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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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## Table of contents

Abstract .....	4
Introduction .....	4
Material and methods .....	5
Ponerine ecology and behavior: A brief review .....	8
Social organization and mating systems .....	9
Foraging behavior .....	10
Morphological characters .....	11
Classification of Ponerinae proposed here .....	15
Keys to Ponerine genera .....	17
Key to New World genera of Ponerinae .....	18
Key to African and Malagasy genera of Ponerinae .....	24
Key to Eurasian and Australian genera of Ponerinae .....	36
Subfamily Ponerinae Lepeletier de Saint-Fargeau .....	46
Tribe Platythyreini Emery .....	47
<i>Platythyrea</i> Roger .....	48
Tribe Ponerini Lepeletier de Saint-Fargeau .....	52
<i>Harpegnathos</i> genus group .....	53
<i>Harpegnathos</i> Jerdon .....	53
<i>Hypoponera</i> genus group .....	57
<i>Hypoponera</i> Santschi .....	57
<i>Odontomachus</i> genus group .....	64
<i>Anochetus</i> Mayr .....	65
<i>Asphinctopone</i> Santschi .....	70
<i>Bothropone</i> Mayr .....	72
<i>Brachyponera</i> Emery .....	77
<i>Buniapone</i> gen. nov. ....	81
<i>Euponera</i> Forel .....	83
<i>Fisheropone</i> gen. nov. ....	87
<i>Hagensia</i> Forel .....	89
<i>Leptogenys</i> Roger .....	92
<i>Megaponera</i> Mayr .....	104
<i>Mesoponera</i> Emery .....	107
<i>Myopias</i> Roger .....	111
<i>Odontomachus</i> Latreille .....	114
<i>Odontoponera</i> Mayr .....	119
<i>Ophthalmopone</i> Forel .....	122
<i>Paltothyreus</i> Mayr .....	124
<i>Phrynoponera</i> Wheeler .....	127
<i>Promyopias</i> Santschi .....	129
<i>Pseudoneoponera</i> Donisthorpe .....	131
<i>Streblognathus</i> Mayr .....	135
<i>Pachycondyla</i> genus group .....	138
<i>Belonopelta</i> Mayr .....	138
<i>Dinoponera</i> Roger .....	140
<i>Mayaponera</i> gen. nov. ....	143
<i>Neoponera</i> Emery .....	145
<i>Pachycondyla</i> Smith, F. ....	152
<i>Simopelta</i> Mann .....	156
<i>Thaumatomyrmex</i> Mayr .....	159
<i>Plectroctena</i> genus group .....	161
<i>Boloponera</i> Fisher .....	162
<i>Centromyrmex</i> Mayr .....	164
<i>Dolioponera</i> Brown .....	168
<i>Feroponera</i> Bolton & Fisher .....	170
<i>Loboponera</i> Bolton & Brown .....	171
<i>Plectroctena</i> Smith .....	174
<i>Psolidomyrmex</i> André .....	177
<i>Ponera</i> genus group .....	179
<i>Austroponera</i> gen. nov. ....	180
<i>Cryptopone</i> Emery .....	182
<i>Diacamma</i> Mayr .....	186
<i>Ectomomyrmex</i> Mayr .....	191

<i>Emeryopone</i> Forel . . . . .	194
<i>Iroponera</i> gen. nov. . . . .	196
<i>Parvaponera</i> gen. nov. . . . .	198
<i>Ponera</i> Latreille . . . . .	200
<i>Pseudoponera</i> Emery . . . . .	205
<i>Rasopone</i> gen. nov. . . . .	208
Acknowledgements . . . . .	210

## 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.**), *Ectomomyrmex* (**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.

For example, the genus *Pachycondyla* has recently been recognized as a highly paraphyletic assemblage with no justification for the species placed there (Keller, 2011; Mariano *et al.*, 2011; Schmidt, 2013). The goal of the present study is to revise the tribe- and genus-level classification of Ponerinae to reflect its internal phylogeny. While several areas of uncertainty remain, and some genera recognized here will likely prove to be non-monophyletic in future studies, the new classification provides a foundation for future phylogenetic and taxonomic refinements.

## Material and methods

The taxonomic changes made in this revision are based on a combination of molecular and morphological evidence. Schmidt's (2013) molecular phylogeny of Ponerinae served as the framework upon which taxonomic changes were based. A consideration of morphological characters was used to assess the plausibility of the molecular phylogeny, to define tribal and generic boundaries, to assign species to genera, and to develop hypotheses about the phylogenetic positions of those genera that were not included in the phylogeny.

The guiding principles for taxonomic changes were as follows:

1. Ponerine classification should reflect evolutionary relationships, so demonstrably non-monophyletic groups should not be recognized.
2. Genus-group and higher taxonomic ranks are arbitrary, so their most valuable roles are in facilitating identification. Genera were therefore defined mainly by morphological distinctiveness, rather than strict observance of an arbitrary age cutoff (in practice there was relatively little conflict between these two criteria, with *Dinoponera* being the most notable exception).
3. Taxonomic changes should be conservative in order to minimize unnecessary disruptions to the end users of ponerine taxonomy. Generally, changes were made only if they were supported by both molecular and morphological data, with minor exceptions.

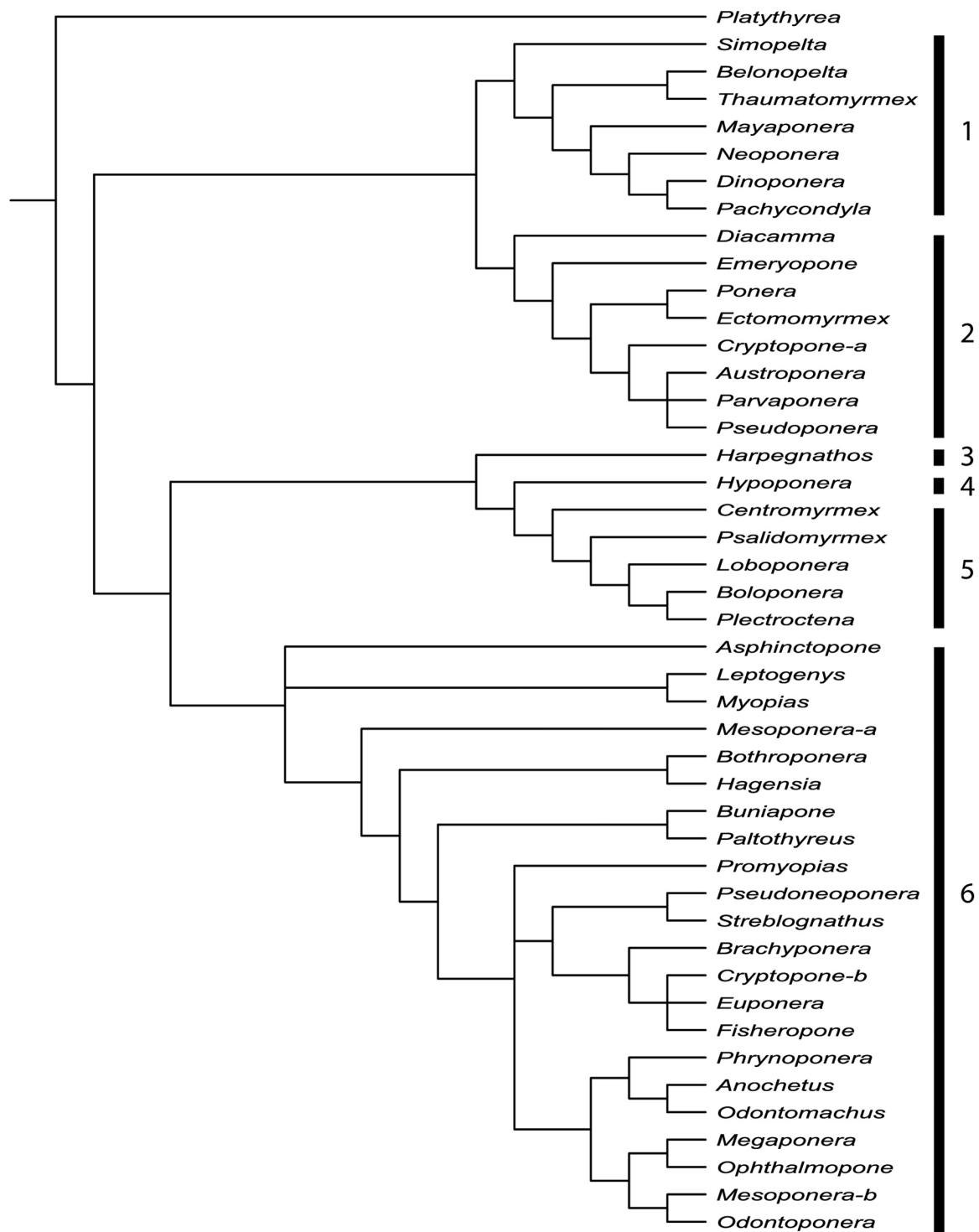
Adherence to these principles resulted in a conservative set of taxonomic changes within Ponerinae. The revised classification incorporates one tribal synonymization (Thaumatomyrmecini as a junior synonym of Ponerini), the division of *Pachycondyla* into 19 genera (six of them new), several new synonymizations of former *Pachycondyla* synonyms and the description of one entirely new genus. In addition, the genera within Ponerini are arranged into six informal genus groups, which are analogous to subtribes but not formally defined as such. Justifications for particular changes are given under the relevant tribe or genus descriptions.

Not all ponerine species were examined to assess their generic placement. Most ponerine genera are taxonomically stable and have clear diagnostic characters and uncontroversial species compositions. For these genera, representative sets of species were examined to provide information on the morphological variation within each genus, supplemented with a review of the original descriptions for the other species and any recent revisionary work.

The species of the former genus *Pachycondyla* were given special attention in order to determine their generic placements. In most cases this was straightforward, as the boundaries of the separate “*Pachycondyla*” lineages largely corresponded to the former genera synonymized under *Pachycondyla*. Particular areas of uncertainty in species placement remain in the genera *Bothroponera*, *Cryptopone* and *Mesoponera* (see their individual descriptions for details).

Adjustments to this taxonomic framework will undoubtedly become necessary in the future as additional molecular and morphological data are obtained. Likely changes that we foresee but do not feel comfortable making at this time include the following:

1. Removal of the African (and potentially other) species currently placed in *Cryptopone* to separate genera.
2. The division of *Mesoponera* into smaller, monophyletic genera.
3. Synonymization of *Anochetus* under *Odontomachus*, should either prove to be non-monophyletic.



**FIGURE 1.** Relationships among the genera of Ponerinae based on Schmidt (2013) with additional unpublished data from P.S. Ward. These two sources differ in their included taxa but have the majority of overlapping clades identical. Where sister-group relationships were inconsistent between these two studies taxa were inserted as unresolved nodes or, in cases where this was not possible, placed as indicated in one of the studies. The numbers on the right represent the following genus groups: 1, *Pachycondyla*; 2, *Ponera*; 3, *Harpegnathos*; 4, *Hypoponera*; 5, *Plectroctena*; 6, *Odontomachus*. *Cryptopone-a* represents *C. hartwigi*, *Cryptopone-b* represents *C. gilva* and *C. testacea*, *Mesoponera-a* represents *M. melanaria* and *Mesoponera-b* represents *M. ambigua*.



**FIGURE 2.** Dated phylogeny of Ponerinae based on Schmidt (2013, figure 7, see there for details on analytical methods and confidence values relating to this phylogeny). Genus groups within Ponerini are demarcated by branch color. Taxonomic names are updated to include those recognized in this study. The following taxa were not included in the analysis of Schmidt (2013) but subsequent data suggest the following placements: *Promyopias* is in an unresolved relationship with the clades *Streblognathus* to *Bothroponera* and *Megaponera* to *Odontomachus*. *Asphinctopone* is in an unresolved relationship with the other members of the *Odontomachus* species group. *Belonopelta* is sister to *Thaumatomyrmex*. *Boloponera* is sister to *Plectroctena*. *Fisheropone* is sister to *Euponera*. *Parvaponera* is in an unresolved relationship with *Austroponera* and *Pseudoponera*. The placements of the following taxa are unknown: *Dolioponera*, *Feroponera*, *Iroponera* and *Rasopone*.

**Specimens.** We examined specimens of ponerine taxa in several museum and personal collections, in addition to specimens obtained through our own collection efforts and through personal loans and gifts from many generous researchers. Collection codes are as follows:

ALWC	Alex L. Wild personal collection, Urbana, Illinois, USA.
ANIC	Australian National Insect Collection, Canberra, Australia.
BMNH	The Natural History Museum, London, UK.
CASC	California Academy of Sciences, San Francisco, California, USA.
CSC	Chris A. Schmidt personal collection, Tucson, Arizona, USA.
JWC	Jeannette Wheeler Collection, Tucson, Arizona, USA.
MCZC	Museum of Comparative Zoology, Cambridge, Massachusetts, USA.
PSWC	Phil S. Ward personal collection, Davis, California, USA.
UAIC	University of Arizona Entomology collection, Tucson, Arizona, USA.
USNM	Smithsonian National Museum of Natural History, Washington, D.C., USA.

**Distribution data.** Distribution information for each genus is reported by political units and biogeographic region. These data are derived primarily from material examined during this study supplemented with records from the published literature and [www.antweb.org](http://www.antweb.org). The maps are based on those prepared by B. Guenard and M.D. Weiser (Guenard *et al.*, 2010) and updated by [www.antwiki.org](http://www.antwiki.org), together with data collected during this study. Regions shown as “present” are those with known occurrence records, “likely present” indicates a high probability of presence but no actual specimens are known, “uncertain” flags regions where a taxon may be present but is likely rare and has yet to be collected there and “present as exotic” are regions with known established but introduced populations.

### Ponerine ecology and behavior: A brief review

Most ponerines retain a suite of social and ecological traits that are probably ancestral within Formicidae, and as a result have often been considered “primitive” relative to most other ants (Hölldobler & Wilson, 1990; Wilson & Hölldobler, 2004). This characterization is only partially accurate, however, as ponerines in fact display a remarkable diversity of derived morphological, ecological and behavioral traits. This diversity is detailed in the individual genus accounts but is briefly reviewed below, with an emphasis on ponerine social, reproductive and foraging behaviors.

Based on a review of the diversity within Ponerinae, it is possible to characterize the “typical” ponerine species. Note that the following description is not necessarily a hypothesis about ancestral conditions, but is rather a composite sketch of the most common features among members of the subfamily. Probably very few ponerine taxa entirely fit the following description, but it serves as a useful starting point to discuss the behavioral diversity within the group:

Colonies of the typical ponerine contain a few dozen to a few hundred adult workers and a single dealate queen. Nesting occurs in preformed cavities in soil, leaf litter or decaying wood. Workers are monomorphic. The queen is morphologically similar to the workers except for its larger eyes, ocelli, modified thoracic flight sclerites, and enlarged gaster. Workers retain ovaries and spermathecae and may lay haploid eggs, but do not mate. Colony reproduction occurs through independent semiclaustal colony foundation by single mated queens. Colony emigration occurs via social carrying and through the use of weak chemical orientation cues. Division of labor among the workers follows a typical pattern of age polyethism, with younger workers performing nest duties and older workers foraging. The workers, which are fairly large (roughly 8 mm long) and have moderately large eyes, hunt individually on the ground and in leaf litter for a wide variety of arthropods. They also scavenge opportunistically. Nestmates are not recruited to food sources. Prey is stung and hence paralyzed before its retrieval to the nest, where it is fed directly to the mandibulate larvae. Trophallaxis does not occur between adults or between adults and larvae. Pupae are enclosed in cocoons.

## Social organization and mating systems

The colony sizes of most ponerine species (and many genera) are unknown, but most taxa seem to have relatively small mature colonies, usually with between a few dozen and a few hundred workers. This is the case, for example, in *Anochetus* (Brown, 1976), *Centromyrmex* (e.g., Léveux, 1976; Déjean & Fénéron, 1999), *Diacamma* (e.g., André *et al.*, 2001), *Dinoponera* (e.g., Monnin & Peeters, 2008), *Harpegnathos* (e.g., Peeters *et al.*, 2000), *Hagensia* (Duncan & Crewe, 1994a), *Platythyrea* (e.g., Villet *et al.*, 1990b), *Plectroctena* (e.g., Bolton *et al.*, 1979), *Streblognathus* (Ware *et al.*, 1990; Peeters, 1993), and most *Hypoponera* (e.g., Yamauchi *et al.*, 1996), *Leptogenys*, *Myopias* (e.g., Gobin *et al.*, 2006), *Neoponera* (e.g., Gobin *et al.*, 2003a; D'Etterre *et al.*, 2006; Longino, 2013) and *Odontomachus* (Brown, 1976). Larger colonies of over a thousand workers are known in some species of *Brachyponera* (Haskins & Haskins, 1950; Déjean & Lachaud, 1994), *Leptogenys*, *Megaponera* (Hölldobler *et al.*, 1994), *Neoponera* (Leal & Oliveira, 1995), *Odontomachus* (Colombel, 1970a), *Paltothyreus* (Braun *et al.*, 1994), and *Simopelta* (Gotwald & Brown, 1967). Very large colonies of 10,000 or more workers are known in some *Leptogenys* (up to 50,000 workers in certain members of the *L. processionalis* group), *Neoponera* (*N. luteola*: Yu & Davidson, 1997), and *Odontomachus* (*O. opaciventris*: de la Mora *et al.*, 2007). At the other end of the spectrum, very small mature colonies with 20 or fewer workers are typical for *Pseudoneoponera* (e.g., Sommer *et al.*, 1994), and exceptionally small colonies of about five workers on average have been reported for some *Thaumatomyrmex* (Jahyny *et al.*, 2002). The ecological and social factors responsible for this diversity in colony sizes are unknown and undoubtedly numerous and varied, but large colonies tend to be correlated with obligate collective foraging behavior and small colonies are often correlated with a reproductive system dominated by gamergate workers (see below).

Monomorphic workers are nearly universal in the subfamily, but polymorphic workers occur in several groups, including *Brachyponera sennaarensis* (Déjean & Lachaud, 1994), the *Centromyrmex bequaerti* species group (Déjean & Fénéron, 1996, 1999), *Megaponera* (Crewe & Villet, 1984), and some *Neoponera* (*N. laevigata* and *N. marginata*; Wheeler, 1936, Longino, 2013). The phylogenetic distribution of these taxa (Schmidt, 2013) suggests that worker polymorphism has probably evolved at least five times independently in Ponerinae. In most cases it is correlated with group foraging behavior (*Centromyrmex*, *Megaponera* and *Neoponera*), while polymorphism in *B. sennaarensis* may be related to its granivorous habits.

Similarly, most ponerines show relatively little morphological differentiation between the worker and queen castes, other than the characters normally associated with reproduction and dispersal (including wings and larger eyes). In one sense, this similarity is taken to an extreme in those taxa without a distinct queen caste (see below). A common trend in ponerine evolution is the supplementation or replacement of winged queens with wingless ergatoid queens. Ergatoid queens are often morphologically extremely similar to the worker caste, as is the case in most *Leptogenys*, whose ergatoid queens differ only very subtly from conspecific workers (Bolton, 1975a). Among ponerine taxa with fully winged queens, worker-queen dimorphism is at its minimum in *Harpegnathos*, as workers and queens basically differ only in the occurrence of wings and associated modifications of the thoracic sclerites (queens are also very slightly larger; Peeters *et al.*, 2000). *Harpegnathos* workers even have ocelli, which are otherwise virtually unknown in ponerine workers (also observed only in some populations of *Paltothyreus tarsatus*: CAS, pers. obs. and B. Bolton, pers. comm.). Large worker-queen size dimorphism has evolved in only a handful of ponerine taxa, including some *Brachyponera* (*B. sennaarensis* and *B. luteipes*; Wheeler, 1933b; Déjean & Lachaud, 1994) and the *Centromyrmex bequaerti* group (Déjean & Fénéron, 1996, 1999). In addition, queens of *Simopelta* are dichthadiigyne and differ greatly from the workers (e.g., Gotwald & Brown, 1967).

Ponerines have evolved a remarkable diversity of reproductive strategies. While most retain the basic (and probably ancestral) pattern in which reproduction is performed by a single dealate queen, many other taxa have modified this strategy in various ways. Two of the most common variations are reproduction by ergatoid queens and gamergate workers. Ergatoids may occur alongside alate queens (e.g., *Mayaponera*, some *Anochetus*, *Hypoponera*, and *Myopias*; Brown, 1978, Foitzik *et al.*, 2002; Gobin *et al.*, 2006; Longino, 2013) or may replace them (e.g., *Megaponera*, some *Anochetus*, *Odontomachus*, *Plectroctena*, most *Leptogenys*, and possibly *Doloponera*; Arnold, 1915; Bolton, 1974, 1975a; Fisher, 2006; Gobin *et al.*, 2006; Molet *et al.*, 2007).

In addition to the frequent evolution of ergatoid queens in Ponerinae, reproduction by mated gamergate workers has arisen numerous times in the subfamily. Gamergates are rare among the other ant subfamilies but have evolved perhaps as many as nine times or more in Ponerinae (Schmidt, 2013). Like ergatoids, gamergates may

occur alongside distinct queens (e.g., *Harpegnathos* and some *Platythyrea* and *Pseudoneoponera*; Villet, 1993; Ito, 1995; Peeters & Hölldobler, 1995) or may entirely replace them (e.g., *Bothroponera kruegeri*, *Diacamma*, *Dinoponera*, *Hagensia*, *Ophthalmopone*, *Streblognathus*, some *Leptogenys*, *Platythyrea* and *Pseudoneoponera*; Peeters & Crewe, 1986b; Peeters & Higashi, 1989; Peeters, 1987, 1991a, 1993; Villet *et al.*, 1990b; Villet, 1991b, 1991c; Sledge *et al.*, 2001; Jahyny *et al.*, 2002; Monnin *et al.*, 2003; Gobin *et al.*, 2008; Monnin & Peeters, 2008). Colonies with gamergates are commonly polygynous (e.g., *Ophthalmopone* and some *Pseudoneoponera*), though in many taxa a dominance hierarchy may exist in which only a single dominant gamergate performs reproduction for the colony (e.g., *Bothroponera kruegeri*, *Diacamma*, *Dinoponera*, *Hagensia*, *Streblognathus*, and some *Pseudoneoponera*).

Both ergatoids and gamergates are correlated with reduced dispersal abilities when they act as the sole reproductives in a colony, but they represent distinct evolutionary pathways and have never been found together in the same species (Molet & Peeters, 2006). Ergatoids and gamergates necessitate a form of colony reproduction characterized by budding, in which new ergatoids or gamergates leave their natal nest (either before or after mating), usually with an entourage of workers, and found new colonies a short distance away. While it is tempting to conjecture that these reduced dispersal capabilities may help drive speciation due to increased genetic isolation, most genera with ergatoids or gamergates are relatively species-poor (e.g., *Dinoponera*, *Hagensia*, *Harpegnathos*, *Megaponera*, *Ophthalmopone* and *Streblognathus*), with *Leptogenys* being a major exception.

## Foraging behavior

Ponerine evolution has been marked by a rich diversification in foraging behaviors. Most of this diversity involves variation in foraging location, prey specialization, method of prey capture, and degree of cooperation among foraging nestmates. We consider these topics separately below.

Ponerines can be broadly categorized as being either cryptobiotic or epigeic foragers depending on the microhabitats where they forage, though many taxa are intermediate between these extremes. Epigeic foraging occurs on the surface of the ground or on low vegetation, and is typical of many ponerines. Rarely, foraging occurs arboreally (e.g., most *Platythyrea*, many *Neoponera*, and a small number of taxa in a few other genera). Epigeic ponerines tend to be relatively large and to have well developed eyes. Cryptobiotic foraging occurs in soil, leaf litter, rotting wood, or other concealed microhabitats, and is also common among ponerines. Cryptobiotic taxa variously show several morphological traits that are correlated with life in tight and dark conditions. For example, cryptobiotic ponerines are typically small bodied, which is taken to an extreme in many *Cryptopone*, *Dolioponera*, *Hypoponera*, and *Ponera*. The compound eyes are typically greatly reduced in size or even entirely absent (including *Boloponera*, *Centromyrmex*, *Dolioponera*, *Feroponera*, *Promyopias*, and some *Cryptopone* and *Hypoponera*). Most cryptobiotic ponerines have at least mildly clubbed antennae, perhaps facilitating movement and prey detection in low light conditions. The legs are often short and stocky, and are sometimes armed with stout setae to increase traction in soil or wood (these are present in *Centromyrmex*, *Feroponera*, *Promyopias*, and most *Cryptopone*). As with the eyes, some other morphological characters show various degrees of reduction, including pigmentation, the number of labial and maxillary palp segments, and the number of tibial spurs. Most cryptobiotic ponerines have only a single metatibial spur, reflecting a loss from the likely ancestral condition of two spurs. This character has often been considered to divide Ponerinae into two groups (discussed by Brown, 1963), but molecular phylogenetic results (Schmidt, 2013) suggest that the loss of a metatibial spur has occurred several times independently during the course of ponerine evolution, with cryptobiotic taxa probably evolving from epigeic ancestors multiple times.

Prey specialization probably drove much of the morphological and behavioral diversification within Ponerinae. While many ponerines are generalist predators and scavengers, a large number have specialized to various degrees on specific types of prey. Many taxa are more or less specialist predators of termites (e.g., *Centromyrmex*, *Megaponera*, *Ophthalmopone*, *Paltothyreus*, some *Leptogenys* and *Neoponera*, and scattered species in other genera). Other taxa are specialist predators of earthworms (*Psalidomyrmex*), isopods (most *Leptogenys*), millipedes (*Plectroctena*, *Thaumatomyrmex*, and some *Myopias*), or other ants (*Simopelta* and some *Myopias*). Prey specialization in these taxa is often correlated with highly specialized mandibular structure (e.g., in *Leptogenys*, *Plectroctena*, and *Thaumatomyrmex*). From this observation it is possible to predict that several other



genera, whose prey preferences are unknown, are probably specialist predators. For example, *Belonopelta*, *Dolioponera*, *Emeryopone*, and *Promyopias* all have highly modified mandibles that are probably adapted to the capture of specific prey types, but the identities of their prey are unknown.

Most ponerines capture their prey by standard means, using their antennae to locate prey, their more or less unspecialized mandibles to seize it, and finally one to several stings to rapidly subdue and paralyze it. A few ponerine taxa have evolved more unusual methods of prey capture: *Harpegnathos* employs its huge eyes to locate its prey, and then uses its jumping capabilities and rapidly closing forceps-like mandibles to capture it. *Anochetus* and *Odontomachus* use their extremely fast and forceful trap jaws to skewer, crush or stun their prey, and *Plectroctena* sometimes uses its snap mandibles to stun its prey. Finally, *Thaumatomyrmex* uses its pitchfork-like mandibles to grasp polyxenid millipedes, which are covered in noxious hairs, and employs its front tarsi to scrape the hairs off.

Ponerines typically forage individually without any nestmate recruitment to food sources, though this basic pattern has been modified by many lineages. In some cases, recruitment is facultative and only employed to large prey sources. In others, recruitment is a standard component of foraging. Such obligately collective foraging occurs in *Megaponera*, the *Neoponera laevigata* species group, *Simopelta*, and some *Leptogenys* (*L. diminuta* and relatives, as well as the *L. processionalis* species group). Some members of the *L. processionalis* species group conduct swarm raids, as in many of the true army ants of the doryline section (Brady, 2003). *Simopelta* has converged most extensively with a true army ant lifestyle, as it conducts mass raids on other ants, is nomadic, and has dichthadii-gyne queens with pulsed reproduction. Recruitment in ponerine taxa may occur either via tandem running or chemical trails.

## Morphological characters

The traditional lack of a robust taxonomic framework for ponerines is unsurprising given their apparently rapid rate of morphological change and their frequent convergence, as suggested by the inferred molecular phylogeny of the subfamily (Schmidt, 2013). Below we review some of the morphological characters of ponerine workers and queens that were utilized in this revision. This review is not intended to be comprehensive, but rather to give a sense of the morphological variation in the subfamily and the utility of each character as a diagnostic or phylogenetic tool. We end with a brief mention of some additional characters which were not examined for this study but which would likely prove highly useful in future studies. We generally follow the morphological terms of Bolton (1994, 2003).

**Body Size and Build.** In the genus descriptions that follow, the known range of body sizes is listed for each genus, and is given as the smallest and largest total body lengths (in mm) reported in the literature for the described species of that genus. Given that these lengths were inconsistently reported and were measured by many different authors using different methods, these ranges should be treated as only very rough estimates of the size range for that genus. No effort was made to determine the average body length among members of a genus. Body size varies within a fairly small range in many ponerine genera, but is highly variable in many other genera (e.g., *Anochetus*, *Bothroponera*, *Centromyrmex*, *Leptogenys*, *Myopias*, *Odontomachus*, *Platythyrea*, and *Plectroctena*). This high intrageneric variation makes body size a generally poor character for phylogenetic inference and of only limited utility for diagnoses. Still, some phylogenetic trends in body size are apparent in ponerine evolution: three of the six genus groups within Ponerini are predominantly small bodied (the *Ponera*, *Hypoconera* and *Plectroctena* groups), while the other three (the *Harpegnathos*, *Pachycondyla* and *Odontomachus* groups) are predominantly large bodied in comparison. *Platythyrea* is highly variable in this respect. Small bodied ponerines apparently have arisen from large bodied ancestors many times independently. Most ponerines have a moderately slender build, but some (e.g., *Bothroponera*, *Phrynoponera*, and *Pseudoneoponera*) are more robust, and others (e.g., most *Leptogenys*) are very slender.

**Color, Sculpturing and Pilosity.** Color, sculpturing and pilosity are highly variable characters within Ponerinae. Color ranges from light yellow-brown in some hypogeic taxa, through various shades of red and brown to black, the latter color typical of most large ponerines. The most common type of sculpturing in ponerines is dense to sparse punctations associated with standing pilosity or pubescence. Some taxa have a more or less smooth and glassy cuticle, with little to no pilosity or pubescence. A few groups (*Platythyrea*, *Belonopelta*, and the *Leptogenys*

*maxillosa* species group) have evolved pruinose sculpturing, which gives the ants a frosted appearance and is associated with an extremely dense pubescence and usually little to no standing pilosity. Many groups have foveate or foveolate sculpturing (e.g., *Harpegnathos*, *Bothroponera*, *Phrynoponera*, and many members of the *Plectroctena* group), and still others are at least partially striate (e.g., *Diacamma*, *Ectomomyrmex*, *Odontoponera*, *Pachycondyla*, *Paltothyreus*, and *Pseudoneoponera*). In short, sculpturing is highly variable within Ponerinae and does not appear to be useful as a marker for deeper phylogenetic relationships (this is also true for pilosity and pubescence). On the other hand, pilosity and sculpturing are generally fairly consistent within individual genera, making them useful characters for diagnosis of some genera. For example, shaggy golden or red pilosity and deep longitudinal striations on the dorsum of A3 are characteristic of most species of *Pseudoneoponera*.

**Mandibles.** The mandibles contain some of the most important diagnostic characters in ponerine taxonomy and provide a wealth of insight into the ecological niches of their carriers, though there are few mandibular characters that have proven useful as synapomorphies linking two ponerine genera (the trap mandibles of *Anochetus* and *Odontomachus* are an obvious exception). The ancestral ponerine probably had more or less triangular mandibles with distinct basal and masticatory margins, several small teeth, and a basal groove. This is still the condition in most extant ponerines, but several lineages have evolved unusual mandibular pits or grooves whose functions are unclear (they may have a role in pheromone dispersal; Brown, 1963). *Hagensia* has perhaps the most striking of these grooves, on the dorsal surface of its mandibles. *Plectroctena* also has dorsal grooves on its mandibles, though of a different form than in *Hagensia*. *Euponera*, *Brachyponera*, and most *Cryptopone* have a basal pit near the mandibular insertion. The ancestral basal groove has become lost or nearly lost in many ponerines, is variable even within many genera, and is generally not a useful diagnostic character.

A substantial diversity of mandible shapes and dentitions occurs in the subfamily, and these are usually correlated with specialized prey preferences or hunting strategies. Hence we find that the mandibles of many isopod-specialist *Leptogenys* species are thin and outwardly bowed, enabling them to grasp their hard round prey. Similar adaptations occur in *Plectroctena* and *Myopias*, which specialize on millipedes (which are also hard and round). *Thaumatomyrmex* has evolved long attenuated teeth to enable capture of polyxenid millipedes, which are covered in irritating hairs. *Belonopelta* and *Emeryopone* have also evolved attenuated mandibular teeth, though their prey preferences are unclear. The mandibles of *Anochetus* and *Odontomachus* are perhaps the most highly derived, as they arise from the midline of the head, are long and straight, and function as trap jaws, snapping shut with tremendous speed and force. The mandibles of *Harpegnathos* are also unusual, being long, upwardly curved, and serrated, apparently facilitating the capture of fast moving prey. *Dolioponera* has a unique set of setose teeth on the inner margins of its mandibles; their function is unknown but may indicate a specialized diet. Many other ponerine genera have evolved less extremely derived mandibular shapes, often by reducing the relative length of the masticatory margin (a mandible shape referred to as “subtriangular”).

**Clypeus and Frontal Lobes.** The clypeus is an important source of characters for ponerine systematics. In most ponerines the clypeus is unremarkable, having a nearly straight or gently convex anterior margin, often with a slight emargination medially. In several genera (e.g., *Buniapone*, *Myopias* and *Paltothyreus*) the clypeus bears a blunt median projection, and in others (e.g., some *Belonopelta* and *Emeryopone*) there is a short but sharp tooth. Some other genera have evolved two (*Dinoponera*, *Feroponera* and *Streblognathus*) or numerous (*Odontoponera*) blunt teeth on the anterior clypeal margin.

The frontal lobes provide some useful diagnostic characters within Ponerinae, as well as some clear synapomorphies. The relative spacing of the frontal lobes is one of the main morphological distinctions between *Platythyrea* and Ponerini, with the frontal lobes widely separated in the former genus but closely approximated in nearly all Ponerini (*Thaumatomyrmex* is the single exception, but its frontal lobes are even more widely spaced than in *Platythyrea*). Within Ponerini, the frontal lobes show a wide diversity of sizes and shapes. In most large bodied members of Ponerini (e.g., *Diacamma*, most members of the *Pachycondyla* group, and many members of the *Odontomachus* group) the frontal lobes are moderately large, with a relatively large separation at their anterior end (created by a posterior triangular projection of the clypeus) but only a narrow or nonexistent separation posteriorly. This particular frontal lobe structure may be the ancestral condition within Ponerini, given its wide phylogenetic distribution. In many other Ponerini (e.g., most members of the *Ponera* group, *Hypoponera*, *Mesoponera*, *Leptogenys*, *Anochetus*, and *Odontomachus*) the frontal lobes are small and closely approximated for nearly their entire length; this type of frontal lobe is often correlated with small body size. Finally, some taxa have greatly expanded frontal lobes (*Bothroponera* and most members of the *Plectroctena* group, taken to an extreme in

*Boloponera* and *Loboponera*). Another character is the shape of the lateral margins of the frontal lobes, which are typically triangular or semicircular. This character is highly variable and rarely useful for diagnoses.

*Eyes and Ocelli.* The size and location of the eyes are important characters in ponerine systematics. Eye size varies substantially among genera. While most ponerines have moderately large eyes, *Harpegnathos* and *Ophthalmopone* both have strikingly large eyes, and many ponerines have very small eyes in the worker caste or have lost them altogether. The reduction or loss of eyes is generally correlated with a reduction in body size and the adoption of hypogeic foraging behavior, and is typical of most members of the *Ponera* group (except *Diacamma*), *Hypoponera*, most members of the *Plectroctena* group, and some members of the *Odontomachus* group. A complete loss of eyes occurs in some *Cryptopone* and *Hypoponera* species, as well as *Boloponera*, *Feroponera*, *Promyopias*, and *Centromyrmex*.

Eye location is generally consistent within genera and even within larger clades, making it a useful diagnostic character. In most large bodied ponerines the eyes are situated at or just anterior of the head midline (though the eyes are posterior to the head midline in *Ophthalmopone*). Most small bodied ponerines, on the other hand, have the eyes located far anterior on the sides of the head, often practically abutting the mandibular articulations. *Harpegnathos* is unusual in having its huge eyes situated at the extreme anterior end of the head, while *Anochetus* and *Odontomachus* are unusual in having their eyes situated on lateral ocular prominences. An additional character related to the eyes is the presence or absence of preocular carinae, which are present only in *Megaponera*, *Odontoponera* and some *Neoponera*. Finally, ocelli are almost universally absent in ponerine workers (though present in queens), but are present in workers of *Harpegnathos* and some populations of *Paltothyreus*.

*Mesosoma.* The thorax and propodeum (which together constitute the mesosoma) have a number of characters that are useful for diagnosis of ponerine genera, and some of these have useful synapomorphies for higher level phylogenetic analysis. The pronotum has rounded or bluntly angular lateral margins in most ponerines, but the margins are sharply ridged in *Hagensia*, most *Neoponera*, some *Pachycondyla*, and some *Centromyrmex*, and *Odontoponera* has a single blunt projecting tooth at each anterolateral corner of its pronotum. The mesopleuron is usually undivided in ponerines, but several ponerine groups have the mesopleuron divided by a transverse groove (e.g., *Ectomomyrmex*, *Euponera*, many *Neoponera* and *Pachycondyla*, many members of the *Plectroctena* group, and rarely in other genera such as *Anochetus* and *Brachyponera*). Though this character is variable within many genera, it is still useful for diagnosis of some genera. A possible synapomorphy of *Plectroctena*, *Loboponera* and *Boloponera* is the apparent fusion of the dorsal section of the mesopleuron to the mesonotum. *Dolioponera* has a similar fusion, but its mesopleuron is undivided.

The metanotal groove is an important character in ponerine systematics. In most ponerines the mesonotum and propodeum are separated by a suture or very shallow groove (the metanotal groove), but a deeply impressed metanotal groove is characteristic of *Brachyponera* and *Mayaponera*, as well as some members of several other genera. In contrast, several groups have entirely lost any vestiges of the metanotal groove, and the mesonotum and propodeum form a continuous structure dorsally (e.g., *Harpegnathos*, *Bothroponera*, *Phrynoponera*, *Pseudoneoponera*, most members of the *Plectroctena* group, and most *Platythyrea*).

The propodeum has a number of useful characters. The propodeal dorsum varies from being roughly as broad as the mesonotum (especially common in those taxa without a metanotal groove) to being very sharply narrowed (e.g., *Brachyponera*, *Hagensia*, and many *Mesoponera* and *Hypoponera*), with most taxa having an intermediate condition in which the propodeal dorsum is moderately narrowed and continuously convex in posterior view. An apparent synapomorphy of *Austroponera*, *Cryptopone* and *Pseudoponera* is the characteristic shape of their propodeal dorsum, which is flattened and has a distinct pinched-in appearance anteriorly. The posterior propodeal margin is unadorned in most ponerines, but *Phrynoponera*, *Streblognathus* and most *Anochetus* have a pair of teeth (of varying structure) at the posterodorsal margin of the propodeum. In *Boloponera*, *Loboponera* and *Plectroctena*, the posterolateral margins of the propodeum are drawn out into lamellae (this is apparently a synapomorphy of these genera). Finally, the shape of the propodeal spiracles is a useful diagnostic character within Ponerinae. It varies from slit-shaped to ovoid to round, and is usually correlated with body size (slit-shaped in large taxa, round in small taxa).

*Metapleural Gland Orifice.* The metapleural gland orifice appears to be a rich source of characters for ponerine systematics, but we have been able to give it only a cursory consideration in this study. The location and direction of opening of the metapleural gland orifice varies a great deal among ponerines. In *Platythyrea*, *Harpegnathos*, and members of the *Plectroctena* group the metapleural gland orifice opens laterally and somewhat anterior of the

posteroventral corner of the propodeum (this may be the ancestral condition within Ponerinae). In most other ponerines the orifice opens posterolaterally at the posteroventral corner of the propodeum, though in some taxa (e.g., *Hypoponera* and many members of the *Ponera* group) the orifice is located on the posterior face of the propodeum and opens posteriorly. Some ponerine groups have accessory grooves or cuticular flanges associated with the metapleural gland orifice, and these are often useful diagnostic or phylogenetic characters. For example, many *Platythyrea* and many members of the *Pachycondyla* group have a lateral longitudinal groove leading up to the metapleural gland orifice, possibly functioning to facilitate the spread of gland contents. The presence of cuticular flanges anterior and posterior to the orifice is synapomorphic for *Buniapone* and *Paltothyreus*. Members of the *Pachycondyla* group, as well as *Diacamma* and *Bothroponera* (s.s.) have a characteristic U-shaped cuticular lip posterior to the orifice. Future examination of both external and internal metapleural gland structure in ponerines will likely yield additional informative characters.

*Legs.* The legs bear a number of useful diagnostic characters, including the number and type of meso-/metatibial spurs, the number of preapical tarsal claws, the prominence of the arolia, the presence of femoral and metatibial glands, and the presence of stout traction setae on the mesotibiae. For an overview of these glands see Billen (2009). Most ponerines have two mesotibial and two metatibial spurs, and this is undoubtedly the ancestral condition (Bolton, 2003). In *Platythyrea* all spurs are pectinate, while in most Ponerini one spur of each pair is pectinate and the other is simple or barbate. The loss of the second metatibial spur has occurred repeatedly in ponerine evolution, and is particularly common in small bodied hypogeic taxa (e.g., *Ponera*, *Simopelta*, *Thaumatomyrmex*, *Fisheropone*, *Hypoconera*, and nearly all members of the *Plectroctena* group). A few genera (e.g., *Cryptopone*, *Centromyrmex* and *Anochetus*) are variable for this character. The number of metatibial spurs was traditionally thought to split Ponerini into two groups, but the phylogenetic distribution of taxa with only a single spur clearly demonstrates that they are non-monophyletic. Despite the variability of this character within some genera, its often subjective scoring (as discussed by Brown, 1963), and its poor utility as a phylogenetic marker, the number of metatibial spurs is still generally a useful diagnostic character within Ponerinae in combination with other characters.

The presence and number of preapical teeth on the tarsal claws is a valuable diagnostic character for several genera. Most ponerines have unarmed tarsal claws, but several large-bodied genera have a single preapical tooth (e.g., *Dinoponera*, *Hagensia*, *Harpegnathos*, *Megaponera*, *Paltothyreus*, most *Platythyrea*, and some *Ophthalmopone*) and in most *Leptogenys* the tarsal claws are pectinate (rarely with only one or two preapical teeth). The arolia are also useful characters, as they are enlarged and prominent (even bright white) in several ponerine genera (*Platythyrea*, *Harpegnathos*, *Diacamma*, *Simopelta*, *Mayaponera*, and most *Neoponera*). Prominent arolia may be plesiomorphic within Ponerinae, given their phylogenetic distribution. Another leg character is the presence of longitudinal and probably glandular grooves in the meso- and/or metafemora of *Boloponera*, *Loboponera* and *Plectroctena* (the grooves are probably synapomorphic for these three genera). Visually, the gland at the apex of the metatibia varies from an obvious subcuticular sac, to a relatively smooth patch of cuticle (the pore plate) to a dense cluster of (often spatulate) hairs, to a small cluster of unspecialized hairs only slightly more dense than the remaining hairs on the tibia (Hölldobler *et al.*, 1996b). This gland is broadly present across the subfamily although it is not visible externally in some species of *Mesoponera*, *Odontoponera* and *Pseudoponera* and appears to be absent from *Parvaponera* and *Streblognathus* (although this absence needs to be confirmed through dissection). Finally, several hypogeic genera have stout traction setae on the mesotibiae (and often metatibiae): *Centromyrmex*, *Ferapone*, *Promyrmex*, and most *Cryptopone* and *Parvaponera*. These setae can be helpful in diagnosis.

*Petiole.* The petiole is highly variable within Ponerinae and provides many useful diagnostic characters. In a few genera the petiole is much longer than it is broad (e.g., *Dolioponera*, *Harpegnathos* and most *Platythyrea*), but in most ponerines the petiole is either roughly cuboidal (about as long as broad) or squamiform (scale-like, much broader than long). The phylogenetic distribution of different petiole structures suggests that petioles change rapidly in evolutionary time, though the adaptive benefits (if any) of each petiole shape are unclear. The exact shape of the petiole is highly variable among taxa, with many genera having important diagnostic characters in their petioles. The two most extreme examples are the petioles of *Streblognathus*, which is unique among ants in having a long posterodorsal keel (reminiscent of the dorsal fins of sharks or whales), and of *Phrynoponera*, which has five sharp spines or teeth jutting posteriorly from the posterodorsal margin of the petiole. Other examples of diagnostic petiole shapes include the dorsally semicircular petioles of *Pseudoneoponera*, the bispinose cuboidal

petioles of *Diacamma*, the emarginate petioles of *Odontoponera* and many *Anochetus*, the coniform and often unispinose petioles of *Odontomachus* and some *Anochetus*, and the sharply margined squamiform petiole of *Hagensia*. The subpetiolar process is undoubtedly a source of many useful characters, but we did not attempt a full evaluation of its diversity. Some notable diagnostic characters of the subpetiolar process include the presence of an anterior fenestra (*Ponera*, *Emeryopone*, and maybe some *Hypoponera*) and the presence of paired posterior teeth. Some members of the *Plectroctena* group have highly modified anteroventral petiolar articulations (see discussion under that group).

**Gaster.** The last set of characters considered for this revision are gaster (abdominal segments 3 to 11, abbreviated as A3, A4, etc.) characters. Most members of Ponerini (and a few *Platythyrea*) have the helcium, to which the petiole attaches, projecting from low on the anterior face of A3. In nearly all of these taxa, A3 has a high vertical face above the helcium, with the one exception being *Harpegnathos*, in which the vertical face is shortened. In a few groups within Ponerini, as well as nearly all *Platythyrea*, the helcium projects from near midheight on the anterior face of A3. All Ponerini with this character state are hypogeic: *Boloponera*, *Buniapone*, *Centromyrmex*, *Dolioponera*, *Feroponera*, *Promyopias*, and some *Cryptopone*. This suggests that a high helcium has an adaptive benefit in hypogeic ponerines, perhaps by enabling more efficient gaster curling while hunting in tight spaces.

Another somewhat useful character is the degree of constriction between the presclerites and postsclerites of A4. While generally consistent within genera, this character is often difficult to assess, and in many cases is of limited utility as a diagnostic tool. In most ponerines the constriction is moderately deep and girdles the sclerites, but in some taxa the constriction is particularly deep (e.g., many members of the *Plectroctena* group) and in others it is absent (e.g., *Asphinctopone* and *Phrynoponera*). The presence of a stridulitrum on the pretergite of A4 is also a useful character, but it again can be difficult to assess, and its presence is variable in many genera. In *Loboponera* and some *Emeryopone* the tergite of A4 is strongly vaulted, probably as an adaptation to hunting in tight spaces. Finally, some lineages have evolved rows of stout setae on the hypopygium on either side of the sting apparatus (this is the case in *Dinoponera*, *Ophthalmopone*, *Pachycondyla*, *Paltothyreus*, some *Leptogenys*, and rarely in *Ponera*).

An additional gastral character is the prora, a cuticular process or prominence that projects forward from the anterior surface of abdominal sternite III, below the helcium. It occurs throughout the Ponerini and is large and obvious in most genera, being easily visible in lateral and ventral view as a U-shaped ridge of cuticle, a tubercle of very variable size, or a distinct prow. However, the prora is reduced and not externally visible in three genera, *Brachyponera*, *Iroponera* and *Phrynoponera*. There is no evidence that this reduction is a synapomorphy for these groups but is rather a convergent loss. See Bolton & Fisher (2008b) for a detailed discussion of this character within *Phrynoponera*.

**Characters for Future Consideration.** This study emphasizes external characters of the worker caste (which are generally also present in the queen caste). Two important characters which were not evaluated here are the number of labial and maxillary palp segments, which could be useful diagnostic characters (Brown, 1963; Bolton, 2003). A wealth of additional characters useful for diagnosis or phylogenetic analysis are likely to come from careful considerations of the mesosoma venter, helcium, mouthparts, details of abdominal segment articulation, internal structure (Hashimoto, 1996), ultrastructure, and histological variation, as well as reproductive characters of all castes and both sexes, wing characters for alate queens and males, all other characters of males, and larval characters. Keller (2011) examined a wealth of morphological characters in his analysis of poneromorph relationships; these deserve deeper study to determine their utility for phylogenetic and diagnostic purposes within the Ponerinae. Finally, as described above, careful study of ponerine metapleural gland orifices and subpetiolar processes are also likely to yield many additional useful characters.

## Classification of Ponerinae Proposed Here

Ponerinae contains two tribes, Platythyreini, with the single genus *Platythyrea*, and Ponerini with the remaining genera. Ponerini is here divided into six informal genus groups based on molecular phylogenetic results (Schmidt, 2013). Firm morphological synapomorphies have not been found for all of these groups, and their relationships are still unresolved, but the monophyly of each is generally well supported by the available evidence.

Platythyreini

*Platythyrea* Roger

= *Eubothroponera* Clark

### **Ponerini**

= Thaumatomyrmecini **syn. nov.**

*Harpegnathos* Genus Group

*Harpegnathos* Jerdon

= *Drepanognathus* Smith, F.

*Hypoponera* Genus Group

*Hypoponera* Santschi

*Odontomachus* Genus Group

*Anochetus* Mayr

= *Myrmapatetes* Wheeler, W.M.

= *Stenomyrmex* Mayr

*Asphinctopone* Santschi (*incertae sedis*)

= *Lepidopone* Bernard

*Bothroponera* Mayr

*Brachyponera* Emery **gen. rev.**

*Buniapone* **gen. nov.**

*Euponera* Forel **gen. rev.**

*Fisheropone* **gen. nov.**

*Hagensia* Forel **gen. rev.**

*Leptogenys* Roger

= *Dorylozelus* Forel

= *Lobopelta* Mayr

= *Machaerogenys* Emery

= *Microbolbos* Donisthorpe

= *Odontopelta* Emery

= *Prionogenys* Emery

*Megaponera* Mayr **gen. rev.**

*Mesoponera* Emery **gen. rev.**

= *Xiphopelta* Forel **syn. nov.**

*Myopias* Roger

= *Bradyponera* Mayr

= *Trapeziopelta* Mayr

*Odontomachus* Latreille

= *Champsomyrmex* Emery

= *Myrtoteras* Matsumura

= *Pedetes* Bernstein

= *Thempsomyrmex* Forel

*Odontoponera* Mayr

*Ophthalmopone* Forel **gen. rev.**

*Paltothyreus* Mayr **gen. rev.**

*Phrynoponera* Wheeler

*Promyopias* Santschi

*Pseudoneoponera* Donisthorpe **gen. rev.**

*Streblognathus* Mayr

*Pachycondyla* Genus Group  
*Belonopelta* Mayr  
     = *Leiopelta* Baroni Urbani  
*Dinoponera* Roger  
*Mayaponera* **gen. nov.**  
*Neoponera* Emery **gen. rev.**  
     = *Eumecopone* Forel  
     = *Syntermitopone* Wheeler **syn. nov.**  
     = *Termitopone* Wheeler **syn. nov.**  
*Pachycondyla* Smith  
*Simopelta* Mann  
*Thaumatomyrmex* Mayr

*Plectroctena* Genus Group  
*Boloponera* Fisher  
*Centromyrmex* Mayr  
     = *Glyphopone* Forel  
     = *Leptopone* Arnold  
     = *Spalacomyrmex* Emery  
     = *Typhloteras* Karavaiev  
*Dolioponera* Brown (*incertae sedis*)  
*Feroponera* Bolton & Fisher (*incertae sedis*)  
*Loboponera* Bolton & Brown  
*Plectroctena* Smith  
     = *Cacopone* Santschi  
*Psalidomyrmex* André

*Ponera* Genus Group  
*Austroponera* **gen. nov.**  
*Cryptopone* Emery  
     = *Wadeura* Weber **syn. nov.**  
*Diacamma* Mayr  
*Ectomomyrmex* Mayr **gen. rev.**  
*Emeryopone* Forel  
*Iroponera* **gen. nov.** (*incertae sedis*)  
*Parvaponera* **gen. nov.**  
*Ponera* Latreille  
     = *Pseudocryptopone* Wheeler  
     = *Pteroponera* Bernard  
     = *Selenopone* Wheeler  
*Pseudoponera* Emery **gen. rev.**  
     = *Trachymesopus* Emery  
*Rasopone* **gen. nov.** (*incertae sedis*)

## Keys to Ponerine genera

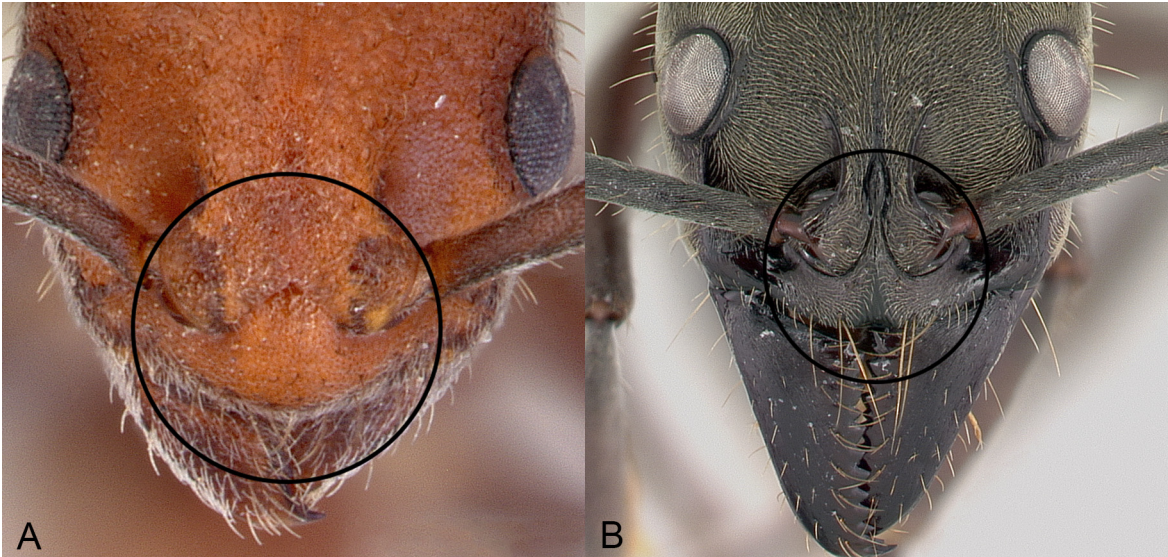
The dichotomous keys that follow are based on morphological characters of the worker caste, though in most cases they will also allow identification of the queen caste. Separate keys are presented for the three major biogeographic provinces of ponerine diversity to facilitate rapid identification.



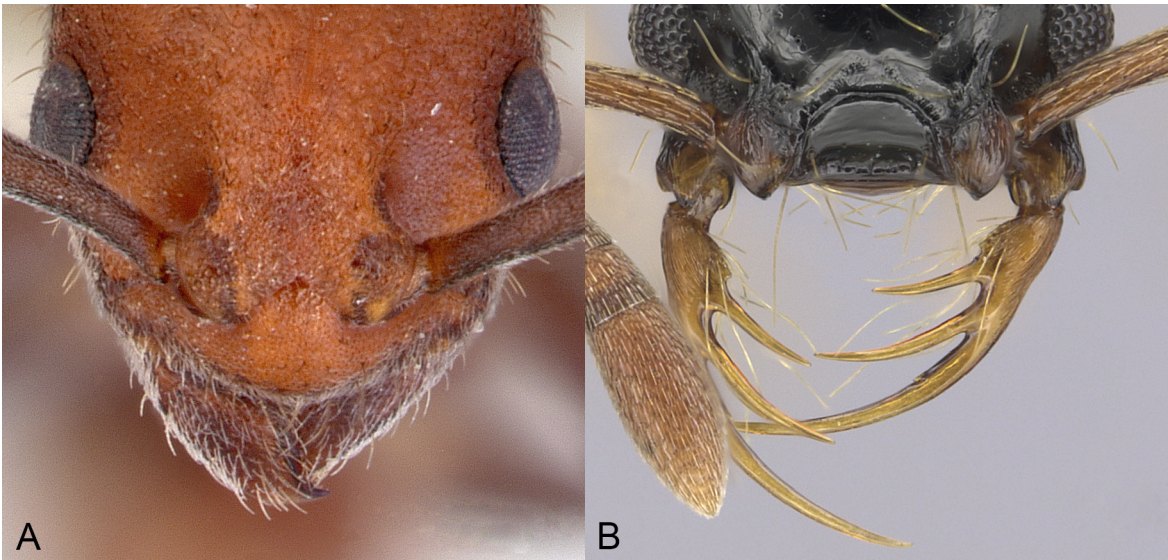
**Key to New World genera of Ponerinae**

Including all of North, Central and South America and the islands of the Caribbean.

- 1     Clypeus broadly inserted between frontal lobes, which appear flattened in frontal view (Fig. A). Antennal sockets widely separated . . . . . 2  
-     Clypeus usually narrowly inserted between frontal lobes (Fig. B). Antennal sockets usually closely approximated . . . . . 3

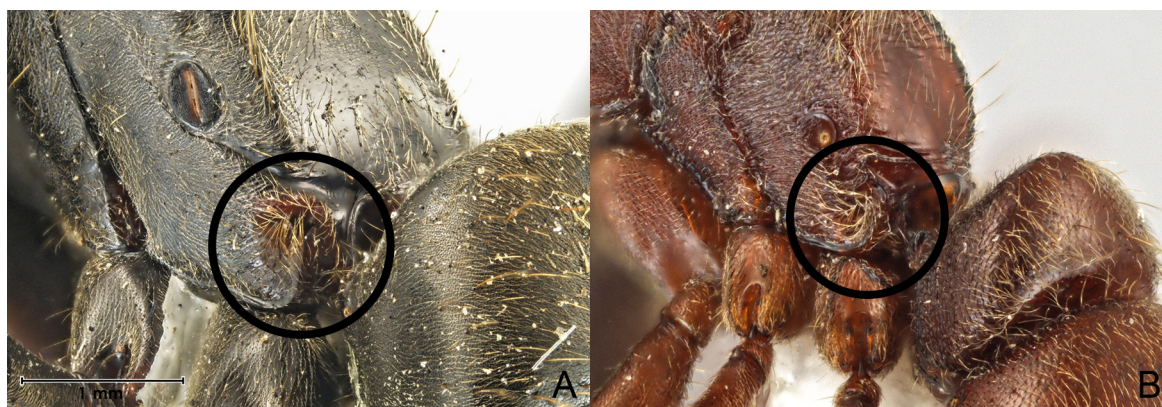


- 2(1)     Mandibles subtriangular, with numerous short teeth (Fig. A). . . . . *Platythyrea*  
-     Mandibles with three long and attenuated teeth (Fig. B) . . . . . *Thaumatomyrmex*



- 3(1)     Metapleural gland orifice with a posterior, inverted U-shaped cuticular lip (opening lateral and anterior of posterior propodeal face) (Fig. A). . . . . 4  
-     Metapleural gland orifice without a posterior U-shaped cuticular lip (opening separated from posterior propodeal face by a very narrow, low flange) (Fig. B) . . . . . 9

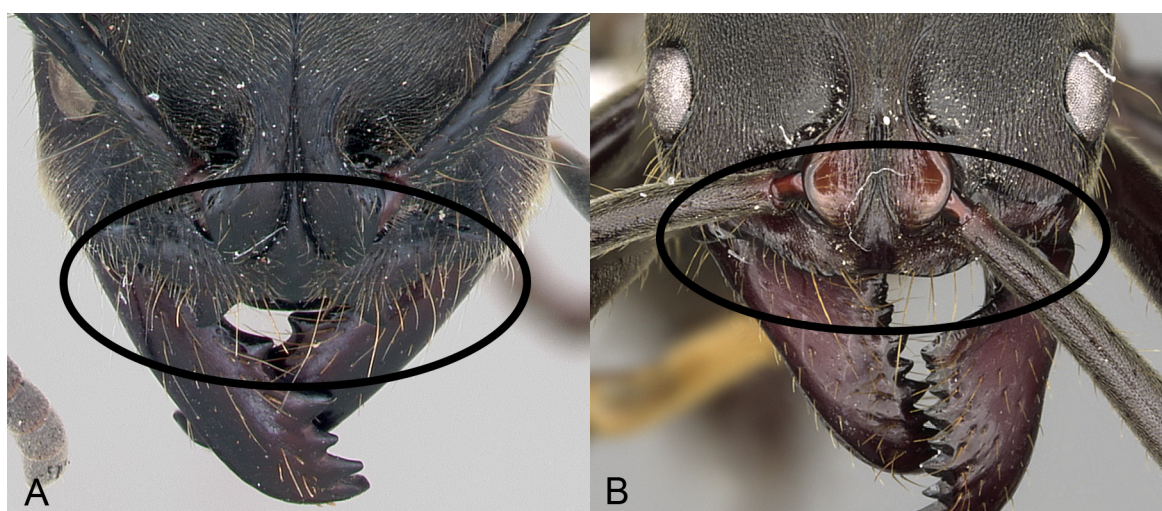




- 4(3) Propodeal spiracle slit-shaped (Fig. A) . . . . . 5  
 - Propodeal spiracle round or ovoid (Fig. B) . . . . . 7

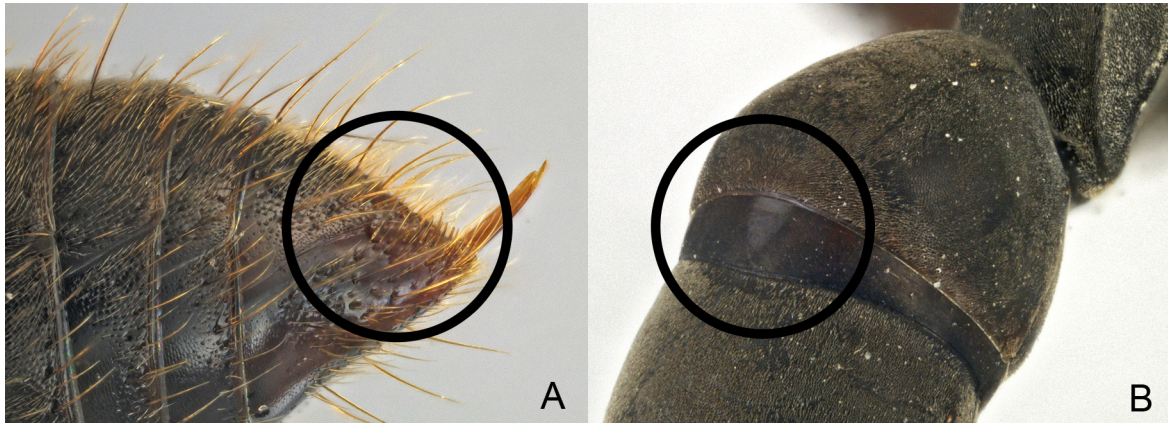


- 5(4) Massive ants (head width greater than 4.0 mm). Anterior clypeal margin with a pair of large projecting teeth (Fig. A) . . . . . *Dinoponera*  
 - Smaller ants (head width less than 4.0 mm). Anterior clypeal margin without a pair of large projecting teeth (Fig. B) . . . . . 6

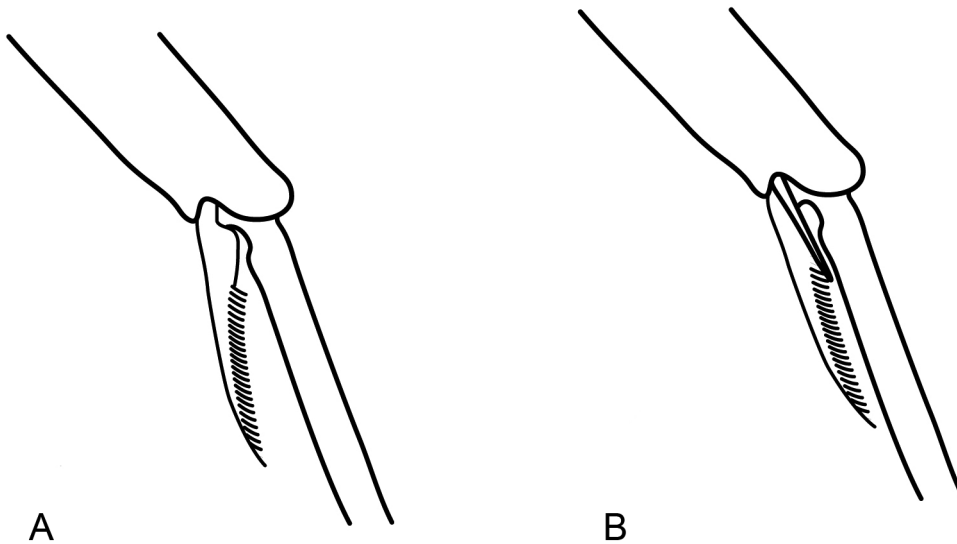


- 6(5) Hypopygium with a row of stout setae along each side of the sting (sometimes partially hidden by surrounding thinner hairs) (Fig. A). Stridulatory organ absent from A4 pretergite. Arolia not prominent and white. Preocular carinae absent . . . . . *Pachycondyla*  
 - Hypopygium without a row of stout setae along each side of the sting. Stridulatory organ present on A4 pretergite (Fig. B). Arolia prominent, projecting and usually bright white. Preocular carinae present or absent . . . . . *Neoponera* (in part)

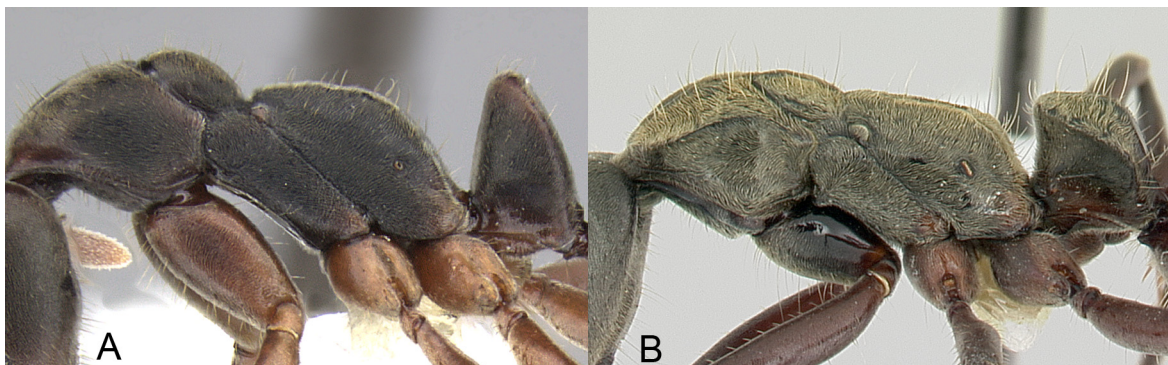




- 7(4) Ventral apex of the metatibia with a single spur, which is pectinate (Fig. A) . . . . . *Simopelta*  
 - Ventral apex of the metatibia with a large pectinate spur and a smaller simple spur (Fig. B) . . . . . 8



- 8(7) Metanotal groove strongly developed and angular, the propodeum well below the mesonotum (Fig. A) . . . . . *Mayaponera*  
 - Metanotal groove essentially absent to weakly developed, the propodeum level with the mesonotum (Fig. B) . . . . .  
 . . . . . *Neoponera* (in part)



- 9(3) Mandibles long and straight, inserted medially on the front of the head. Head with prominent ocular prominences (Fig. A) 10  
 - Mandibles inserted toward the sides of the front of the head. Head without prominent ocular prominences (Fig. B) . . . . . 11

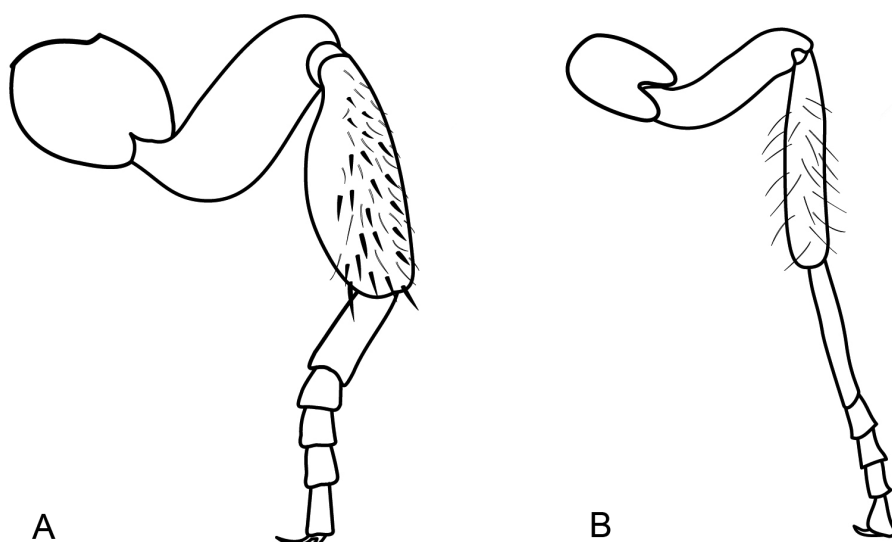




- 10(9) Nuchal carina continuously curved, the posterior surface of the head lacking a pair of dark apophyseal lines (Fig. A). . . . . *Anochetus*  
 - Nuchal carina medially V-shaped, the posterior surface of the head with a pair of dark converging apophyseal lines (Fig. B) . . . . . *Odontomachus*



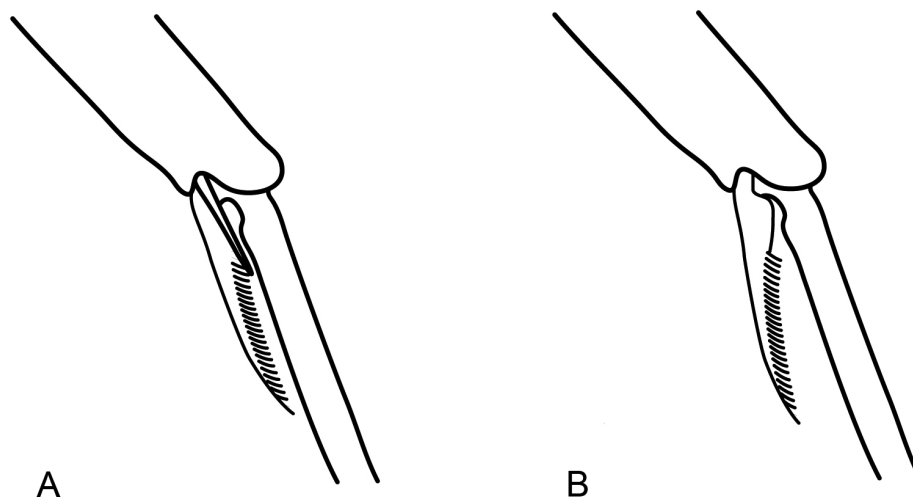
- 11(9) Mesotibiae dorsally with abundant stout traction setae (Fig. A). . . . . 12  
 - Mesotibiae dorsally without abundant stout traction setae (a few stout setae sometimes present near tarsus but never extending along length of tibia) (Fig. B) . . . . . 13



- 12(11) Eyes absent in workers, but present in queens. Metapleural gland orifice opening laterally. Head and body without a dense pubescence. Mandible with a basal groove (Fig. A) . . . . . *Centromyrmex*
- Eyes usually present in both workers and queens (rarely absent in workers). Metapleural gland orifice opening posteriorly at the posteroventral corner of the metapleuron. Head and body covered by a dense pubescence. Mandible without a basal groove but often with a basal pit (Fig. B) . . . . . *Cryptopone*

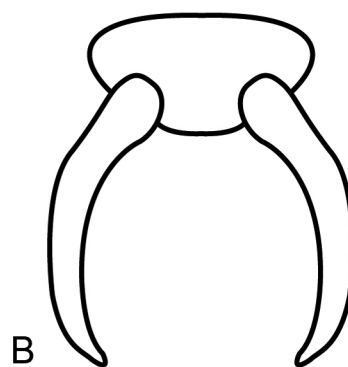
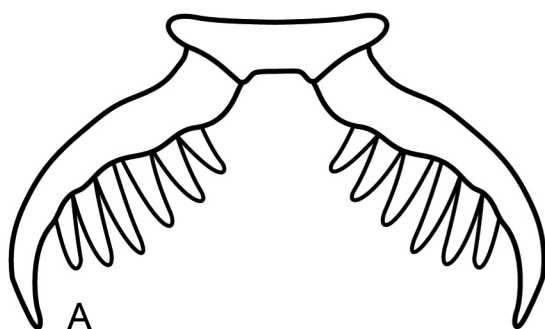


- 13(11) Ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur (Fig. A) . . . . . 14
- Ventral apex of the metatibia with a single spur, which is pectinate (Fig. B) . . . . . 17

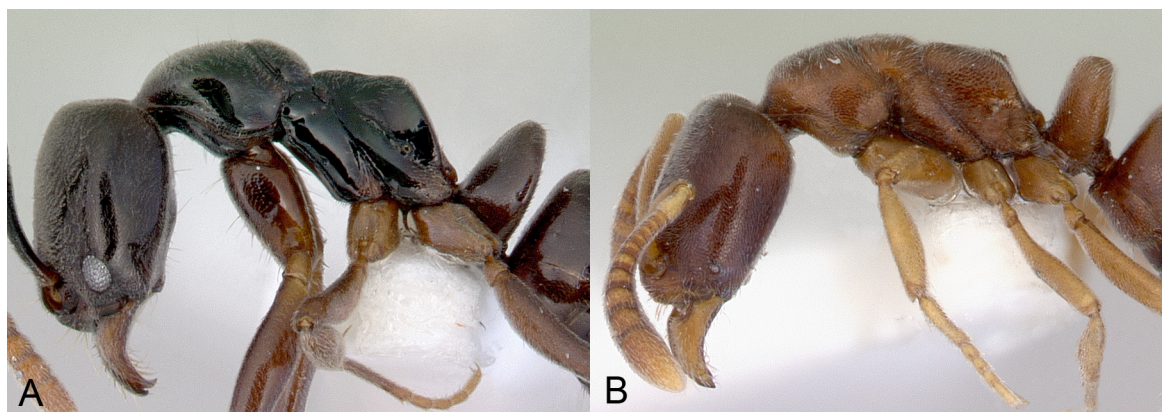




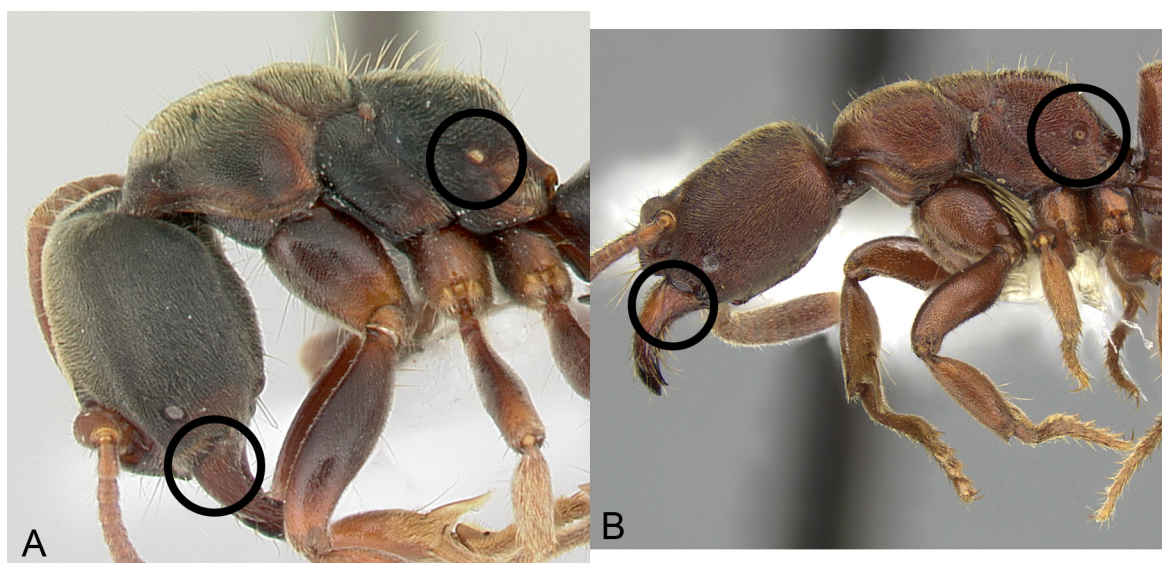
- 14(13) Tarsal claws usually pectinate, rarely armed with one to three preapical teeth (Fig. A) ..... *Leptogenys*  
 - Tarsal claws unarmed (Fig. B) ..... 15



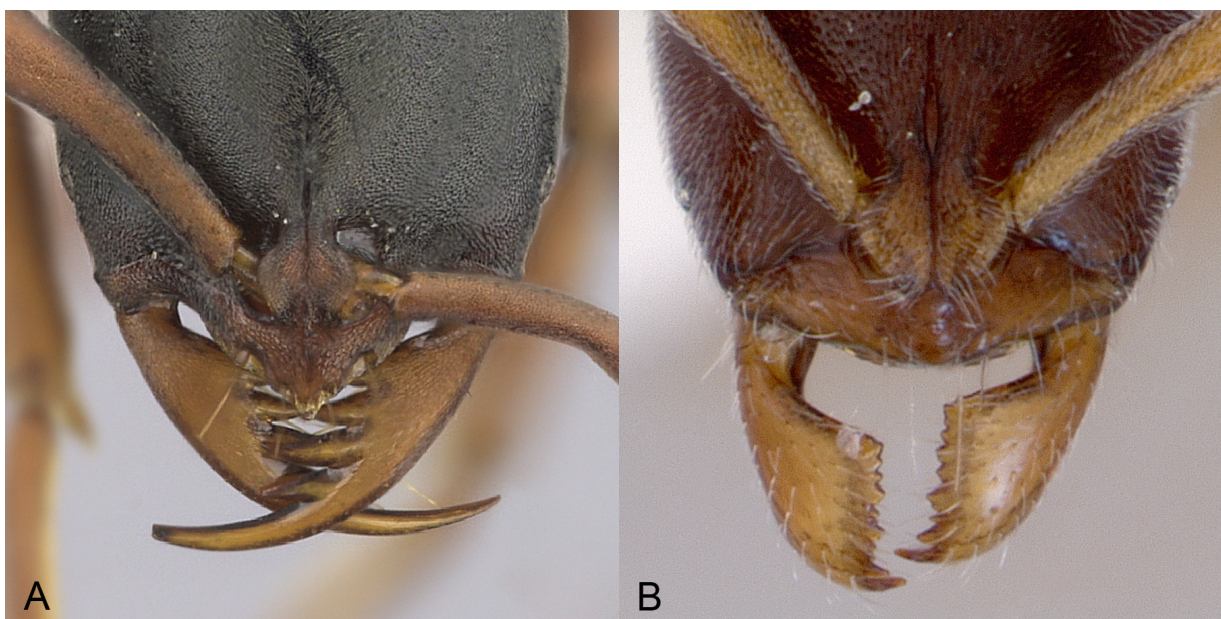
- 15(14) Mesosomal profile discontinuous, the propodeum lower than the mesonotum. Mandible with a basal pit or groove. Propodeal spiracle round. Prora absent from anterior margin of first gastral sternite (Fig. A) (Introduced in SE USA) .... *Brachyponera*  
 - Mesosomal profile nearly continuous, the metanotal groove shallow or absent. Either mandible without a basal pit or groove and propodeal spiracle round or ovoid, or mandible with a basal pit or groove and propodeal spiracle slit-shaped. Prora present on anterior margin of first gastral sternite (Fig. B) ..... 16



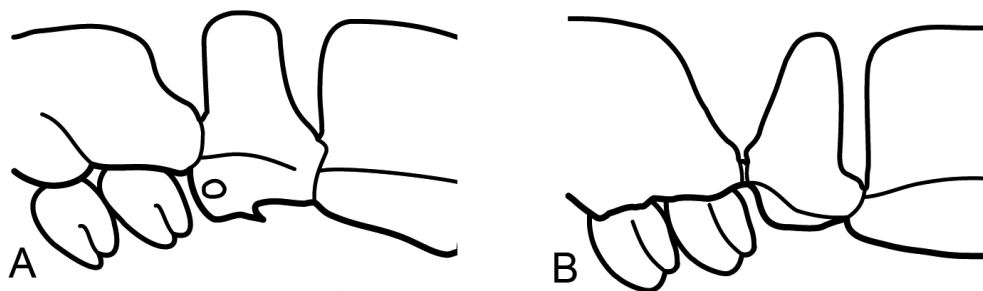
- 16(15) Mandible with a basal groove (occasionally weakly developed). Propodeal spiracle slit-shaped (Fig. A) ..... *Pseudoponera*  
 - Mandible without a basal groove (but a ridge sometimes present). Propodeal spiracle round or ovoid (Fig. B) ..... *Rasopone*



- 17(13) Mandibles narrow, with several long attenuated teeth (Fig. A) ..... *Belonopelta*  
 - Mandibles triangular and without long attenuated teeth (Fig. B) ..... 18



- 18(17) Subpetiolar process with an anterior fenestra and paired posteroventral teeth (Fig. A) ..... *Ponera*  
 - Subpetiolar process without both an anterior fenestra and paired posteroventral teeth (Fig. B) ..... *Hypoponera*



## Key to African and Malagasy Genera of Ponerinae

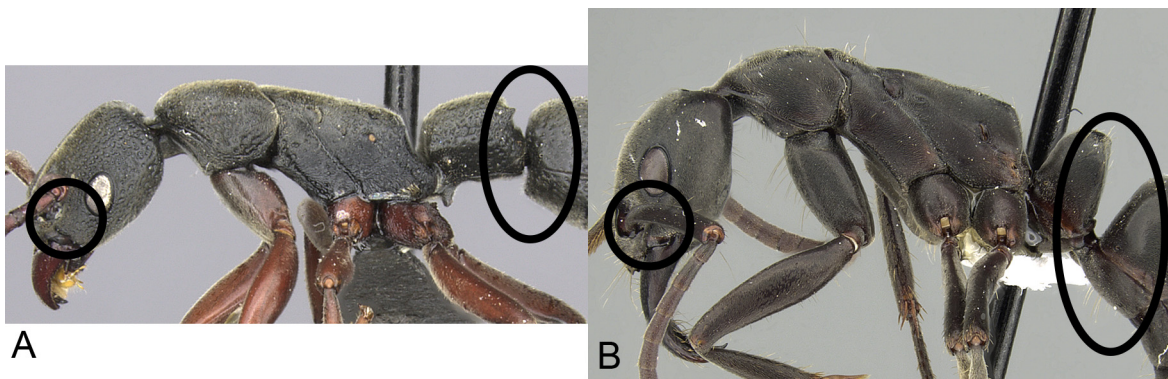
Including all of Africa, Madagascar, and the western islands of the Indian Ocean.

- 1 Clypeus broadly inserted between frontal lobes, which appear flattened in frontal view, the antennal sockets widely separated (Fig. A). Metatibiae with two pectinate spurs. Tarsal claws armed with a single preapical tooth ..... 2  
 - Clypeus narrowly inserted between frontal lobes, the antennal sockets closely approximated (Fig. B). Metatibiae with one or two spurs. Tarsal claws usually unarmed, sometimes pectinate or armed with one or two preapical teeth ..... 3





- 2(1) Preocular carinae absent. Petiole attached at approximately midheight of anterior face of first gastral segment (Fig. A) . . . . .  
 - Preocular carinae present. Petiole attached low on the anterior face of the first gastral segment (Fig. B). . . . . *Megaponera*



- 3(1) Mandibles long and linear, inserted medially on the front of the head. Eyes set on prominent ocular prominences (Fig. A) . . 4  
 - Mandibles variously shaped, inserted at or near the anterolateral corners of the head. Eyes not set on prominent ocular prominences (Fig. B) . . . . . 5

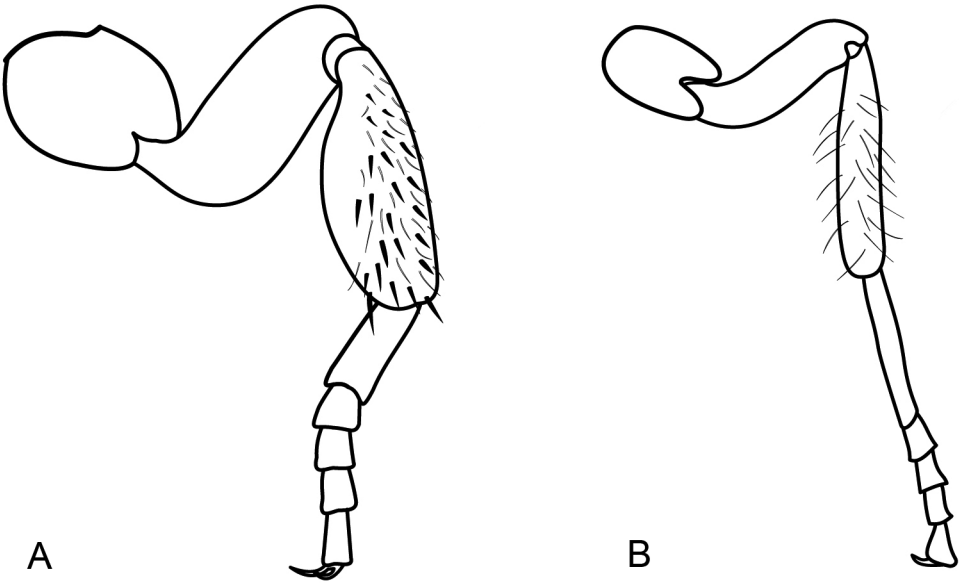




- 4(3) Nuchal carina continuously curved, the posterior surface of the head lacking a pair of dark apophyseal lines (Fig. A). . . . . *Anochetus*  
- Nuchal carina medially V-shaped, the posterior surface of the head with a pair of dark converging apophyseal lines (Fig. B) . . . . . *Odontomachus*



- 5(3) Mesotibiae dorsally with abundant stout traction setae (Fig. A). . . . . 6  
- Mesotibiae dorsally without abundant stout traction setae (a few stout setae sometimes present near tarsus but never extending along length of tibia) (Fig. B) . . . . . 9

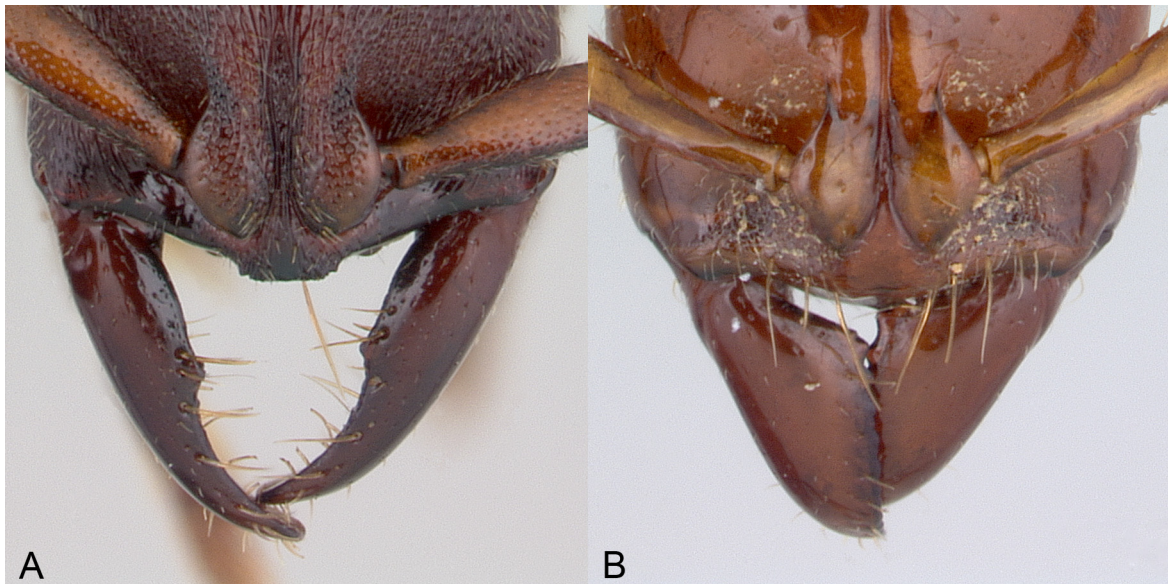


- 6(5) Mandibles triangular, with a basal pit. Metanotal groove distinct. Spiniform setae absent from meso- and metabasitarsi. Eyes present (but small) or absent in workers (Fig. A) . . . . . *Cryptopone* (in part)  
- Mandibles variously shaped, but never with a basal pit. Metanotal groove usually obsolete. Spiniform setae present on meso- and metabasitarsi. Eyes absent in workers (Fig. B) . . . . . 7

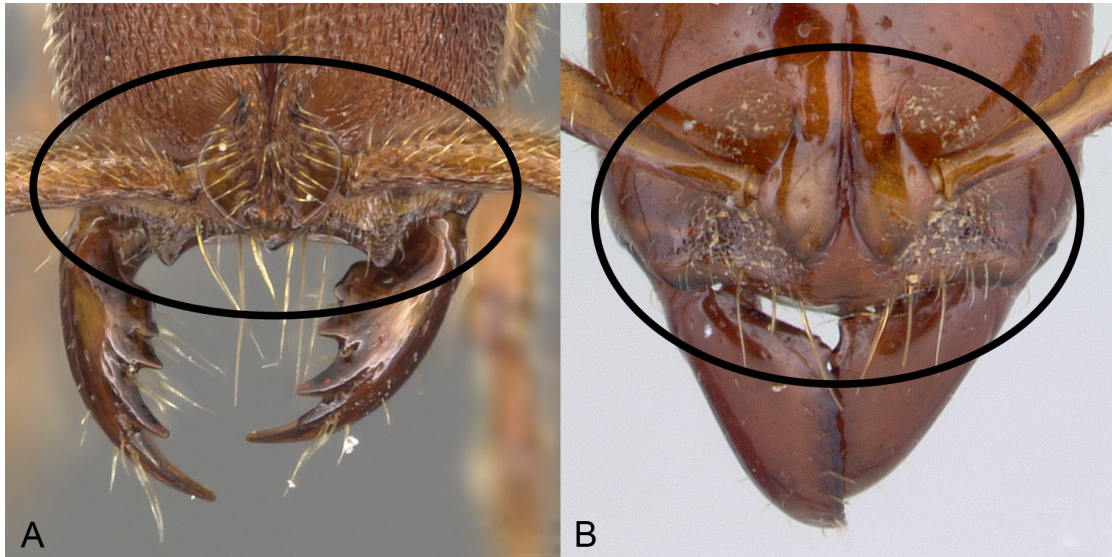




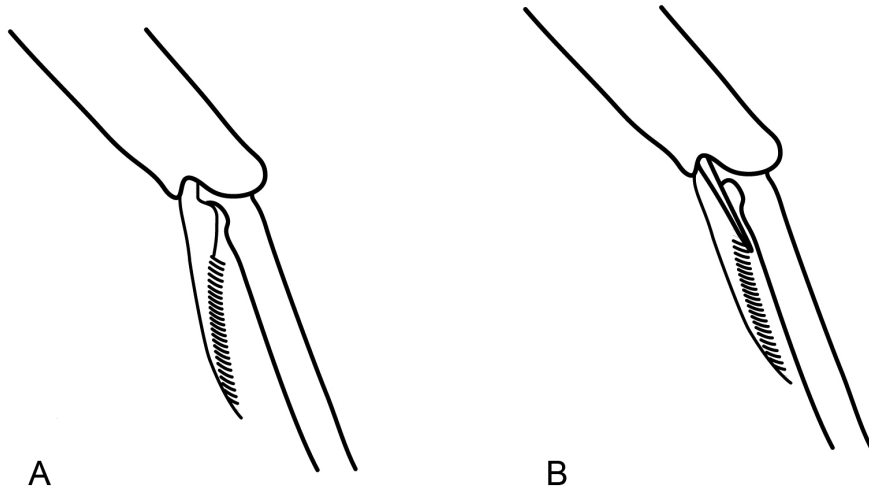
- 7(6) Mandibles linear. Anterior margin of clypeus with a blunt medial projection (Fig. A) ..... *Promyopias*  
 - Mandibles triangular to subtriangular. Anterior margin of clypeus without a blunt medial projection (Fig. B) ..... 8



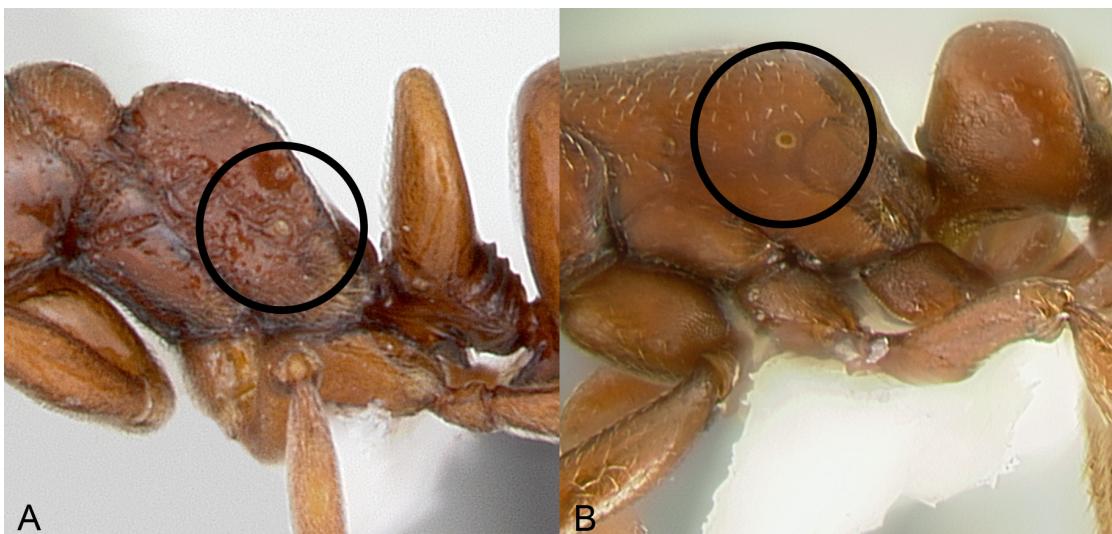
- 8(7) Anterior clypeal margin with a pair of small lateral projecting teeth. Frontal lobes closely approximated and overhanging the anterior clypeal margin. (Fig. A) Metapleural gland orifice located near the posteroventral corner of the metapleuron ..... *Feraponera*  
 - Anterior clypeal margin without a pair of projecting teeth. Frontal lobes not closely approximated and not overhanging the anterior clypeal margin. (Fig. B) Metapleural gland orifice located near the propodeal spiracle and opening laterally ..... *Centromyrmex*



- 9(5) Ventral apex of the metatibia with a single spur, which is pectinate (Fig. A) . . . . . 10  
 - Ventral apex of the metatibia with one pectinate and one simple or barbulate spur (Fig. B) . . . . . 19



- 10(9) Propodeal spiracle slit-shaped (Fig. A) . . . . . 11  
 - Propodeal spiracle round or ovoid (Fig. B) . . . . . 12

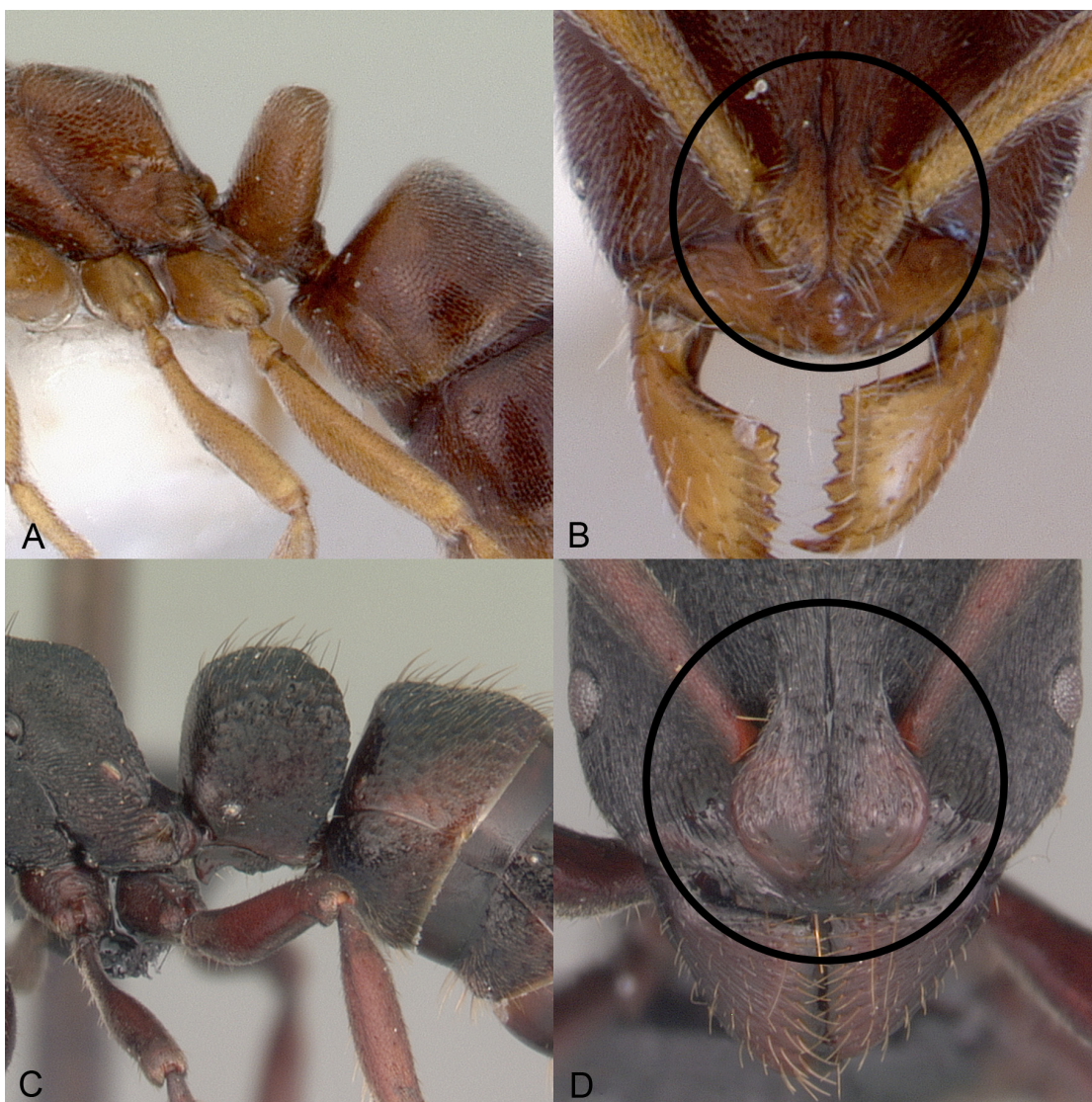




- 11(10) Eyes present. Metanotal groove strongly impressed and “V”-shaped (Fig. A) ..... *Asphinctopone*  
 - Eyes absent (or present only as a pigmented spot). Metanotal groove angular, the propodeum depressed below the mesonotum (Fig. B) ..... *Fisheropone*

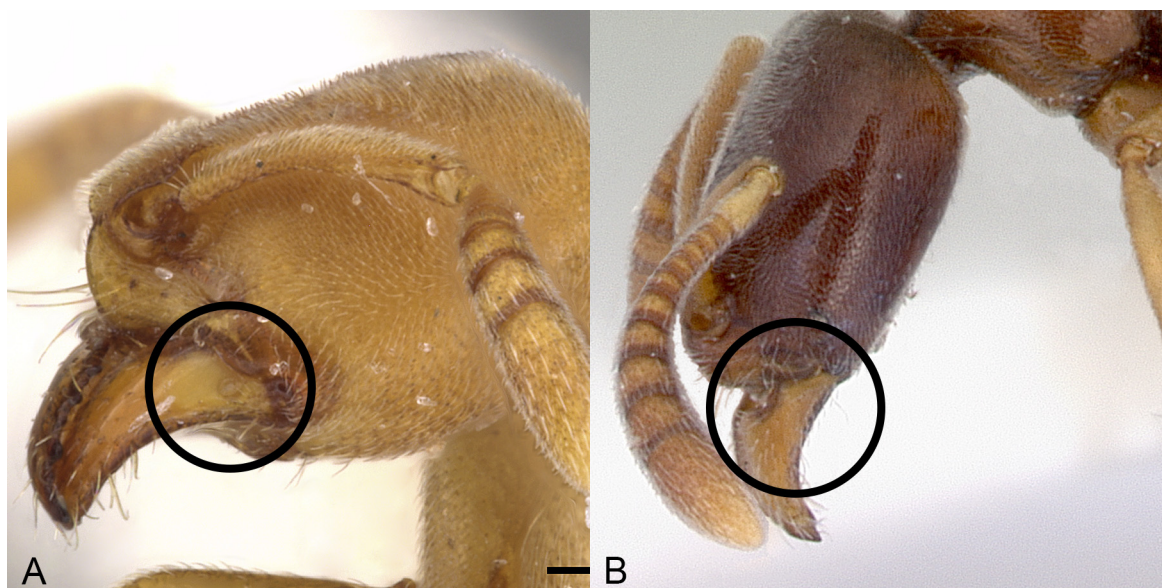


- 12(10) Petiole scale-like and thin (Fig. A). Frontal lobes small (Fig. B) ..... 13  
 - Petiole surmounted by a thick node (Fig. C). Frontal lobes large (Fig. D) ..... 15

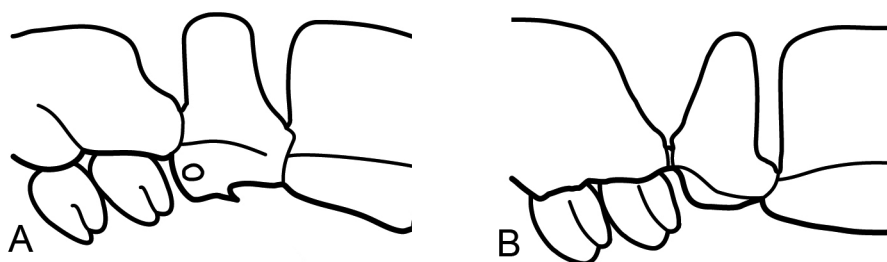




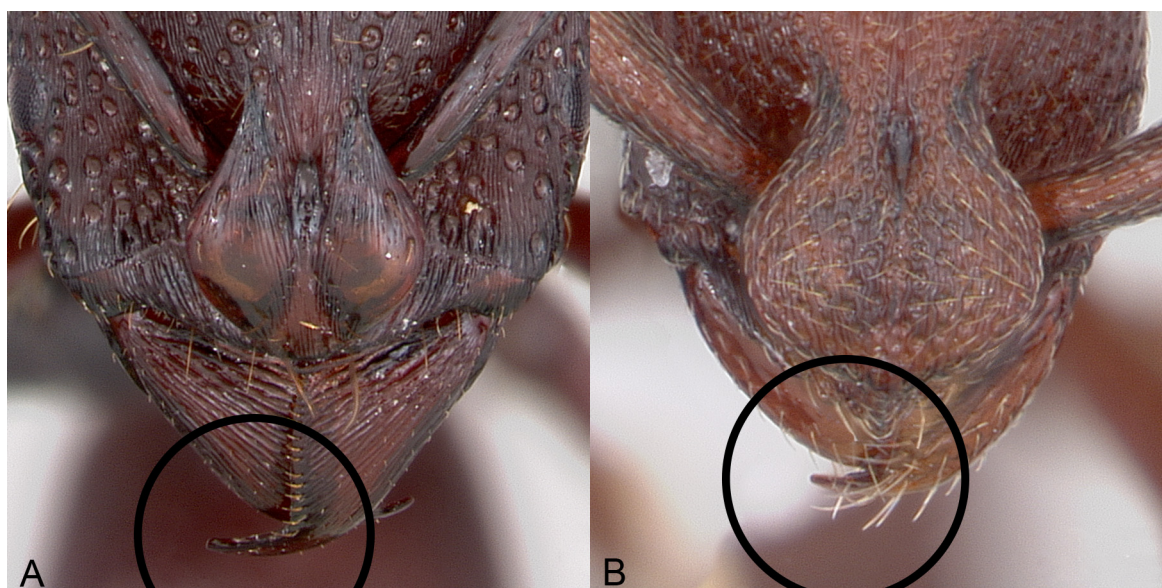
- 13(12) Mandibles with a basal pit or fovea (Fig. A) ..... *Cryptopone* (in part)  
 - Mandibles without a distinct basal pit or fovea (Fig. B)..... 14



- 14(13) Subpetiolar process with an anterior fenestra and paired posteroventral teeth (Fig. A) ..... *Ponera*  
 - Subpetiolar process without both an anterior fenestra and paired posteroventral teeth (Fig. B) ..... *Hypoponera*

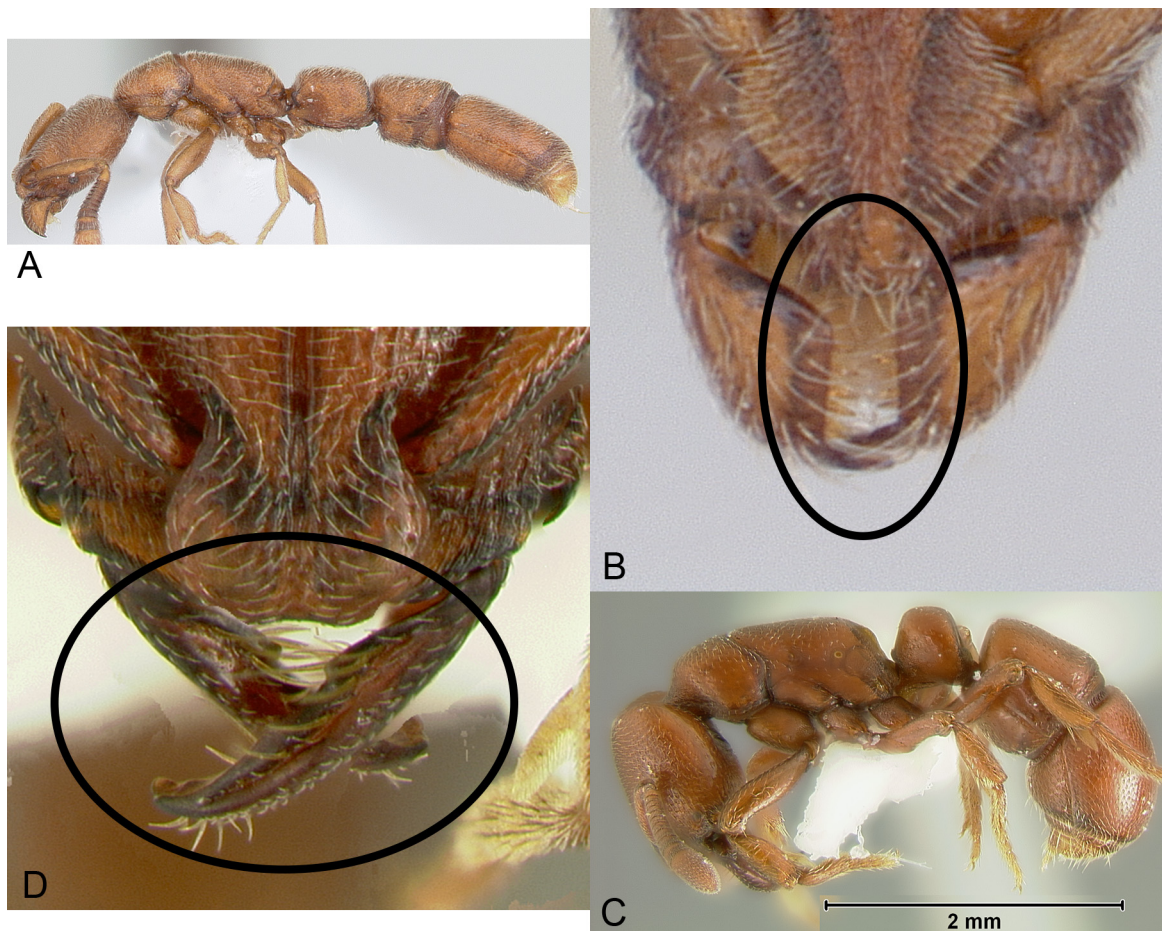


- 15(12) Mandible with a long curved attenuated apical tooth (Fig. A). Labrum projecting beyond the anterior clypeal margin. ....  
 ..... *Psalidomyrmex*  
 - Mandible without a long attenuated apical tooth (Fig. B). Labrum not projecting beyond the anterior clypeal margin ..... 16

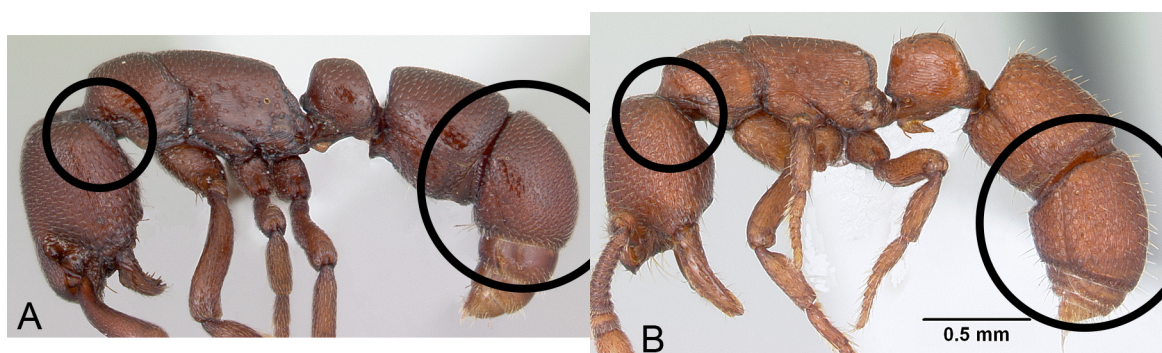




- 16(15) Body extremely elongate (Fig. A). Mandibles with a row of peg-like setae on their inner margins (Fig. B). Posterior propodeal margins not expanded to form lamellae. Metafemur without a dorsal groove ..... *Dolioponera*
- Body not extremely elongate (Fig. C). Mandibles without a row of peg-like setae on their inner margins (Fig. D). Posterior propodeal margins expanded posteriorly to form lamellae. Metafemur with a dorsal groove ..... 17

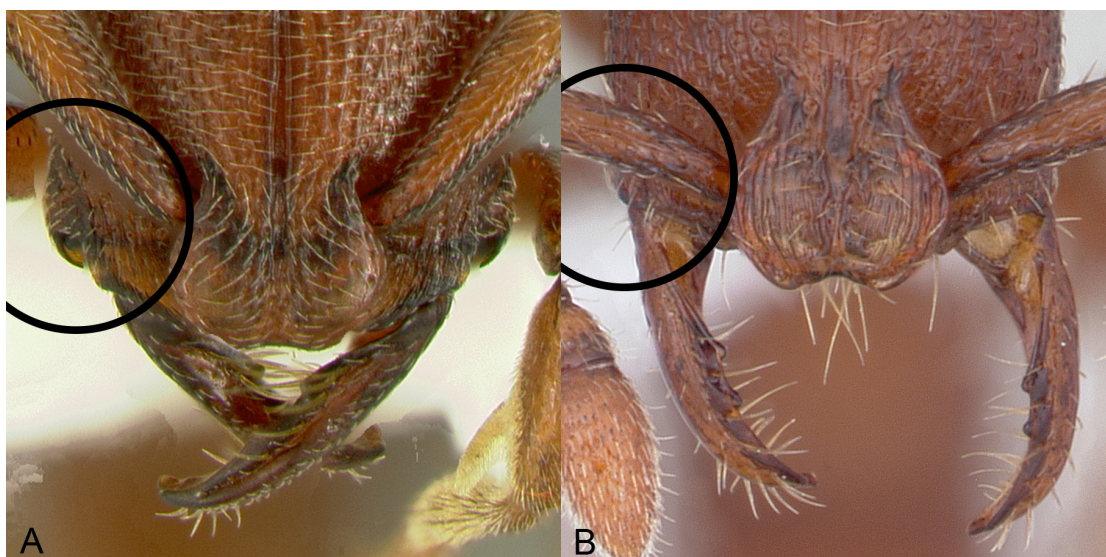


- 17(16) A4 tergite strongly vaulted, the gaster downcurved posteriorly. Posteroventral corners of head with a projecting flange (Fig. A) ..... *Loboponera*
- A4 tergite not strongly vaulted. Posteroventral corners of head without a projecting flange (Fig. B) ..... 18



- 18(17) Mandible thin and curved, with both a dorsal and a lateral longitudinal groove (Fig. A). Clypeus with a lateral excavation at the base of each mandible (Fig. A). Eyes generally present, varying from moderately large to very small, rarely absent ..... *Plectroctena*
- Mandible triangular, with only a lateral longitudinal groove (Fig. B). Clypeus without lateral excavations (Fig. B). Eyes absent ..... *Boloponera*





- 19(9) Tarsal claws usually pectinate (Fig. A), sometimes armed with only one to three preapical teeth. Gaster generally with a strong girdling constriction (sometimes constriction essentially absent). Frontal lobes very small. Body slender. . . . . *Leptogenys*
- Tarsal claws unarmed (Fig. B) or at most armed with one preapical tooth, in which case the gaster lacks a strong girdling constriction, the frontal lobes are of moderate size, and the body is not especially slender . . . . . 20

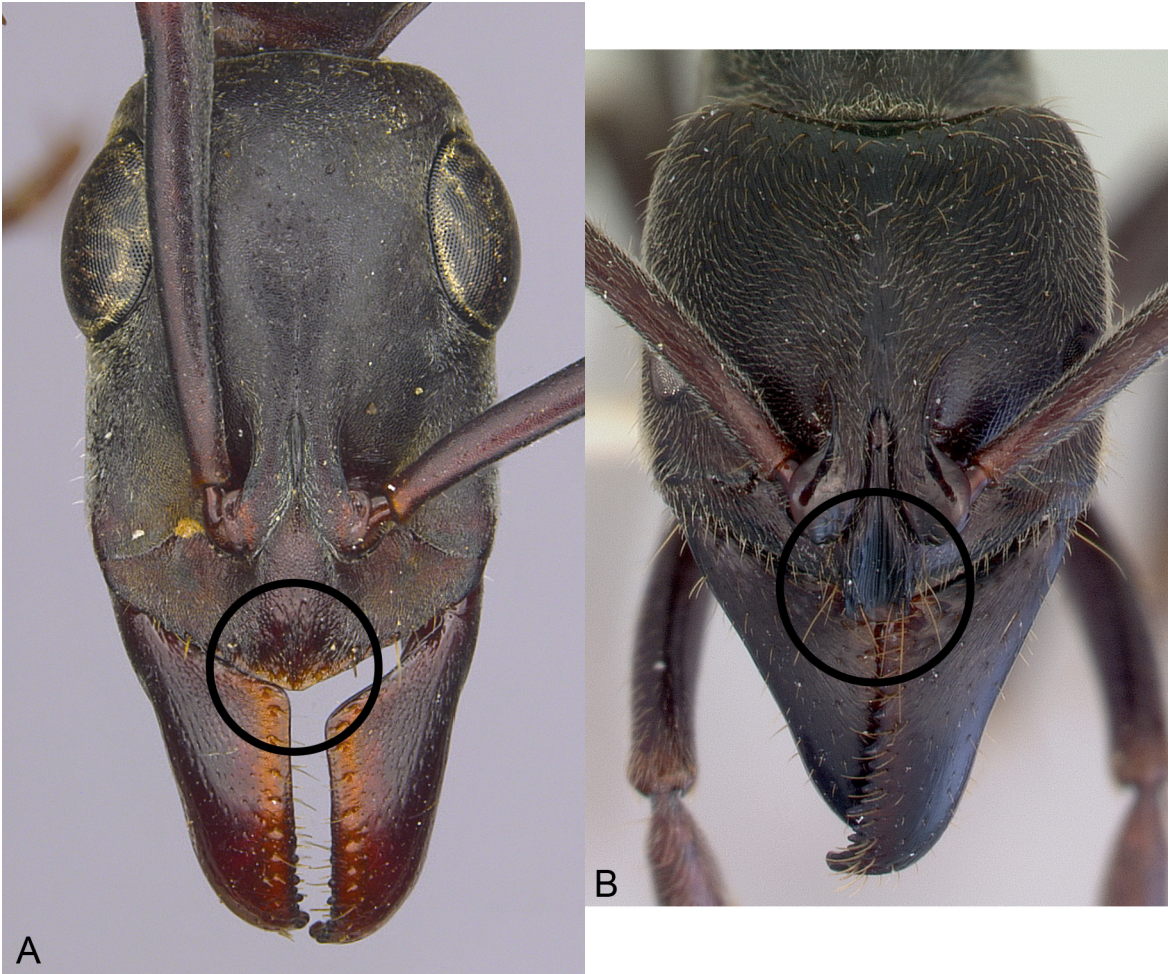


- 20(19) Hypopygium with a row of stout setae along each side of the sting (sometimes partially hidden by surrounding thinner hairs) (Fig. A) . . . . . 21
- Hypopygium without a row of stout setae along each side of the sting . . . . . 22

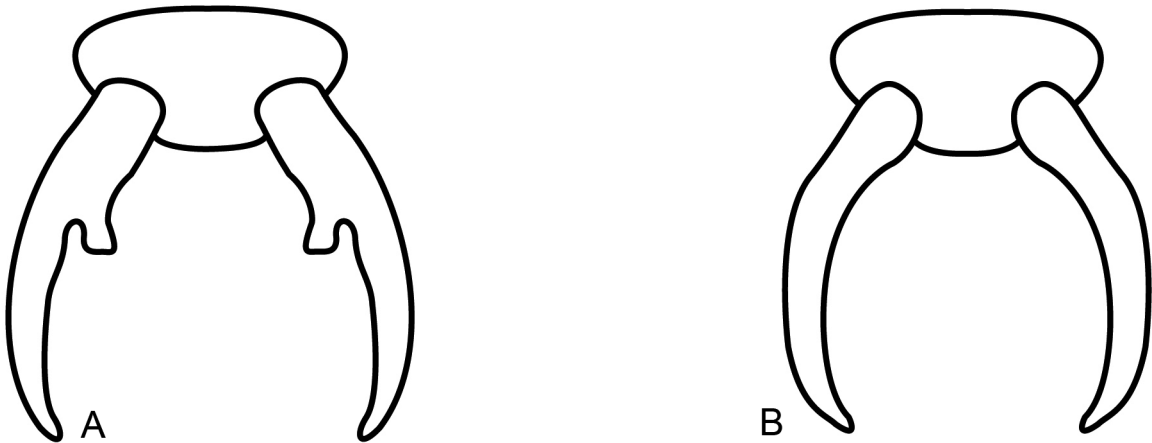




- 21(20) Eyes very large, located at or posterior to the head midline (Fig. A). Clypeus without a blunt medial anterior projection (Fig. A). Propodeal spiracle slit-shaped. .... *Ophthalmopone*
- Eyes of moderate size, located anterior to the head midline (Fig. B). Clypeus with a blunt medial anterior projection (Fig. B). Propodeal spiracle ovoid. .... *Paltothyreus*

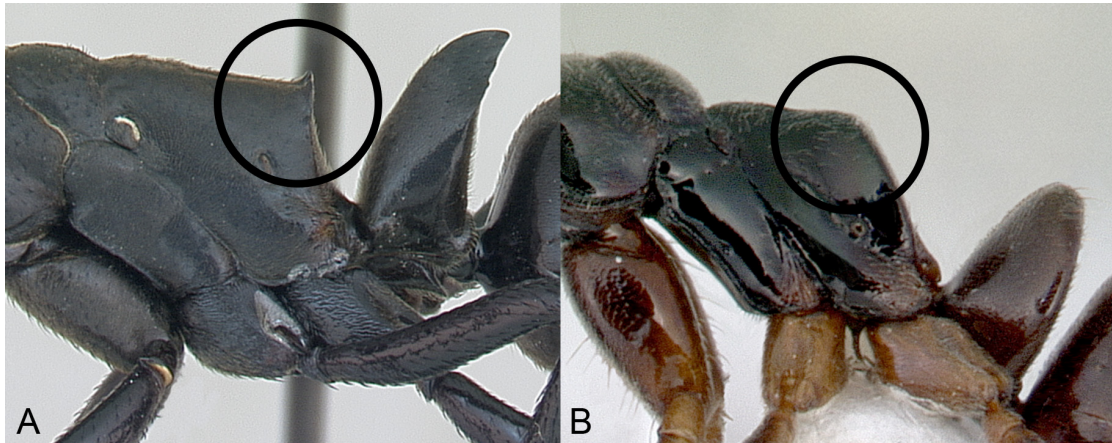


- 22(20) Tarsal claws armed with a single preapical tooth (Fig. A) ..... *Hagensia*
- Tarsal claws unarmed (Fig. B) ..... 23

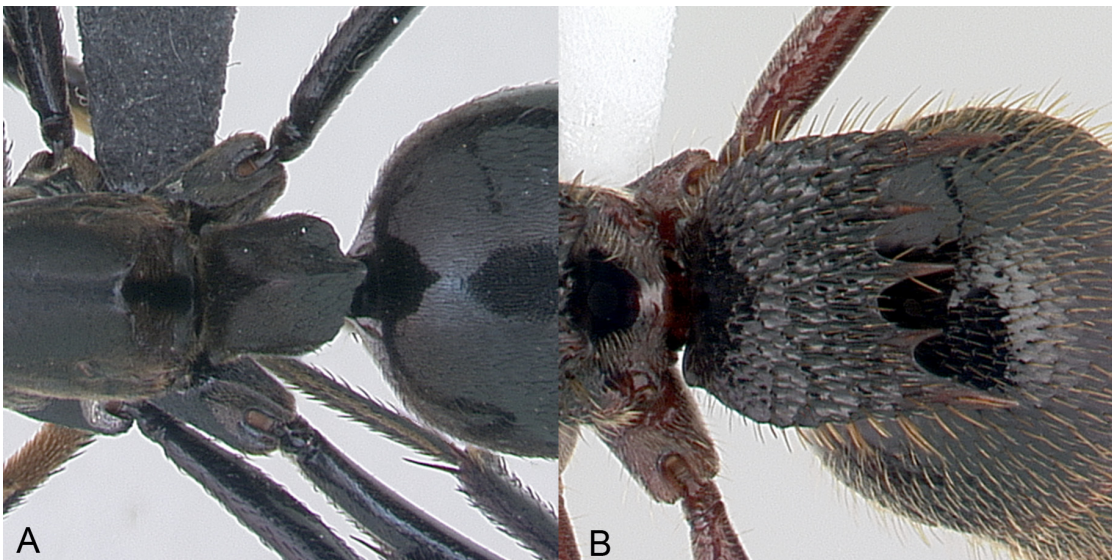


- 23(22) Propodeum with a pair of spines or teeth on the posterodorsal margin (near the angle) (Fig. A) ..... 24
- Propodeum without a pair of spines or teeth on the posterodorsal margin (near the angle) although teeth sometimes present along the posterior propodeal face (Fig. B). .... 25

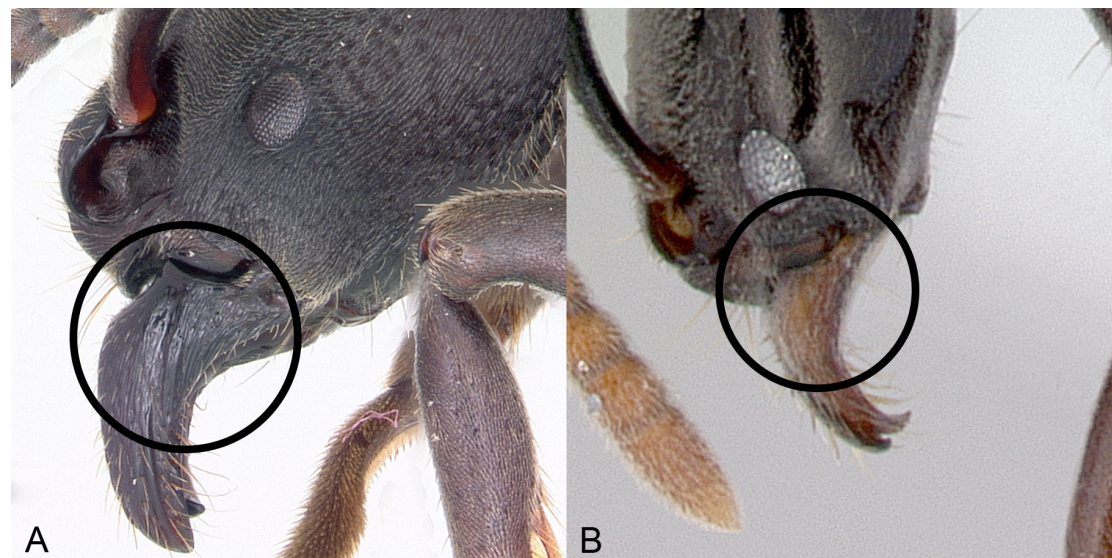




- 24(23) Petiole tall and fin-like, with sharp lateral margins and a longitudinal dorsal carina (Fig. A) . . . . . *Sirebolognathus*  
 - Petiole with five sharp posteriorly-projecting teeth on the posterodorsal margin (Fig. B). . . . . *Phrynoponera*

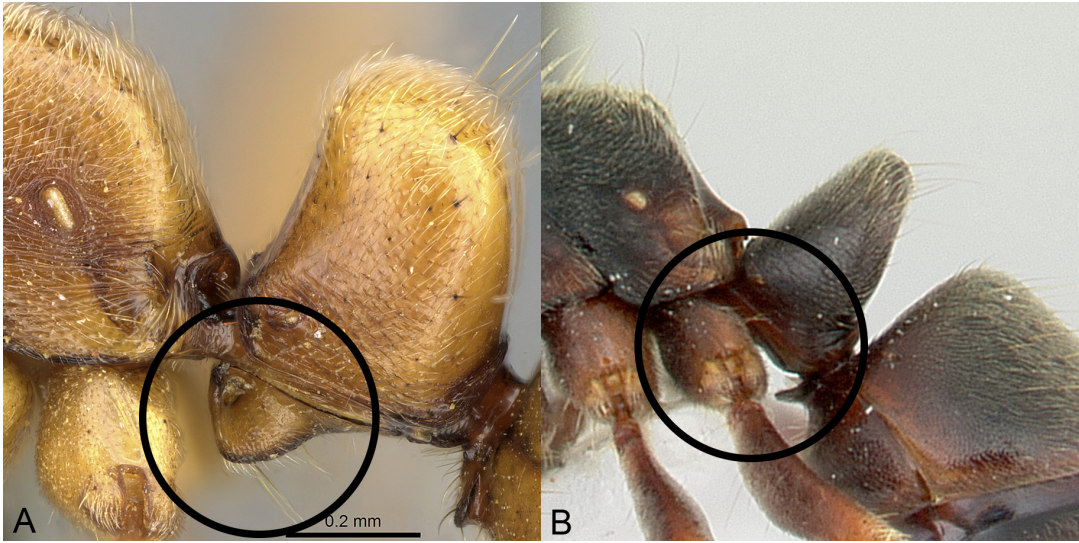


- 25(23) Mandible smooth or with an elongate suture basally, but never with a pit or short groove (Fig. A) . . . . . 26  
 - Mandible with a small basal pit or short groove, but never with an elongate basal suture (Fig. B). . . . . 28

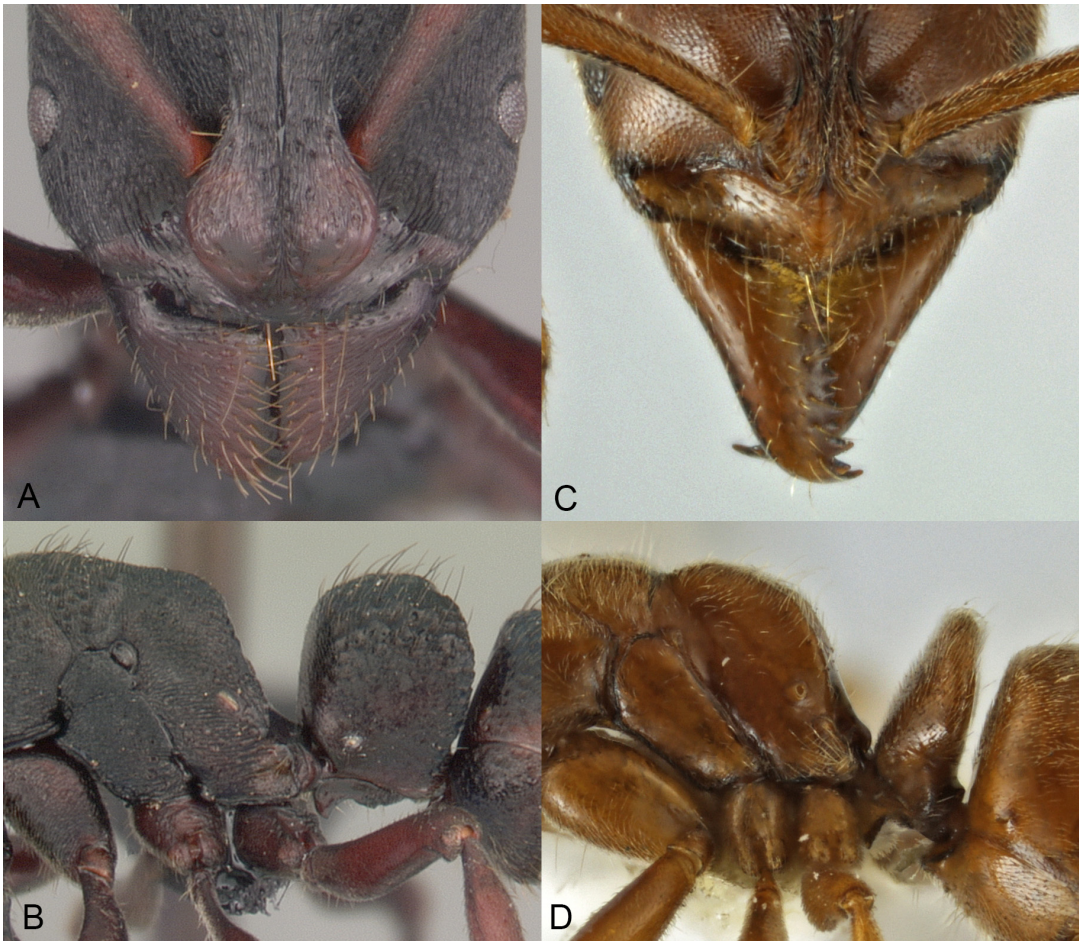




- 26(25) Compound eyes small (with 2-4 facets) or absent. Subpetiolar process with an anterior fenestra and/or a pair of teeth (Fig. A).  
 ..... *Parvaponera*  
 - Compound eyes present and larger, with numerous facets. Subpetiolar process simpler, without a fenestra or teeth (but sometimes various small projections) (Fig. B) ..... 27

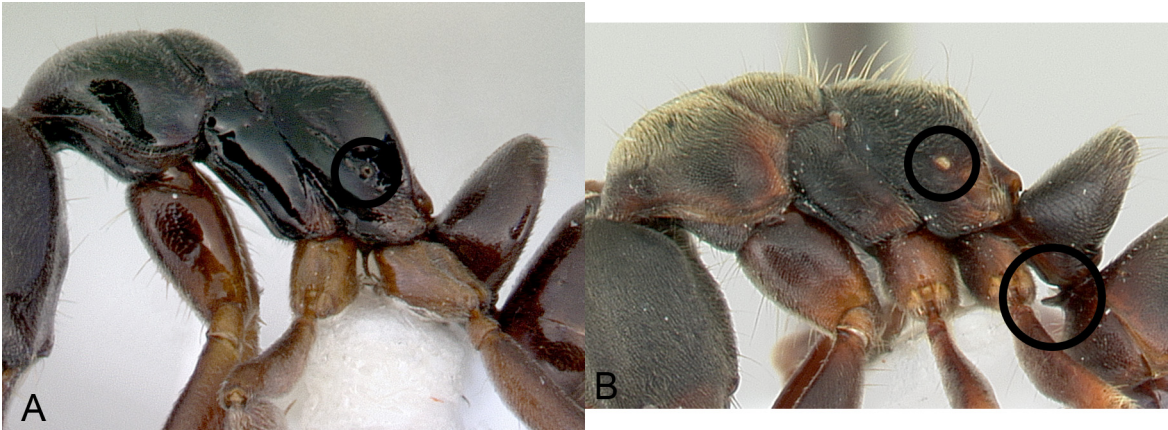


- 27(26) Mandible relatively short and often with an elongate basal suture (Fig. A). Metanotal groove absent. Propodeal spiracle elongate. Petiole surmounted by a thick node (Fig. B) ..... *Bothroponera*  
 - Mandible generally elongate and never with a basal suture (Fig. C). Metanotal groove impressed (weakly to strongly). Propodeal spiracle round or elongate. Petiolar node generally scale-like and thin (Fig. D), sometimes broader but never thick. ....  
 ..... *Mesoponera* (in part)





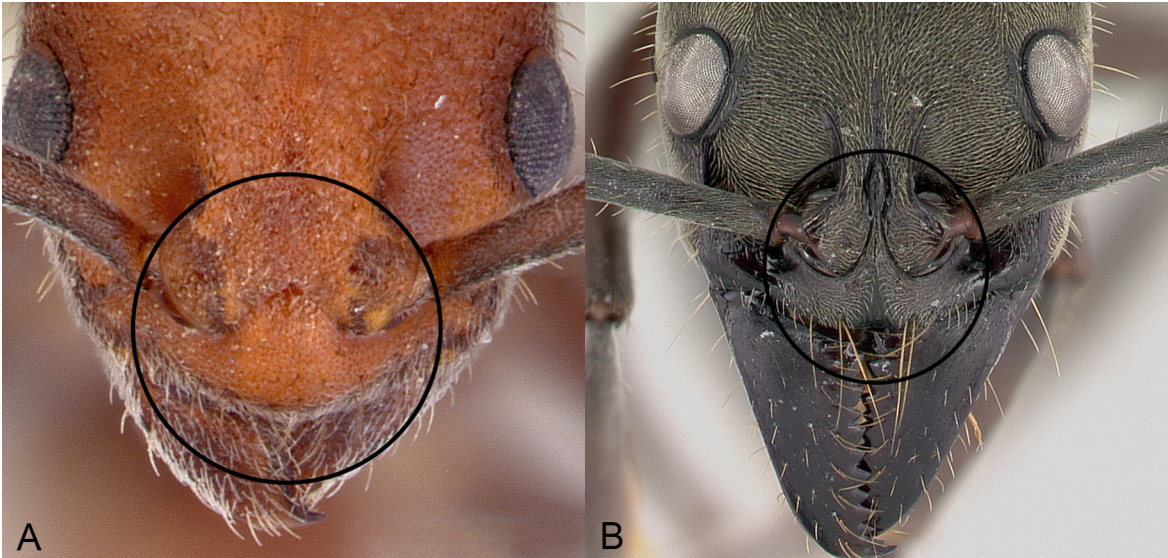
- 28(27) Metanotal groove distinct. Propodeal spiracle round or ovoid. Prora absent from anterior margin of first gastral sternite (Fig. A). . . . . *Brachyponera*
- Metanotal groove obsolete or distinct. Propodeal spiracle slit-shaped. Prora present on anterior margin of first gastral sternite (Fig. B) . . . . . *Euponera*



**Key to Eurasian and Australian Genera of Ponerinae**

Including all of Europe, Asia, Australia, Melanesia, and Polynesia.

- 1 Clypeus broadly inserted between frontal lobes, which appear flattened in frontal view, the antennal sockets widely separated (Fig. A). Metatibia with two pectinate spurs. Tarsal claws usually armed with a single preapical tooth (rarely unarmed). Petiole usually attached at approximately midheight of anterior face of first gastral segment (attached low on the anterior face in Australian species). Sculpturing usually uniformly pruinose (less pronounced in Australian species) . . . . . *Platythyrea*
- Clypeus narrowly inserted between frontal lobes, the antennal sockets closely approximated (Fig. B). Metatibia with either one or two spurs. Tarsal claws usually unarmed, sometimes pectinate or armed with a single tooth. Petiole attached low on the anterior face of the first gastral segment. Sculpturing rarely uniformly pruinose. (Tribe Ponerini) . . . . . 2

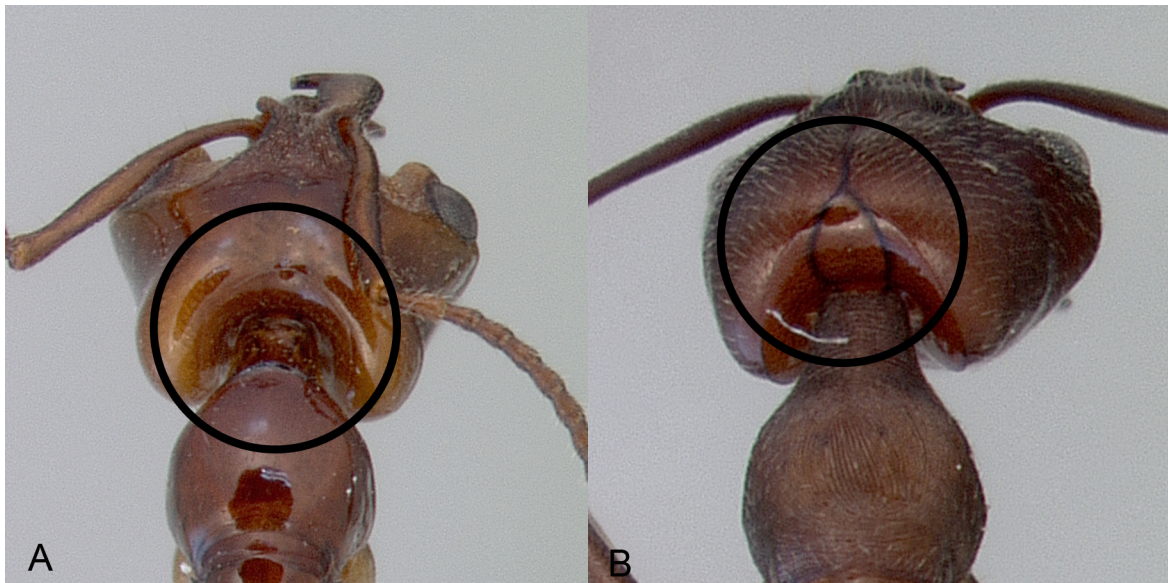


- 2(1) Mandibles long and linear, inserted medially on the front of the head. Head with prominent ocular prominences (Fig. A). . . 3
- Mandibles inserted toward the sides of the front of the head. Head without prominent ocular prominences (Fig. B) . . . . . 4

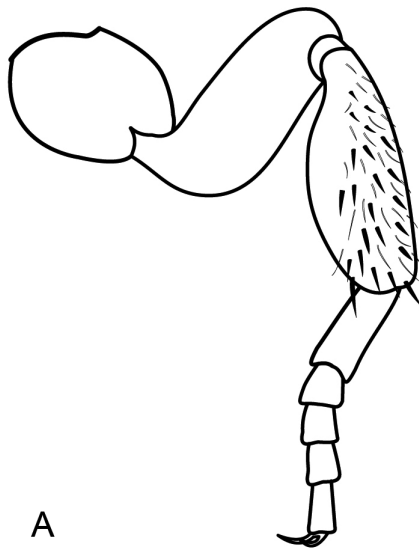




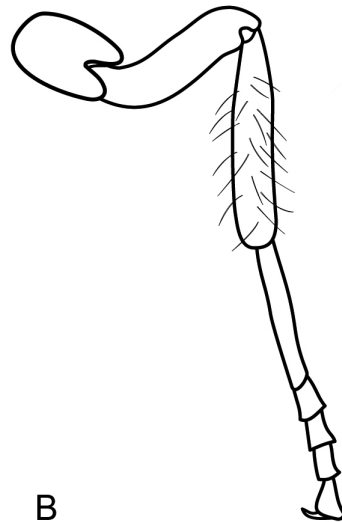
- 3(2) Nuchal carina continuously curved, the posterior surface of the head lacking a pair of dark apophyseal lines (Fig. A) . . . . . *Anochetus*  
 - Nuchal carina medially V-shaped, the posterior surface of the head with a pair of dark converging apophyseal lines (Fig. B) . . . . . *Odontomachus*



- 4(2) Mesotibiae dorsally with abundant stout traction setae (Fig. A) . . . . . 5  
 - Mesotibiae dorsally without abundant stout traction setae (a few stout setae sometimes present near tarsus but never extending along length of tibia) (Fig. B) . . . . . 6



A



B

- 5(4) Metapleural gland orifice opening laterally (Fig. A). Head and body without a dense pubescence. Mandible with a lateral longitudinal groove (Fig. A). . . . . *Centromyrmex*  
 - Metapleural gland orifice opening posteriorly at the posteroventral corner of the metapleuron (Fig. B). Head and body covered by a dense pubescence. Mandible with a basal pit but without a lateral longitudinal groove (Fig. B). . . . . *Cryptopone*

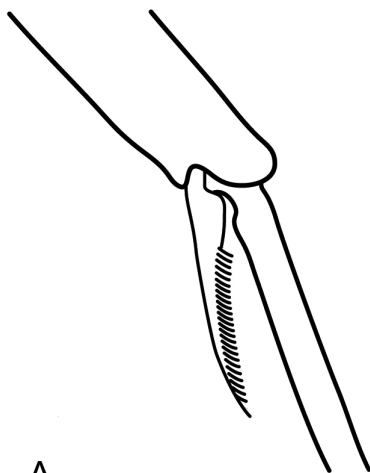


A

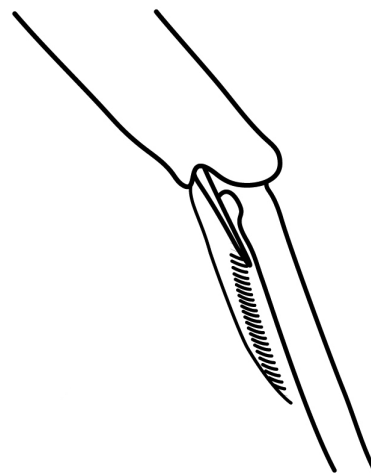


B

- 6(4) Ventral apex of the metatibia with a single spur, which is pectinate (Fig. A). . . . . 7  
 - Ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur (Fig. B) . . . . . 10



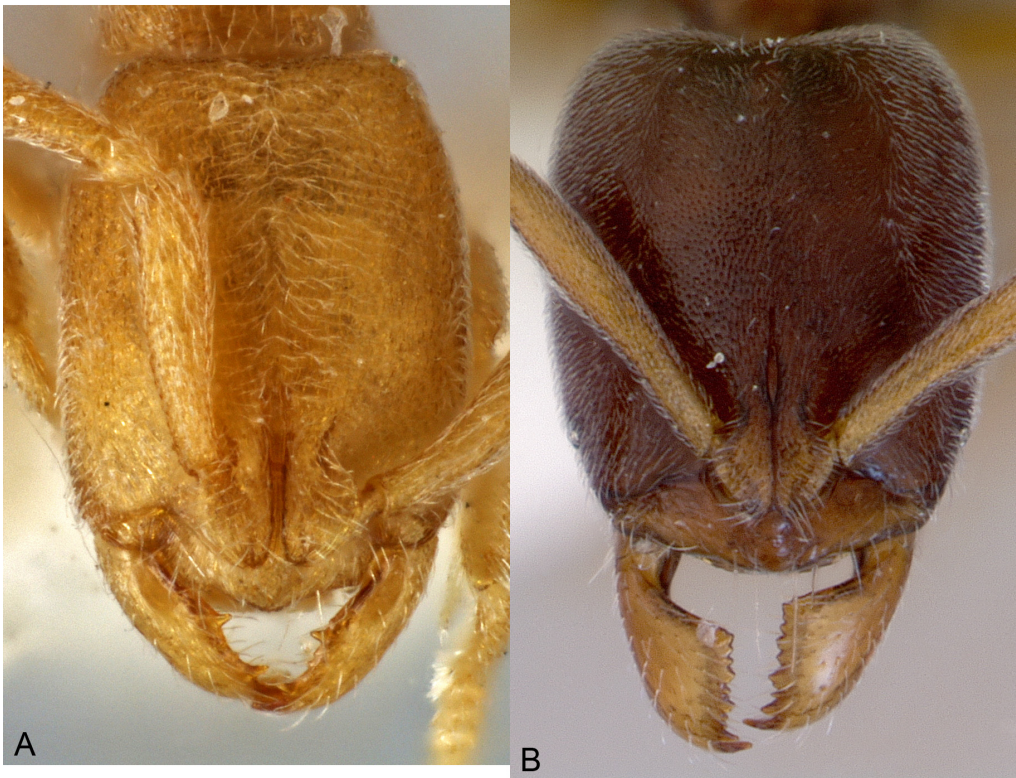
A



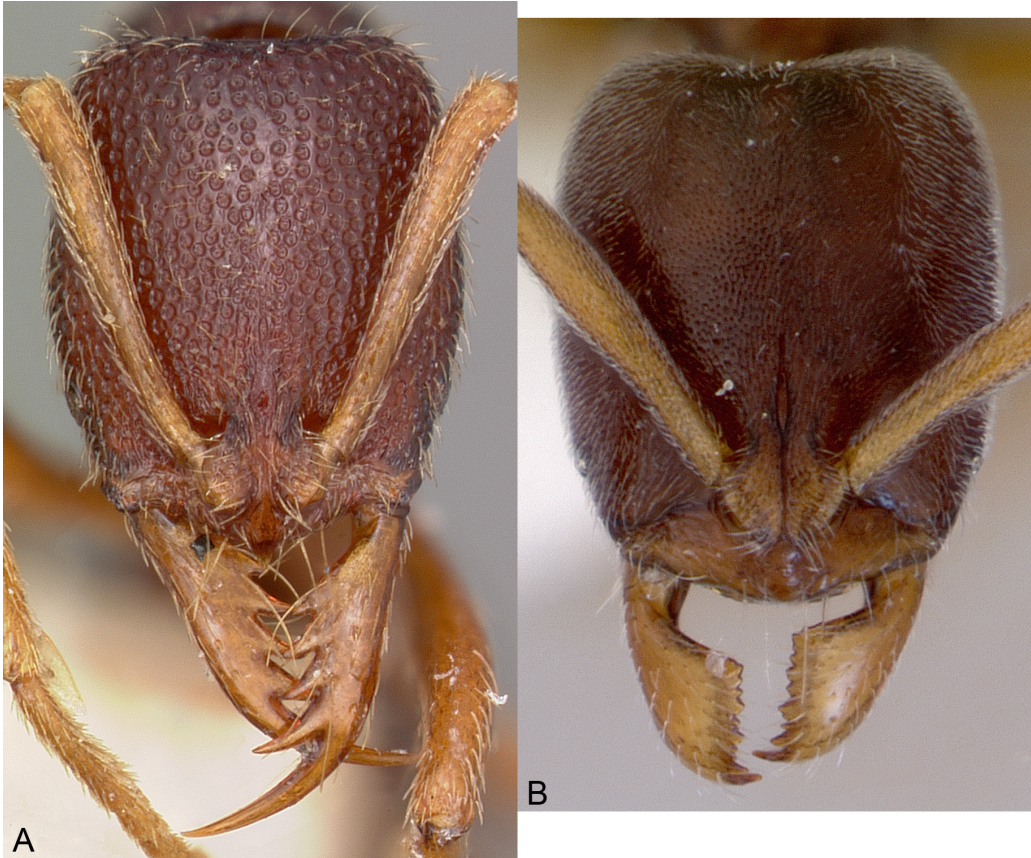
B



- 7(6) Eyes absent. Mandibles elongate and narrow, the teeth small and widely spaced (Fig. A) . . . . . *Iroponera*  
- Eyes present (although sometimes very small). Mandibles generally triangular but occasionally elongate, the teeth generally moderately sized (occasionally elongate) and evenly spaced (Fig. B) . . . . . 8

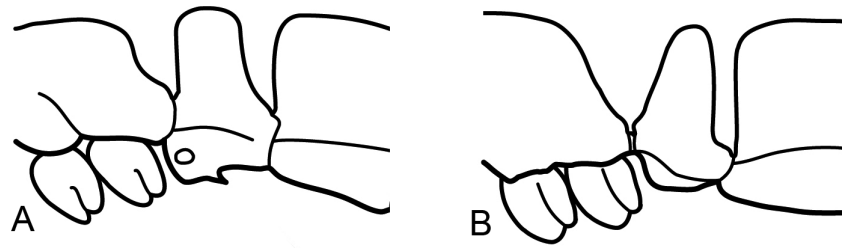


- 8(7) Mandibles thin, with long attenuated teeth (Fig. A) . . . . . *Emeryopone*  
- Mandibles triangular, the teeth not long and attenuated (Fig. B) . . . . . 9





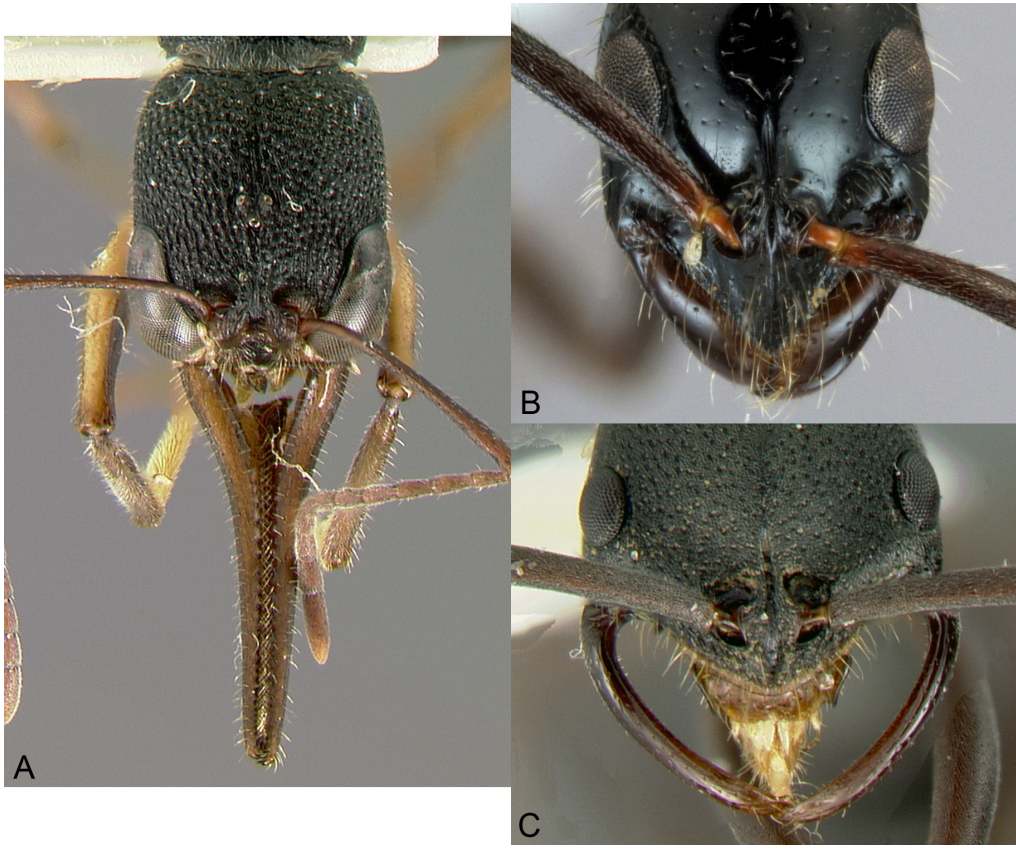
- 9(8) Subpetiolar process with an anterior fenestra and paired posteroventral teeth (Fig. A) ..... *Ponera*
- Subpetiolar process without both an anterior fenestra and paired posteroventral teeth (Fig. B) ..... *Hypoponera*



- 10(6) Tarsal claws pectinate (Fig. A) or armed with one or two preapical teeth ..... 11
- Tarsal claws unarmed (Fig. B) ..... 12



- 11(10) Eyes extremely large and located at the extreme anterior end of the head (Fig. A). Mandibles long, narrow, upcurved and parallel, with two rows of small teeth on the masticatory margins (Fig. A). Tarsal claws armed with a single preapical tooth. Arolia prominent and white ..... *Harpegnathos*
- Eyes variable in size, but not extremely large, and typically located at or near the midline of the head (Figs B, C). Mandibles triangular (Fig. B) or thin and curved (Fig. C). Tarsal claws usually pectinate, sometimes with only one to three preapical teeth. Arolia not prominent and white ..... *Leptogenys*

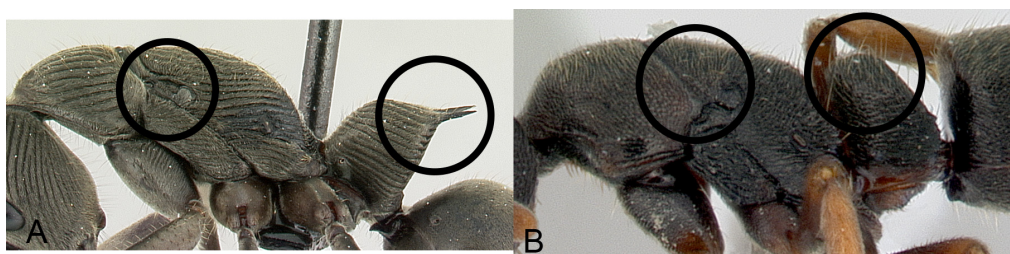




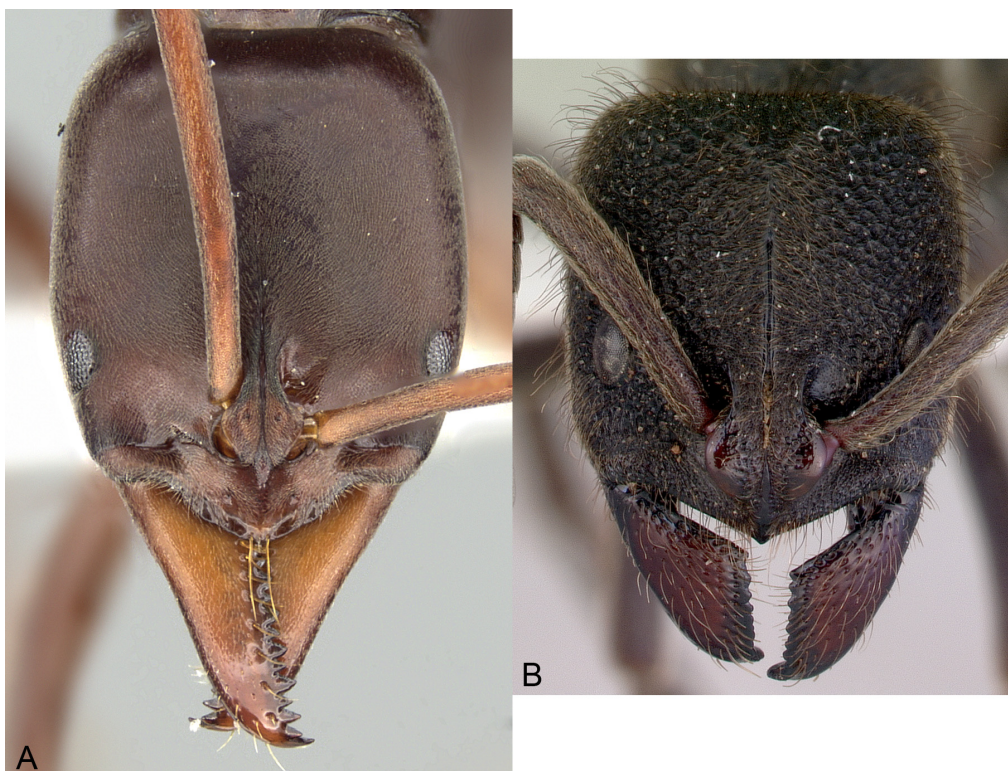
12(10) Propodeal spiracle slit-shaped (Fig. A).....	13
- Propodeal spiracle round or ovoid (Fig. B).....	20



13(12) Mesosoma with a deep pit anterior to each metanotal spiracle (Fig. A). Petiole with a pair of spines on the posterodorsal margin (Fig. A). Arolia prominent and white.....	<i>Diacamma</i>
- Mesosoma without deep pits laterally (Fig. B). Petiole rounded dorsally, without a pair of spines (Fig. B). Arolia not prominent and white.....	14

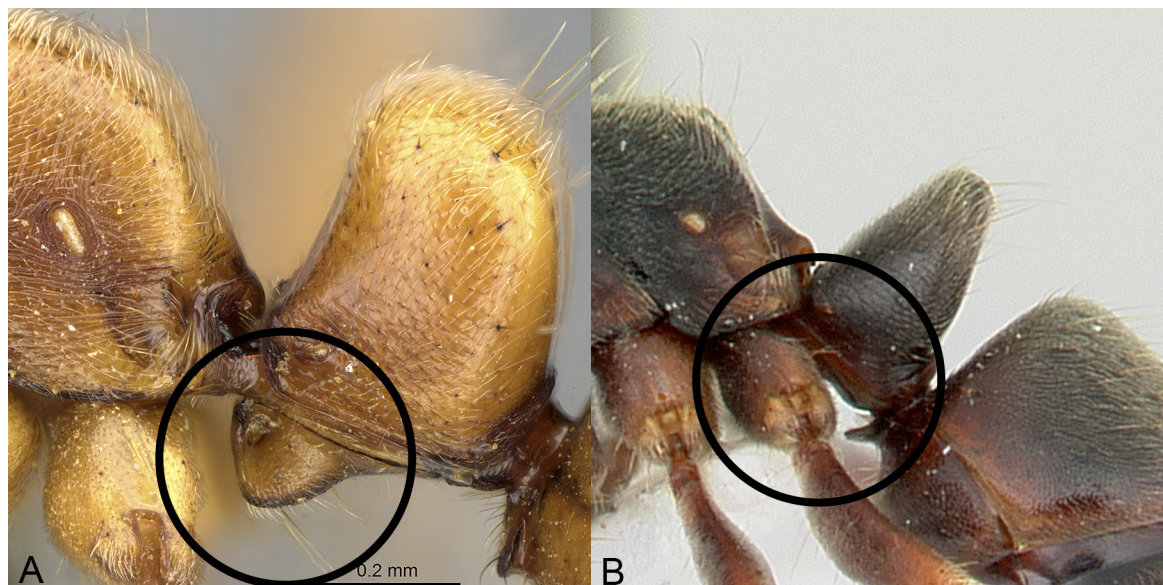


14(13) Mandibles are very long, approximately ½ length of head (Fig. A). Mandibles without basal pits or grooves.....	<i>Mesoponera</i> (in part)
- Mandibles shorter, much less than ½ length of head (Fig. B). Mandibles with or without basal pits or grooves.....	15

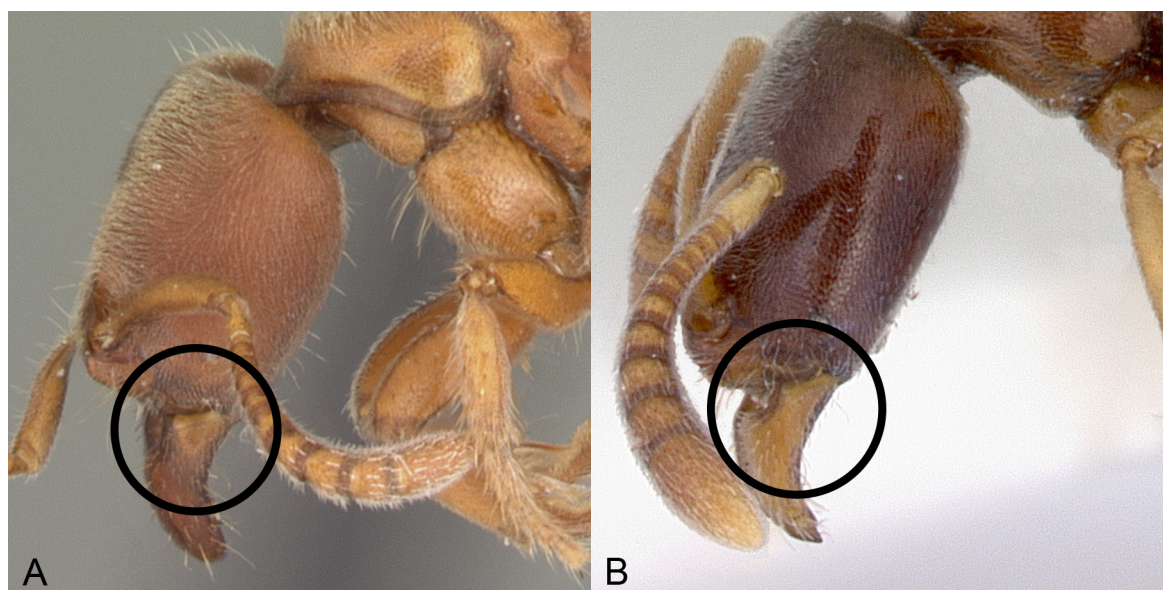




- 15(14) Compound eyes small (with 2-4 facets) or absent. Subpetiolar process with an anterior fenestra and/or a pair of teeth (Fig. A).  
 ..... *Parvaponera*  
 - Compound eyes present and larger, with numerous facets. Subpetiolar process simple, without an anterior fenestra (Fig. B). . .  
 ..... 16

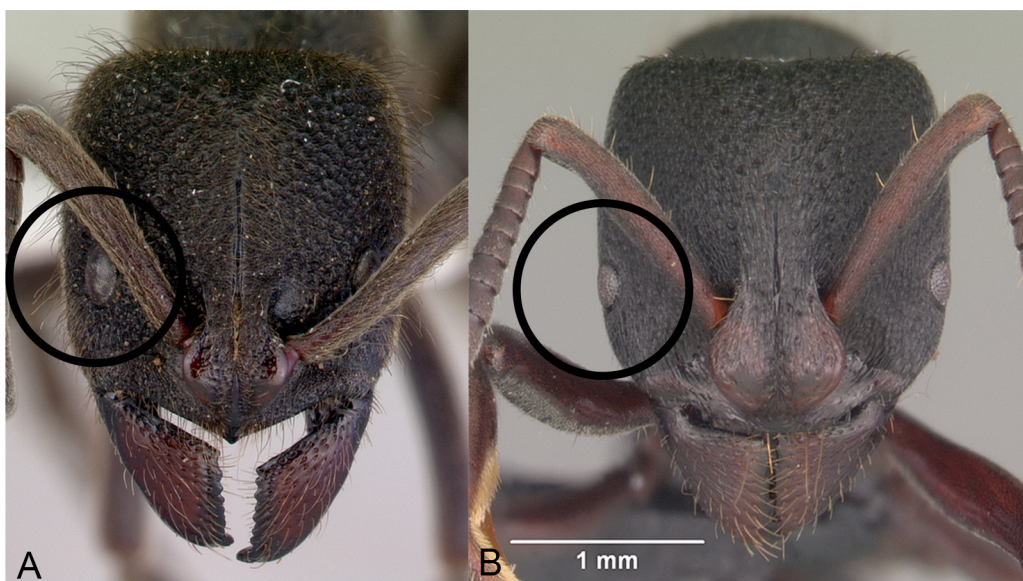


- 16(15) Mandible with a basal pit (Fig. A) ..... *Euponera*  
 - Mandible lacking a basal pit (Fig. B) but a groove generally present (sometimes weakly developed) ..... 17

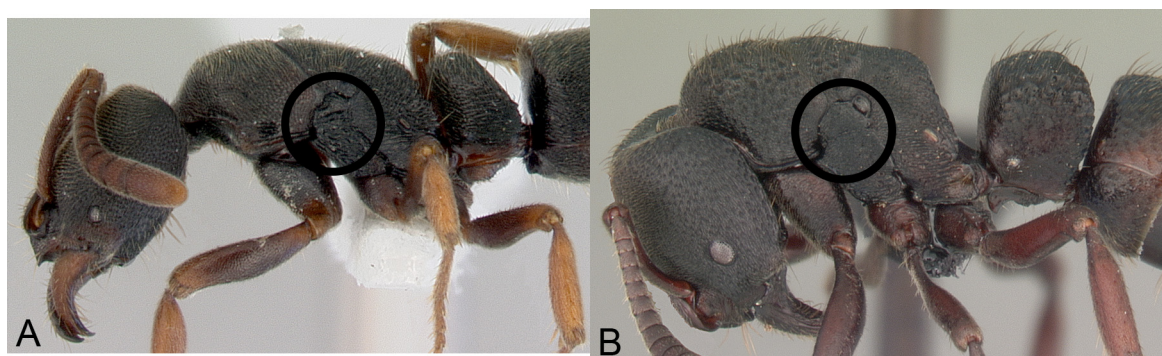


- 17(16) In frontal view, eyes located dorsally on head and separated from the lateral margin by a small gap (Fig. A). Additionally, with the following combination of characters: Head and body usually with both dense pilosity and dense pubescence; propodeum broad dorsally; petiole semicircular in dorsal profile and usually with a row of small teeth or denticles on the posterodorsal margin (angled or ridged in some Australian species); A3 tergite usually longitudinally striate ..... *Pseudoneoponera*  
 - In frontal view, eyes located laterally on head and touching or extending beyond the lateral margin (Fig. B). Additional characters not as above. .... 18

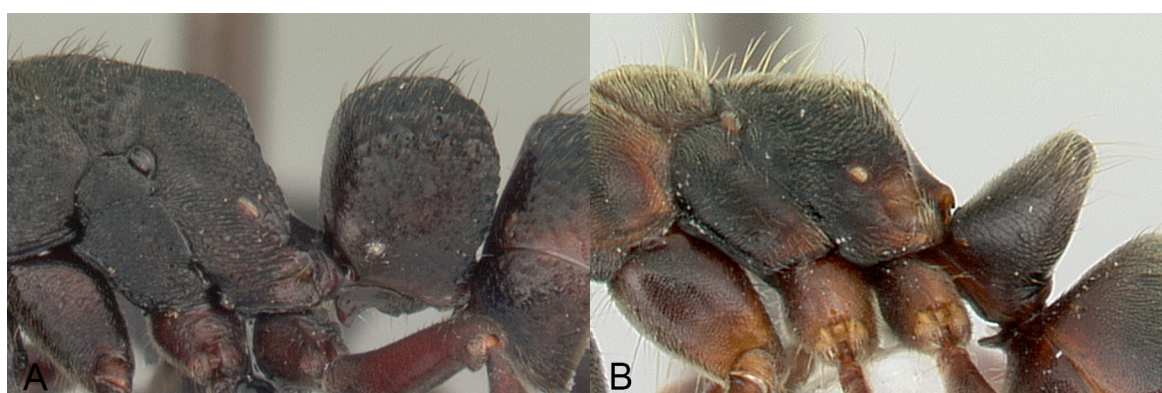




- 18(17) Head and body strongly sculptured (usually striate). Mesopleuron divided by a transverse groove. Petiolar node in dorsal view generally convex anteriorly and flat posteriorly (a few exceptions). Posterolateral margins of head angular (Fig. A) . . . . . *Ectomomyrmex*
- Head and body not strongly sculptured. Mesopleuron not divided. Petiolar node scale-like or block-like. Posterolateral margins of head rounded (Fig. B) . . . . . 19



- 19(18) Metanotal groove absent or essentially absent. Petiole generally block-like (Fig. A) . . . . . *Bothroponera*
- Metanotal groove present as a shallow impression. Petiole generally scale-like (Fig. B) . . . . . *Pseudoponera*



- 20(12) Mandibles linear or subtriangular. Clypeus with a blunt anteromedial rectangular projection (Fig. A) . . . . . 21
- Mandibles triangular. Clypeus without a blunt anteromedial rectangular projection (Fig. B) . . . . . 22





- 21(20) Anteromedial clypeal projection short and broad (Fig. A). Eyes extremely small (Figs A, B). Mandibles subtriangular, with several distinct teeth (Fig. A). Metanotal suture obsolete dorsally. Petiole a thick scale. Gaster with only a moderate girdling constriction (Fig. B) ..... *Buniapone*
- Anteromedial clypeal projection long and narrow (Fig. C). Eyes small to moderate (Figs C, D). Mandibles thin and curved, with only a few teeth. Metanotal suture distinct dorsally. Petiole with a small but thick node. Gaster with a strong girdling constriction (Fig. D) ..... *Myopias*

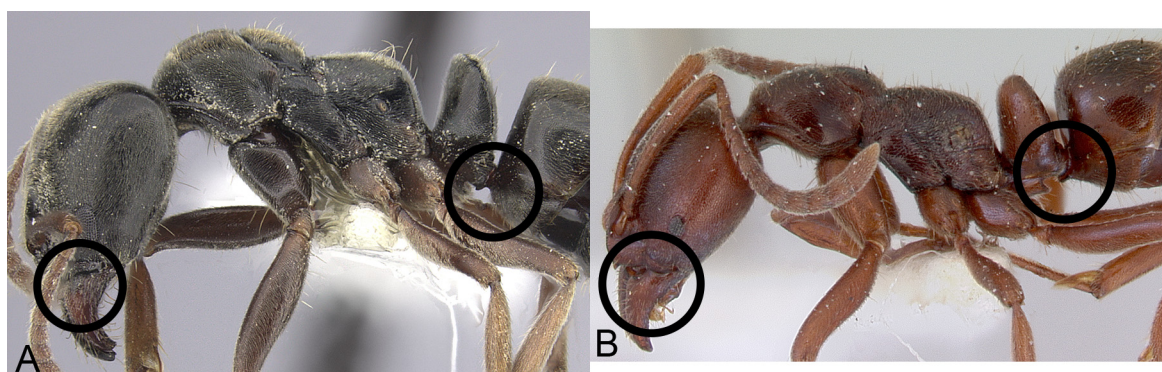




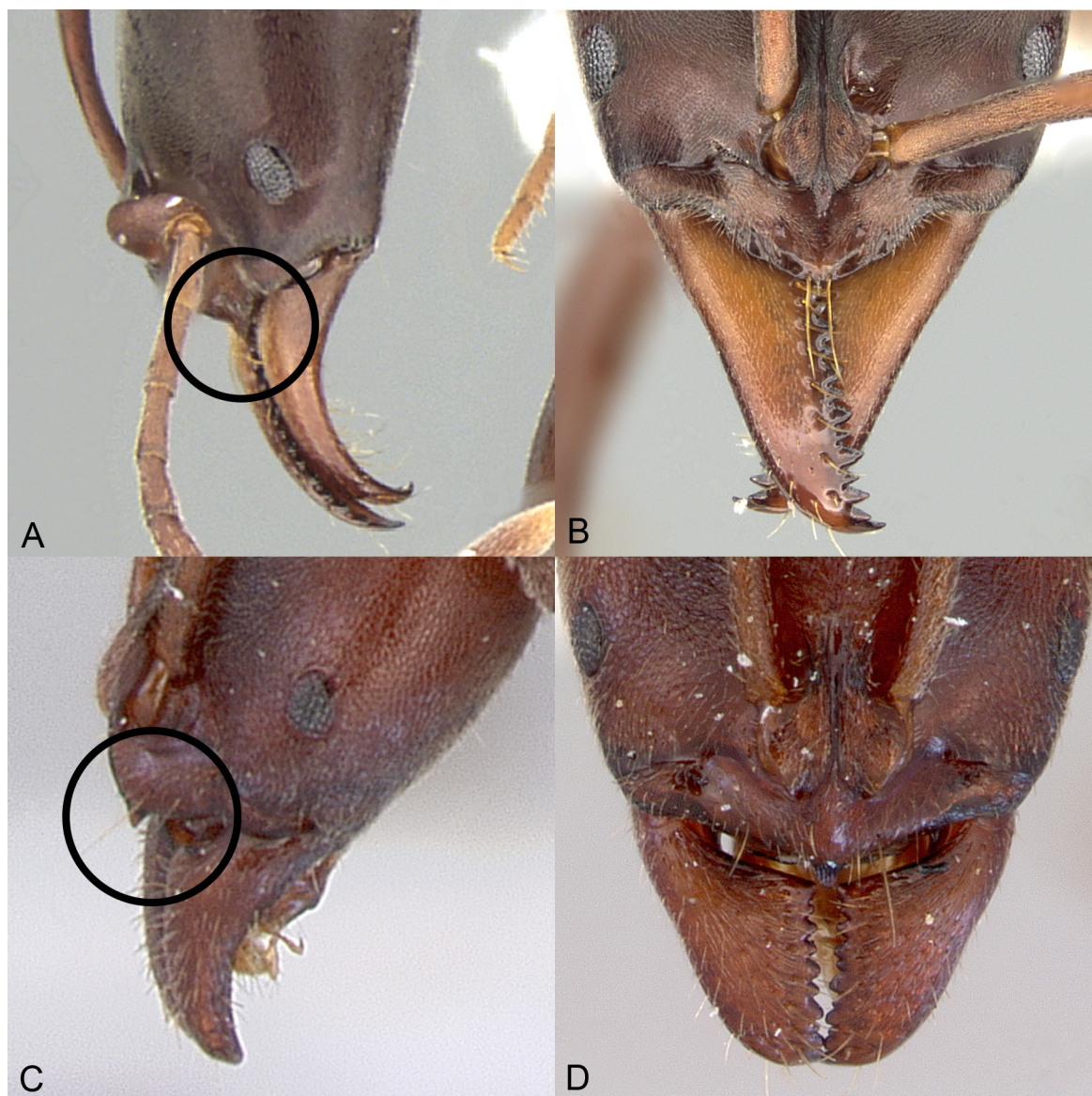
- 22(20) Head and body strongly striate. Pronotum with a distinct tooth at each anterodorsal corner. Dorsal margin of petiole emarginate-denticulate. Anterior clypeal margin with a series of small teeth (Fig. A) . . . . . *Odontoponera*
- Head and body not strongly striate, though light striations may be present on the sides of the mesosoma. Pronotum without a tooth at each anterodorsal corner. Dorsal margin of petiole not emarginate-denticulate. Anterior clypeal margin without teeth . . . . . 23



- 23(22) Mandible with a basal pit or groove. Prora absent from anterior margin of first gastral sternite (Fig. A) . . . . . *Brachyponera*
- Mandible without a basal pit or groove. Prora present on anterior margin of first gastral sternite (Fig. B). . . . . 24



- 24(23) In side view anterior clypeal margin angular and located against the mandibles (Fig. A). Mandibles elongate, their outer margins generally broadly and shallowly concave (Fig. B) . . . . . *Mesoponera* (in part)
- In side view anterior clypeal margin rounded, the anterior-most point located above the mandibles and clypeus meeting mandibles posteriorly to this point (Fig. C). Mandibles shorter, their outer margins generally flat or with separate convex sections separated by a slight medial angle (Fig. D). . . . . *Austroponera*



### Subfamily Ponerinae Lepeletier de Saint-Fargeau

Ponérites Lepeletier de Saint-Fargeau, 1835: 185 (as group name). Type genus: *Ponera* Latreille, 1804: 179. Dalla Torre, 1893: 13 (Ponerinae).

Ponerinae is the largest ant subfamily outside the formicoid clade, and is rivaled or exceeded in diversity only by Dolichoderinae, Formicinae and Myrmicinae within that clade. The tribal and generic organization of Ponerinae is here revised to reflect new molecular phylogenetic results (Schmidt, 2013) and a reassessment of ponerine morphological diversity.

#### Included Tribes.

Platythyreini Emery

Ponerini Lepeletier de Saint-Fargeau

= Thaumatomyrmecini Emery **syn. nov.**

**Diagnosis.** The following formal diagnosis for Ponerinae is adapted from Bolton (2003): Torulus fused to frontal lobe. Antenna with 12 segments (13 in males). Lateral margins of frontal lobes form short semicircles or blunt triangles, with a pinched-in appearance posteriorly. Promesonotal suture flexible. Metapleural gland orifice without a dorsal cuticular flange or flap. Propodeal lobes present. Petiole (A2) distinctly separated posteriorly from



A3 and with only a narrow attachment to it. Petiole without tergosternal fusion. A3 continuous with the remainder of the gaster. A3 and A4 with tergosternal fusion. A4 with presclerites and usually a girdling constriction between pre- and postsclerites. Spiracles of A5–A7 concealed by posterior margins of preceding tergites. Sting present and strongly developed.

Ponerines are most readily identified by the following combination of traits: toruli fused to frontal lobes, frontal lobes prominent and with a pinched-in appearance posteriorly, waist formed of a single segment (petiole, A3) which attaches narrowly to the undifferentiated postpetiole (A4), petiole without tergosternal fusion, and sting present and well-developed. The identity of ponerine synapomorphies is uncertain. Bolton (2003) gave the complete fusion of the toruli to the frontal lobes as an autapomorphy of Ponerinae, but noted the presence of similar fusion (to various degrees) among some members of Amblyoponinae. Bolton also listed the characteristic shape of the frontal lobes in Ponerinae as synapomorphic for the subfamily, but similar frontal lobe structure occurs in many amblyoponines (pers. observation). Given the close but incompletely resolved relationship between Ponerinae and Amblyoponinae, we consider the ancestral condition of these characteristics (torular fusion and frontal lobe shape) to be ambiguous within the poneroid clade and are therefore hesitant to treat them as apomorphies of Ponerinae.

We tentatively recognize the loss of tergosternal fusion of the petiole as a possible synapomorphy of Ponerinae. Bolton (2003) treated the absence of petiolar tergosternal fusion as plesiomorphic within Formicidae, but recent molecular phylogenies (Moreau *et al.*, 2006; Brady *et al.*, 2006; Rabeling *et al.*, 2008; Schmidt, 2013) suggest that the ancestral ant may have had a fused petiole. The phylogenetic distribution of this character implies that Ponerinae secondarily lost tergosternal fusion of the petiole, though this interpretation depends on the phylogenetic rooting of Formicidae and could conceivably be symplesiomorphic, with repeated evolution of a fused petiole in other poneroid lineages.

**Discussion.** Ponerinae has had a more convoluted taxonomic history than any other ant subfamily. First appearing as a group of Formicidae under the name Ponérites (Lepeletier de Saint-Fargeau, 1835), Ponerinae gradually came to represent an assemblage of ant taxa that were highly divergent but nonetheless placed together due to their relatively simple social organizations and shared morphological characters (such as tergosternal fusion of A3 and A4; Baroni Urbani *et al.*, 1992; Ward, 1994). At various times Ponerinae has included taxa that are now considered to represent eight distinct subfamilies: Amblyoponinae, Proceratiinae, Paraponerinae, Ectatomminae, Heteroponerinae, Aenictogitoninae, Cerapachyinae, and Ponerinae itself (Bolton, 2003). Cerapachyinae and Aenictogitoninae were removed from Ponerinae by Bolton (1990) and Baroni Urbani *et al.* (1992), respectively, but the remaining taxa continued to be included in Ponerinae until Bolton (2003) finally recognized the symplesiomorphic nature of the defining “ponerine” traits, and took the important step of breaking Ponerinae into its component subfamilies. Subsequent molecular studies (Saux *et al.*, 2004; Moreau *et al.*, 2006; Brady *et al.*, 2006; Schmidt, 2013) have confirmed most aspects of Bolton’s reclassification at the subfamily and tribe levels, with some notable exceptions: Apomyrminae has been shown to be a junior synonym of Amblyoponinae (Saux *et al.*, 2004), and Thaumatomyrmecini is now known to be a junior synonym of Ponerini (Brady *et al.*, 2006; Schmidt, 2013). With the changes made in the present study, the taxonomy of Ponerinae is finally brought to relative stability, though with some additional genus-level changes likely to come in the future. The major issues in ponerine taxonomy are now generally resolved: the monophyly of Ponerinae (*sensu* Bolton, 2003), the monophyly of Ponerini if *Thaumatomyrmex* is included, and the non-monophyly of *Pachycondyla*.

### Tribe Platythyreini Emery

Platythyrei Emery, 1901: 36 (as tribe of Ponerinae). Type genus: *Platythyrea* Roger, 1863a: 172. Emery, 1911: 28 (Platythyreini).

Tribe Platythyreini contains the single genus *Platythyrea* Roger. These ants are notable for their arboreal habits and frequent (probably nearly universal) presence of gamergate workers.

**Diagnosis.** See the diagnosis and synoptic description under *Platythyrea* below.

**Discussion.** The deep separation between *Platythyrea* and Ponerini has been recognized at least since Emery (1901), who placed *Platythyrea* in its own tribe Platythyrei (later renamed Platythyreini; Emery, 1911). Two sources of taxonomic confusion have arisen since Emery’s original designation of tribal status: the proper location

of *Probolomyrmex* and the status of *Eubothroponera*. *Probolomyrmex* Mayr superficially resembles *Platythyrea* in overall gestalt and in the presence of pruinose sculpturing, though there are many major differences between them. It has been placed by some authors within Platythyreini (e.g., Brown, 1952, and most subsequent authors), though Perrault (2000) placed it in its own subfamily, Probolomyrmecinae. Bolton (2003) moved *Probolomyrmex* to its own tribe within Proceratiinae; many early authors had placed the genus in tribe Proceratiini of that subfamily (e.g., Emery, 1911). Molecular phylogenetic evidence (e.g., Moreau *et al.*, 2006; Brady *et al.*, 2006; Schmidt, 2013) confirms the placement of *Probolomyrmex* within Proceratiinae and demonstrates that its superficial similarity to *Platythyrea* is likely the result of convergence. See the discussion under *Platythyrea* (below) for a consideration of *Eubothroponera* Clark, a genus confirmed here as a junior synonym of *Platythyrea*.

## ***Platythyrea* Roger**

Fig. 3

*Platythyrea* Roger, 1863a: 172 (as genus). Type-species: *Pachycondyla punctata* Smith, F., 1858: 108; by subsequent designation of Bingham, 1903: 73.

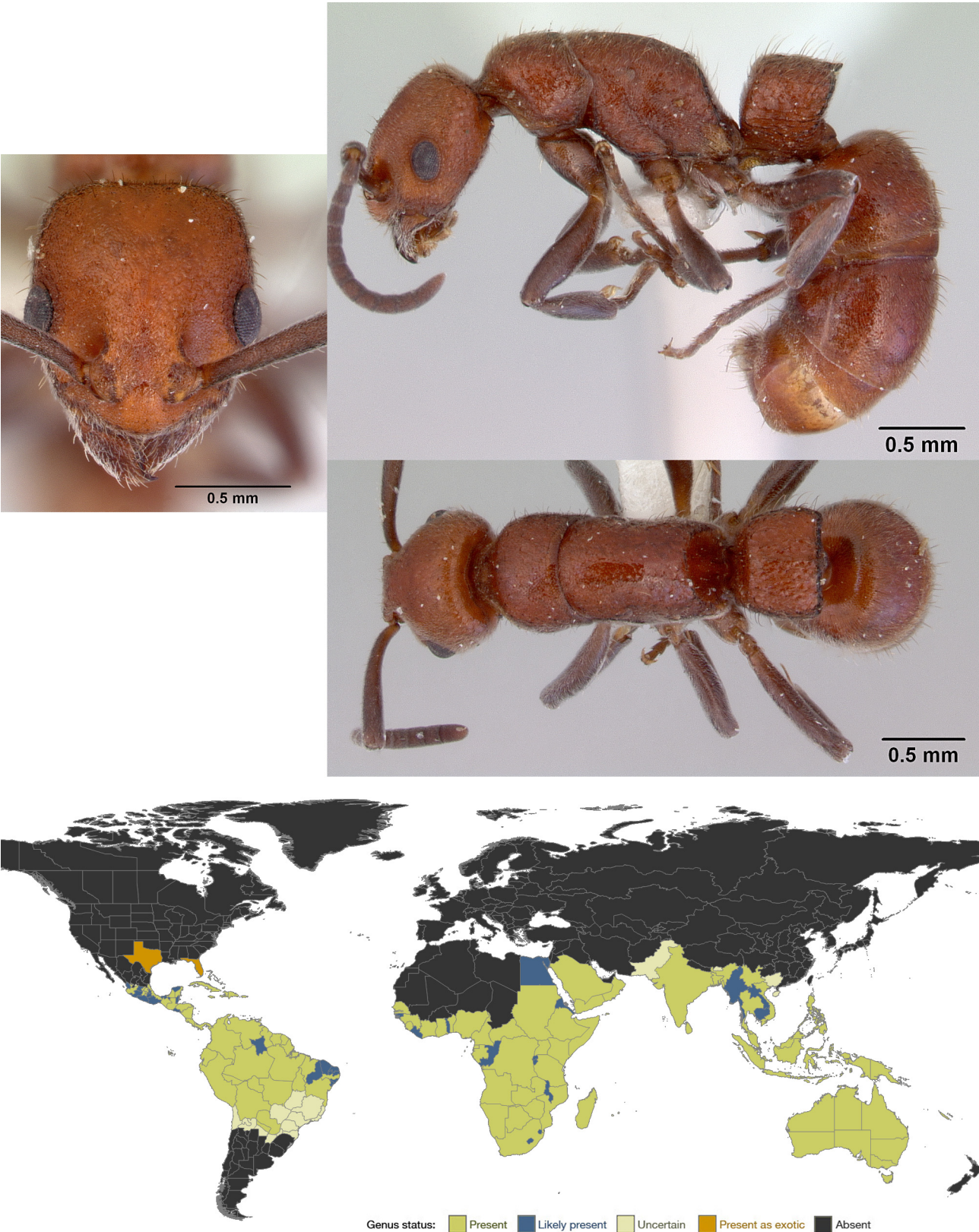
*Eubothroponera* Clark, 1930: 8 (as genus). Type-species: *Eubothroponera dentinodis* Clark, 1930: 9; by original designation. Brown, 1975: 6 (*Eubothroponera* as junior synonym of *Platythyrea*).

*Platythyrea* is a moderately large (38 described extant species) pantropical genus and is the only member of Platythyreini. *Platythyrea* workers are notable for their rapid movement, arboreal habits and frequent presence of gamergates.

**Diagnosis.** *Platythyrea* workers are distinctive and not easily confused with those of other genera, though the genus lacks unequivocal autapomorphies. Diagnostic characters of *Platythyrea* workers and queens include (in combination) pruinose sculpturing, broad insertion of the clypeus between the frontal lobes and the consequently widely spaced frontal lobes and antennal insertions, laterally opening metapleural gland orifice, metatibiae with two pectinate spurs, toothed tarsal claws, and projection of the helcium from near midheight on the anterior face of A3. Pruinose sculpturing is rare within Ponerini (only present in some *Leptogenys* and in *Belonopelta*, both of which lack the high helcium and broad clypeal insertion of *Platythyrea*), but is also shared with the proceratiine genus *Probolomyrmex*. *Probolomyrmex* differs from *Platythyrea*, however, in numerous characters, most obviously in its lack of frontal lobes and eyes, its single metatibial spur, its simple tarsal claws, and its lack of a stridulitrum on the pretergite of A4. In most Ponerini the clypeus is only narrowly inserted between the frontal lobes, but *Thaumatomyrmex* has a broad clypeal insertion (even broader than in *Platythyrea*). *Thaumatomyrmex* otherwise differs dramatically from *Platythyrea*, and they are unlikely to be confused. A small number of genera in Ponerini have a relatively high helcium as in *Platythyrea*, but these genera all lack the broad clypeal insertion and pruinose sculpturing of *Platythyrea*. Finally, the Australian *Platythyrea dentinodis* species group (formerly *Eubothroponera*) have a relatively low helcium, as in most Ponerini, and lack the fine pruinose sculpturing of most *Platythyrea*, but can be distinguished from Ponerini by their broad clypeal insertion and presence of two pectinate metatibial spurs.

**Synoptic description.** *Worker*. Small to very large (TL 4–20 mm; Brown, 1975) ants with the standard characters of Platythyreini. Mandibles triangular, edentate or with multiple distinct teeth on the masticatory margin, and often with a basal groove. Clypeus with a flat or convex anterior margin, and a broad posterior insertion between the frontal lobes. Frontal lobes moderately large and widely separated. Eyes large to moderate in size, located anterior to head midline. Metanotal groove usually obsolete, rarely present and shallowly impressed (e.g., *P. lamellosa*). Propodeum broad dorsally, the posterior margins distinct and usually with a short blunt tooth at each posterodorsal corner. Propodeal spiracle usually round, rarely slit-shaped (e.g., *P. lamellosa*). Metapleural gland orifice opening laterally, near the posteroventral corner of the propodeum, sometimes with a shallow lateral longitudinal groove. Metatibial spur formula (1p, 1p). Tarsal claws usually armed with a single preapical tooth. Arolia prominent and bright white. Petiole nodiform, the node usually much longer than wide, with parallel sides and a distinct dorsal face, the posterodorsal margin often bi- or tridentate. Helcium usually projects from near midheight on the anterior face of A3 (projects from lower down in the *P. dentinodis* group). Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and body usually uniformly pruinose (having a frosted appearance due to extremely dense fine punctations combined with a dense short pubescence), usually also with scattered foveolations, and usually with little to no upright pilosity.

Members of the *P. dentinodis* group lack the pruinose condition and have denser upright pilosity. Color variable, yellowish brown to black. See descriptions by Brown (1975) and Bolton (2003) for further details of worker structure in *Platythyrea*.



**FIGURE 3.** Worker caste of *Platythyrea dentinodis*: lateral and dorsal view of body and full-face view of head (CASENT0172409, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Platythyrea*.

**Queen.** Very similar to conspecific workers but usually winged, with the corresponding modifications of the thoracic sclerites and usually with ocelli (though they are sometimes absent, which is a unique condition among alate ant queens) (Brown, 1975). Queens are ergatoid in some species and are completely absent in others (reviewed by Molet & Peeters, 2006).

**Male.** See descriptions by Brown (1975) and Yoshimura & Fisher (2007).

**Larva.** Described by Wheeler & Wheeler (1952, 1971a, 1976, 1989) and Villet *et al.* (1990a).

**Geographic distribution.** *Platythyrea* is pantropical, with some species also occurring in subtropical regions of the New World, Africa, Asia, and Australia (Brown, 1975; Bolton *et al.*, 2006).

**Ecology and behavior.** *Platythyrea* is an ecologically and behaviorally interesting genus. Unusually among ponerines, many *Platythyrea* species are arboreal, nesting in hollow branches or other preformed cavities in live or fallen trees, and foraging on tree trunks or other vegetation (Brown, 1975; Djitéto-Lordon *et al.*, 2001b; Yéo *et al.*, 2006; Molet & Peeters, 2006). Some large African species (*e.g.*, *P. lamellosa*) are terrestrial and nest at the base of termitaria or under rocks (Arnold, 1915; Brown, 1975). *Platythyrea* colonies are of the typical size for ponerines, with on average usually a few hundred workers or fewer (*P. conradti*: 100 to 500 workers; Lévieux, 1976; Molet & Peeters, 2006; Yéo *et al.*, 2006; *P. lamellosa*: 115 workers; Villet *et al.*, 1990b; *P. modesta*: up to 50 workers; Djitéto-Lordon *et al.*, 2001b; *P. parallela*: 50 workers; Wilson, 1959b; *P. punctata*: 23-51 workers; Hartmann *et al.*, 2005b; *P. quadridenta*: 19 workers; Ito, 1995; *P. schultzei*: 21 workers; Villet, 1991b; *P. tricuspidata*: 21 workers; Ito, 1995).

*Platythyrea* workers are very fast runners, and their speed combined with their potent venomous stings enable them to rapidly catch and subdue a wide range of prey (Brown, 1975; Djitéto-Lordon *et al.*, 2001a, 2001b). Some *Platythyrea* species are generalist predators (*e.g.*, *P. conradti*: Yéo *et al.*, 2006; Molet & Peeters, 2006; *P. lamellosa*: Villet, 1990c; *P. modesta*: Djitéto-Lordon *et al.*, 2001a, 2001b), but many reportedly specialize on termites (*e.g.*, Arnold, 1915; Brown, 1975) and at least one species (*P. arnoldi*) is apparently a specialist on adult beetles (Arnold, 1915). In an unusual behavior, *P. conradti* workers collect nectar onto part of their body surface for transport to the nest; the liquid is retained via surface tension (Déjean & Suzzoni, 1997). Lévieux (1983) lists an unidentified *Platythyrea* species as eating seeds, though this has not been confirmed (Hölldobler & Wilson, 1990). *Platythyrea* workers typically forage individually (*e.g.*, Villet, 1990c), but Djitéto-Lordon *et al.* (2001b) observed nestmate recruitment in *P. modesta* to aid in retrieval of large prey. Interestingly, workers of this species sometimes carry larvae directly to their prey, rather than bringing the prey back to their nest; this behavior is otherwise unknown within the Ponerinae. *P. modesta* conducts frequent emigrations to new nest sites, with recruitment occurring via use of chemical trails (Djitéto-Lordon *et al.*, 2001b). The use of chemical trails by other *Platythyrea* species has not been reported.

*Platythyrea* has perhaps the highest diversity of reproductive strategies known for any ponerine genus (Villet, 1992b; Molet & Peeters, 2006). Nearly all examined *Platythyrea* species have gamergates, with the only exception being *P. conradti*, which is also the only *Platythyrea* species known to have ergatoid queens (Molet & Peeters, 2006). In *P. conradti*, queens and workers aggressively interact to form a dominance hierarchy, but high-ranking workers do not reproduce unless the queen dies. Among those species known to have gamergates, some also have alate queens (*P. quadridenta*, *P. tricuspidata* and *P. arnoldi*; Villet, 1993; Ito, 1995), but some have gamergates only (*P. lamellosa*, *P. schultzei*, and *P. cf. cribrinodis*; Peeters, 1987; Villet *et al.*, 1990b; Villet, 1991b, 1991c). In addition, the reproductive strategy of *P. punctata* is perhaps the most variable known for any ponerine species (see below). Villet (1990c, 1991b, 1992b) examined the division of labor in colonies of *P. cf. cribrinodis*, *P. lamellosa*, and *P. schultzei* and found typical age-related polyethism in all species, with unmated workers of *P. cf. cribrinodis* laying only inviable haploid eggs.

*Platythyrea punctata* is a fascinating species from the standpoint of social and reproductive behavior, as it variously has alate queens, parthenogenetic intercaste queens, mated gamergates, and parthenogenetic workers (Schilder *et al.*, 1999a, 1999b; Hartmann *et al.*, 2005b). In many populations of this species, reproduction occurs via thelytokous parthenogenesis (Heinze & Hölldobler, 1995), which is not known to occur in any other ponerine. Workers in parthenogenetic colonies of *P. punctata* aggressively compete and form dominance hierarchies, with reproduction restricted to only a small number of high-ranking individuals and with workers attacking “surplus reproductives”, as communicated by their cuticular hydrocarbon profiles (Heinze & Hölldobler, 1995; Hartmann *et al.*, 2005a). The presence of worker policing in such colonies is surprising, since they are virtually clonal (Schilder *et al.*, 1999b) and therefore lack any genetic conflict among colony members (Hartmann *et al.*, 2003). The reason



for the reproductive conflict is that a reduced number of reproductives leads to increased colony productivity (Hartmann *et al.*, 2003), favoring the maintenance of social control over reproduction.

The chemical ecology of *Platythyrea* has not been extensively studied, but Morgan *et al.* (2003) found that *P. punctata* lacks a Dufour's gland and lacks volatile substances in its venom gland secretions.

Yéo *et al.* (2006) discovered an interesting commensal association between *P. conradti* and the myrmicine *Strumigenys maynei*, which nest together in the same branches. *Strumigenys* colonies were found in association with 75% of the examined *Platythyrea* nests. The *Strumigenys* workers apparently feed on refuse in the *Platythyrea* nest, and are moved without injury by *Platythyrea* workers if they attempt to feed on fresh prey brought into the nest.

**Phylogenetic and taxonomic considerations.** Roger (1863a) erected *Platythyrea* to house four species formerly placed in *Pachycondyla* or *Ponera*. He did not cite a type species, but Bingham (1903) later designated *P. punctata* (Smith, F.) as the type species. Some early authors placed *Platythyrea* in Ponerini (e.g., Forel, 1899; Wheeler, 1910), or even in Ectatommini (Ashmead, 1905), but Emery (1911) moved it to its own tribe, Platythyreini. Subsequent authors have followed Emery's classification, and we continue to do so.

The sole junior synonym of *Platythyrea*, *Eubothroponera*, was described by Clark (1930) with the type species *Eubothroponera dentinodis* Clark (now *Platythyrea dentinodis*). He placed into *Eubothroponera* several Australian species which he considered to be closely related to *Bothroponera*, of Tribe Ponerini. This is understandable, as the members of *Eubothroponera* (now the *Platythyrea dentinodis* group) differ from typical *Platythyrea* in their coarser sculpturing, denser pilosity, and especially in their relatively low helcium, which approximates the condition that is typical of most members of Ponerini.

Brown (1952) recognized the close relationship between *Platythyrea* and *Eubothroponera* and moved *Eubothroponera* into Platythyreini (along with *Probolomyrmex* and its eventual synonym *Escherichia*), and later (Brown, 1975) took the further step of synonymizing *Eubothroponera* under *Platythyrea* based on both worker and larval characters. Schmidt's (2013) molecular phylogeny of the Ponerini confirms this synonymy, as *P. turneri* (unequivocally a member of "*Eubothroponera*", though it was never formerly placed there) is nested within *Platythyrea*. The phylogeny also confirms that *Platythyrea* and *Probolomyrmex* are not closely related, with their extensive morphological similarities presumably being due to convergence.

### Species of *Platythyrea*

Brown (1975) provides a key to *Platythyrea* species that is only slightly outdated due to the subsequent description of two additional species, while De Andrade (2004) provides a key to New World *Platythyrea*, including both extant and fossil species. In the species list below (and throughout this publication) only the country of the type localities is given.

- P. angusta* Forel, 1901: Trinidad
- P. arnoldi* Forel, 1913: Zimbabwe
- P. arthuri* Forel, 1910: Madagascar
- P. bicuspis* Emery, 1899: Madagascar
- P. bidentata* Brown, 1975: Philippines
- P. brunnipes* (Clark, 1938): Australia
- P. clypeata* Forel, 1911: S.E. Asia
- P. conradti* Emery, 1899: Cameroon
- P. cooperi* Arnold, 1915: South Africa
- P. cribrinodis* (Gerstäcker, 1859): Mozambique
- P. crucheti* Santschi, 1911: Angola
- P. dentinodis* (Clark, 1930): Australia
- P. exigua* Kempf, 1964: Brazil
- P. frontalis* Emery, 1899: Cameroon
- P. gracillima* Wheeler, W.M., 1922: DRC
- P. inermis* Forel, 1910: Philippines
- P. lamellosa* (Roger, 1860): South Africa

*P. lenca* De Andrade, 2004: Honduras  
*P. matopoensis* Arnold, 1915: Zimbabwe  
*P. micans* (Clark, 1930): Australia  
*P. mocquerysi* Emery, 1899: Madagascar  
*P. modesta* Emery, 1899: Cameroon  
*P. nicobarensis* Forel, 1905: Nicobar Islands  
*P. occidentalis* André, 1890: Sierra Leone  
*P. parallela* (Smith, F., 1859): Indonesia (Aru Island)  
*P. pilosula* (Smith, F., 1858): Brazil  
*P. prizo* Kugler, 1977: Costa Rica  
*P. punctata* (Smith, F., 1858): Central America  
*P. quadridenta* Donisthorpe, 1941: New Guinea  
*P. sagei* Forel, 1900: India  
*P. schultzei* Forel, 1910: Namibia  
*P. sinuata* (Roger, 1860): Suriname  
*P. strenua* Wheeler, W.M. & Mann, 1914: Haiti  
*P. tenuis* Emery, 1899: Cameroon  
*P. tricuspidata* Emery, 1900: Indonesia (Sumatra)  
*P. turneri* Forel, 1895: Australia  
*P. viehmeyeri* Santschi, 1914: Tanzania  
*P. zodion* Brown, 1975: Ecuador

#### Fossil species

† *P. dentata* Lattke, 2003: Dominican Amber  
 † *P. dluskyi* Aria, *et al.* 2011: Oise Amber  
 † *P. primaeva* Wheeler, W.M., 1915: Baltic Amber  
 † *P. procera* Lattke, 2003: Dominican Amber  
 † *P. pumilio* De Andrade, 2004: Dominican Amber  
 † *P. scalpra* Lattke, 2003: Dominican Amber

### Tribe Ponerini Lepeletier de Saint-Fargeau

Ponériles Lepeletier de Saint-Fargeau, 1835: 185 (as group name). Type genus: *Ponera* Latreille, 1804: 179. Ashmead, 1905: 382 (Ponerini).  
 Odontomachidae Mayr, 1862: 708 (as subfamily of Formicidae). Type genus: *Odontomachus* Latreille, 1804: 179. Bolton, 1994: 164 (Odontomachini, as junior synonym of Ponerini).  
 Leptogenyi Forel, 1893a: 162 (as tribe of Ponerinae). Type genus: *Leptogenys* Roger, 1861: 41. Brown, 1963: 3 (Leptogenysii, as junior synonym of Ponerini).  
 Harpegnathii Forel, 1900a: 63 (as tribe of Ponerinae). Type genus: *Harpegnathos* Jerdon, 1851: 116. Bolton, 1994: 164 (Harpegnathini, as junior synonym of Ponerini).  
 Drepanognathini Ashmead, 1905: 382 (as tribe of Pachycondylinae). Type genus: *Drepanognathus* Smith, F., 1858: 81 (unnecessary replacement name for *Harpegnathos* Jerdon, 1851). Bolton, 1994: 164 (as junior synonym of Ponerini).  
 Pachycondylinae Ashmead, 1905: 382 (as subfamily of Ponerinae). Type genus: *Pachycondyla* Smith, F., 1858: 105. Bolton, 1994: 164 (Pachycondylini, as junior synonym of Ponerini).  
 Euponerinae Emery, 1909: 355 (as group of Ponerinae). Type genus: *Euponera* Forel, 1891: 126. Bolton, 1994: 164 (Euponerini, as junior synonym of Ponerini).  
 Centromyrmicini Emery, 1911: 57 (as subtribe of Ponerini). Type genus: *Centromyrmex* Mayr, 1866: 894. Brown, 1953a: 9 (as junior synonym of Ponerini).  
 Plectroctenini Emery, 1911: 92 (as subtribe of Ponerini). Type genus: *Plectroctena* Smith, F., 1858: 101. Bolton, 1994: 164 (as junior synonym of Ponerini).  
 Dorylozelini Wheeler, 1922b: 646 (as tribe of Ponerinae). Type genus: *Dorylozelus* Forel, 1915a: 24 (junior synonym of *Leptogenys* Roger, 1861: 41). Taylor, 1969: 132 (as junior synonym of Ponerini).  
 Pseudoneoponerini Chapman & Capco, 1951: 77 (as tribe of Ponerini). Type genus: *Pseudoneoponera* Donisthorpe, 1943a: 439. Bolton, 2003: 159 (as junior synonym of Ponerini).  
 Archiponerini Dlussky & Fedoseeva, 1988: 78 (as tribe of Ponerini). Type genus: *Archiponera* Carpenter, 1930: 27. Bolton,

2003: 172 (*Archiponera* as *incertae sedis* in Ponerinae). Bolton, 1994: 164 (as junior synonym of Ponerini).  
Thaumatomyrmecini Emery, 1901: 36 (as tribe of Ponerini). Type genus: *Thaumatomyrmex* Mayr, 1887: 530.  
Thaumatomyrmecini as junior synonym of Ponerini: **Syn. nov.**

Tribe Ponerini contains the vast majority of ponerine generic and species diversity. Bolton (2003) provided a diagnosis for Ponerini which is still mostly accurate, though our inclusion of *Thaumatomyrmex* necessitates some minor changes.

**Diagnosis.** The only unequivocal autapomorphy of Ponerini is the vestigial nature of the mandibles in males. Differentiation of the female castes between Ponerini and Platythyreini (*Platythyrea*) is less straightforward. Ponerini workers can generally be identified by their closely approximated frontal lobes and antennal sockets, by their lack of two pectinate metatibial spurs, by the projection of their helcium low on the anterior face of A3 (which has a high vertical anterior face), and by their non-pruinose sculpturing. Exceptions to each of these character states exist within Ponerini, however, and the occurrence of some of these states in certain *Platythyrea* species (the Australian species formerly placed in *Eubothroponera*) complicates the tribe's diagnosis. The spacing of the frontal lobes and antennal sockets is the most consistent difference between the tribes, with the exception of *Thaumatomyrmex*, which has very widely spaced frontal lobes but is a member of Ponerini. *Thaumatomyrmex* has derived pitchfork-like mandibles, in contrast to the triangular mandibles present in all *Platythyrea*, and also lacks the paired pectinate metatibial spurs, high helcium, and pruinose sculpturing present in nearly all *Platythyrea*. The following diagnosis is adapted from that of Bolton (2003), with a change to reflect the inclusion of *Thaumatomyrmex*.

**Worker.** With the standard characters of Ponerinae. Frontal lobes and antennal sockets usually closely approximated medially; if these are widely spaced (*Thaumatomyrmex*), the mandibles are pitchfork-like, with a few highly attenuated teeth. Metacoxal cavities closed, fully fused or with a suture in the annulus (not evaluated in this study). Helcium usually projecting from low on the anterior face of A3, which has a high vertical anterior face above the helcium (the helcium projects from near midheight on the anterior face of A3 in *Boloponera*, *Buniapone*, *Dolioponera*, *Feroponera*, *Promyopias*, some *Cryptopone* species, and some *Centromyrmex* species; *Harpegnathos* has a relatively low anterior face above the helcium).

**Queen.** Similar to worker but typically winged, slightly larger, and with ocelli and larger compound eyes. The queen caste has frequently been modified during the course of ponerine evolution. Ergatoid queens are common, and the queens of *Simopelta* are dichthadiigyne. Some taxa with gamergates have lost the queen caste (e.g., *Diacamma*, *Dinoponera*, *Hagensia* and *Streblognathus*).

**Male.** Mandibles highly reduced and vestigial. Palp formula often higher than in conspecific females.

**Larva.** See references under individual genera.

**Discussion.** Ponerini first appeared in the literature under the informal group name Ponérites (Lepeletier de Saint-Fargeau, 1835). Subsequent authors recognized Ponerini as a tribe of Ponerinae, with early authors using the names Ponerii or Poneri (e.g., Forel 1893a, 1895). Ashmead (1905) was the first to use the name Ponerini, which has been used by all subsequent authors.

Ponerini has a large number of junior synonyms, as various authors have erected family-group names for many of the most morphologically derived ponerine genera, as well as some more plesiomorphic genera. These taxa are now known to share a strong synapomorphy in the vestigial mandibles of males, as well as generally similar worker and queen structure. Molecular phylogenetic evidence (Schmidt, 2013) confirms the synonymic status of these groups, and demonstrates that an additional synonymy is necessary: Thaumatomyrmecini, recognized by Bolton (2003) and earlier authors as a distinct tribe, is nested within a non-monophyletic Ponerini. This result is also supported by morphological evidence (see discussion under *Thaumatomyrmex*), so we are newly synonymizing Thaumatomyrmecini under Ponerini.

## ***Harpegnathos* Genus Group**

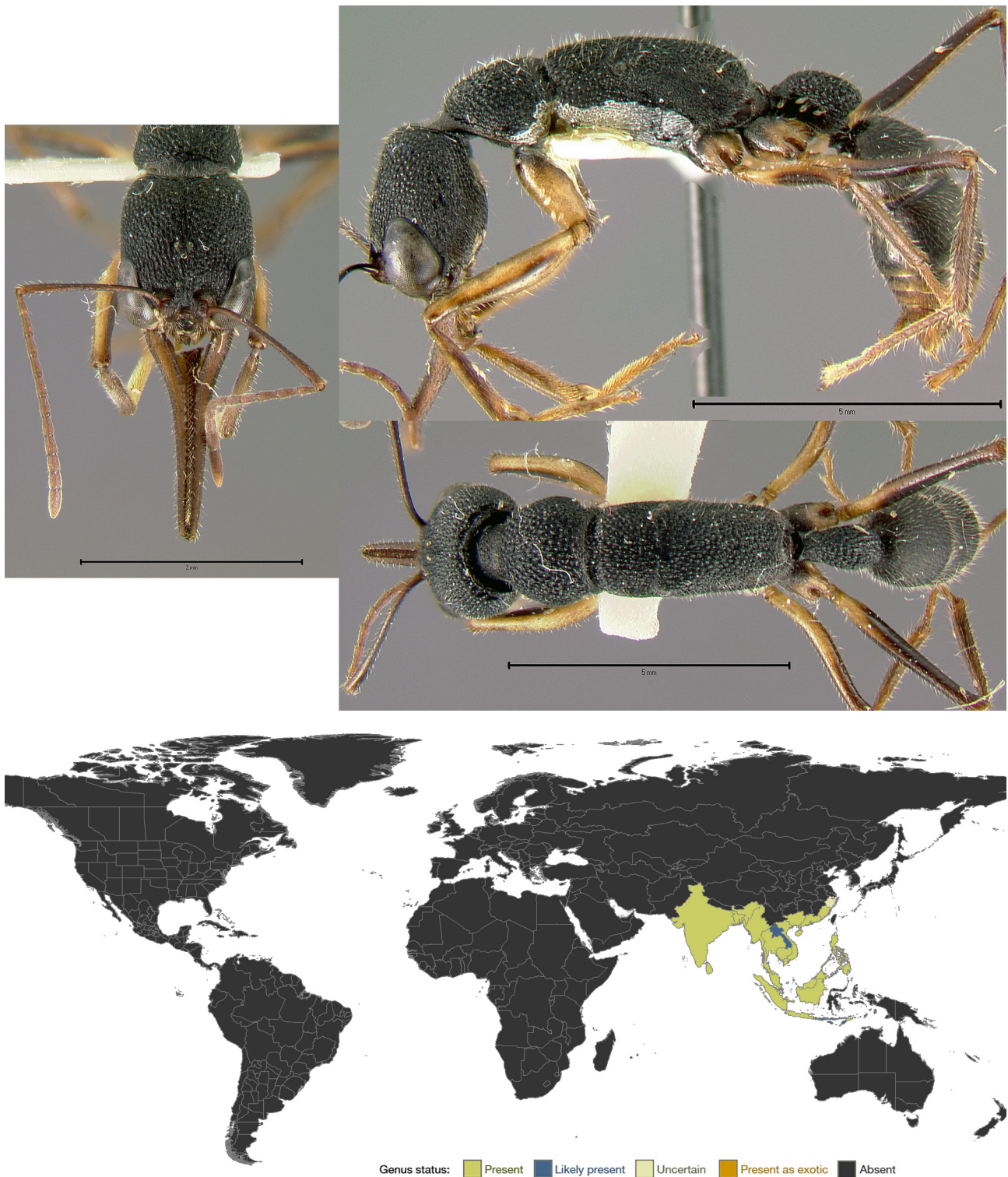
### ***Harpegnathos* Jerdon**

Fig. 4

*Harpegnathos* Jerdon, 1851: 116 (as genus). Type-species: *Harpegnathos saltator* Jerdon, 1851: 117; by monotypy.

*Drepanognathus* Smith, F., 1858: 81 (in Poneridae [unnecessary replacement name for *Harpegnathos*]). Type-species: *Harpegnathos saltator* Jerdon, 1851: 117; by subsequent designation of Bingham, 1903: 49.

*Harpegnathos* is a small genus restricted to Southeast Asia. These ants are notable for their remarkable morphological traits, foraging behaviors, complex nest architecture, and unusual reproductive behaviors.



**FIGURE 4.** Worker caste of *Harpegnathos venator*: lateral and dorsal view of body and full-face view of head (Philippines, G.Alpert, MCZC); world distribution of *Harpegnathos*.

**Diagnosis.** Workers of *Harpegnathos* are virtually impossible to confuse with those of any other genus. They



are among the most morphologically unique of all ponerines, and their scythe-shaped mandibles and huge anteriorly set eyes instantly identify them. Other diagnostic characters (in combination) include the presence of ocelli, an obsolete metanotal groove, a laterally opening metapleural gland orifice, toothed tarsal claws, prominent arolia, a long nodiform petiole, a short rounded anterior face of A3, and a strong girdling constriction between pre- and postsclerites of A4.

**Synoptic description.** *Worker*. Large to very large (TL 14–20 mm) ants with the standard characters of Ponerini, except that the anterior face of A3 is short and rounded, not vertical. Mandibles long, upturned and scythe-shaped, with a small ventral edge bearing a few teeth and a long medial edge bearing two rows of small denticles. Clypeus shallow and with a nearly straight anterior margin. Frontal lobes very small. Eyes greatly enlarged, nearly half the length of the head, and located at the extreme anterolateral corners of the head. Ocelli present. Metanotal groove obsolete dorsally. Propodeum broad dorsally. Propodeal spiracles slit-shaped. Metapleural gland orifice opening laterally within a deep depression. Tarsal claws with a single preapical tooth. Arolia prominent and bright white. Metatibial spur formula (1s, 1p). Petiole longer than wide, becoming wider dorsally and posteriorly. Anterior face of A3 short and rounded, not vertical. Gaster with a strong girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and mesosoma foveate and striate, the gaster punctate or foveolate. Head and body with abundant short pilosity and little to no pubescence. Color variable, orange to black.

*Queen*. Very similar to worker, but winged and slightly larger (Peeters *et al.*, 2000).

*Male*. See descriptions in Bingham (1903), Emery (1911), and Donisthorpe (1942).

*Larva*. Not described.

**Geographic distribution.** The range of *Harpegnathos* encompasses the area bounded by India, the Philippines, southern China, and Java (Donisthorpe, 1937).

**Ecology and behavior.** *Harpegnathos* is morphologically and behaviorally one of the most unusual and interesting of all ponerines. Its bizarre scythe-shaped mandibles and huge eyes are instantly recognizable, and its jumping abilities and visual hunting strategy are unique within the Ponerinae and matched among ants only by *Myrmecia* (Myrmeciinae) and *Gigantiops* (Formicinae) (Wheeler, 1922a; Tautz *et al.*, 1994). *Harpegnathos* is also notable for its nest architecture, which is unusually complex for a ponerine, and for its unique social system in which reproduction is performed both by dealate queens and gamergates. Nearly everything known about the ecology and behavior of the genus comes from studies of the Indian species *H. saltator*, so the following discussion mainly concerns that species unless otherwise noted. The general applicability of these observations to other *Harpegnathos* species is unknown.

*Harpegnathos* are formidable hunters, and their excellent vision, long mandibles, venomous sting, and jumping capabilities make them superbly adapted to hunting fast moving prey (Maschwitz, 1981). Their eyes have the largest number of ommatidia of any ant examined and enable them to be visually oriented to a degree that is rare in ants (Baroni Urbani *et al.*, 1994). Their mandibles are designed for rapid closure, rather than extreme force, with a preponderance of fast muscle fibers controlling mandibular closure (Paul & Gronenberg, 1999; Paul, 2001). *Harpegnathos* workers have powerful paralyzing stings which rapidly subdue prey (Maschwitz *et al.*, 1979; Maschwitz, 1981) and are also effectively used in defense (*e.g.*, Jerdon, 1851; Wroughton, 1892). The paralysis is permanent, and paralyzed prey may be stored for short periods before consumption (Maschwitz *et al.*, 1979).

The jumping abilities of *Harpegnathos* have been noted in the literature since the original description of the genus (Jerdon, 1851). Early observers (*e.g.*, Jerdon, 1851; Wroughton, 1892; Bingham, 1903) generally described the jumping as an escape response, but more recent studies have demonstrated that *Harpegnathos* utilizes its jumping for at least four distinct purposes: escape, normal locomotion, an unusual behavior called “group jumping”, and prey capture (Musthak Ali *et al.*, 1992; Baroni Urbani *et al.*, 1994). When disturbed, *Harpegnathos* workers jump repeatedly and then hide under leaf litter (Shivashankar *et al.*, 1989). Of all the jumps made by *Harpegnathos*, these escape jumps cover the longest distance (3 to 21 cm; Musthak Ali *et al.*, 1992). During normal locomotion, *Harpegnathos* typically make slow, deliberate movements (Crosland, 1995), but apparently also employ jumping (Soans & Soans, 1969; Baroni Urbani *et al.*, 1994). Musthak Ali *et al.* (1992) observed a strange behavior in *H. saltator* which they termed “group jumping”: an individual worker will sometimes start jumping in an uncoordinated fashion for several minutes, and eventually other workers in the vicinity follow suit. The function of this behavior is unknown, but it may serve to flush out prey or to prevent attacks by parasitoids (Musthak Ali *et al.*, 1992). *Harpegnathos* workers also jump to capture fast prey and can even catch flying insects

in midair, but do not jump at slow prey such as termites (Shivashankar *et al.*, 1989; Musthak Ali *et al.*, 1992; Ke *et al.*, 2008). These predatory jumps tend to cover shorter distances than the escape jumps (Musthak Ali *et al.*, 1992). Wheeler (1922a) hypothesized that the mandibles must be involved in generating the forces necessary for leaping, but recent studies of *Harpegnathos* jumping have confirmed that it is the legs which drive the jumps (though the biomechanics involved are unclear: Baroni Urbani *et al.*, 1994; Tautz *et al.*, 1994).

*Harpegnathos* are crepuscular foragers, requiring daylight to locate prey but preferring to avoid the heat of midday (Shivashankar *et al.*, 1989). They hunt individually in leaf litter and among low vegetation for a diversity of arthropods (Jerdon, 1851; Maschwitz *et al.*, 1979; Maschwitz, 1981; Shivashankar *et al.*, 1989; Peeters *et al.*, 1994; Liebig & Poethke, 2004), though a substantial proportion of their diet consists of fast-running or jumping prey such as crickets, cockroaches, cicadas, flies, and spiders (Maschwitz, 1981; Shivashankar *et al.*, 1989). By enabling them to utilize such prey, which might normally be difficult for an ant to capture, the specialized adaptations of *Harpegnathos* allow it to fill a niche which is otherwise not fully exploited by ants.

Liebig & Poethke (2004) found no evidence of intercolony aggression in *H. saltator* despite potentially overlapping foraging ranges, and Maschwitz (1981) found no evidence of chemical recruitment in either foraging or emigrations of *H. saltator* (emigrations occur via social carrying). The chemical ecology of *Harpegnathos* has not been extensively studied, though Nascimento *et al.* (1993) examined the exocrine secretions of *H. saltator* and Gobin *et al.* (2003b) discovered a unique epidermal gland in *H. saltator* which may be involved in hydrocarbon production.

Peeters *et al.* (1994) studied the nests of *H. saltator* and discovered that they are exceptionally complex by ponerine standards. In a mature colony the nest consists of a series of stacked chambers forming a nearly spherical structure, surmounted by a thick vaulted roof and separated from the surrounding soil by a hollow space. A tunnel leads down to a separate refuse chamber. Peeters *et al.* (1994) hypothesized that this nest design is an adaptation to survive periodic flooding, which is common in the areas inhabited by *H. saltator*. This idea is supported by the fact that *H. saltator* “wallpapers” the surfaces of its nests with discarded cocoons, insect parts, and plant matter. This wallpaper is glued down and probably helps keep the chambers dry. Shivashankar *et al.* (1989) further observed that *H. saltator* nest entrances are purposefully plugged with rodent feces or plant matter. The nests of *H. venator* are comparatively simple, consisting of two disc-shaped chambers separated by a unique funnel-like opening (Crosland, 1995); this funnel could make the inner chamber accessible only via jumping, an effective defense mechanism.

Like most ponerines, *Harpegnathos* have small colonies, with an average of 65 to 225 workers in *H. saltator* (Peeters *et al.*, 2000) and 35 workers in *H. venator* (Crosland, 1995). New colonies are founded by a single dealate queen (Peeters & Hölldobler, 1995; Peeters *et al.*, 2000; some polygynous queenright colonies have been observed in *H. venator*: Crosland, 1995). Like most ponerines, virgin alate queens leave their natal nests, mate, found new colonies, and continue to forage until the first crop of workers are mature, though from this point on the colony’s reproductive life cycle is highly unusual (Peeters & Hölldobler, 1995). *Harpegnathos* workers retain functional spermathecae (J. Billen, pers. comm. in Peeters *et al.*, 2000), and many of them will mate with their brothers inside the nest (Peeters *et al.*, 2000). These mated workers do not begin to lay eggs until the colony’s short-lived queen senesces or dies (Peeters & Hölldobler, 1995). In newly orphaned colonies, mated workers aggressively compete in order to achieve reproductive status (Liebig, 1998; Liebig *et al.*, 2000). Those that are successful develop their ovaries and begin laying eggs (they are now considered gamergates; Liebig *et al.*, 1998, 2000; Peeters *et al.*, 2000). As the active gamergates gradually lose fecundity or die, new gamergates arise to take their place, and as a result a *Harpegnathos* colony is theoretically immortal (Peeters *et al.*, 2000).

This complex reproductive system has recently been examined by several research groups. Whereas queenright colonies are generally monogynous, queenless colonies typically contain a large number of mated workers, of which a significant fraction are reproductively active gamergates (Peeters & Hölldobler, 1995). The reproductive status of a *Harpegnathos* worker is communicated via its cuticular hydrocarbon profile (Liebig *et al.*, 2000), allowing low-ranking workers to detect sexual maturation by their nestmates and potentially prevent it through aggression (Liebig *et al.*, 1999; Hoyer *et al.*, 2005). Since gamergates do not work as much as normal workers (as demonstrated by their reduced brain volumes: Gronenberg & Liebig, 1999), the number of gamergates in a queenless colony is tightly regulated to optimize reproduction versus productivity (Monnin & Ratnieks, 2001).

Colonies of most ponerine species die along with their queens, and new colonies arise via independent foundation by a fertilized alate queen (exceptions include species with ergatoid queens). In contrast, *Harpegnathos* emphasizes long-term stability (even immortality) of existing colonies. This likely stems from two related factors:

the high mortality rates of new *Harpegnathos* colonies (Liebig & Poethke, 2004), and their elaborate nests, which represent major investments of time and energy. Successful *Harpegnathos* queens typically only live for two or three years (Peeters & Hölldobler, 1995; Liebig & Poethke, 2004), but by extending the colony's lifespan through multiple generations of gamergates the colony can utilize the nests for longer periods and produce many more alate queens (Peeters *et al.*, 2000). Colony emigrations and colony fissions are unknown in *Harpegnathos* and are unlikely, given the major investment represented by the nest and given that gamergate colonies emphasize production of new queens over workers (Peeters *et al.*, 1994; Peeters & Hölldobler, 1995; Peeters *et al.*, 2000).

**Phylogenetic and taxonomic considerations.** *Harpegnathos* was erected by Jerdon (1851) to house the single species *H. saltator* Jerdon. Soon afterward, Smith (1858) replaced the genus name with *Drepanognathus*, based on some confusion over possible homonymy with a genus of staphilinid beetles (discussed by Donisthorpe, 1937). Subsequent authors alternated between treating *Harpegnathos* or *Drepanognathus* as the valid name (*e.g.*, Roger, 1863a; Forel, 1893a; Dalla Torre, 1893; Bingham, 1903), but eventually the proper consensus was reached recognizing the validity of the original name *Harpegnathos* (Donisthorpe, 1937). *Harpegnathos* has also experienced some instability at the tribal level, being variously placed in Ponerini (*e.g.*, Wheeler, 1910), its own tribe Harpegnathii (Forel, 1900b; Drepanognathini: Ashmead, 1905), or its own subtribe Harpegnathini in Ponerini (*e.g.*, Emery, 1911). Smith (1871) even grouped it with *Odontomachus* in his family Odontomachidae.

Both molecular and morphological evidence support the placement of *Harpegnathos* in its own “genus group” within Ponerini. Schmidt's (2013) molecular phylogeny of the Ponerinae confirms that *Harpegnathos* is very closely related to the rest of Ponerini, if not deeply nested within the tribe. The exact placement of *Harpegnathos* in the phylogeny of Ponerinae is unresolved, possibly due to long branch issues (Schmidt, 2013). The best supported phylogenetic position of *Harpegnathos* is as sister to the remainder of the Ponerini, but other placements cannot be statistically rejected. Commonly resolved alternative placements include as sister to *Hypoponera*, the *Plectroctena* group, or *Hypoponera* plus the *Plectroctena* group. Morphological data suggests that *Harpegnathos* may be sister to the remainder of Ponerini, though it is still an open question. The phylogenetic position of *Harpegnathos* is arguably the single most important outstanding question in ponerine phylogenetics, given its implications for reconstructions of ancestral ponerine structure, ecology and behavior.

### Species of *Harpegnathos*

- H. empesoi* Chapman, 1963: Philippines
- H. hobbyi* Donisthorpe, 1937: Borneo
- H. macgregori* Wheeler & Chapman, 1925: Philippines
- H. medioniger* Donisthorpe, 1942: Philippines
- H. pallipes* (Smith, F., 1858): Java
- H. saltator* Jerdon, 1851: India
- H. saltator cruentatus* (Smith, F. 1858): China
- H. saltator taprobanae* Forel, 1909: Sri Lanka
- H. venator* (Smith, F., 1858): India
- H. venator chapmani* Donisthorpe, 1937: Philippines
- H. venator rugosus* (Mayr, 1862): China

### *Hypoponera* genus group

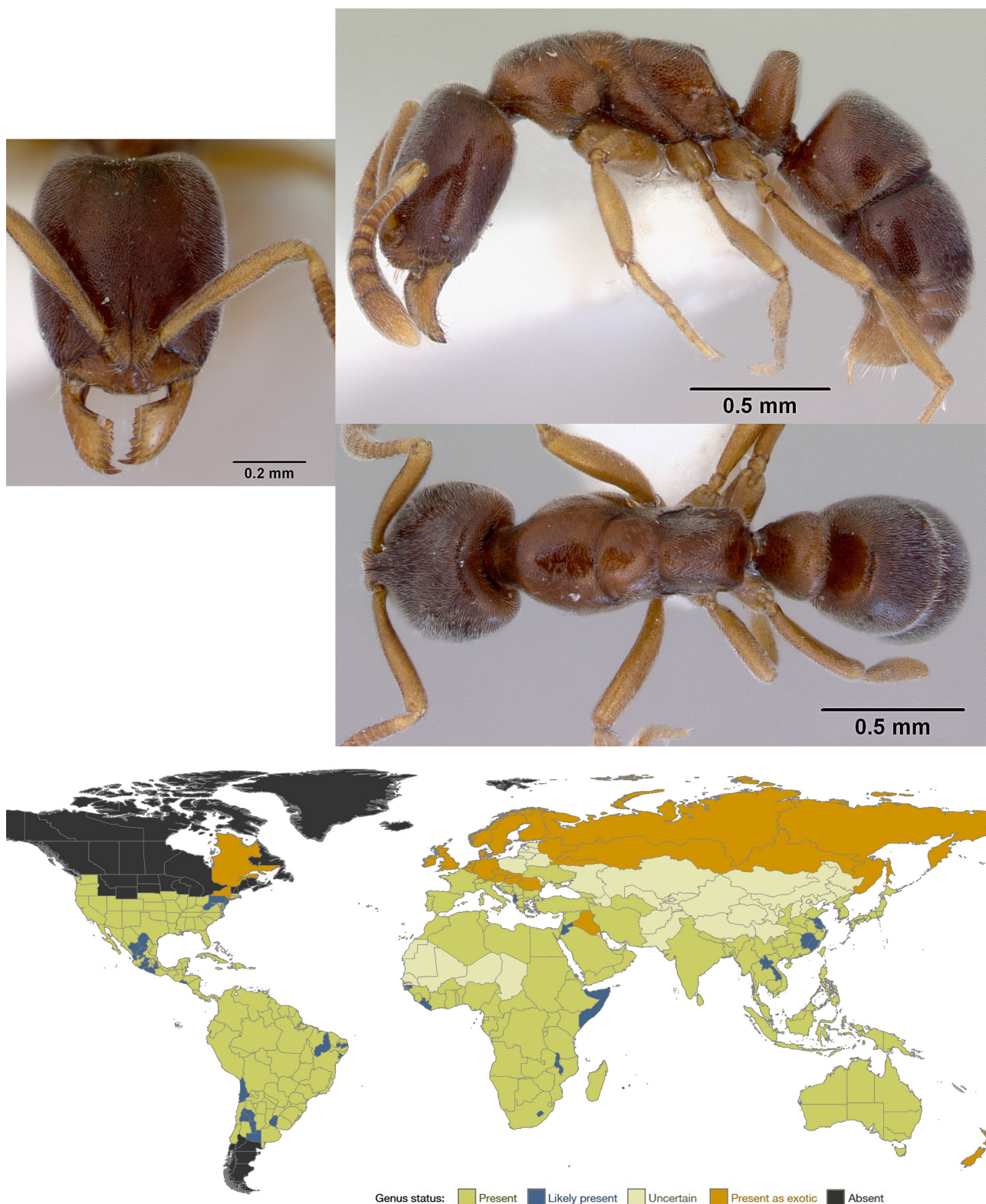
#### *Hypoponera* Santschi

Fig. 5

*Hypoponera* Santschi, 1938: 79 (as subgenus of *Ponera*). Type-species: *Ponera abeillei* André, 1881: 61, xlviii; by original designation.

*Hypoponera* is a large (approximately 170 described extant species) cosmopolitan genus of small cryptic ponerines. Most *Hypoponera* are generalist predators, and some are widespread tramp species. Several are known to have highly unusual reproductive strategies, including the presence of combative ergatoid males.





**FIGURE 5.** Worker caste of *Hypoponera eduardi*: lateral and dorsal view of body and full-face view of head (CASENT0172333, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Hypoponera*.

**Diagnosis.** *Hypoponera* is morphologically the most generalized of the cryptobiotic ponerine genera, as it lacks any obvious autapomorphies. The genus also shows greater variability than most ponerine genera in many characters typically useful for generic diagnosis. Despite these complications, *Hypoponera* workers are generally diagnosable by the following combination of characters: mandibles triangular, with a variable number of small

teeth and without basal pits or grooves; frontal lobes small and closely approximated; metanotal groove usually shallowly depressed; mesotibiae and meso-/metabasitarsi without stout traction setae; metatibial spur formula (1p); petiole squamiform; subpetiolar process a rounded lobe without paired teeth posteriorly, and usually without an anterior fenestra; and head and body without strong sculpturing and usually with a relatively dense pubescence. *Hypoponera* is morphologically most similar to *Ponera*, *Cryptopone*, *Pseudoponera*, *Brachyponera*, some *Euponera*, *Belonopelta*, and *Emeryopone*. *Hypoponera* most consistently differs from *Ponera* in the structure of the subpetiolar process: in *Ponera* the subpetiolar process has an anterior fenestra and a pair of teeth posteriorly, whereas in *Hypoponera* the subpetiolar process is a simple rounded lobe, only rarely with an anterior fenestra. *Hypoponera* differs from *Cryptopone* in lacking stout spines on the middle and hind legs, from *Euponera*, *Pseudoponera* and *Brachyponera* in having only a single metatibial spur, and from *Belonopelta* and *Emeryopone* in having triangular mandibles without a series of long attenuated teeth.

**Synoptic description.** *Worker.* Very small to small (TL 1.4–5.5 mm) slender to robust ants with the standard characters of Ponerini. Mandibles triangular, with a variable number of teeth and without a distinct basal groove (though a shallow pit or vestigial groove may be present). Frontal lobes small and closely approximated. Apical segments of antennae sometimes enlarged into a distinct club. Eyes sometimes absent, but usually present, very small and located far anterior on the sides of the head. Mesopleuron usually not divided by a transverse groove, though occasionally faintly present. Metanotal groove usually present and shallowly depressed, though sometimes reduced to a suture, and rarely absent altogether. Propodeum usually moderately to strongly narrowed dorsally, but occasionally broad. Propodeal spiracles round. Metatibial spur formula (1p). Petiole squamiform. Subpetiolar process a rounded lobe, without paired teeth posteriorly and only rarely with an anterior fenestra. Gaster with a weak to strong girdling constriction between pre- and postsclerites of A4. Stridulitrum sometimes present on pretergite of A4. Head and body occasionally glossy, usually finely punctate, sometimes lightly striate on the sides of the mesosoma. Head and body with sparse to scattered pilosity and usually a dense pubescence. Color variable, testaceous to black.

*Queen.* Similar to worker; usually alate, with ocelli and larger compound eyes. Queens are sometimes ergatoid or intermorphic (Yamauchi *et al.*, 1996). See further description in Taylor (1967) and Bolton & Fisher (2011).

*Male.* Usually winged, but sometimes ergatoid. See general description in Taylor (1967) and Bolton & Fisher (2011) and descriptions of ergatoid males in Yamauchi *et al.* (1996).

*Larva.* *Hypoponera* larvae were described generically by Taylor (1967) and for various species by Wheeler & Wheeler (1964, 1971a, 1990). Detailed histological or morphological studies of *Hypoponera* larvae were performed by Peeters & Hölldobler (1992) and Escoubas *et al.* (1987). Unusually among ponerines, sufficient research has been conducted on *Hypoponera* larval structure to yield a meaningful diagnostic character: *Hypoponera* larvae have two pairs of sticky tubercles on A4 and A5, whereas *Ponera* larvae have three or four pairs (Taylor, 1967).

**Geographic distribution.** *Hypoponera* is the most cosmopolitan of all ponerine genera, occurring on every continent except Antarctica and extending into many temperate regions. Endemic species are apparently absent from many island groups (*e.g.*, Polynesia), but several widespread tramp species have become established even in these locations (Taylor, 1967; Ingram *et al.*, 2006).

**Ecology and behavior.** *Hypoponera* is probably the most common and diverse ponerine genus worldwide and is consistently one of the most abundant and diverse ant genera collected in quantitative surveys of leaf litter and soil ant communities, especially in the tropics (*e.g.*, Argentina: Theunis *et al.*, 2005; Australia: King *et al.*, 1998; Brazil: Soares & Schoederer, 2001; Costa Rica: Longino *et al.*, 2002; Ghana: Belshaw & Bolton, 1994; Guyana: LaPolla *et al.*, 2007; Madagascar: Fisher, 1999; Melanesia and New Caledonia: Wilson, 1976; generally: Ward, 2000). Though *Leptogenys* currently boasts many more described species than *Hypoponera*, the true species diversity of *Hypoponera* is probably grossly underestimated and may rival or exceed that of *Leptogenys* given their cryptobiotic habits, lack of revisionary taxonomic work, and the likely occurrence of cryptic species complexes. Fisher (1999) found that *Hypoponera* diversity was a good surrogate for total ant diversity in forests in eastern Madagascar, indicating that it may be a useful indicator genus for faunal surveys.

Except for their unusual reproductive and larval behaviors (see below), surprisingly little work has been done on the ecology and behavior of *Hypoponera*. They are cryptobiotic, nesting in soil, under rocks, or in rotting wood, and foraging there or in leaf litter and other sheltered microhabitats (Wilson, 1958c; Onoyama, 1989; Yamauchi *et al.*, 1996; Terayama, 1999; Foitzik *et al.*, 2002; pers. obs.). Reports on the sizes of *Hypoponera* colonies are scarce,

but colonies usually have fewer than 100 workers and only occasionally more (e.g., Wilson, 1958c; Villet *et al.*, 1991; Peeters & Hölldobler, 1992; Peeters, 1993; Hashimoto *et al.*, 1995; Yamauchi *et al.*, 1996; Foitzik *et al.*, 2002). They are typically reported to be generalist predators of small arthropods or scavengers (e.g., Wilson, 1958c; Agbogba, 1984; Escoubas *et al.*, 1987; Brown, 2000; Seifert, 2004), though some species probably have stricter diets (e.g., one African species is reported to feed principally on collembolans; Lévieux, 1983). Foraging is probably generally performed by solitary workers, though at least one species is known to recruit nestmates to help dismember large prey (Agbogba, 1984). Hölldobler (1985) observed tandem running in an unidentified *Hypoponera* species but did not clarify its purpose.

While in most respects *Hypoponera* are fairly typical ponerines, members of the genus exhibit many unusual social or reproductive traits, including one of only two known instances of adult trophallaxis in the Ponerinae (Hashimoto *et al.*, 1995), as well as obligate worker sterility (Villet *et al.*, 1991; Ito & Ohkawara, 1994; Yamauchi *et al.*, 2001), male polymorphism, and larval cannibalism. As a genus *Hypoponera* displays an interesting diversity of reproductive strategies, with species variously having almost every conceivable combination of alate and intermorphic queens and alate and ergatoid males. At least three *Hypoponera* species are known to have both winged and ergatoid males (*H. eduardi*, *H. nubatama* and *H. opacior*), at least three species apparently have only ergatoid males (*H. ergatandria*, *H. gleadowi* and *H. punctatissima*), and still other species are thought to have only winged males (Yamauchi *et al.*, 2001; Bolton & Fisher, 2011). A similar variation occurs in the queen caste, with some species having both alate and intermorphic queens and others probably having only one or the other (e.g., Hashimoto *et al.*, 1995; Yamauchi *et al.*, 1996, 2001). In what are probably the most complex mating systems known for any ponerine, *H. nubatama* and *H. opacior* have alate queens, intermorphic queens, alate males, and ergatoid males, often all in the same colony (Yamauchi *et al.*, 2001; Foitzik *et al.*, 2002; Rüger *et al.*, 2008). Some colonies of *H. opacior* are polygynous and polydomous, with 2 to 15 intermorphic queens and multiple nest sites connected by subterranean tunnels. Ergatoid males remain in their natal nest and mate with virgin queens (either alate or intermorphic) which are still in their puparia (Foitzik *et al.*, 2002).

The behavior of ergatoid *Hypoponera* males is both unusual and varied within the genus. At one extreme is *H. ergatandria*, whose males are dimorphic, the minor males mimicking females and utilizing a sneaky mating strategy, and the major males fighting and killing one another to secure mating opportunities (Yamauchi *et al.*, 1996). Similar fighting was also observed among ergatoid males of *H. punctatissima*, though it's unclear whether they are dimorphic (Hamilton, 1979). Ergatoid males of *H. nubatama* do not fight directly but instead kill other males before they eclose from their puparia (Yamauchi *et al.*, 2001). Finally, ergatoid males of *H. opacior* do not fight but monopolize their mates by copulating with them for up to 40 hours, the longest copulations ever observed in ants (Foitzik *et al.*, 2002). Given the presence of ergatoid males in virtually all tramp species of *Hypoponera*, Taylor (1967) hypothesized that the consequent simplification of the mating process in these species may facilitate their spread.

*Hypoponera* larvae have two pairs of sticky tubercles, with which they are stuck to the walls and ceilings of their nest cavities (Taylor, 1967; Escoubas *et al.*, 1987; Peeters & Hölldobler, 1992). This may assist the larvae in feeding or may function to protect the larvae from excess humidity (Peeters & Hölldobler, 1992), but may also function to separate larvae sufficiently to prevent larval cannibalism, which has been observed in at least three species (Rüger *et al.*, 2008).

**Phylogenetic and taxonomic considerations.** Santschi (1938) erected *Hypoponera* as a subgenus of *Ponera* to house those *Ponera* species with shallow metanotal grooves. Taylor (1967) raised *Hypoponera* to full genus status, recognized that Santschi's definition of the subgenus was phylogenetically meaningless, and instead differentiated the genus from *Ponera* by its palp formula (1,1 in *Hypoponera*), absence of an anterior fenestra or posterior teeth in the subpetiolar process, several male characters, and the number of sticky tubercles on the larvae. *Hypoponera* workers are superficially quite similar to those of *Ponera*, but they are distantly separated in Schmidt's (2013) molecular phylogeny of the Ponerinae, suggesting that their morphological similarities are the result of convergence due to their similar cryptobiotic lifestyles. *Hypoponera* is phylogenetically distinct from other major lineages of Ponerini, diverging from its closest relative (probably the *Plectroctena* group) quite early in the radiation of the tribe.

Given the absence of strong autapomorphies for the genus and its relatively high morphological diversity, it is possible that *Hypoponera* as presently defined is non-monophyletic. Schmidt (2013) included in his molecular phylogeny several *Hypoponera* species presenting maximum morphological diversity from across the range of the



genus, to begin to test the monophyly of the genus. To his surprise these species formed a tight clade with strong phylogenetic support. Even more surprising was that three sympatric *Hypoponera* species from Malaysia, which he included in the phylogeny because they are morphologically quite divergent from one another (to the point that he expected them all to represent distinct genera) turned out to be very closely related to one another, indicating an impressive recent adaptive radiation.

### Species of *Hypoponera*

*Hypoponera* is in desperate need of a thorough species level revision, as the genus has never received any comprehensive revisionary work, many synonyms exist, and a great many species await description (Taylor, 1967). The only exception to this is the Afrotropical and western Palaearctic faunas, which were recently revised by Bolton & Fisher (2011). Examining the remaining fauna will be a monumental task, as the true diversity of the genus is probably dramatically higher than presently known.

*H. abeillei* (André, 1881): France (Corsica)  
*H. agilis* (Borgmeier, 1934): Surinam  
*H. albopubescens* (Menozzi, 1939): Indonesia (Sumatra)  
*H. aliena* (Smith, F., 1858): Brazil  
*H. angustata* (Santschi, 1914): Guinea  
*H. aprora* Bolton & Fisher, 2011: Tanzania  
*H. argentina* (Santschi, 1922): Argentina  
*H. assmuthi* (Forel, 1905): India  
*H. austra* Bolton & Fisher, 2011: South Africa  
*H. beebei* (Wheeler, W.M., 1924): Ecuador (Galapagos Islands)  
*H. beppin* Terayama, 1999: Japan  
*H. biroi* (Emery, 1900): New Guinea  
*H. blanda* Bolton & Fisher, 2011: Central African Republic  
*H. boerorum* (Forel, 1901): South Africa  
*H. bugnioni* (Forel, 1912): Indonesia (Sumatra)  
*H. bulawayensis* (Forel, 1913): Zimbabwe  
*H. butteli* (Forel, 1913): Indonesia (Sumatra)  
*H. camerunensis* (Santschi, 1914): Cameroon  
*H. ceylonensis* (Mayr, 1897): Sri Lanka  
*H. clavatula* (Emery, 1906): Argentina  
*H. coeca* (Santschi, 1914): Cameroon  
*H. collegiana* (Santschi, 1925): Brazil  
*H. collegiana paranensis* (Santschi, 1925): Brazil  
*H. comis* Bolton & Fisher, 2011: Tanzania  
*H. confinis* (Roger, 1860): Sri Lanka  
*H. confinis aitkenii* (Forel, 1900): India  
*H. confinis epinotalis* (Viehmeyer, 1916): Singapore  
*H. confinis javana* (Forel, 1905): Indonesia (Java)  
*H. confinis singaporensis* (Viehmeyer, 1916): Singapore  
*H. confinis wroughtonii* (Forel, 1900): India  
*H. congrua* (Wheeler, W.M., 1934): Australia  
*H. convexiuscula* (Forel, 1900): Australia  
*H. creola* (Menozzi, 1931): Costa Rica  
*H. decora* (Clark, 1934): Australia  
*H. defessa* Bolton & Fisher, 2011: Ghana  
*H. dema* Bolton & Fisher, 2011: Rwanda  
*H. dis* Bolton & Fisher, 2011: Tanzania  
*H. distinguenda* (Emery, 1890): Venezuela

*H. distinguenda dispar* (Santschi, 1925): Brazil  
*H. distinguenda histrio* (Forel, 1912): Brazil  
*H. distinguenda inexpedita* (Forel, 1911): Brazil  
*H. distinguenda vana* (Forel, 1909): Guatemala  
*H. dulcis* (Forel, 1907): Tanzania  
*H. eduardi* (Forel, 1894): Algeria  
*H. elliptica* (Forel, 1900): Australia  
*H. emeryi* (Donisthorpe, 1943): New Guinea  
*H. ergatandria* (Forel, 1893): West Indies  
*H. eutrepta* (Wilson, 1958): Fiji Islands  
*H. exigua* Bolton & Fisher, 2011: Ethiopia  
*H. exoecata* (Wheeler, W.M., 1928): China  
*H. faceta* (Menozzi, 1931): Costa Rica  
*H. faex* Bolton & Fisher, 2011: Ethiopia  
*H. fatiga* Bolton & Fisher, 2011: Ghana  
*H. fenestralis* (Gallardo, 1918): Argentina  
*H. fiebrigi* (Forel, 1908): Paraguay  
*H. fiebrigi antoniensis* (Forel, 1912): Colombia  
*H. fiebrigi famini* (Forel, 1912): Colombia  
*H. fiebrigi transiens* (Santschi, 1925): Argentina  
*H. foeda* (Forel, 1893): West Indies  
*H. foeda saroltae* (Forel, 1912): Brazil  
*H. foreli* (Mayr, 1887): Brazil  
*H. gibbinota* (Forel, 1912): Great Britain  
*H. gleadowi* (Forel, 1895): India  
*H. gracilicornis* (Menozzi, 1931): Costa Rica  
*H. grandidieri* (Santschi, 1921): Madagascar  
*H. hawkesi* Bolton & Fisher, 2011: Tanzania  
*H. hebes* Bolton & Fisher, 2011: Rwanda  
*H. herbertonensis* (Forel, 1915): Australia  
*H. idelettae* (Santschi, 1923): Brazil  
*H. ignavia* Bolton & Fisher, 2011: Zimbabwe  
*H. ignigera* (Menozzi, 1927): Costa Rica  
*H. iheringi* (Forel, 1908): Brazil  
*H. importuna* Bolton & Fisher, 2011: Gabon  
*H. inaudax* (Santschi, 1919): DRC  
*H. indigens* (Forel, 1895): Madagascar  
*H. indigens bellicosa* (Forel, 1895): Madagascar  
*H. inexorata* (Wheeler, W.M., 1903): United States  
*H. inexorata fallax* (Forel, 1909): Guatemala  
*H. jeanneli* (Santschi, 1935): Kenya  
*H. jocosa* Bolton & Fisher, 2011: Ethiopia  
*H. johannae* (Forel, 1891): Madagascar  
*H. juxta* Bolton & Fisher, 2011: Ethiopia  
*H. lamellosa* (Forel, 1907): West Malaysia  
*H. lassa* Bolton & Fisher, 2011: Ghana  
*H. lea* (Santschi, 1937): Sierra Leone  
*H. leninei* (Santschi, 1925): Brazil  
*H. lepida* Bolton & Fisher, 2011: Ghana  
*H. longiceps* (Forel, 1913): Java  
*H. ludovicae* (Forel, 1892): Madagascar  
*H. lumpurensis* (Forel, 1907): West Malaysia



*H. lumpurensis slamatana* (Forel, 1913): Indonesia (Sumatra)  
*H. mackayensis* (Forel, 1900): Australia  
*H. macradelphe* (Wilson, 1958): New Guinea  
*H. madeccasa* (Santschi, 1938): Madagascar  
*H. malayana* (Wheeler, W.M., 1929): West Malaysia  
*H. menozzii* (Santschi, 1932): Costa Rica  
*H. meridia* Bolton & Fisher, 2011: South Africa  
*H. mixta* Bolton & Fisher, 2011: Kenya  
*H. molesta* Bolton & Fisher, 2011: Gabon  
*H. monticola* (Mann, 1921): Fiji Islands  
*H. natalensis* (Santschi, 1914): South Africa  
*H. neglecta* (Santschi, 1923): Brazil  
*H. nippona* (Santschi, 1937): Japan  
*H. nitidula* (Emery, 1890): Costa Rica  
*H. nivariana* (Santschi, 1908): Spain (Canary Islands)  
*H. nubatama* Terayama & Hashimoto, 1996: Japan  
*H. obtunsa* Bolton & Fisher, 2011: Zimbabwe  
*H. occidentalis* (Bernard, 1953): Guinea  
*H. odiosa* Bolton & Fisher, 2011: Cameroon  
*H. opaciceps* (Mayr, 1887): Brazil  
*H. opaciceps cubana* (Santschi, 1930): Cuba  
*H. opaciceps gaigei* (Forel, 1914): Colombia  
*H. opaciceps jamaicensis* (Aguayo, 1932): Jamaica  
*H. opaciceps pampana* (Santschi, 1925): Argentina  
*H. opacior* (Forel, 1893): West Indies  
*H. orba* (Emery, 1915): Ethiopia  
*H. pallidula* (Emery, 1900): New Guinea  
*H. papuana* (Emery, 1900): New Guinea  
*H. parva* (Forel, 1909): Guatemala  
*H. perparva* Bolton & Fisher, 2011: South Africa  
*H. perplexa* (Mann, 1922): Honduras  
*H. petiolata* (Bernard, 1953): Guinea  
*H. pia* (Forel, 1901): New Guinea  
*H. producta* Bolton & Fisher, 2011: Gabon  
*H. pruinosa* (Emery, 1900): New Guinea  
*H. pulchra* Bolton & Fisher, 2011: Equatorial Guinea  
*H. punctatissima* (Roger, 1859): Poland and Germany  
*H. punctatissima indifferens* (Forel, 1895): Madagascar  
*H. punctiventris* (Emery, 1901): New Guinea  
*H. pygmaea* (Forel, 1907): West Malaysia  
*H. quaestio* Bolton & Fisher, 2011: Tanzania  
*H. queenslandensis* (Forel, 1900): Australia  
*H. ragusai* (Emery, 1894): Italy (Sicily)  
*H. rectidens* (Clark, 1934): Australia  
*H. regis* Bolton & Fisher, 2011: Tanzania  
*H. reichenspergeri* (Santschi, 1923): Brazil  
*H. rigida* Bolton & Fisher, 2011: Uganda  
*H. sabronae* (Donisthorpe, 1941): New Guinea  
*H. sakalava* (Forel, 1891): Madagascar  
*H. sakalava excelsior* (Forel, 1892): Madagascar  
*H. sauteri* Onoyama, 1989: Taiwan  
*H. schmalzi* (Emery, 1896): Brazil

*H. schmalzi fugitans* (Forel, 1912): Brazil  
*H. schmalzi paulina* (Forel, 1913): Brazil  
*H. schwebeli* (Forel, 1913): Brazil  
*H. scitula* (Clark, 1934): Australia  
*H. segnis* Bolton & Fisher, 2011: Rwanda  
*H. silvestrii* (Donisthorpe, 1947): China  
*H. sinuosa* (Bernard, 1953): Guinea  
*H. siremps* (Forel, 1901): Papua New Guinea (Bismarck Archipelago)  
*H. sororcula* (Wilson, 1958): New Guinea  
*H. spei* (Forel, 1910): South Africa  
*H. stoica* (Santschi, 1912): Uruguay  
*H. sulcatinasis* (Santschi, 1914): South Africa  
*H. sulciceps* (Clark, 1928): Australia  
*H. surda* Bolton & Fisher, 2011: Kenya  
*H. taprobanae* (Forel, 1913): Sri Lanka  
*H. tecta* Bolton & Fisher, 2011: Kenya  
*H. tenella* (Emery, 1901): New Guinea  
*H. traegaordhi* (Santschi, 1914): South Africa  
*H. transvaalensis* (Arnold, 1947): South Africa  
*H. trigona* (Mayr, 1887): Brazil  
*H. trigona cauta* (Forel, 1912): Brazil  
*H. tristis* Bolton & Fisher, 2011: Rwanda  
*H. truncata* (Smith, F., 1860): Indonesia (Sulawesi)  
*H. turaga* (Mann, 1921): Fiji Islands  
*H. ursa* (Santschi, 1924): DRC  
*H. vanreesi* (Forel, 1912): Java  
*H. venusta* Bolton & Fisher, 2011: Rwanda  
*H. vernacula* (Kempf, 1962): Brazil  
*H. viri* (Santschi, 1923): Brazil  
*H. vitiensis* (Mann, 1921): Fiji Islands  
*H. wilsoni* (Santschi, 1925): Brazil  
*H. zwaluwenburgi* (Wheeler, W.M., 1933): Hawaii

#### *Incertae sedis*

*H. leveillei* (Emery, 1890): Venezuela (**comb. nov.**)

#### Fossil species

† *H. atavia* (Mayr, 1868): Baltic Amber

### ***Odontomachus* genus group**

The *Odontomachus* genus group is a large and heterogeneous clade of predominantly Old World epigeic ponerines. The genus-level diversity of the group arose during an explosive period of radiation between about 40 and 30 MYA (Schmidt, 2013). As a result, most generic relationships within the group are unresolved.

**Discussion.** The monophyly of the *Odontomachus* genus group is strongly supported by molecular data (Schmidt, 2013) and is subtended by a long stem branch, but we have been unable to discern a single morphological synapomorphy for the group. Relationships within the group are generally very poorly resolved, suggesting a rapid basal radiation in the group. *Leptogenys* and *Myopias* are most frequently inferred as sisters and together as sister to the remainder of the group, except that the position of *Mesoponera* (*s.s.*) is uncertain and may form a clade with *Leptogenys* and *Myopias*. *Paltothyreus* and *Buniapone* are strongly inferred as sisters by molecular evidence; this relationship is corroborated by several morphological synapomorphies. *Megaponera* and *Ophthalmopone* are sisters, and this too is corroborated by morphological data. Recent preliminary data (P.S. Ward,

pers. comm.) has placed *Promyopias* near *Phrynoponera* and *Odontoponera* but further study will be required to confirm this placement. Finally, *Odontomachus* and *Anochetus* form a clade, though their reciprocal monophyly is not yet certain. All other generic relationships within the *Odontomachus* group are unresolved.

The monophyly of both *Bothroponera* and *Mesoponera* is uncertain. We divide *Bothroponera* here into two groups: the *Bothroponera pumicosa* species group (*Bothroponera s.s.*) and the *Bothroponera sulcata* species group. The *B. sulcata* group was not sampled in the molecular phylogeny, and we have not been able to discern any synapomorphies linking it to *Bothroponera s.s.*, but we are retaining it within *Bothroponera* for now until its true phylogenetic position can be discerned. A monophyletic *Mesoponera* (as defined here) was not inferred in the molecular phylogeny, but could not be rejected. The *Mesoponera melanaria* species group (*Mesoponera s.s.*) and *Mesoponera ingesta* species group are not united by any definite synapomorphies, though they have many superficial similarities. These same character states have also evolved in other ponerine genera, however, reducing the strength of the characters as phylogenetic markers. We are retaining the *M. ingesta* group within *Mesoponera* until their relationships can be more definitively determined.

We tentatively include *Asphinctopone* in the *Odontomachus* genus group despite any strong morphological argument for doing so. The genus lacks the putative synapomorphies of both the *Plectroctena* and *Pachycondyla* groups, and is not obviously related to *Hypoconera*, *Harpegnathos*, or the *Ponera* group. The 28S phylogeny of Oullette *et al.* (2006) grouped *Asphinctopone* with *Anochetus*, but this relationship is not supported by any morphological synapomorphies. 28S is not a highly informative gene at these depths within Ponerinae, so this result should not be taken too seriously. Still, it is the best lead available at this time, so we are considering *Asphinctopone* as *incertae sedis* within the *Odontomachus* group for now. Its geographic range (the Afrotropics) is consistent with this placement, as the *Odontomachus* group appears to have witnessed the bulk of its diversification in Sub-Saharan Africa.

## ***Anochetus* Mayr**

Fig. 6

*Anochetus* Mayr, 1861: 53 (as genus in Ponerinae [Poneridae]). Type-species: *Odontomachus ghilianii* Spinola, 1851: 55; by monotypy.

*Stenomyrmex* Mayr, 1862: 711 (as genus in Formicidae, Odontomachidae). Type-species: *Myrmecia emarginata* Fabricius, 1804: 426; by subsequent designation of Wheeler, W.M., 1911: 173. Forel, 1887: 381; Brown, 1978: 552 (*Stenomyrmex* as junior synonym of *Anochetus*).

*Myrmapatetes* Wheeler, W.M., 1929: 6, 7 (as genus in Dolichoderinae). Type-species: *Myrmapatetes filicornis* Wheeler, W.M., 1929: 6; by original designation. Brown, 1953b: 2 (*Myrmapatetes* as junior synonym of *Anochetus*).

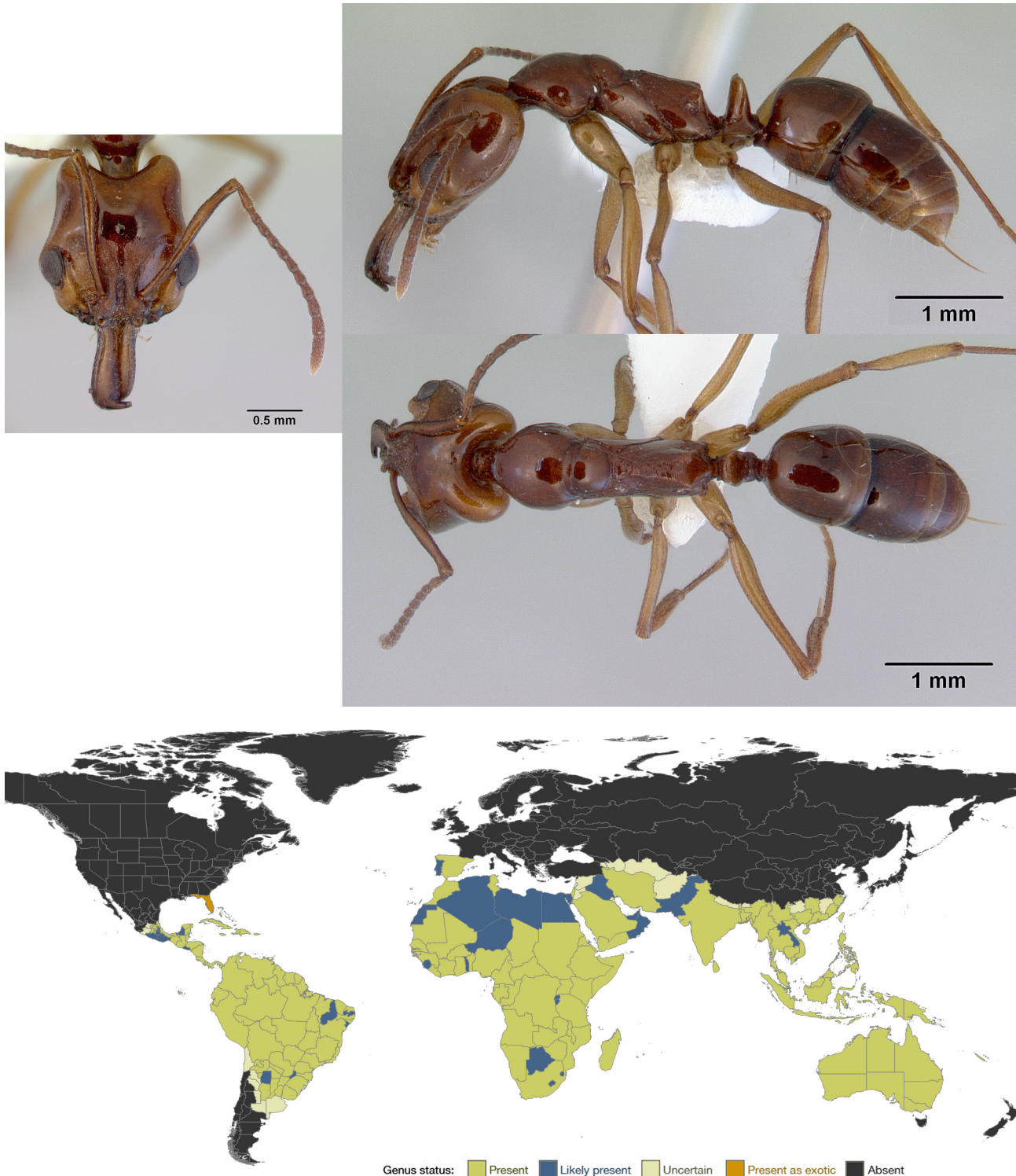
*Anochetus* is a large genus, with 95 described extant species and eight described fossil species. It is widespread and abundant in the tropical and subtropical regions of the world, with a few species extending into temperate regions. Like its sister genus *Odontomachus*, *Anochetus* is remarkable for its specialized trap mandibles and associated behaviors.

**Diagnosis.** Workers of *Anochetus* are so distinctive that they would be difficult to confuse with those of any other genus except *Odontomachus*, its sister genus. The unusual trap mandibles and head shape of *Anochetus* are synapomorphic with *Odontomachus*, but the genera are readily differentiated by examination of the rear of the head. In *Odontomachus* the nuchal carina is V-shaped medially, and the posterior surface of the head has a pair of dark converging apophyseal lines. In *Anochetus* the nuchal carina is continuously curved and the posterior surface of the head lacks visible apophyseal lines. These genera also tend to differ in size (*Anochetus* are generally smaller, though there is some overlap), propodeal teeth (absent in *Odontomachus* but usually present in *Anochetus*), and petiole shape (always coniform in *Odontomachus*, but variable in *Anochetus*).

**Synoptic description.** *Worker.* Small to medium (TL 3–12 mm; Brown, 1978) slender ants with the standard characters of Ponerini. Mandibles straight and narrow, articulating with the head medially, capable of being held open at 180°, and with a trio of apical teeth and often a row of smaller teeth along the masticatory margin. Head with a pair of long trigger setae below the mandibles. Clypeus truncate laterally and anteriorly. Frontal lobes small. Head strangely shaped: usually about as long as wide (sometimes longer than wide), with a gradual narrowing behind the eyes, the posterior margin of the head strongly concave, the nuchal carina continuously curved, and the posterior surface of the head without a pair of distinct apophyseal lines. Eyes small to moderate in size, located



anterior of head midline on temporal prominences. Mesopleuron rarely divided by a transverse groove. Metanotal groove shallow to deep. Propodeum weakly to strongly narrowed dorsally, the posterior margins often with a pair of short spines or teeth. Propodeal spiracles small and round. Metatibial spur formula (1p) or (1s, 1p). Petiole variable, usually squamiform but sometimes coniform or nodiform, the posterodorsal apex often with one or two spines of variable length and acuity. Girdling constriction between pre- and postsclerites of A4 usually not apparent. Pretergite of A4 usually without a stridulitrum. Head and body shiny, striate or rugoreticulate, with sparse to abundant pilosity and little to no pubescence. Color variable, testaceous to dark brown.



**FIGURE 6.** Worker caste of *Anochetus armstrongi*: lateral and dorsal view of body and full-face view of head (CASENT0172378, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Anochetus*.

*Queen.* Similar to worker but slightly larger, alate and with the other caste differences typical for ponerines (Brown, 1978). Ergatoid queens occur in many species; those of *A. kempfi* differ from conspecific workers by being smaller, with more differentiated thoracic sclerites and a larger gaster (Torres *et al.*, 2000).

*Male.* See descriptions in Brown (1978) and Yoshimura & Fisher (2007).

*Larva.* Larvae of various *Anochetus* species have been described by Wheeler & Wheeler (1952, 1964, 1971a, 1976).

**Geographic distribution.** Like its sister genus *Odontomachus*, *Anochetus* is widespread in the tropical and subtropical regions of the world. A few species encroach on temperate areas of South America, southern Africa, Europe (southern Spain), and Australia (reviewed in Brown, 1978).

**Ecology and behavior.** Despite their interesting mandibular structures and associated behaviors, relatively little is known about the habits of *Anochetus*. Brown (1976, 1978) reviewed what was known about *Anochetus* at the time. Torres *et al.* (2000) performed the most detailed study of the ecology and behavior of a single *Anochetus* species (*A. kempfi*), though the applicability of these observations to other species is uncertain. The lack of information on *Anochetus* likely stems from the fact that its sister genus, *Odontomachus*, is more conspicuous and more easily studied. *Anochetus* are generally smaller than *Odontomachus* (TL 3–12 mm versus TL 6–20 mm). Colonies of *Anochetus* also tend to be smaller, typically containing fewer than 100 workers versus several hundred for *Odontomachus* (Brown, 1976, 1978), though colonies of *A. faurei* were found to have about 400 workers (Villet *et al.*, 1991). *Anochetus* also tend to nest and forage more cryptically than the epigeic *Odontomachus*; when they do forage above ground, *Anochetus* are more likely to be nocturnal than are *Odontomachus* (Brown, 1978). *Anochetus* typically nest in tight places such as in rotten twigs, under bark, or in small spaces in the soil (Wilson, 1959b; Brown, 1976, 1978; Lattke, 1986), some are apparently arboreal (Brown, 1976, 1978), and some nest in termitaries (Wheeler, 1936; Déjean *et al.*, 1996, 1997). *Anochetus* often feign death when disturbed, unlike *Odontomachus*, which tend to attack and sting intruders (Brown, 1978).

Like *Odontomachus*, *Anochetus* use their trap-jaws to catch insect prey and can also use their mandibles to bounce themselves away from danger (Brown, 1978). The structure and neurobiology of the *Anochetus* trap-jaw mechanism were studied by Gronenberg & Ehmer (1996). The hunting strategy used by *Anochetus* tends to be more like that of some dacetines than that of *Odontomachus*, in that they are slower (Gronenberg & Ehmer, 1996) and more liable to ambush prey than to actively seek them out (Brown, 1978; Schatz *et al.*, 1999). Mandibular strikes on prey are followed by a paralyzing sting (Schatz *et al.*, 1999). The prey preferences of most *Anochetus* are unknown, though many appear to be specialist predators of termites (*e.g.*, *A. traegordhi*; Schatz *et al.*, 1999).

Very little is known about the social and reproductive behavior of *Anochetus*. Ergatoid queens are apparently common, and some species (such as members of the *A. inermis* group; Brown, 1978) have both ergatoid and alate queens, while others may have only ergatoids (*e.g.*, *A. kempfi* and an unidentified species from Indonesia; Torres *et al.*, 2000; Gobin *et al.*, 2006). Workers of *A. faurei*, *A. bequaerti*, and *A. katonae* were found to lack ovarioles, which is fairly unusual among ponerines (Villet *et al.*, 1991). Torres *et al.* (2000) observed a novel behavior in *A. kempfi*, in which nursery workers hold unhatched eggs in their mandibles until they hatch, and never allow them to be set down on the substrate of the nest. Another interesting behavior in this species involves the execution of excess queens by the workers of a colony. *A. emarginatus* appears to reproduce via gamergates (C. Starr, pers. comm.).

The chemical ecology of *Anochetus* has received little attention, though *A. grandidieri* (Madagascar) was reported to be a source of toxic alkaloids in poison frogs (Clark *et al.*, 2005).

**Phylogenetic and taxonomic considerations.** *Anochetus* was erected by Mayr (1861) to house the species *Odontomachus ghilianii* Spinola. Like *Odontomachus*, *Anochetus* has had a stable taxonomic history at the genus level. Though Brown (1973) provisionally synonymized *Anochetus* under *Odontomachus*, he reversed himself (1976) after discovering the consistent differences in head structure between the two groups. *Anochetus* itself has two junior synonyms, *Stenomymex* (often treated as a subgenus of *Anochetus*; Mayr, 1862) and *Myrmapatetes* (Wheeler, 1929). Like *Odontomachus*, the history of family-level taxonomy for *Anochetus* has been complex (see discussion under *Odontomachus*). Schmidt's (2013) molecular phylogeny of Ponerinae confirms that *Anochetus* is a member of tribe Ponerini and that its sister group is *Odontomachus*. It is possible that *Anochetus* may not be mutually monophyletic with *Odontomachus* (see discussion under that genus), but we are retaining *Anochetus* as a distinct genus for now. This is consistent with the treatment by Santos *et al.* (2010), who could find no evidence that both are not monophyletic.

## Species of *Anochetus*

Brown (1978) revised the species-level taxonomy of *Anochetus*, and his keys are still the most complete for the genus despite being slightly outdated; the Malagasy species have recently been examined by Fisher & Smith (2008) while the Australia species were revised by Shattuck & Slipinska (2012).

- A. africanus* (Mayr, 1865): Ghana
- A. agilis* Emery, 1901: Borneo
- A. alae* Shattuck & Slipinska, 2012: Australia
- A. altisquamis* Mayr, 1887: Brazil
- A. angolensis* Brown, 1978: Angola
- A. armstrongi* McAreavey, 1949: Australia
- A. avius* Shattuck & Slipinska, 2012: Australia
- A. bequaerti* Forel, 1913: DRC
- A. bispinosus* (Smith, F., 1858): Brazil
- A. boltoni* Fisher, 2008: Madagascar
- A. brevis* Brown, 1978: Philippines
- A. bytinskii* Kugler & Ionescu, 2007: Israel
- A. cato* Forel, 1901: New Britain
- A. chirichinii* Emery, 1897: New Guinea
- A. chocoensis* Zabala, 2008: Colombia
- A. consultans* (Walker, 1859): Sri Lanka
- A. diegensis* Forel, 1912: Colombia
- A. elegans* Lattke, 1987: Colombia
- A. emarginatus* (Fabricius, 1804): Central America
- A. evansi* Crawley, 1922: Iran
- A. faurei* Arnold, 1948: South Africa
- A. filicornis* (Wheeler, W.M., 1929): New Guinea
- A. fricatus* Wilson, 1959: New Guinea
- A. fuliginosus* Arnold, 1948: South Africa
- A. ghilianii* (Spinola, 1851): Morocco
- A. gladiator* (Mayr, 1862): Indonesia (Misool Island)
- A. goodmani* Fisher, 2008: Madagascar
- A. graeffei* Mayr, 1870: Samoa
- A. grandidieri* Forel, 1891: Madagascar
- A. haytianus* Wheeler, W.M. & Mann, 1914: Haiti
- A. hohenbergiae* Feitosa & Delabie, 2012: Brazil
- A. horridus* Kempf, 1964: Brazil
- A. inca* Wheeler, W.M., 1925: Peru
- A. incultus* Brown, 1978: Philippines
- A. inermis* André, 1889: Trinidad
- A. isolatus* Mann, 1919: Solomon Islands
- A. jonesi* Arnold, 1926: South Africa
- A. kanariensis* Forel, 1900: India
- A. katonae* Forel, 1907: Tanzania
- A. kempfi* Brown, 1978: Puerto Rico
- A. levaillanti* Emery, 1895: South Africa
- A. longifossatus* Mayr, 1897: Sri Lanka
- A. longispinus* Wheeler, W.M., 1936: Haiti
- A. madagascarensis* Forel, 1887: Madagascar
- A. madaraszi* Mayr, 1897: Sri Lanka
- A. maynei* Forel, 1913: DRC
- A. mayri* Emery, 1884: Antilles Islands



*A. micans* Brown, 1978: Costa Rica  
*A. minans* Mann, 1922: Honduras  
*A. miserabilis* González-Campero & Elizalde, 2008: Argentina  
*A. mixtus* Radchenko, 1993: Vietnam  
*A. modicus* Brown, 1978: Borneo  
*A. muzzioli* Menozzi, 1932: Indonesia (Sumatra)  
*A. myops* Emery, 1893: West Malaysia  
*A. natalensis* Arnold, 1926: South Africa  
*A. neglectus* Emery, 1894: Brazil  
*A. nietneri* (Roger, 1861): Sri Lanka  
*A. obscuratus* Santschi, 1911: Tanzania  
*A. obscurior* Brown, 1978: India  
*A. orchidicola* Brown, 1978: Mexico  
*A. oriens* Kempf, 1964: Brazil  
*A. orientalis* André, 1887: Vietnam  
*A. pangens* (Walker, 1859): Sri Lanka  
*A. paripungens* Brown, 1978: Australia  
*A. pattersoni* Fisher, 2008: Seychelles  
*A. pellucidus* Emery, 1902: Cameroon  
*A. peracer* Brown, 1978: New Guinea  
*A. princeps* Emery, 1884: Java  
*A. pubescens* Brown, 1978: Zimbabwe  
*A. punctaticeps* Mayr, 1901: South Africa  
*A. pupulatus* Brown, 1978: India  
*A. rectangularis* Mayr, 1876: Australia  
*A. renatae* Shattuck & Slipinska, 2012: Australia  
*A. risii* Forel, 1900: Hong Kong  
*A. rothschildi* Forel, 1907: Somalia  
*A. rufolatus* Shattuck & Slipinska, 2012: Australia  
*A. rufostenus* Shattuck & Slipinska, 2012: Australia  
*A. rufus* (Jerdon, 1851): India  
*A. rugosus* (Smith, F., 1857): Singapore  
*A. sedilloti* Emery, 1884: Tunisia  
*A. seminiger* Donisthorpe, 1943: New Guinea  
*A. shohki* Terayama, 1996: Japan  
*A. simoni* Emery, 1890: Venezuela  
*A. siphneus* Brown, 1978: Ivory Coast  
*A. splendidulus* Yasumatsu, 1940: Caroline Islands  
*A. striatulus* Emery, 1890: Costa Rica  
*A. strigatellus* Brown, 1978: West Malaysia  
*A. subcoecus* Forel, 1912: Taiwan  
*A. taiwaniensis* Terayama, 1989: Taiwan  
*A. talpa* Forel, 1901: South Africa  
*A. targionii* Emery, 1894: Bolivia  
*A. testaceus* Forel, 1893: Antilles Islands  
*A. traegaordhi* Mayr, 1904: Sudan  
*A. tua* Brown, 1978: West Malaysia  
*A. turneri* Forel, 1900: Australia  
*A. vallensis* Lattke, 1987: Colombia  
*A. variegatus* Donisthorpe, 1938: New Guinea  
*A. veronicae* Shattuck & Slipinska, 2012: Australia  
*A. vexator* Kempf, 1964: Brazil

*A. wiesiae* Shattuck & Slipinska, 2012: Australia

*A. yerburyi* Forel, 1900: Sri Lanka

*A. yunnanensis* Wang, 1993: China

#### Fossil species

† *A. ambiguus* De Andrade, 1994: Dominican Amber

† *A. brevidentatus* MacKay, 1991: Dominican Amber

† *A. conisquamis* De Andrade, 1994: Dominican Amber

† *A. corayi* Baroni Urbani, 1980: Dominican Amber

† *A. dubius* De Andrade, 1994: Dominican Amber

† *A. exstinctus* De Andrade, 1994: Dominican Amber

† *A. intermedius* De Andrade, 1994: Dominican Amber

† *A. lucidus* De Andrade, 1994: Dominican Amber

### *Asphinctopone* Santschi

Fig. 7

*Asphinctopone* Santschi, 1914: 318 (as genus). Type-species: *Asphinctopone silvestrii* Santschi, 1914: 318; by monotypy.

*Lepidopone* Bernard, 1953: 207 (in Ponerinae, Ponerini). Type-species: *Lepidopone lamottei* Bernard, 1953: 208 (junior synonym of *Asphinctopone silvestrii* Santschi, 1914); by monotypy. Brown, 1953b: 2 (*Lepidopone* as junior synonym of *Asphinctopone*).

*Asphinctopone* is a small genus (three described species) restricted to tropical Africa. Nothing is known about its habits.

**Diagnosis.** *Asphinctopone* is morphologically distinctive and unlikely to be confused with any other genus. Important diagnostic apomorphies of the genus include the complex clypeus (see description below), the long apical antennomere, the strongly impressed metanotal groove, the divided mesopleuron, and the lack of differentiated presclerites in A4. Additional apomorphies of *Asphinctopone* include characters of the subpetiolar process and the helcium (described in detail by Bolton & Fisher, 2008a). The presence of a small process on the basal mandibular margin and strongly impressed promesonotal suture, previously thought to be apomorphies, do not occur in all known species and are therefore not of use in diagnosing this genus (Hawkes, 2010). Superficially, workers of *Asphinctopone* perhaps most resemble small *Brachyponera*, due to their similarly impressed metanotal grooves, strongly narrowed propodeal dorsa, round or ovoid propodeal spiracles, squamiform petioles, and absent or weak gastral constriction. These genera strongly differ in many characters, however, including those of the mandibles (triangular and with a basal pit in *Brachyponera*, subtriangular and with a unique process on the basal margin in *Asphinctopone*) and clypeus (broadly convex in *Brachyponera*, complex in *Asphinctopone*), their metatibial spur count (two in *Brachyponera*, one in *Asphinctopone*), and many other characters.

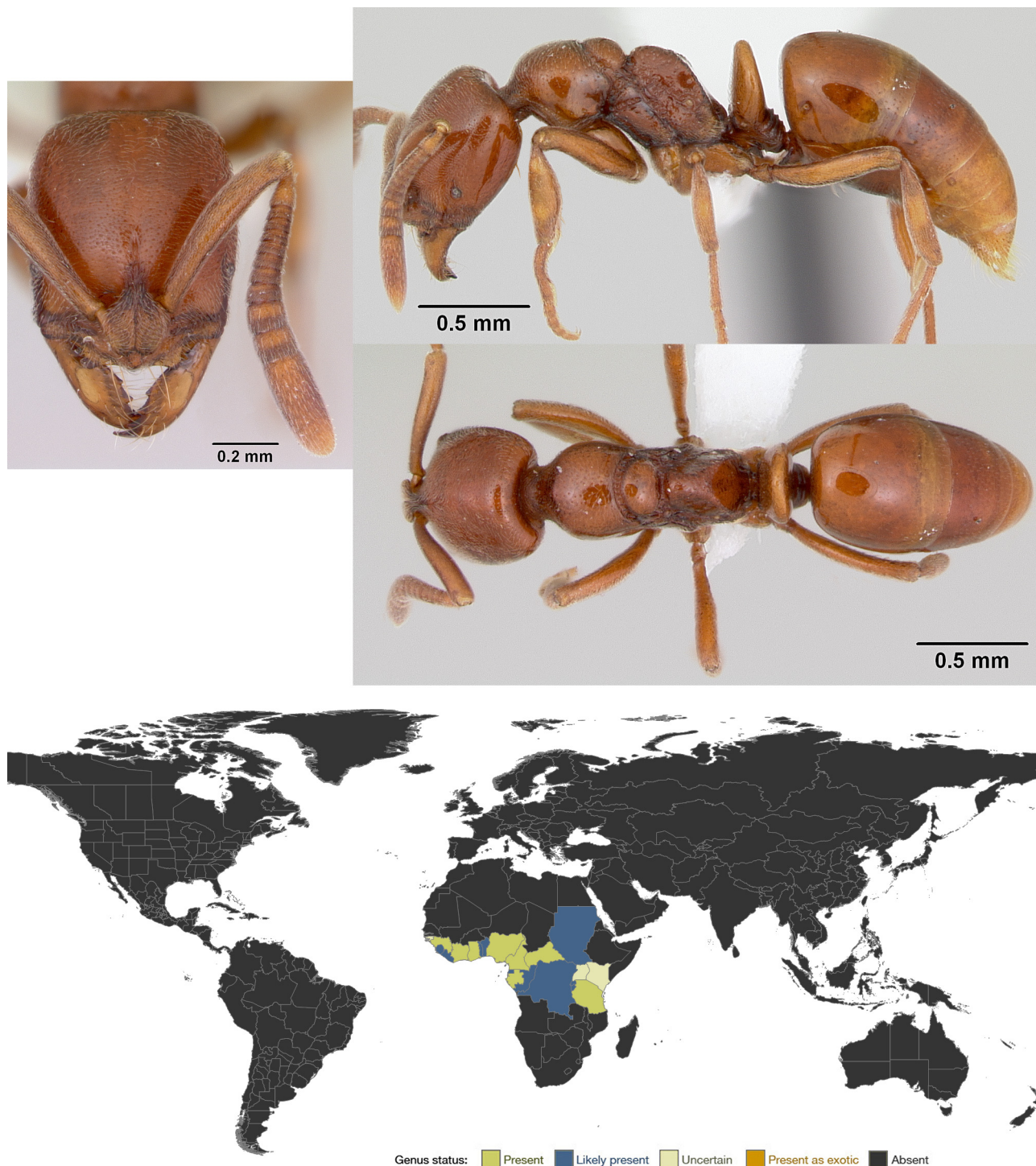
**Synoptic description.** *Worker.* Small (TL 3.3–3.7 mm) ants with the standard characters of Ponerini. Mandibles subtriangular, with five teeth, a small process on the basal margin near the mandibular articulation present in some species, and a faint basal groove. Clypeus projecting anteriorly, with a small rounded lobe medially, on either side of which is a shallow concavity and then an angular projection. Frontal lobes closely approximated and of moderate size. Antennae with the three or four apical antennomeres forming a weak club, the apical antennomere longer than the preceding five (or four) segments combined. Eyes small, located anterior of head midline. Promesonotal suture sometimes relatively deeply impressed, the metanotal groove always deeply impressed. Mesopleuron divided by a transverse groove. Propodeal dorsum strongly narrowed and relatively short, the posterior face relatively long. Propodeal spiracles ovoid. Metatibial spur formula (1p). Petiole squamiform, the scale thin in side view but broad in dorsal view. A4 without differentiated presclerites, and hence the gaster without a girdling constriction. Head and body shiny to very sparsely punctate, with sparse pilosity and pubescence. Color orange to reddish brown. See description by Bolton & Fisher (2008a) and Hawkes (2010) for further details and for discussion of additional important characters, such as those of the helcium and subpetiolar process.

*Queen.* Similar to worker but slightly larger, winged, with ocelli and larger eyes, and with the other characters typical of winged ponerine queens (Bolton & Fisher, 2008a).

*Male.* Unknown.

*Larva.* Not described.

**Geographic distribution.** *Asphinctopone* is rarely collected and seems to be at low density where it occurs, but is widespread in central and western Africa with a single species known from eastern Africa, having been collected in the Ivory Coast, Nigeria, Cameroon, the Central African Republic, Ghana, Guinea, Gabon and Tanzania (Bolton & Fisher, 2008a; Hawkes, 2010).



**FIGURE 7.** Worker caste of *Asphinctopone silvestrii*: lateral and dorsal view of body and full-face view of head (CASENT0006811, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Asphinctopone*.

**Ecology and behavior.** Nothing definite is known about the habits of *Asphinctopone*. Specimens have been collected in leaf litter, soil, rotting wood, and an abandoned termitary (Déjean *et al.*, 2006; Bolton & Fisher, 2008a)



while one worker was collected during the evening (Hawkes, 2010). The presence of *Asphinctopone* workers in these microhabitats, along with their reduced eyes, implies a cryptobiotic existence. Bolton & Fisher (2008a) suggest that the derived mandibular structure of the genus is indicative of prey specialization, though its feeding habits remain unknown.

**Phylogenetic and taxonomic considerations.** Santschi (1914) described *Asphinctopone* as a monotypic genus to hold his new species *A. silvestrii*. Bernard (1953) later erected the genus *Lepidopone* for his new species *L. lamottei*. Bernard differentiated his new genus from the obviously closely related *Asphinctopone* by supposed differences of the coxae, petiole and gaster. Brown (1953c) concluded that the justification for separating *Lepidopone* from *Asphinctopone* was weak, and synonymized them. Bolton & Fisher (2008a) revised the species-level taxonomy of *Asphinctopone*.

Schmidt (2013) was unable to include *Asphinctopone* in his phylogeny of Ponerinae, and the morphological traits of the genus give only a few clues to its phylogenetic position. Ouellette *et al.* (2006) included an unidentified *Asphinctopone* species in their 28S phylogeny of the poneroid subfamilies, and found weak support for a close relationship between *Asphinctopone* and *Odontomachus* or *Anochetus*, suggesting membership of *Asphinctopone* in the *Odontomachus* Genus Group. Morphological evidence does not give a strong indication of the phylogenetic relationships of *Asphinctopone*, though after considering the various possibilities we conclude that *Asphinctopone* most likely is a member of the *Odontomachus* Group, as suggested by Ouellette *et al.*'s (2006) molecular results. Bolton & Fisher (2008a) found similarities in the structure of the petiolar sternite and helcium in *Asphinctopone*, *Phrynonopone*, and *Brachyponera*, though they argued against these similarities representing synapomorphies of all three genera or any given pair of them. Still, the possibility cannot be rejected, especially given other superficial similarities between *Asphinctopone* and both *Phrynonopone* and *Brachyponera*.

The presence of only a single metatibial spur in *Asphinctopone* would be unusual among *Odontomachus* group genera, but some species of *Anochetus* have a similar reduction in spur count. Spur count is roughly correlated with body size, so the loss of the second spur in *Asphinctopone* could be the result of a reduction in body size, and would not exclude its placement in the *Odontomachus* group. Other morphological arguments for a placement in the *Odontomachus* group include the unconstricted gaster (present to a less extreme degree in most members of the group), the impressed metanotal groove (more commonly impressed in the *Odontomachus* group than in other genus groups), and the relatively large frontal lobes, which would argue against a placement in the *Ponera* group, nearly all of which have very small frontal lobes. A placement of *Asphinctopone* within the *Plectroctena* group is unlikely, given its posteriorly-opening metapleural gland orifice, impressed metanotal groove, and narrowed propodeal dorsum. The possibility of a close relationship between *Asphinctopone* and *Hypoconopone* cannot be rejected, but is not supported by any particular putative synapomorphy. Finally, the biogeography of *Asphinctopone* (restricted to central and western Africa) lends credibility to a placement in either the *Plectroctena* or *Odontomachus* groups, which are apparently Afrotropical in origin. Weighing all the evidence, we find it most likely that *Asphinctopone* is simply an unusually small member of the *Odontomachus* group, and we therefore tentatively include it there.

### Species of *Asphinctopone*

For synonyms see Bolton & Fisher (2008a) and for key to species see Hawkes (2010).

*A. differens* Bolton & Fisher, 2008: Central African Republic

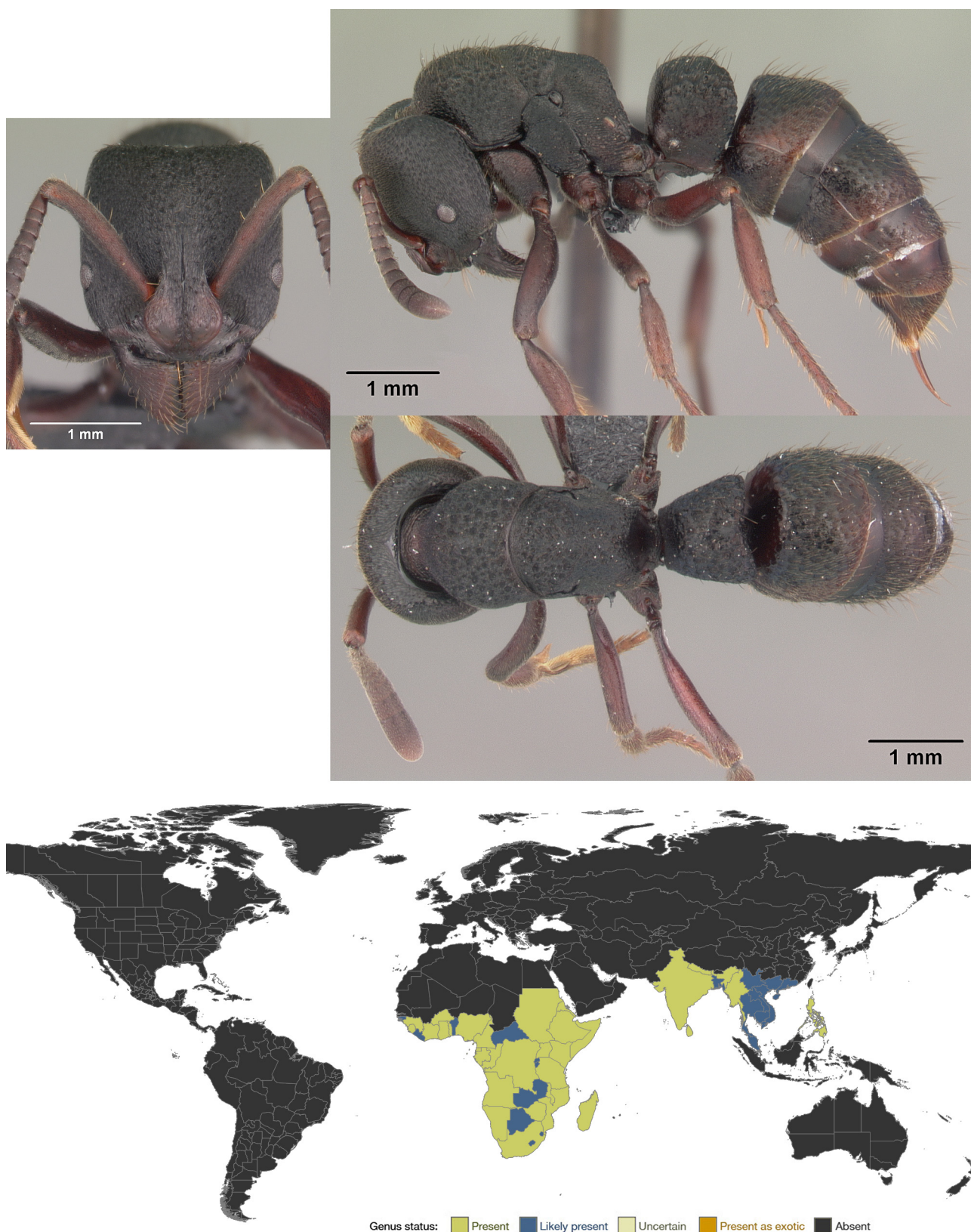
*A. pilosa* Hawkes, 2010: Tanzania

*A. silvestrii* Santschi, 1914: Nigeria

### *Bothroponera* Mayr

Fig. 8

*Bothroponera* Mayr, 1862: 713, 717 (as genus in Ponerinae [Poneridae]). Type-species: *Ponera pumicosa* Roger, 1860: 290; by subsequent designation of Emery, 1901: 42. **Gen. rev.**



**FIGURE 8.** Worker caste of *Bothroponera cambouei*: lateral and dorsal view of body and full-face view of head (CASENT0034474, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Bothroponera*.

*Bothroponera* is a moderately large genus, with 53 described species and subspecies. The sister group of *Bothroponera* is unresolved, and the genus may be non-monophyletic as defined here. *Bothroponera* (*sensu stricto*)

is restricted to Africa and Madagascar, while the *B. sulcata* species group ranges from Africa to the Philippines. Relatively little is known about *Bothroponera* ecology and behavior.

**Diagnosis.** *Bothroponera* workers lack any obvious autapomorphies within the Ponerinae, and are therefore more difficult to diagnose than those of most ponerine genera. They can generally be distinguished by the following combination of characters: Body without a long dense golden pilosity, mesopleuron usually not divided by a transverse groove, metanotal groove obsolete, propodeal dorsum without spines or teeth, propodeal spiracles slit-shaped, petiole nodiform (and not semicircular in top view) and without posterodorsal spines or teeth, tergite of A3 without strong longitudinal striations, gaster with a strong constriction between A3 and A4, and metatibiae with two spurs. Species of *Bothroponera* (s.s.) also have strong sculpturing, large cordate frontal lobes, a broad propodeal dorsum, and a U-shaped cuticular lip posterior to the metapleural gland orifice, though members of the *B. sulcata* group lack these characters. Superficially, *Bothroponera* workers most closely resemble those of *Phrynoponera* and *Pseudoneoponera*, but they lack the bispinose propodeum, five-spined petiole, and unconstricted gaster of *Phrynoponera* and the shaggy pilosity, semicircular petiole, and longitudinally striate tergite A3 of *Pseudoneoponera*. *Bothroponera* can also be confused with *Ectomomyrmex*, though *Bothroponera* lacks the small eyes, angular sides of the head, divided mesopleuron (except in a few species), and weakly constricted gaster of *Ectomomyrmex*, and Asian *Bothroponera* species lack the strong sculpturing of *Ectomomyrmex*. The workers of *Bothroponera* (s.s.) also somewhat resemble the workers of *Loboponera* and *Boloponera*, given their stocky build, coarse sculpturing, large frontal lobes, obsolete mesopropodeal suture, broad propodeal dorsum, and nodiform petioles, but are readily separated from these genera by their metatibial spur formulae (two spurs versus one), propodeal spiracles (slit-shaped versus round), and metapleural gland orifice (opening posterolaterally versus laterally), among other characters.

**Synoptic description.** *Worker.* Medium to large (TL 5.5–16 mm) slender to robust ants with the standard characters of Ponerini. Mandibles triangular, usually with a faint basal groove. Frontal lobes either moderately large (*B. sulcata* group) or very large and cordate (*Bothroponera* s.s.). Eyes of moderate size and placed anterior of head midline. Mesopleuron usually not divided by a transverse groove. Metanotal groove obsolete dorsally. Propodeum broad dorsally. Propodeal spiracles slit-shaped. Distinct pale glandular patch on posterior surface of metatibia, close to spur, present (*B. sulcata* group) or absent (*Bothroponera* s.s.). Metatibial spur formula (1s, 1p). Petiole nodiform, widening posteriorly in dorsal view, with vertical anterior and posterior faces. Girdling constriction between pre- and postsclerites of A4 apparent. Stridulitrum either present (*Bothroponera* s.s.) or absent (*B. sulcata* group) on pretergite of A4. Head and body either coarsely sculptured with abundant pilosity and moderate pubescence (most *Bothroponera* s.s.; *B. laevissima* is shiny, with only weak sculpturing and sparse pilosity) or finely punctate with scattered pilosity and dense pubescence (*B. sulcata* group). Color dark brown to black.

*Queen.* Similar to the worker but slightly larger, winged and with ocelli (Wheeler, 1922b). Queens are absent in *B. kruegeri*, in which reproduction is performed by gamergate workers.

*Male.* See description in Wheeler (1922b).

*Larva.* Described by Wheeler & Wheeler (1952, 1971b, 1976).

**Geographic distribution.** *Bothroponera* (sensu stricto) is restricted to Sub-Saharan Africa and Madagascar, while the *B. sulcata* group occurs from Sub-Saharan Africa through southern Asia to the Philippines. References in the literature to Australian “*Bothroponera*” species (and many Asian species as well) are actually references to *Pseudoneoponera*, which we are reviving as a distinct genus.

**Ecology and behavior.** Relatively little is known about *Bothroponera*, and all studies of the ecology and behavior of these ants have focused on species in the *B. sulcata* group, so even less is known about the habits of *Bothroponera* (s.s.), with most information coming from anecdotal observations. *B. mlanjiensis* is reported to dwell in shady forest habitats and to nest in the ground (Arnold, 1946), collection data for several other species indicates that they also nest in the ground and are often collected in leaf litter, and *B. pachyderma* has been found nesting inside abandoned termitaries (Déjean *et al.*, 1996), but otherwise ecological notes on *Bothroponera* (s.s.) are sorely lacking. At least some species feign death when disturbed (e.g., *B. pachyderma*; Wheeler, 1922b). *B. pachyderma* is reported to be a generalist predator (Déjean *et al.*, 1999), but the prey preferences of other species are unknown. Some larger species, such as *B. pachyderma*, stridulate audibly when distressed (B. Bolton, pers. comm.).

Perhaps the best studied species of *Bothroponera* is *B. tesseronoda*, a South Asian member of the *B. sulcata* group. This species forms subterranean nests, with from 50 to 170 workers per colony (Jessen & Maschwitz, 1986).



*B. tesseronoda* is apparently a generalist predator of arthropods, with termites making up a large portion of its diet (Shivashankar *et al.*, 1995), though it is also known to visit extrafloral nectaries (Agarwal & Rastogi, 2008). Workers recruit nestmates to food sources and new nest sites via tandem running, which is initiated by mechanical stimulation and a colony-specific chemical trail derived from the entire body surface (Maschwitz & Mühlenberg, 1973; Maschwitz *et al.*, 1974; Jessen & Maschwitz, 1985 and 1986; Maschwitz & Steghaus-Kovac, 1991). Nest entrances are marked with a colony-specific chemical cue, and foraging workers also employ chemical signaling while scouting a new area for food. Remarkably, individual workers can identify their own trails and show a preference for them over that of other individuals (Jessen & Maschwitz, 1986). Alarm pheromones and defensive secretions are produced in the mandibular glands, poison gland, and Dufour's gland (Maschwitz *et al.*, 1974).

An African species in the *B. sulcata* group, *B. crassa*, also uses tandem running for nestmate recruitment (Hölldobler & Wilson, 1990). Workers of another African member of the *B. sulcata* group, *B. soror*, use tandem running to recruit nestmates to large prey items or to groups of prey, but are also capable of recruiting nestmates from up to 150 mm away using a multicomponent mandibular gland secretion (Longhurst *et al.*, 1980; Déjean, 1991). Arnold (1915) reports that workers of *B. soror* smell strongly like cockroaches; the mandibular gland secretions are possibly responsible for this. *B. soror* is a generalist predator of arthropods and a scavenger (Longhurst *et al.*, 1980; Déjean *et al.*, 1999). Déjean (1991) describes some behavioral adaptations of *B. soror* to termite predation, and Orivel & Déjean (2001) measured the toxicity of *B. soror* venom. Nests are typically located under stones or in termitaries (Déjean *et al.*, 1996, 1997), and colonies are small with about two dozen workers (Arnold, 1915). Haskins (1941) found that *B. soror* queens display semi-claustral nest founding during which they forage outside the nest but also metabolize their flight muscles, and that they prefer to build nests in soil around rotting logs and even in the logs. Ground nesting is probably the rule for *Bothroponera*, though *B. silvestrii* has also been reported nesting in rotting wood (Taylor, 2008). Queenless but apparently self-sustaining populations of *B. soror* have been observed (Longhurst, 1977; Villet & Wildman, 1991).

An unusual member of the *B. sulcata* group is the South African species *B. kruegeri*, which has lost the queen caste and reproduces only via gamergate workers (Peeters & Crewe, 1986b). Colonies each have only a single gamergate, which is the only inseminated individual in the colony and the only individual with mature ovaries. Gamergates suppress the ovarian development of the other workers. This is apparently accomplished through chemical means, as no physical interactions between gamergates and non-gamergates have been observed (Wildman & Crewe, 1988; Villet & Wildman, 1991). Villet & Wildman (1991) examined division of labor in this species. In the population studied by Wildman & Crewe (1988), colony size ranged from 8 to 100 workers (mean = 43). This species is a generalized predator of arthropods (Wildman & Crewe, 1988) and nests in the ground (Villet & Wildman, 1991).

Discussions in the literature of foamy defensive secretions from the sting apparatus of *Bothroponera* (e.g., Wheeler, 1922b) apparently all refer to species of *Pseudoneoponera*, which we consider a distinct genus. True *Bothroponera* presumably lack these unusual secretions, though data are lacking either way.

**Phylogenetic and taxonomic considerations.** *Bothroponera* was erected by Mayr (1862) to house the single species *Ponera pumicosa* Roger. Emery (1895d) treated it as a subgenus of *Ponera*, and later (Emery, 1901) as a subgenus of *Pachycondyla*. Bingham (1903) revived *Bothroponera* to genus status, and subsequent authors variously treated it as a distinct genus or as a subgenus of *Pachycondyla*. Most authors since Hölldobler & Wilson (1990) have taken the latter approach (but see Tiwari, 1999). Wilson (1958c) placed *Pseudoneoponera* as a junior synonym of *Bothroponera*. The type species of *Phrynoponera*, *Ph. gabonensis*, was originally placed in *Bothroponera* but was moved to a separate genus by Wheeler (1920).

Recently Joma & Mackay (2013) removed *Bothroponera* from synonymy with *Pachycondyla*, treating it as a valid genus. However, little justification was provided and they included species we consider as belonging to *Bothroponera*, *Ectomomyrmex*, *Pseudoneoponera* and *Ophthalmopone*. Additionally, only about half of the species we place in *Bothroponera* were transferred, the remainder being placed in *Pachycondyla*. While we agree that *Bothroponera* should be given full genus status, our broader analysis of the subfamily Ponerinae suggests that the previous concept of the genus, that which included *Pseudoneoponera* as a junior synonym as well as various species placed at one time or another in the genera, should be modified. We are restricting *Bothroponera* to a subset of the species previously considered as belonging to the genus.

Our concept of *Bothroponera* is based on both morphological and molecular evidence. Morphologically, *Bothroponera* (*s.s.*) most closely resembles *Phrynoponera* and *Pseudoneoponera*, as they all generally have robust

builds, strong sculpturing, and obsolete metanotal grooves. These characters have evolved on multiple occasions in other ponerine genera, however, and are therefore unlikely to be good phylogenetic markers. In addition, the *B. sulcata* species group of *Bothroponera* lacks the robust build and strong sculpturing (but see below).

Schmidt's (2013) molecular phylogeny of the Ponerinae places *Bothroponera* with strong support within the *Odontomachus* group. Members of *Bothroponera* (s.s.) have a U-shaped cuticular lip at the posterior edge of the metapleural gland orifice, which is a possible synapomorphy of the *Pachycondyla* group but was apparently independently derived in *Bothroponera* (and also maybe in *Diacamma*). The sister group of *Bothroponera* is unresolved, but it is not closely related to *Pachycondyla*. Though a sister group relationship with either *Phrynoponera* or *Pseudoneoponera* cannot be statistically rejected, we consider *Bothroponera*, *Phrynoponera* and *Pseudoneoponera* to be separate genera, given their morphological distinctiveness and phylogenetic age consistent with that of other ponerine genera.

Emery (1911) divided the species of *Bothroponera* into four groups: the *B. pumicosa*, *B. rufipes-piliventris*, *B. sulcata*, and *B. perroti* groups. The *B. rufipes-piliventris* group is actually the genus *Pseudoneoponera*. Schmidt's (2013) molecular phylogeny indicates that the *B. perroti* group is simply a Malagasy clade nestled within a non-monophyletic African *B. pumicosa* group. This group is *Bothroponera* (sensu stricto), as it includes the type species of the genus, *B. pumicosa*. Emery's *B. sulcata* group is problematic, as there is no obvious morphological synapomorphy linking it to *Bothroponera* (s.s.), and molecular data are lacking for this group. The *B. sulcata* group may form a monophyletic sister clade, or even paraphyletic basal grade, with respect to *Bothroponera* (s.s.), or it may represent an entirely independent lineage. For now we are choosing to be conservative by retaining the *B. sulcata* group species within *Bothroponera*, with the explicit caveat that it may actually be a distinct lineage requiring a new genus name.

### Species of *Bothroponera*

For keys to African *Bothroponera* species see Wheeler (1922b) or Arnold (1952; South African species only) and for Malagasy species see Rakotonirina & Fisher (2013).

*Bothroponera* (sensu stricto: *B. pumicosa* group)

*B. cambouei* Forel, 1891: Madagascar

*B. cariosa* Emery, 1895: Mozambique

*B. cavernosa* (Roger, 1860): South Africa

*B. cavernosa montivaga* Arnold, 1947: South Africa

*B. comorensis* (André, 1887): Madagascar

*B. cribrata* (Santschi, 1910): Congo (**comb. rev.**)

*B. fugax* (Forel, 1907): Tanzania (**comb. rev.**)

*B. granosa* (Roger, 1860): South Africa

*B. laevissima* (Arnold, 1915): South Africa

*B. laevissima aspera* Arnold, 1962: South Africa

*B. masoala* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*B. mlanjiensis* Arnold, 1946: Malawi (**comb. rev.**)

*B. pachyderma* (Emery, 1901): Cameroon (**comb. rev.**)

*B. pachyderma attenata* (Santschi, 1920): DRC (**comb. nov.**)

*B. pachyderma funerea* Wheeler, W.M. 1922: DRC (**comb. rev.**)

*B. pachyderma postsquamosa* (Santschi, 1920): Congo (**comb. nov.**)

*B. perroti* Forel, 1891: Madagascar

*B. planicornis* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*B. pumicosa* (Roger, 1860): South Africa

*B. pumicosa sculpturata* (Santschi, 1912b): Zimbabwe (**comb. nov.**)

*B. rubescens* Santschi, 1937: DRC (**comb. rev.**)

*B. sanguinea* (Santschi, 1920): DRC (**comb. rev.**)

*B. strigulosa* Emery, 1895: South Africa

*B. talpa* André, 1890: Sierra Leone (**comb. rev.**)

*B. talpa variolata* (Santschi, 1912): Congo (**comb. nov.**)  
*B. tavaratra* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*B. umgodikulula* Joma and Mackay, 2013: South Africa  
*B. variolosa* Arnold, 1947: South Africa  
*B. wasmannii* Forel, 1887: Madagascar  
*B. vazimba* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*Bothroponera* (*incertae sedis*: *B. sulcata* group)

*B. crassa* (Emery, 1877): Ethiopia (**comb. rev.**)  
*B. crassa crassior* Santschi, 1930: Kenya (**comb. rev.**)  
*B. crassa ilgii* (Forel, 1910): Ethiopia (**comb. nov.**)  
*B. glabripes* Emery, 1893: Philippines  
*B. henryi* (Donisthorpe, 1942): India  
*B. kenyensis* Santschi, 1937: Kenya (**comb. rev.**)  
*B. kruegeri* (Forel, 1910): South Africa  
*B. kruegeri asina* (Santschi, 1912): Kenya (**comb. rev.**)  
*B. kruegeri rhodesiana* (Forel, 1913): Zimbabwe (**comb. rev.**)  
*B. lamottei* Bernard, 1953: Guinea (**comb. rev.**)  
*B. picardi* (Forel, 1901): Angola (**comb. rev.**)  
*B. rubiginosa* (Emery, 1889): Myanmar  
*B. silvestrii* (Santschi, 1914): Ghana (**comb. rev.**)  
*B. silvestrii nimba* Bernard, 1953: Guinea (**comb. rev.**)  
*B. soror* (Emery, 1899): Cameroon (**comb. rev.**)  
*B. soror ancilla* (Emery, 1899): Congo (**comb. rev.**)  
*B. soror suturalis* (Forel, 1907): Ethiopia (**comb. nov.**)  
*B. sulcata* (Mayr, 1867): “Vaterland unbekannt”  
*B. sulcata fossulata* (Forel, 1900): India  
*B. sulcata sulcatotesserinoda* (Forel, 1900): India  
*B. tesseronoda* (Emery, 1877): India  
*B. williamsi* Wheeler, W.M. & Chapman, 1925: Philippines  
*B. zumpti* Santschi, 1937: Cameroon (**comb. nov.**)

## ***Brachyponera* Emery**

Fig. 9

*Brachyponera* Emery, 1900a: 315 (as subgenus of *Euponera*). Type-species: *Euponera* (*Brachyponera*) *croceicornis* Emery, 1900a: 315; by monotypy. **Gen. rev.**

*Brachyponera* is a fairly large genus, with 24 described species and subspecies, and ranges from southern Africa to Australia. *Brachyponera* is unusual among ponerines in having a distinct size dimorphism between workers and queens, and in the invasiveness of some of its species.

**Diagnosis.** Workers of *Brachyponera* can be differentiated from those of other ponerine genera by the following combination of characters: Mandibles usually with a basal pit (obsolete or vestigial in some species), eyes small and placed near the mandibular insertions, metanotal groove deep, propodeum at a lower elevation than the thorax and usually strongly narrowed dorsally, propodeal spiracle small and round, petiole squamiform, prora reduced and not externally visible, gaster with only a slight girdling constriction, and metatibiae with two spurs. None of these characters is autapomorphic within the *Odontomachus* group, but this combination of characters is unique. *Brachyponera* is most likely to be confused with species of *Pseudoponera*, but *Pseudoponera* lacks the mandibular pits, deep metanotal groove, and lowered propodeal elevation of *Brachyponera*.





**FIGURE 9.** Worker caste of *Brachyponera croceicornis*: lateral and dorsal view of body and full-face view of head (CASENT0172432, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Brachyponera*.

**Synoptic description.** *Worker.* Small to medium (TL 3–7 mm) ants with the standard characters of Ponerini. Mandibles triangular and usually with a small basal groove/pit. Frontal lobes small. Eyes small and placed far anterior near the mandibular insertions. Mesopleuron sometimes fully or partially divided by a shallow transverse groove. Metanotal groove deeply impressed. Propodeum at a lower elevation than the thorax, and usually strongly narrowed dorsally. Propodeal spiracle small and round. Metatibial spur formula (1s, 1p). Petiole squamiform. Girdling constriction between pre- and postsclerites of A4 apparent. Stridulitrum sometimes present on pretergite of A4. Head and body shiny to lightly punctate, sometimes with lateral striations on the mesosoma. Head and body with sparse pilosity and patchy pubescence. Color orange to black.

*Queen.* Similar to worker but larger (sometimes much larger, as in *B. lutea*; Wheeler, 1933b), winged, with a wider and broader petiole, and with the other caste differences typical in ponerines. See description by Ogata (1987) for further details.

*Male.* See description by Ogata (1987).

*Larva.* Described by Wheeler & Wheeler (1971a, 1976, 1986b).

**Geographic distribution.** *Brachyponera* is widespread from Africa through southern Asia to Australia. It is most species-rich in Southeast Asia. *B. chinensis* was accidentally introduced to the southeastern United States and is now locally abundant (Nelder *et al.*, 2006); it has also been introduced to New Zealand.

**Ecology and behavior.** *Brachyponera* workers are among the smallest of the *Odontomachus* group, but like most members of the group are solitary epigeic generalist predators and scavengers. Nests are generally constructed in soil or rotten wood (*B. chinensis*: Ogata, 1987; Matsuura, 2002; Matsuura *et al.*, 2002; Gotoh & Ito, 2008; *B. croceicornis*: Wilson, 1958c; *B. lutea*: Wheeler, 1933b; Haskins & Haskins, 1950; *B. luteipes*: Kikuchi *et al.*, 2007; *B. mesoponeroides*: Radchenko, 1993; *B. pilidorsalis*: Yamane, 2007). *Brachyponera* is unusual among ponerines in that it displays a marked reproductive dimorphism between workers and queens, with the workers having completely lost their reproductive organs and queens having a large number of ovarioles (Ito & Ohkawara, 1994; Gotoh & Ito, 2008). *Brachyponera* also has the distinction of containing some of the only ponerine species considered to be pests: *B. chinensis* and *B. sennaarensis*, which are invasive and have potentially dangerous stings (see below).

Due to its pest ant status, *B. chinensis* has received more attention than most *Brachyponera* species. It seems to be fairly representative of the genus. *B. chinensis* is a generalist predator and scavenger, (Teranishi, 1929; Matsuura, 2002; Matsuura *et al.*, 2002; Matsuura & Nishida, 2002), its nests are apparently polydomous (Gotoh & Ito, 2008), and its colonies average between 30 and 100 workers (Gotoh & Ito, 1998; Matsuura, 2002). Colony founding in *B. chinensis* is apparently semi-claustral (Koriba, 1963), and both monogynous and polygynous colonies have been observed (Gotoh & Ito, 1998). It is an invasive pest ant in the southeastern United States, having been accidentally introduced sometime before 1932 (Smith, 1934). The species is a public health concern due to the relative frequency of life-threatening anaphylaxis and other reactions to its venom (in Japan: Fukuzawa *et al.*, 2002; in Korea: Cho *et al.*, 2002; in the United States: Leath *et al.*, 2006; Nelder *et al.*, 2006).

*B. sennaarensis* is another invasive *Brachyponera* species. It is widespread in Sub-Saharan Africa and has recently been spreading northeastward through the Middle East (reaching as far as Iran), where it takes advantage of the relatively cooler and wetter climatic conditions provided by urban areas (Collingwood *et al.*, 1999; Tigrari & Paknia, 2005; Paknia, 2006; Wetterer, 2012b). The species is very adaptable, occurring in both dry and humid habitats in its native range and having a very flexible diet (Déjean & Lachaud, 1994; L, 1994; Déjean *et al.*, 1999). *B. sennaarensis* is a generalist omnivore but like many other *Brachyponera* species (and unusually for ponerines) will utilize seeds for food (Arnold, 1925; Lévieux & Diomande, 1978; Lévieux, 1979; Déjean & Lachaud, 1994; Lachaud & Déjean, 1994). Workers forage individually and will only recruit nestmates in times of general starvation (Lachaud & Déjean, 1994). *B. sennaarensis* is notable for the large size of its colonies (about 1,000 workers on average) and the striking size dimorphism between workers and queens (Déjean & Lachaud, 1994). Even more unusual is the presence of size polymorphism within the worker caste, which is rare among ponerines (Déjean & Lachaud, 1994). *B. sennaarensis* nests are constructed in soil and are multichambered, the chambers being connected by tunnels (Déjean & Lachaud, 1994). Tandem-running is used during emigrations to new nest sites (Lachaud & Déjean, 1994). Like *B. chinensis*, the sting of *B. sennaarensis* can cause life-threatening anaphylaxis (Dib *et al.*, 1992). Longhurst *et al.* (1978) examined the mandibular gland secretions of *B. sennaarensis*.

The abundant and adaptable Australian species *B. lutea* displays even more extreme size differences between

the workers and queens than does *B. sennaarensis* (Wheeler, 1933b). The workers are tiny and hypogeic (unlike most *Brachyponera*). The large size of the queens enables claustral colony founding, though semiclastral founding also occurs, as is the case with *B. sennaarensis* (Haskins & Haskins, 1950; Lachaud & Déjean, 1991b; Déjean & Lachaud, 1994). *B. lutea* has large colonies of over 2,000 workers, and is apparently largely predacious (Wheeler, 1933b; Haskins & Haskins, 1950).

Very little has been reported about other species of *Brachyponera*. *B. luteipes* is polygynous and may be polydomous or uniclonal, though the data on this are not conclusive (Takahashi *et al.*, 2005; Kikucho *et al.*, 2007). Interestingly, *B. luteipes* workers are aggressive toward queens of foreign colonies but not toward foreign workers (Kikucho *et al.*, 2007). Like *B. sennaarensis*, *B. luteipes* is known to feed on seeds (Zhou *et al.*, 2007). Wilson (1958c) reports that *B. croceicornis* is one of the most abundant and widespread ants in New Guinea, inhabiting a wide array of habitats; its colonies have about 100 workers.

**Phylogenetic and taxonomic considerations.** *Brachyponera* first appeared in the literature as a subgenus of *Euponera* (Emery, 1900a), with *B. croceicornis* Emery as the type species. The next year, Emery (1901) again described *Brachyponera* as new and designated *B. sennaarensis* Mayr as the type species, though this was unjustified given the earlier designation of *B. croceicornis*. Most authors continued to treat *Brachyponera* as a subgenus of *Euponera* (except Bingham, 1903) until Wilson (1958c) raised it to full genus status, where it generally remained until Brown (in Bolton, 1994) synonymized it with *Pachycondyla* (see also Snelling, 1981).

We are reviving *Brachyponera* to full genus status based on both molecular and morphological evidence. Schmidt's (2013) molecular phylogeny of the Ponerinae places *Brachyponera* with strong support within the *Odontomachus* group. Its sister group is unresolved, but *Brachyponera* is not closely related to *Pachycondyla*, and a sister relationship with *Euponera* cannot be rejected.

Morphologically, *Brachyponera* does not share any obvious apomorphies with any other genera, with the possible exception of basal mandibular pits, which also occur in *Euponera*, and the lack of a prora, which is also absent in *Iroponera* and *Phrynoponera*. *Brachyponera* and *Euponera* also share deep metanotal grooves and divided mesopleura (only in some *Brachyponera*), though these easily could be convergent. The lack of the prora is most likely convergent as there is little additional evidence suggesting a close relationship among these three genera. *Brachyponera*'s round propodeal spiracle suggests a possible placement near *Myopias* and *Leptogenys*, though the absence of a strong gastral constriction argues against this placement. In sum, both the molecular and morphological evidence is inconclusive about the exact phylogenetic position of *Brachyponera*, though it is certainly distinctive enough to warrant full genus status.

### Species of *Brachyponera*

- B. arcuata* (Karavaiev, 1925): Indonesia (**comb. rev.**)
- B. atrata* (Karavaiev, 1925): Indonesia (**comb. rev.**)
- B. bataak* (Yamane, 2007): Indonesia (Sumatra) (**comb. nov.**)
- B. brevidorsa* Xu, 1994: China
- B. chinensis* (Emery, 1895): China (**comb. rev.**)
- B. christmasi* (Donisthorpe, 1935): Christmas Island (**comb. nov.**)
- B. croceicornis* (Emery, 1900): New Guinea (**comb. rev.**)
- B. flavipes* (Yamane, 2007): Myanmar (**comb. nov.**)
- B. jerdonii* (Forel, 1900): India (**comb. rev.**)
- B. jerdonii glabricollis* (Stärcke, 1930): Indonesia (**comb. nov.**)
- B. lutea* (Mayr, 1862): Australia (**comb. rev.**)
- B. luteipes* (Mayr, 1862): Nicobar Islands (**comb. rev.**)
- B. luteipes continentalis* (Karavaiev, 1925): India (**comb. nov.**)
- B. mesoponeroides* Radchenko, 1993: Vietnam (**comb. rev.**)
- B. nakasujii* (Yashiro, *et al.* 2010): Japan (**comb. nov.**)
- B. nigrata* (Emery, 1895): Myanmar (**comb. rev.**)
- B. nigrata nigratella* (Stärcke, 1930): Indonesia (**comb. nov.**)
- B. obscurans* (Walker, 1859): Sri Lanka (**comb. nov.**)
- B. pilidorsalis* (Yamane, 2007): Malaysia (**comb. nov.**)



*B. sennaarensis* (Mayr, 1862): Sudan (**comb. rev.**)  
*B. sennaarensis decolor* (Santschi, 1921): Congo (**comb. nov.**)  
*B. sennaarensis ruginota* (Stitz, 1916): Cameroon (**comb. nov.**)  
*B. tianzun* (Terayama, 2009): Taiwan (**comb. nov.**)  
*B. wallacei* (Yamane, 2007): Lombok (**comb. nov.**)

***Buniapone* gen. nov.**

Fig. 10

Type-species: *Ponera amblyops* Emery, 1887: 434; by present designation.

*Buniapone* is a monotypic genus restricted to Southern and Southeast Asia. Very little is known about its habits.

**Etymology.** *Buniapone* is named after the *Orang Bunian*, a race of invisible forest beings in the traditional folklore of Malaysia (where the genus is common), reflecting the hypogeic sylvan habits of these ants. The suffix *-pone* is derived from the subfamily name Ponerinae.

**Diagnosis.** *Buniapone* is a morphologically distinctive genus and its workers are readily identified by the following combination of characters: long and narrow toothed mandibles, blunt medial clypeal projection, greatly reduced eyes, obsolete metanotal groove, ovoid propodeal spiracles, complex metapleural gland orifice, and squamiform petiole. Superficially, *Buniapone* most closely resembles *Centromyrmex*, *Promyopias*, and certain Neotropical *Cryptopone* species, but *Buniapone* has eyes, lacks the anterolateral position of the metapleural gland orifice of *Centromyrmex*, lacks the linear mandibles of *Promyopias*, and lacks the small closely approximated frontal lobes and circular propodeal spiracles of *Cryptopone*. Though *Buniapone* shares several apomorphies with its sister genus *Paltothyreus*, they are superficially very different and unlikely to be confused. *Myopias* also has a blunt medial clypeal projection, but it is much more pronounced than in *Buniapone*, and *Myopias* lacks the other characters diagnostic of *Buniapone*.

**Synoptic description.** *Worker.* Medium-sized (TL 5.5–6.5 mm; Emery, 1887) ants with the standard characters of Ponerini. Mandibles long and narrow, with seven prominent teeth on the masticatory margin, a short basal margin, and a basal groove. Anterior clypeal margin forming a narrow blunt medial projection. Frontal lobes moderately large. Eyes very small (with about four ommatidia), located anterior of head midline. Metanotal groove obsolete. Propodeum narrowed dorsally. Propodeal spiracles ovoid. Metapleural gland orifice opening posterolaterally, with anterior and posterior cuticular flanges. Mesotibae and meso-/metabasitarsi with stout traction setae. Metatibial spur formula (1s, 1p). Petiole squamiform. Helcium projecting from near midheight of anterior face of A3. Girdling constriction between pre- and postsclerites of A4 apparent. Head, gaster and mesosomal dorsum punctate, the sides of the mesosoma longitudinally striate. Head and body with scattered pilosity and a dense pubescence. Color orange.

*Queen.* Similar to worker, but larger (TL 9.25 mm; Emery, 1889) and winged.

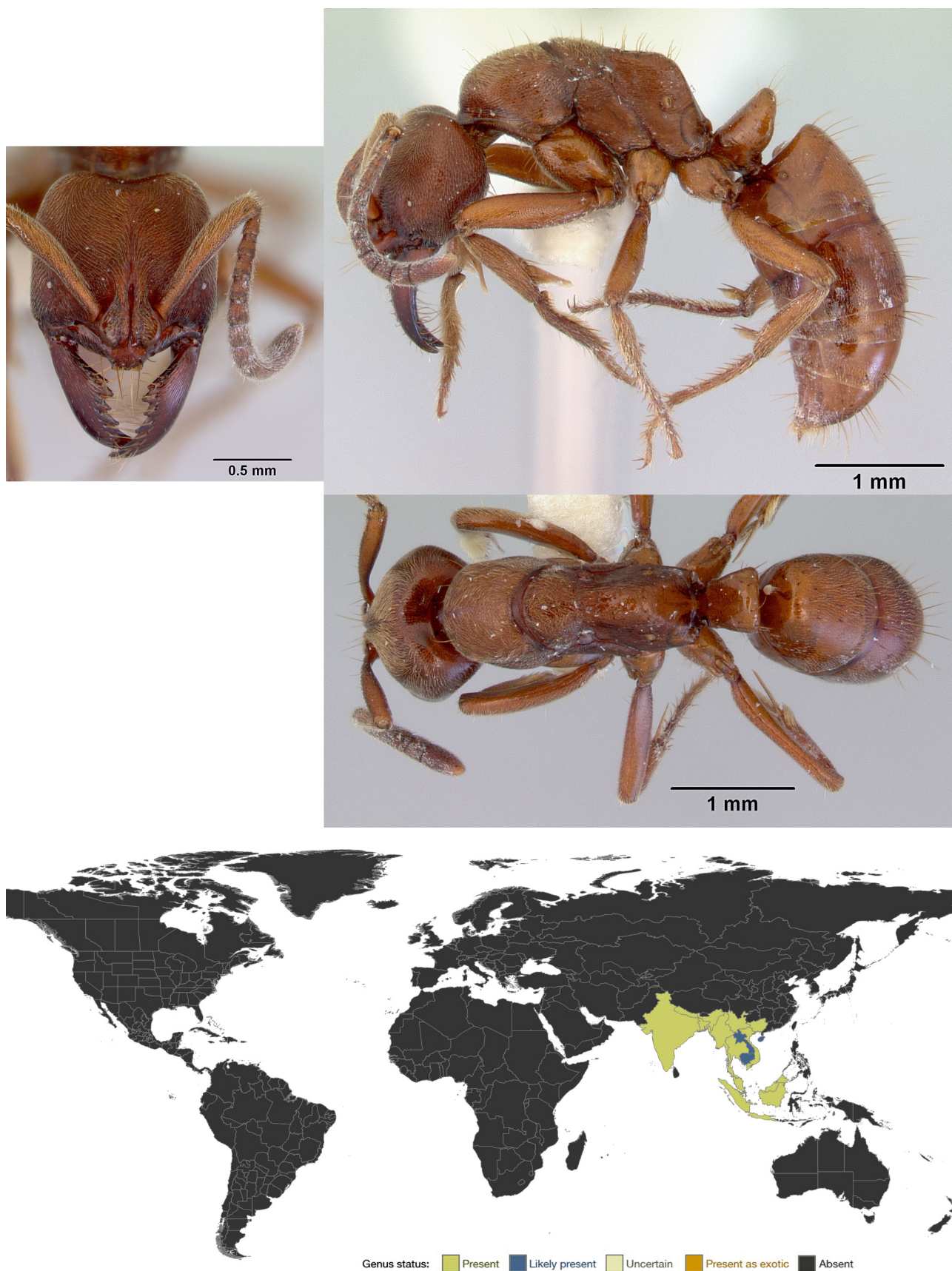
*Male.* See description in Santschi (1928).

*Larva.* Not described.

**Geographic distribution.** *Buniapone* is restricted to Southern and Southeast Asia, ranging from southern China to the islands of southern Indonesia and as far west as India.

**Ecology and behavior.** Virtually nothing is known about the habits of *Buniapone*, other than that they are hypogeic. They are presumably predatory, though their prey preferences are unknown. One of us (CS) observed large numbers of *B. amblyops* workers congregated at a palm oil bait sunk into the ground, suggesting that they are not strictly carnivorous and that they may employ some kind of nestmate recruitment to food sources, like their sister genus *Paltothyreus*.

**Phylogenetic and taxonomic considerations.** We are erecting *Buniapone* as a new genus to house the single species *Ponera amblyops* Emery (1887) (currently *Pachycondyla amblyops*). This species has had probably the most convoluted taxonomic history of any ponerine. It was originally placed in *Ponera* (Emery, 1887), then moved to *Trapeziopelta* (= *Myopias*; Emery, 1889), *Belonopelta* (Emery, 1897a), *Pachycondyla* (Emery, 1900b), *Pseudoponera* (Emery, 1901; Bingham, 1903), *Euponera* (Forel, 1905), and most recently *Pachycondyla* again (W. L. Brown, in Bolton, 1995). Emery (1901) designated it the type species of *Pseudoponera*, despite having



**FIGURE 10.** Worker caste of *Buniapone amblyops*: lateral and dorsal view of body and full-face view of head (CASENT0172431, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Buniapone*.

implicitly erected *Pseudoponera* the previous year with a different type species (what is now *Ps. stigma*; Emery, 1900a). This mistake was repeated throughout much of the subsequent taxonomic literature, but was finally noted by Bolton (2003).

The confusion over the taxonomic placement of *B. amblyops* is understandable given its unique structure. Schmidt's (2013) molecular phylogeny of the Ponerinae resolves this uncertainty, as *Buniapone* is very strongly resolved as sister to *Paltothyreus*, though sister relationships to either *Euponera* or *Myopias* were not statistically rejected. The apparent sister relationship between *Buniapone* and *Paltothyreus* is a novel and surprising result which is nevertheless also strongly supported by morphology (see discussion under *Paltothyreus*). Given that these two genera share several apomorphies and that their divergence is relatively recent, they could arguably be synonymized. We feel that their morphological and ecological differences are stark enough, however, to warrant distinct generic status, similar to the situation with *Dinoponera* and *Pachycondyla*.

*Buniapone*'s close relationship to *Paltothyreus* is perhaps the most surprising result in Schmidt's (2013) molecular phylogeny. *Buniapone* is a medium-sized hypogeic ant restricted to Asia, while *Paltothyreus* is a very large epigeic ant restricted to Sub-Saharan Africa. Given their phylogenetic position within the *Odontomachus* group, it is clear that *Buniapone* is morphologically the more derived of the two genera. The most recent common ancestor of *Buniapone* and *Paltothyreus* was most likely a large epigeic ant like most members of the *Odontomachus* group. Further information about the behavior of *Buniapone* would be invaluable in understanding the remarkable divergence between these two genera.

*Buniapone* bears superficial morphological similarity to some Neotropical *Cryptopone* species (those formerly placed in *Wadeura*) and to *Promyopias*. These similarities are presumably the result of convergence due to their shared hypogeic habits as *Cryptopone* belongs to the *Ponera* group and preliminary results suggest that *Promyopias*, while also belonging to the *Odontomachus* group, is not particularly closely related to *Buniapone* (P.S. Ward, pers. comm.).

### Species of *Buniapone*

*B. amblyops* (Emery, 1887): Indonesia (Sumatra) (**comb. nov.**)

*B. amblyops oculator* (Forel, 1909): Indonesia (Java) (**comb. nov.**)

### *Euponera* Forel

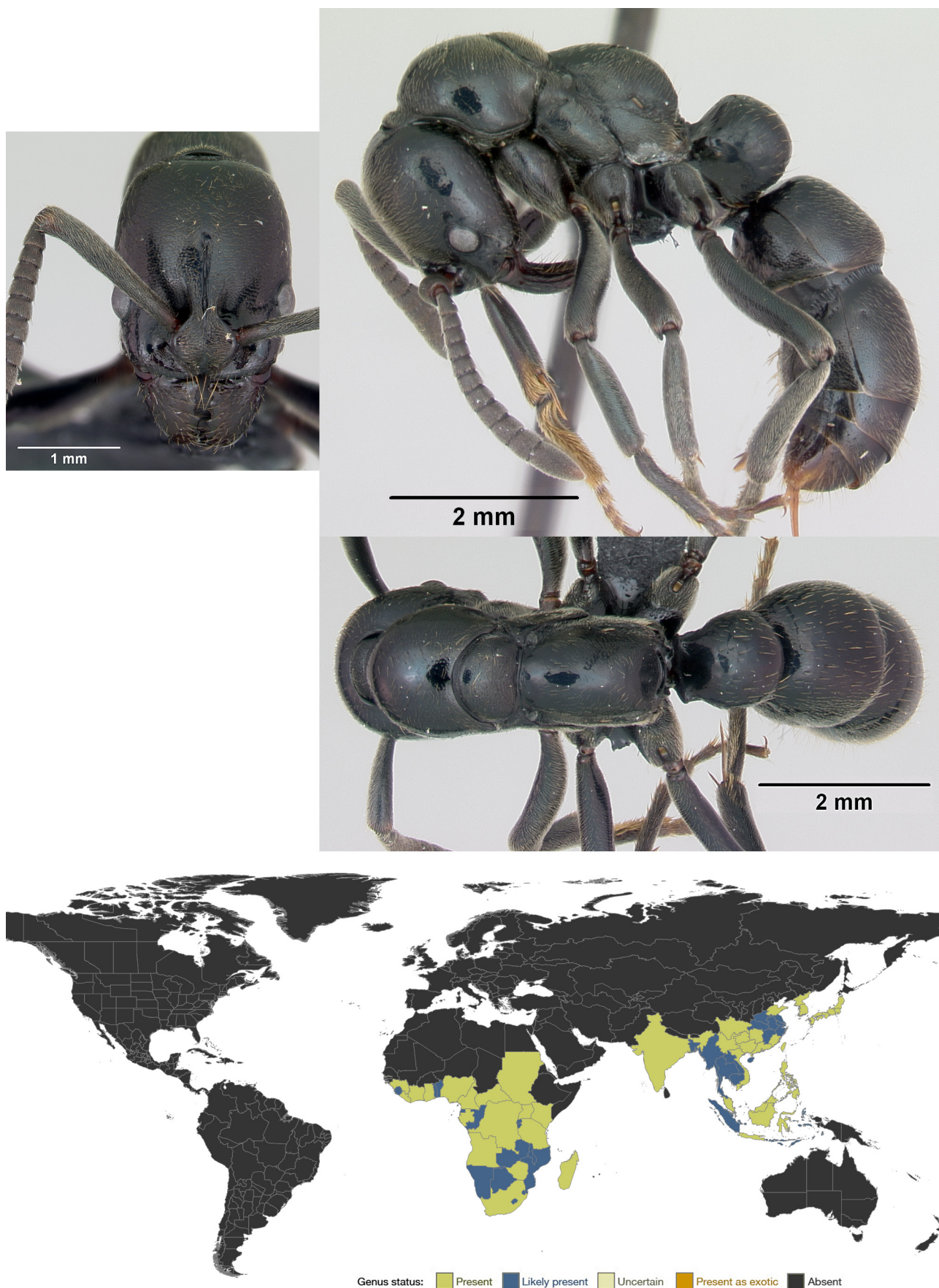
Figs 11, 12

*Euponera* Forel, 1891: 126 (as subgenus of *Ponera*). Type-species: *Ponera* (*Euponera*) *sikorae* Forel, 1891: 127; by monotypy.  
**Gen. rev.**

*Euponera* is a moderately large genus (26 described species) of medium-sized ants occurring in the Afrotropics, Madagascar and eastern Asia. Its habits are poorly known.

**Diagnosis.** *Euponera* species fall into two groups, the first, related to *E. sikorae*, can be diagnosed by the presence of a shiny integument, basal mandibular pits, cordate frontal lobes, divided mesopleuron, deep metanotal groove, and strong gastral constriction. This combination of characters does not occur in any other ponerine genus. The second set of species, which includes *E. sjostedti*, can be separated from others by the presence of basal mandibular pits, obsolete metanotal groove, elongate or slit-shaped propodeal spiracle, simple subpetiolar process without an anterior fenestra and a prora on anterior margin of first gastral sternite. A shiny integument occurs in some other ponerines, but is absent in most large species. Basal mandibular pits occur in most species of *Brachyponera* and *Cryptopone*. Cordate frontal lobes occur in most members of the *Plectroctena* group as well as in *Bothroponera* (*s.s.*). A divided mesopleuron and deep metanotal groove occur in combination only in some *Brachyponera*, *Hagensia* (in which the mesopleuron is only partially divided), and in *Mesoponera subiridescens*. *Euponera* superficially most closely resembles *Bothroponera* (*s.s.*) and *Pseudoponera*, but differs in the presence of basal mandibular pits. Some *Euponera* species are also similar to *Cryptopone*, but these differ in having eyes and lacking mesotibial traction setae. They are also similar to *Mesoponera* but are generally smaller in body size with smaller eyes, larger frontal lobes, a wider head and have shorter mandibles.





**FIGURE 11.** Worker caste of *Euponera sikorae*: lateral and dorsal view of body and full-face view of head (CASENT0487847, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Euponera*.





**FIGURE 12.** Worker caste of *Euponera antsiraka*: lateral and dorsal view of body and full-face view of head (CASENT0317590, Jean Claude Rakotonirina and [www.antweb.org](http://www.antweb.org)).

**Synoptic description.** *Worker.* Large (TL 6–10.5 mm) ants with the standard characters of Ponerini. Mandibles triangular, with numerous teeth and a basal pit. Anterior clypeal margin convex or medially emarginate. Frontal lobes moderate to large, cordate and closely approximated for most of their length (less close in the *E. wroughtonii* group). Eyes small (3–4 facets in diameter) to moderate in size, located just anterior of head midline (in *E. sikorae*) or anteriorly on sides of head (in most species). Mesopleuron sometimes divided by a transverse groove. Metanotal groove varying from little more than a suture to deeply impressed. Metapleural gland orifice opening laterally in the *P. wroughtonii* group. Propodeal spiracle slit-shaped. Metatibial spur formula (1s, 1p). Petiole with a cuboidal node in most species but scale-like in a few. Girdling constriction between pre- and postsclerites of A4 apparent. Head and body varying from shiny and sparsely punctate, with sparse pilosity and pubescence to finely punctate and with abundant pilosity and scattered to dense pubescence. Color variable, ferruginous to black.

*Queen.* Winged but otherwise similar to workers (Rakotonirina & Fisher, 2013).

*Male.* Not described.

*Larva.* Not described.

**Geographic distribution.** *Euponera* occurs in Sub-Saharan Africa and Madagascar and India eastward to Korea and Japan and south through the Philippines to Indonesia.

**Ecology and behavior.** Collections of *Euponera sikorae* have come from rainforest habitats, but nothing else is known about its ecology or behavior. Terayama (1999) reported that *E. sakishimensis* nests in soil and that

workers forage on the ground, and K. Masuko observed very small colony sizes (4–11 workers) in *E. pilosior* (pers. comm. in Peeters, 1993). Villet (1994) studied the colony demographics and reproductive strategy of *E. fossigera*. This species is a generalist predator, forms small colonies (up to 50 workers), and nests in soil, leaf litter, or rotting wood. Reproduction is performed by a single ergatoid.

**Phylogenetic and taxonomic considerations.** Other than *Pachycondyla* itself, *Euponera* has been the focus of the greatest taxonomic lumping within the Ponerinae, having at various times housed *Brachyponera*, *Mesoponera*, *Pseudoponera*, *Xiphopelta* (here treated as a junior synonym of *Mesoponera*) and *Hagensia*, all of which (except *Xiphopelta*) we consider to be distinct genera. *Euponera* was originally erected as a subgenus of *Ponera* by Forel (1891) to house the single species *E. sikorae*. Emery raised *Euponera* to full genus status (1900a) and described *Brachyponera* (1900a) and *Mesoponera* (1900b) as subgenera of *Euponera*. Emery's treatment was generally accepted by most authors (but see Bingham, 1903) until Wilson (1958c) moved both *Brachyponera* and *Mesoponera* to full genus status. Forel (1901a) moved *Pseudoponera* to subgenus status under *Euponera*, where it generally remained until Wheeler (1922b) revived it as a distinct genus (but again see Bingham, 1903). Emery (1911) treated *Trachymesopus* (now *Pseudoponera*) as a subgenus of *Euponera*, though Wilson (1958c) eventually raised it to full genus status. Arnold (1915) synonymized *Hagensia* under *Euponera* (subgenus *Mesoponera*), while Forel (1917) raised *Hagensia* to subgenus status under *Euponera*. Arnold (1926) later raised *Hagensia* to generic status. Forel (1917) placed *Xiphopelta* (= *Mesoponera*) under *Euponera* as a distinct subgenus, where it remained on and off until Brown (1973) synonymized it with *Pachycondyla*. *Euponera* was treated as a distinct genus until W. L. Brown (in Bolton, 1994) lumped it under *Pachycondyla* without phylogenetic justification.

*Euponera* became the type genus for Emery's (1909, 1911) Euponerinae, which he considered a section of Ponerinae and which basically conformed to the present definition of Ponerini. Emery (1911) gave a diagnosis for *Euponera* that included *Brachyponera*, *Mesoponera* and *Trachymesopus* (= *Pseudoponera*) as subgenera. He united these taxa based on characters of their mandibles (subtriangular and toothed, with a distinct angle between the masticatory and basal margins), eyes (located in the anterior third of the head), mesosoma (presence of a distinct metanotal groove), and the alate queens. All of these characters are likely plesiomorphic within the Ponerini, and do not indicate a close relationship among these genera.

We are reviving *Euponera* as a distinct genus based on both molecular and morphological evidence. Schmidt's (2013) molecular phylogeny of the Ponerinae and Ward's (pers. comm.) examination of selected African taxa places *Euponera* with strong support within the *Odontomachus* group, but its sister group is unresolved. It is not closely related to *Pachycondyla* or *Pseudoponera* as these are placed in separate genus groups (*Pachycondyla* group and *Ponera* group, respectively). Morphologically, *Euponera* shares basal mandibular pits and a deep metanotal groove with *Brachyponera*, and while these taxa are otherwise morphologically quite different, Schmidt's and Ward's molecular data suggest a close relationship between them. Ward's molecular results suggest a close relationship between *Euponera* and *Fisheropone*, even though they share few morphological characters. Similarly, the distinctive *Cryptopone hartwigi* was also found to be closely related to *Euponera* (and *Fisheropone*). The highly divergent morphologies among these three close relatives belie their true relationships, and have contributed to the fluidity of generic concepts within the subfamily.

Morphologically, some *Euponera* species are superficially closest to certain members of *Bothroponera*, particularly *Bothroponera comorensis*, while other species are separable from selected *Pseudoponera* species only by careful examination. However, molecular evidence suggests these similarities are due to convergence as they are not closely related.

### Species of *Euponera*

The Malagasy species of this genus were revised by Rakotonirina & Fisher (2013). The remaining species await revision.

*E. aenigmatica* (Arnold, 1949): S. Africa (**comb. nov.**)

*E. agnivo* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*E. antsiraka* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*E. brunoi* (Forel, 1913): Zimbabwe (**comb. nov.**)

*E. daraina* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

*E. fossigera* (Mayr, 1901): South Africa (**comb. nov.**)



*E. gorogota* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. grandis* Donisthorpe, 1947: Vietnam (**comb. nov.**)  
*E. haratsingy* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. ivolo* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. kipyatkovi* (Dubovikoff, 2013): Madagascar (**comb. nov.**)  
*E. maeva* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. malayana* (Wheeler, 1929): Malaysia (**comb. nov.**)  
*E. mialy* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. nosy* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. pilosior* (Wheeler, W.M., 1928): Japan (**comb. nov.**)  
*E. rovana* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. sakishimensis* (Terayama, 1999): Japan (**comb. nov.**)  
*E. sharpi* (Forel, 1901): Singapore (**comb. nov.**)  
*E. sikorae* (Forel, 1891): Madagascar (**comb. rev.**)  
*E. sjostedti* (Mayr, 1896): Cameroon (**comb. rev.**)  
*E. tahary* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. vohitravo* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)  
*E. wrightonii* (Forel, 1901): South Africa (**comb. nov.**)  
*E. wrightonii crudelis* (Forel, 1901): South Africa (**comb. nov.**)  
*E. zoro* (Rakotonirina & Fisher, 2013): Madagascar (**comb. nov.**)

The placement of the following species is uncertain as their true identities could not be confirmed during this study. The limited details available suggest they belong to *Euponera* but this placement awaits confirmation.

*E. butteli* Forel, 1913: Indonesia (Java) (**comb. rev.**)  
*E. pallidipennis* (Smith, 1860): Sulawesi (**comb. nov.**)  
*E. suspecta* (Santschi, 1914): Tanzania (**comb. nov.**)

### ***Fisheropone* gen. nov.**

Fig. 13

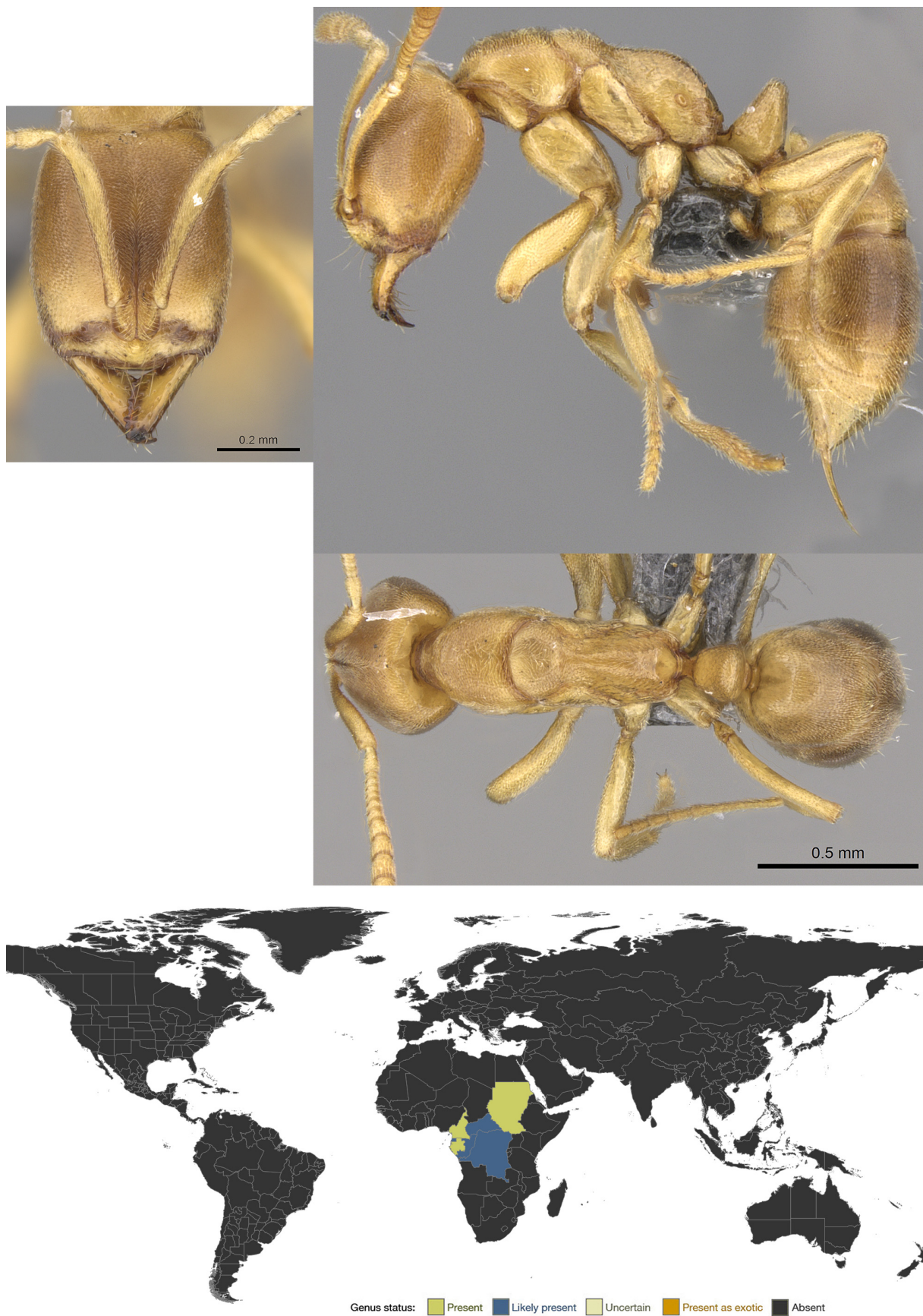
Type-species: *Ponera ambigua* Weber, 1942a: 46; by present designation.

*Fisheropone* is known from a single described and at least one undescribed species which are found in central Africa (Cameroon, Gabon, South Sudan, Tanzania, Uganda). Nothing is known of their biology.

**Etymology.** *Fisheropone* is named in honour of Brian Fisher, acknowledging his tremendous contributions to African and Malagasy myrmecology.

**Diagnosis.** *Fisheropone* workers can be diagnosed by the following unique combination of characters: mandibles narrowly triangular, relatively long and without a basal pit or fovea; clypeus narrowly inserted between small frontal lobes, the antennal sockets closely approximated; propodeal spiracle slit-shaped; mesotibiae dorsally without abundant stout traction setae and ventral apex of the metatibia with a single pectinate spur; and petiole scale-like and thin. These ants bear a superficial resemblance to *Hypoponera* and *Mesoponera* in being relatively slender and with elongate mandibles and an impressed metanotal groove. They can be separated from *Hypoponera* by the slit-shaped rather than round propodeal spiracle, and from *Mesoponera* by the presence of only a single metatibial spur. Separation from the single African species of *Cryptopone* is based on the lack of a basal mandibular pit and mesotibial pusher setae, both of which are present in *Cryptopone*.

**Synoptic description.** *Worker.* Small (TL ca. 2 mm) slender ants with the standard characters of Ponerini. Mandibles narrowly triangular, relatively long. Eyes absent. Frontal lobes very small and closely approximated. Mesopleuron not divided by a transverse groove. Metanotal groove angular. Propodeum narrowed dorsally. Propodeal spiracles elongate. Metatibial spur formula (1p). Petiole squamiform. Gaster with a moderately weak girdling constriction between pre- and postsclerites of A4. Stridulitrum absent from pretergite of A4. Head and body finely punctate, with sparse pilosity but a dense fine pubescence. Color pale yellow.



**FIGURE 13.** Worker caste of *Fisheropone ambigua*: lateral and dorsal view of body and full-face view of head (CASENT0289205, Cerise Chen and [www.antweb.org](http://www.antweb.org)); world distribution of *Fisheropone*.

*Queen*. Unknown.

*Male*. Unknown.

*Larva*. Unknown.

**Geographic distribution.** This genus is apparently restricted to Sub-Saharan Africa from Cameroon and Gabon to South Sudan.

**Ecology and behavior.** Nothing is known about the habits of *Fisheropone*. The lack of eyes, small body size and pale color suggest a hypogeic lifestyle, and this may explain their infrequent collection. However, this remains to be confirmed by field observations.

**Phylogenetic and taxonomic considerations.** The only described species of *Fisheropone* was originally placed in *Ponera* as it has only a single metatibial spur. It is now known that this character occurs across the subfamily in unrelated genera and is of little phylogenetic value. Recent preliminary molecular results provided by P. S. Ward (unpublished) place this genus within the *Odontomachus* genus group, and near species of *Brachyponera* and *Euponera*. While this placement appears well supported the taxon sampling in this preliminary work is limited and further details will be required to determine exact relationships.

### Species of *Fisheropone*

Only a single species has been described from this genus although at least one undescribed species is known. The described species, *F. ambigua* (Weber), has been a junior secondary homonym of *Pachycondyla ambigua* André, 1890 and was replaced by *Pachycondyla gulera* Özdikmen, 2010. However, as these names are here placed in separate genera the replacement name is unnecessary and becomes a junior objective synonym of *F. ambigua* Weber.

Bolton & Fisher (2011) discuss *F. ambigua* and consider it closely related to *weberi* (Bernard, 1953). However, an examination of type material (held in MCZC) of *weberi* (Bernard) support the placement of this species in *Mesoponera* rather than *Fisheropone*, and thus these species are not treated as closely related in this study.

***F. ambigua*** (Weber, 1942): South Sudan (**comb. nov.**)

### *Hagensia* Forel

Fig. 14

*Hagensia* Forel, 1901c: 333 (as subgenus of *Megaloponera* [sic]). Type-species: *Megaloponera* (sic) (*Hagensia*) *havilandi* Forel, 1901c: 333; by monotypy. **Gen. rev.**

*Hagensia* is a small South African genus (two described species and four subspecies), notable for having gamergate workers.

**Diagnosis.** Diagnostic morphological apomorphies of *Hagensia* workers include the presence of a dorsal mandibular groove, sharp pronotal margins, and a squamiform petiole with anterior and posterior faces meeting along a sharp edge. This combination of characters is unique to *Hagensia*. The dorsal mandibular groove is approximated by the condition in *Pseudoponera wroughtonii*, and a sharp pronotal margin is present in some African *Centromyrmex* species as well as some members of *Pachycondyla* and *Neoponera*, but these genera lack the other diagnostic characters of *Hagensia*.

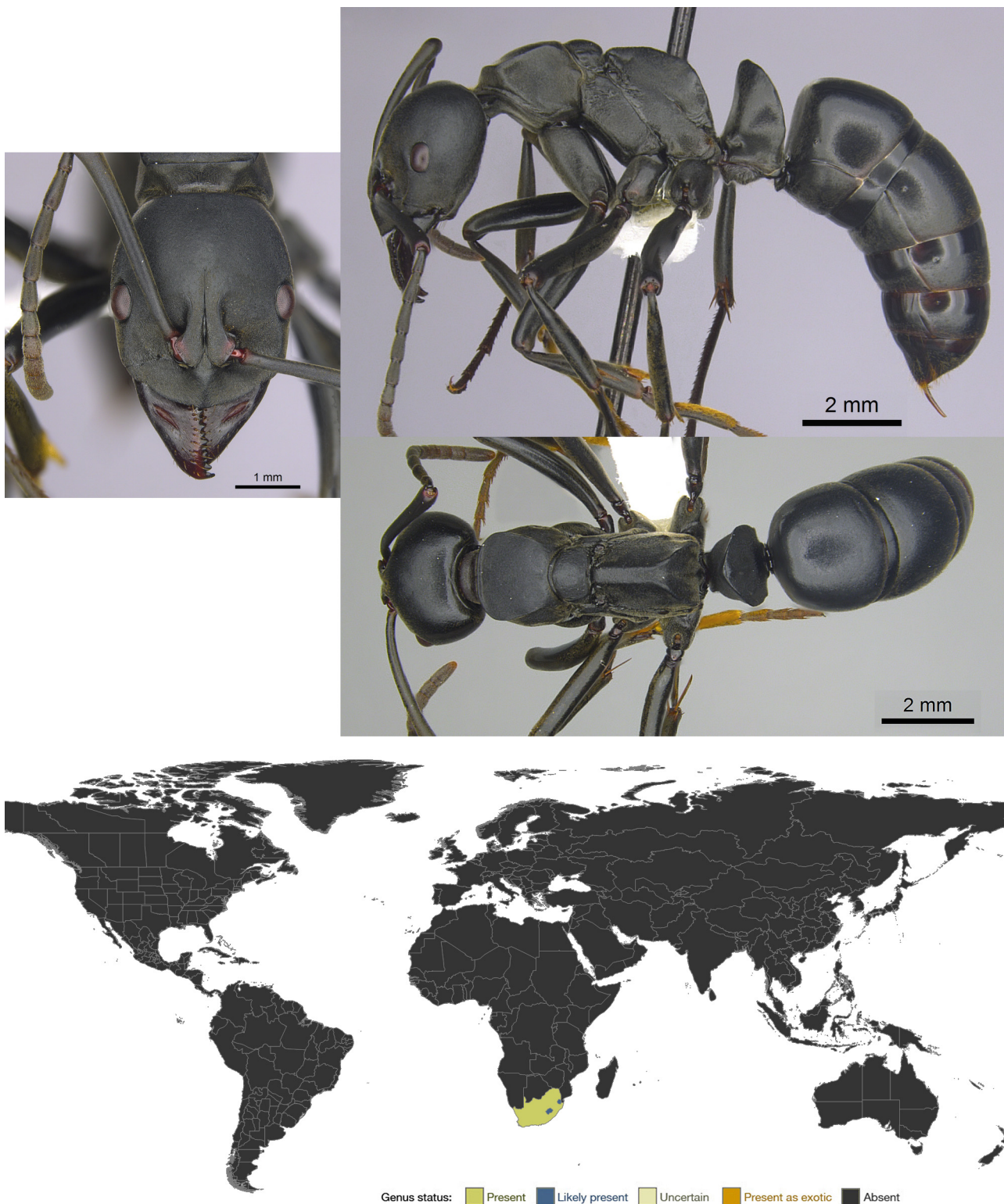
**Synoptic description.** *Worker*. Large (TL 10.5–13.0 mm; Arnold, 1915) ants with the standard characters of Ponerini. Mandibles triangular, with a deep dorsal transverse groove. Eyes moderately large and located near the head midline. Pronotum with sharp dorsolateral margins. Mesopleuron partially divided by a transverse groove. Metanotal groove shallowly to deeply impressed. Propodeum strongly narrowed dorsally. Propodeal spiracles slit-shaped. Tarsal claws with a single preapical tooth. Metatibial spur formula (1s, 1p). Petiole squamiform, the anterior and posterior faces meeting along a sharp edge. Head and body finely punctate, with sparse pilosity and dense pubescence. Color black.

*Queen*. Unknown and apparently absent.

*Male*. See descriptions in Arnold (1915, 1926).

*Larva*. Pupae of *H. peringueyi* were described by Wheeler & Wheeler (1971a).





**FIGURE 14.** Worker caste of *Hagensia havilandi marleyi*: lateral and dorsal view of body and full-face view of head (CASENT0249202, Will Ericson and [www.antweb.org](http://www.antweb.org)); world distribution of *Hagensia*.

**Geographic distribution.** *Hagensia* is restricted to the southern and eastern coastal areas of South Africa.

**Ecology and behavior.** Like most ponerines, *Hagensia* are generalist predators and scavengers. Duncan and Crewe (1994a) studied the foraging behavior of *H. havilandi* and observed exclusively diurnal solitary foraging, with no chemical recruitment (though with occasional tandem running). Foraging occurred in leaf litter, with prey consisting of a diversity of invertebrates and some plant matter; foragers apparently navigated using visual cues.

Arnold (1951) reported diurnal foraging in *H. peringueyi*, but crepuscular and nocturnal foraging in *H. havilandi*, in contrast to both Villet (1992a) and Duncan & Crewe (1994a). *Hagensia* forms subterranean nests, with colony sizes of about 10 to 50 workers in *H. havilandi* (Arnold, 1951; Villet, 1992a; Duncan & Crewe, 1994a). Reproduction occurs via a single mated gamergate worker, the queen caste having been completely lost (Peeters, 1991a). Villet (1992a) found no evidence of a dominance hierarchy among workers of *H. havilandi*.

**Phylogenetic and taxonomic considerations.** *Hagensia* was originally erected by Forel as a subgenus of *Megaponera* to house the newly described species *Megaloponera* [sic] *havilandi* Forel. Forel considered the absence of a preocular carina in this species to be of primary significance but otherwise felt that it was close to *Megaponera* (*sensu stricto*). Arnold (1915) synonymized *Hagensia* with *Euponera* (subgenus *Mesoponera*), based on characters of the males, and Forel (1917) then raised *Hagensia* to subgenus status under *Euponera*. Arnold (1926) later raised *Hagensia* to generic status based on several characters of both the worker and male castes, and revised the species-level taxonomy of the genus (Arnold, 1951). As part of his unfinished revision of ponerine taxonomy, W. L. Brown (in Bolton, 1994) synonymized *Hagensia* under *Pachycondyla* without phylogenetic justification.

We are reviving *Hagensia* to full genus status, given its morphological distinctiveness and phylogenetic age, which is consistent with that of other recognized ponerine genera. Schmidt's (2013) molecular phylogeny of the Ponerinae places *Hagensia havilandi* (the type species) with strong support within the *Odontomachus* group. The sister group of *Hagensia* is unresolved in this phylogeny, and there is no evidence of a close relationship to *Megaponera*, *Euponera*, or *Mesoponera*, though a sister relationship with any of them could not be rejected. *Hagensia* is not closely related to *Pachycondyla*.

*Hagensia*'s dorsal mandibular groove, sharply margined pronotum, and sharply edged squamiform petiole are apparently autapomorphic within the *Odontomachus* group, and hence do not assist in determining its phylogenetic position. Morphologically, *Hagensia* resembles *Megaponera* and *Ophthalmopone* most closely. The workers of these genera share large body size, dark coloration, finely punctate sculpturing, sparse or scattered pilosity, dense pubescence (sparser in minor workers of *Megaponera*), a distinct metanotal suture, narrow propodeal dorsum, slit-shaped propodeal spiracles, a simple metapleural gland orifice which opens posterolaterally, a weak or obsolete gastral constriction between A3 and A4, and toothed tarsal claws (absent in some *Ophthalmopone*). In many cases these similarities are likely plesiomorphic, but some are potentially synapomorphic for these three genera, such as the toothed tarsal claws (though toothed tarsal claws do occur in some other members of the *Odontomachus* group).

In addition, *Hagensia* shares with *Megaponera* and *Ophthalmopone* the loss of alate queens (Peeters, 1991a). Both *Hagensia* and *Ophthalmopone* have lost the queen caste entirely (reproduction is performed by gamergates), while in *Megaponera* the queen is ergatoid. It is tempting to consider this a possible synapomorphy for these taxa, but ponerine reproductive strategies seem to be quite fluid in evolutionary time and may not be good phylogenetic markers. Both gamergates and ergatoids have evolved in many other members of the *Odontomachus* group, such as at least some species of *Streblognathus*, *Leptogenys*, *Bothroponera*, and *Pseudoneoponera*.

Wheeler & Wheeler (1971a) examined *Hagensia* semipupae and found them to be quite different from those of *Megaponera*, though the phylogenetic significance of these differences is uncertain. Still, given their morphological and behavioral similarities, we believe that the most probable phylogenetic placement for *Hagensia* is as sister to *Megaponera* and *Ophthalmopone*. A close relationship with *Streblognathus* is also plausible, though the morphological evidence for this relationship is not particularly compelling.

### Species of *Hagensia*

*Hagensia* is characterized by several morphological autapomorphies that lead us to confidently group *H. peringueyi* with the type species, *H. havilandi*. Taylor (2008) informally divides the genus into three species, but we are following the traditional division of two species until a formal study of species-level taxonomy is published. See Arnold (1951) for a key to species.

*H. havilandi* (Forel, 1901): South Africa (**comb. rev.**)

*H. havilandi fochi* (Forel, 1918): South Africa (**comb. nov.**)

*H. havilandi godfreyi* Arnold, 1926: South Africa (**comb. rev.**)

*H. havilandi marleyi* Arnold, 1926: South Africa (**comb. rev.**)

*H. peringueyi* (Emery, 1899): South Africa (**comb. rev.**)  
*H. peringueyi saldanhae* Arnold, 1951: South Africa (**comb. rev.**)

### ***Leptogenys* Roger**

Fig. 15

*Leptogenys* Roger, 1861: 41 (as genus). Type-species: *Leptogenys falcigera* Roger, 1861: 42; by subsequent designation of Bingham, 1903: 52.  
*Lobopelta* Mayr, 1862: 714, 733 (as genus in Ponerinae [Poneridae]). Type-species: *Ponera diminuta* Smith, F., 1857: 69; by subsequent designation of Bingham, 1903: 54. Forel, 1892: 520 (*Lobopelta* as subgenus of *Leptogenys*); Emery, 1896: 177; Bolton 1975a:240 (*Lobopelta* as junior synonym of *Leptogenys*).  
*Prionogenys* Emery, 1895b: 348 (as genus). Type-species: *Prionogenys podenzanai* Emery, 1895b: 349; by monotypy. Taylor, 1988: 33 (*Prionogenys* as junior synonym of *Leptogenys*).  
*Machaerogenys* Emery, 1911: 100 (as subgenus of *Leptogenys*). Type-species: *Leptogenys truncatirostris* Forel, 1897: 195; by original designation. Brown, 1973: 181; Bolton, 1975a:240 (*Machaerogenys* as junior synonym of *Leptogenys*).  
*Odontopelta* Emery, 1911: 101 (as subgenus of *Leptogenys*). Type-species: *Leptogenys turneri* Forel, 1900a: 67; by monotypy. Brown, 1973: 183; Taylor & Brown, 1985: 32 (*Odontopelta* as junior synonym of *Leptogenys*).  
*Dorylozelus* Forel, 1915b: 24 (as genus). Type-species: *Dorylozelus mjobergi* Forel, 1915b: 25 (junior secondary homonym in *Leptogenys*, replaced by *Leptogenys tricola* Taylor, 1969: 132); by monotypy. Taylor, 1969: 132 (*Dorylozelus* as junior synonym of *Leptogenys*).  
*Microbolbos* Donisthorpe, 1948f: 170 (as genus). Type-species: *Microbolbos testaceus* Donisthorpe, 1948: 170; by original designation. Wilson, 1955b: 136 (*Microbolbos* as junior synonym of *Leptogenys*).

*Leptogenys* is the largest ponerine genus, with 211 described extant species and one described fossil species, and is widespread in the tropical and subtropical regions of the world. It is probably sister to *Myopias*. The genus is notable for its ergatoid queens, frequent specialization on isopods, and for containing species that exhibit an army ant-like lifestyle.

**Diagnosis.** Workers of *Leptogenys* are easily distinguished from those of other ponerine genera. Usually the presence of pectinate tarsal claws is enough to identify the genus (as no other ponerines have pectinate tarsal claws), though the tarsal claws of some *Leptogenys* species are not pectinate. Other diagnostic characters in combination include: slender build, linear mandibles, triangular or distinctly lobed anterior clypeal margin, round propodeal spiracles (rarely slit-shaped), and strong gastral constriction (sometimes only moderately so, and constriction absent in many Afrotropical species of the *L. guineensis* and *L. stuhlmanni* groups). *Leptogenys* is morphologically most similar to *Myopias*, but *Myopias* usually has a blunt rectangular projection on the anterior clypeal margin, has simple tarsal claws, and has more mandibular teeth than *Leptogenys*.

**Synoptic description.** *Worker.* Small to large (TL 2.1–14.5 mm) slender ants with the standard characters of Ponerini. Mandibles subtriangular to curvilinear, often without a distinct basal margin, usually lacking teeth except for a single large apical tooth (mandibles with multiple teeth in the *L. processionalis* group), and articulating with the head at the extreme anterolateral corners of the head; mandibles sometimes with a basal groove. Anterior margin of clypeus angular, with a blunt or sharp point medially, and usually longitudinally carinate medially; sometimes with a narrow blunt lobe medially and a sharp tooth to each side. Frontal lobes small. Eyes small to large, placed at or anterior to head midline. Metanotal groove shallowly to deeply impressed. Propodeum broad to moderately narrowed dorsally. Propodeal spiracles usually small and round, though occasionally a short slit. Tarsal claws usually pectinate, though sometimes with only four or fewer teeth and very rarely simple. Metatibial spur formula (1s, 1p). Petiole usually nodiform (more squamiform in the *L. processionalis* group), though variable in shape. Girdling constriction between pre- and postsclerites of A4 apparent (less pronounced in the *L. processionalis* group, absent in many species of the *L. guineensis* and *L. stuhlmanni* groups). Stridulitrum present on pretergite of A4. Hypopygium occasionally with a row of stout setae on either side of the sting. Head and body usually shining, though often punctate, foveolate, striate, or rugoreticulate. Head and body with scattered to abundant pilosity, and usually no pubescence. Color variable, testaceous to black.

*Queen.* Usually ergatoid, flightless and very similar to the worker but with a broader petiole and larger gaster, and often vestigial ocelli; ergatoids also often differ from conspecific workers in various minor characters. The queens of one species (*L. ergatogyna*) are not ergatoid, but are still wingless; unlike other *Leptogenys* queens, they have the ocelli and thoracic modifications typical of alate ponerine queens (Wheeler, 1922b; Bolton, 1975a). The



queens of at least one species, *L. langi*, are fully winged (Wheeler, 1923a). Queens are fully absent from at least a handful of species in which reproduction is performed by gamergate workers (Davies *et al.*, 1994; Ito, 1997; Gobin *et al.*, 2008).

*Male.* See descriptions in Arnold (1915), Wheeler (1922b), Bolton (1975a), and Yoshimura & Fisher (2007).

*Larva.* The larvae of various *Leptogenys* species have been described by Wheeler & Wheeler (1952, 1964, 1971a, 1974, 1976, 1986b) and Petralia & Vinson (1980).

**Geographic distribution.** *Leptogenys* is abundant and species-rich throughout the tropical regions of the world, and to a lesser extent the subtropical regions (Wheeler, 1922b; Bolton, 1975a). Some members of the *L. maxillosa* species group are widely-distributed tramp species (Bolton, 1975a). *L. falcigera*, for example, was one of the first ants introduced to the Hawaiian Islands (Kirschenbaum & Grace, 2007).

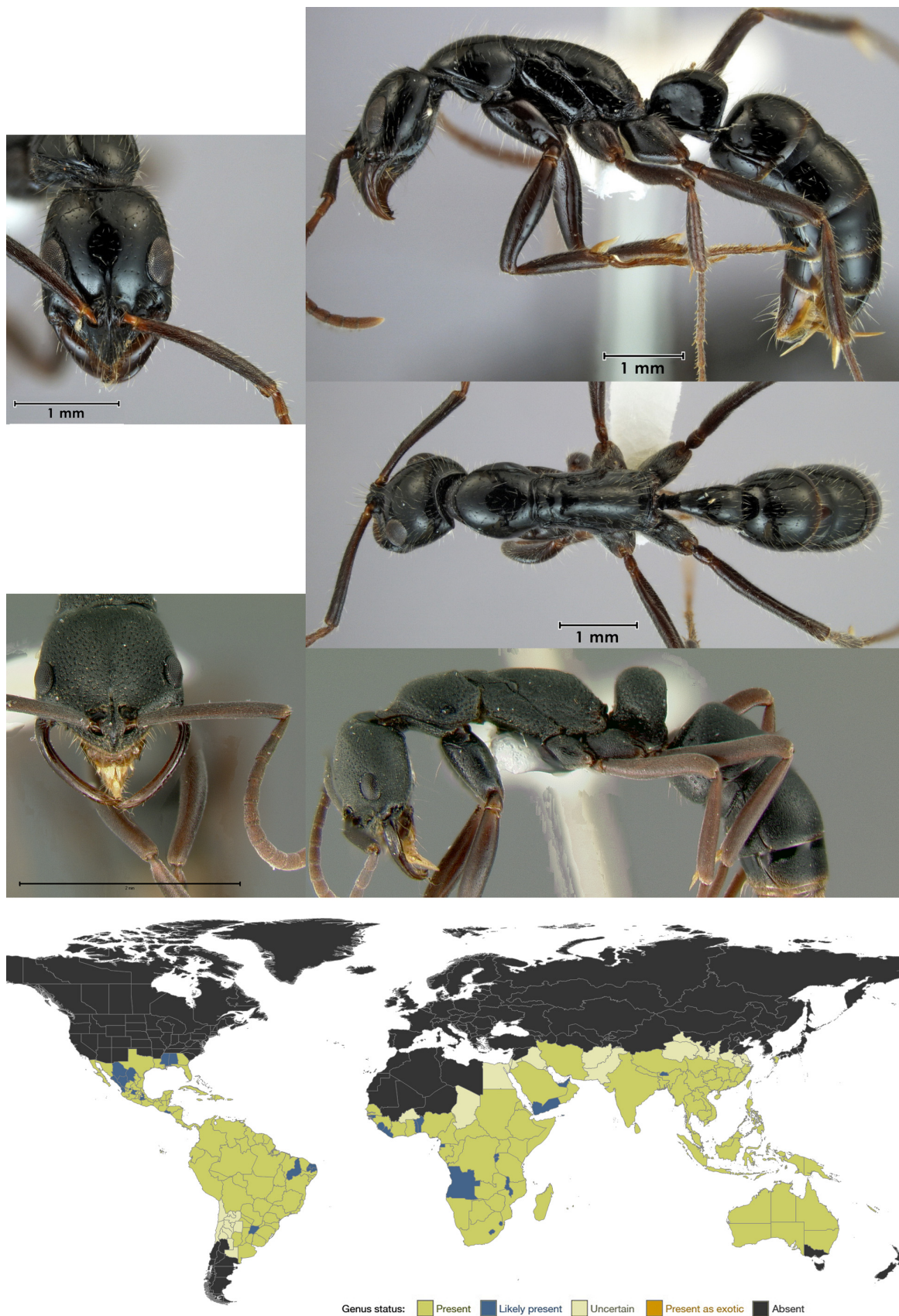
**Ecology and behavior.** *Leptogenys* dwarfs every other ponerine genus in terms of number of described species, accounting for roughly a quarter of the subfamily's species diversity, and is considered to be a major component of many tropical faunas (Peeters & Ito, 2001). Though there are numerous exceptions (see discussion below), most *Leptogenys* species follow a general pattern of having small colonies, nesting in soil or rotting wood, having monomorphic workers which forage individually and are specialist predators of isopods, and having a single ergatoid queen which performs reproduction for the colony.

Average colony sizes vary greatly among *Leptogenys* species. While colonies of most species have between 25 and 300 workers, some Southeast Asian species average fewer than 10 workers per colony (Ito, 1997), and the colonies of the mass raiding members of the *L. processionalis* group can have over 50,000 workers, the largest colonies known in the Ponerinae (Maschwitz *et al.*, 1989; Witte & Maschwitz, 2000).

Most *Leptogenys* occur in tropical forests, and like most ponerines construct their nests in soil, leaf litter, or rotting wood (Forel, 1893b; Arnold, 1915; Mann, 1921; Wheeler, 1922b; Wilson, 1958b; Lenko, 1966; Maschwitz & Mühlenberg, 1975; Bolton, 1975a; Peeters, 1991b; Villet *et al.*, 1991; Duncan & Crewe, 1994b; Ito & Ohkawara, 2000). A few species are known to nest subarborally in dead tree branches (Bolton, 1975a) and some have been found nesting inside abandoned termitaries (Déjean *et al.*, 1996, 1997). Due to the typically ephemeral nature of their nesting sites, many *Leptogenys* conduct frequent emigrations to new nest sites (Maschwitz & Schönegge, 1983; Shivashankar, 1985; Duncan & Crewe, 1994b; Peeters & Ito, 2001). Members of the *L. diminuta* and *L. processionalis* groups are nomadic and form temporary bivouacs similar to those of the true army ants (Wilson, 1958b; Maschwitz & Mühlenberg, 1975; Maschwitz *et al.*, 1989).

*Leptogenys* workers are typically nocturnal or crepuscular epigeic foragers (*e.g.*, Arnold, 1915; Wheeler, 1922b; Bolton, 1975a; Shivashankar, 1985; Maschwitz *et al.*, 1989; Kumar, 1990; Déjean & Evraerts, 1997; Witte & Maschwitz, 2000), although some species forage diurnally (*e.g.*, *L. breviceps*; Wilson, 1958b; *L. intermedia*: Duncan & Crewe, 1994b) and some are cryptobiotic (*e.g.*, *L. testacea*: Bolton, 1975a). Two species, *L. khammouanensis* from Laos, (Roncin & Deharveng, 2003) and an undetermined species from Texas (Cokendolpher *et al.*, 2009) dwell deep inside caves and are the only known troglobitic ponerine species. *Leptogenys* workers are generally very agile, and while some species respond aggressively to nest disturbance and have painful stings, others are more timid (Jerdon, 1851; Wheeler, 1922b; Wilson, 1958b; pers. obs.). As is typical for ponerines, these venomous stings are also used in prey capture. For example, Maschwitz *et al.* (1979) found that *L. chinensis* invariably stings and paralyzes its termite prey. Some *Leptogenys* species also have additional chemical defenses. *L. processionalis* and other species have an abdominal gland (the Jessen's gland) whose secretions have an unpleasant smell and apparently serve a defensive function (Jessen, 1977; Buschinger & Maschwitz, 1984). *L. processionalis* also produces compounds in an unidentified cephalic gland, which are hypothesized to act as an early-warning system for predators (Fales *et al.*, 1992).

Déjean & Evraerts (1997) classified the predatory behavior of *Leptogenys* species in three categories: solitary hunting and retrieval of prey, group predation after recruitment by a scout, and swarm raiding. While this classification is useful, it is somewhat simplistic since *Leptogenys* species show a continuum of foraging behaviors from completely solitary foraging to mass raiding, with various degrees of nestmate recruitment between these extremes (see also Maschwitz & Steghaus-Kovac, 1991). Most species practice solitary hunting and retrieval of prey, and most of these are specialist predators of isopods, though some species are known to specialize on earwigs (*L. sp. nr. kraepelini*: Steghaus-Kovac & Maschwitz, 1993; also *L. rouxi* to a limited extent: Wilson, 1958b), termites (*e.g.*, *L. binghami*: Maschwitz & Mühlenberg, 1975; *L. unistimulosa*: Mill, 1982a) or ant queens (*L. neutralis*: Wheeler, 1933b).



**FIGURE 15.** Worker caste of *Leptogenys*. Upper specimen: *Leptogenys darlingtoni*: lateral and dorsal view of body and full-face view of head (ANIC32-059614). Lower specimen: *Leptogenys maxillosa*: lateral view of body and full-face view of head (Philippines, G.Alpert, MCZC); world distribution of *Leptogenys*.

The frequent specialization on isopods is a unique ecological characteristic of *Leptogenys* and is probably the plesiomorphic condition within the genus (Déjean & Evraerts, 1997). Numerous *Leptogenys* species have been reported as partially or exclusively specializing on isopods, including *L. attenuata* and *L. schwabi* (Duncan & Crewe, 1993; Davies *et al.*, 1994), *L. bohlsi* (Lenko, 1966), *L. bubastis*, *L. camerunensis*, *L. donisthorpei*, *L. mexicana*, *L. wheeleri*, and three undescribed species (Déjean, 1997; Déjean & Evraerts, 1997; Déjean *et al.*, 1999), *L. conradti* and an unidentified species (Lévieux, 1982, 1983), *L. elongata* (Wheeler, 1904), *L. falcigera* (Kirschenbaum & Grace, 2007), *L. manni* (Trager & Johnson, 1988), *L. "propefalcigera"* (Freitas, 1995), *L. rouxi* (Wilson, 1958b), *L. stuhlmanni* (Arnold, 1915), and *L. triloba* (Wilson, 1958b, 1959a). The mandibular structure of *Leptogenys* seems well suited to predation on isopods: the mandibles are typically long, narrow, curved, and articulated at the extreme anterolateral corners of the head (Bolton, 1975a, 1994; Déjean *et al.*, 1999), making them excellent tools for clasping round objects such as rolled-up isopods. The medially pointed clypeus probably contributes to this process as well (Trager & Johnson, 1988). Déjean & Evraerts (1997) studied the behavior of isopod-hunting *Leptogenys* and found that the behavioral sequence employed by a *Leptogenys* worker depends on the length of its mandibles and the species and size of the isopod, with different *Leptogenys* species better adapted to hunting different prey species and sizes. Interestingly, at least one species (*L. mexicana*) chemically attracts its isopod prey to its nest, a remarkable strategy which has not been recorded in any other ant species (Déjean & Evraerts, 1997).

Limited recruitment to clustered or large prey may occur in some predominantly solitary foraging species. For example, the African species *L. schwabi*, which preys on termites, isopods and amphipods, and *L. attenuata*, which feeds on isopods and amphipods, hunt individually but sometimes recruit nestmates to large or clustered prey sources (Arnold, 1915; Duncan & Crewe, 1993; Davies *et al.*, 1994; Déjean & Evraerts, 1997). Limited recruitment was also reported in *L. peugeuti* (Janssen *et al.*, 1997).

True group predation, in which workers engage in obligate collective foraging, is characteristic of several African and Asian *Leptogenys* species (Déjean & Evraerts, 1997). Perhaps the simplest manifestation of this strategy occurs in the generalist Asian species *L. diminuta* and its relatives (*e.g.*, *L. purpurea*; Wilson, 1958a, 1958b; Maschwitz & Mühlenberg, 1975; Maschwitz & Steghaus-Kovac, 1991). Foraging in *L. diminuta* begins when scouts leave the nest in search of arthropod prey. Upon finding prey the successful scout returns to its nest and lays down a chemical trail. Once back at the nest, it recruits a group of from three to nearly 300 workers and leads them to the prey, which they attack and retrieve cooperatively (Maschwitz & Mühlenberg, 1975; Kumar, 1990). Another Asian species, *L. chinensis*, utilizes a similar strategy but is a specialist predator of termites and hunts in groups of 10 to 50 individuals (Maschwitz & Schönegge, 1983). Wheeler (1936; also Bingham, 1903) lists additional Asian *Leptogenys* species that are known to conduct organized raids on termites, including *L. aspera*, *L. binghami*, *L. birmana*, and *L. kitteli*, and provides interesting observations of termite raiding by some other species.

Several *Leptogenys* species have done away with the use of scouts altogether, instead employing swarm raids akin to those of the true army ants. For example, workers of the African species *L. intermedia* form foraging trails from which groups of workers (approximately 30 to 100) cooperatively search for and retrieve leaf litter arthropods (Duncan & Crewe, 1993, 1994b). Members of the Southeast Asian *L. processionalis* species group have increased the scale of this swarm raiding, hunting in massive groups of up to 40,000 workers (Jerdon, 1851; Maschwitz & Mühlenberg, 1975; Maschwitz & Steghaus-Kovac, 1991; Witte & Maschwitz, 2000). The foraging behaviors of three species in the *L. processionalis* group have been studied to date, and while there are many basic similarities among these species, there are also some interesting differences. *L. processionalis* itself is a crepuscular forager which preys predominantly on termites, though it also takes other arthropods and annelids (Shivashankar, 1985). Foraging workers utilize permanent branching trails radiating from the nest, and successful foragers recruit nestmates from the trail to harvest prey, which is collectively dispatched and dismembered but individually retrieved (Maschwitz & Mühlenberg, 1975). Unlike some other members of the *L. processionalis* group, *L. processionalis* does not emigrate frequently, but instead may persist at a nest site and utilize the same trails for up to several months; emigration is initiated by environmental factors (Maschwitz & Mühlenberg, 1975). Ganeshiah & Veena (1991) studied the formation and topology of *L. processionalis* foraging trails and found that they were constructed to maximize travel and prey retrieval efficiency. The flow of individuals in *L. processionalis* trails was modeled by John *et al.* (2008).

One of the best studied members of the *L. processionalis* group is *L. distinguenda*, which is a generalist predator and will take anything from arthropods and other invertebrates to small vertebrates (Witte & Maschwitz,



2000). *L. distinguenda* has taken the army ant lifestyle even further than has *L. processionalis*, as its massive colonies are even larger than those of *L. processionalis* (nearly 50,000 versus 16,000 workers, respectively: Maschwitz & Mühlenberg, 1975; Witte & Maschwitz, 2000). More importantly, *L. distinguenda* colonies emigrate frequently, with emigrations initiated when suitable nest sites are discovered in the course of a raid (Witte & Maschwitz, 2000).

Finally, an undescribed species closely related to *L. mutabilis* was studied by Maschwitz *et al.* (1989) and found to have the largest colonies of any ponerine (over 50,000 workers). These generalist predators forage nocturnally in massive swarms of up to 40,000 workers and capture and retrieve their prey cooperatively. Like *L. distinguenda*, this species emigrates to new bivouac sites frequently, from every several hours to every 10 days. The combination of obligate collective foraging and nomadism in this and related *Leptogenys* species makes them quite close to embracing a full army ant lifestyle (*sensu* Brady, 2003), with the main differences being that they do not display dichthadiigyny or pulsed brood production (Maschwitz *et al.*, 1989).

Chemical communication has been studied in several *Leptogenys* species, especially those which exhibit mass raiding behavior. Jessen *et al.* (1979) characterized the abdominal glands of *L. processionalis* and *L. chinensis*. In both species, recruitment pheromones are produced in both the venom and pygidial glands (Maschwitz & Schönegge, 1977, 1983; Duncan & Crewe, 1994b; Witte & Maschwitz, 2002). In *L. processionalis*, the secretions of these glands act as orientation pheromones, maintaining the cohesiveness of groups of workers, and are utilized in both foraging and emigrations. Due to differences in chemical composition, workers are able to distinguish between raiding and emigration trails (Witte & Maschwitz, 2002). *L. diminuta* produces recruitment pheromones in the pygidial gland (Attygalle *et al.*, 1988, 1991; Steghaus-Kovac *et al.*, 1992), and also produces pheromones in the venom and Dufour glands (Maile *et al.*, 2000). Kern & Bestmann (1993) studied the electrophysiological response of the antennae of *L. diminuta* workers to trail and recruitment pheromones. *L. binghami* also produces a trail pheromone, but it is primarily utilized during emigrations (Maschwitz & Mühlenberg, 1975). Janssen *et al.* (1997) characterized the trail pheromone of *L. peuqueti*, which is produced in the venom gland and is the most complex trail pheromone known in any ant.

The diversity of foraging strategies and recruitment pheromones in *Leptogenys* make it an excellent system for understanding the evolutionary origins of cooperative foraging (Maschwitz & Schönegge, 1983), as well as chemical communication and prey specialization. Most likely, the ancestral *Leptogenys* was a solitary forager (though perhaps with limited recruitment) which specialized at least partially on isopods. Mass raiding species probably arose from this ancestral archetype, through stages with progressively greater emphasis on collective foraging. This progression is illustrated well by extant species of *Leptogenys*. While Schmidt's (2013) phylogenetic data for *Leptogenys* are limited, it appears that the *L. processionalis* group may form the sister group to the remainder of the genus. *L. diminuta* and *L. attenuata*, both species which exhibit at least limited recruitment, are closely related to each other and to species not known to engage in much recruitment. Greater taxon sampling and natural history observations of more species will be required in order to reconstruct the evolutionary history of *Leptogenys* foraging behavior.

Reproduction in nearly all *Leptogenys* species is performed by ergatoid queens. Exceptions to this general rule include one species with fully winged queens (*L. langi*: Wheeler, 1923a) and one species with queens that are flightless but have other characteristics typical of normal alate queens (*L. ergatogyna*: Wheeler, 1922b; Bolton, 1975a). Finally, a few species have completely lost the queen caste and instead reproduce via gamergate workers (*L. schwabi*: Davies *et al.*, 1994; Peeters, 1991b; *L. peuqueti* and three undescribed species: Ito, 1997; Gobin *et al.*, 2008). The near universality of flightlessness in *Leptogenys* queens is probably a major cause of the immense species diversity of the genus, as their poor dispersal ability undoubtedly contributes to reproductive isolation and subsequent allopatric speciation.

Most *Leptogenys* species which have been examined are monogynous (*e.g.*, *L. arnoldi*: Arnold, 1915; *L. attenuata* and *L. castanea*: Villet *et al.*, 1991; *L. diminuta*, *L. kraepelini*, *L. myops*, and five undescribed species: Ito, 1997; *L. intermedia*: Duncan & Crewe, 1994b; *L. sp. nr. kraepelini*: Steghaus-Kovac & Maschwitz, 1993; *L. sp. nr. mutabilis*: Maschwitz *et al.*, 1989; *Leptogenys* in general: Wheeler, 1922b). Among species with ergatoid queens, polygyny has only been observed in a single Neotropical species (K. Okhawara & S. Higashi, pers. comm. cited in Ito, 1997). *L. diminuta* and its relatives are unusual in that their colonies contain a single mated ergatoid queen but also additional unmated ergatoids which perform the same activities as workers; interestingly, the morphological distinction between queens and workers is even less pronounced in this species group than in other

*Leptogenys* (Ito & Ohkawara, 2000). All known *Leptogenys* species with gamergate workers are polygynous (Davies *et al.*, 1994; Ito, 1997; Monnin & Peeters, 2008). Davies *et al.* (1994) found that mated gamergates in *L. schwabi* pheromonally inhibit reproduction by unmated workers; this study also includes one of the only examinations of *Leptogenys* division of labor. Asexual reproduction by *Leptogenys* workers presumably occurs, as it does in many other ponerines, but to our knowledge this has not been documented. While workers of those species with gamergates are obviously sexually reproductive, the workers of several *Leptogenys* species lack ovaries and are completely sterile (*e.g.*, *L. intermedia*, *L. castanea*, and *L. attenuata*; Villet *et al.*, 1991). Probably not coincidentally, queens in these species have an unusually large number of ovarioles (Villet *et al.*, 1991).

As with foraging behavior, the diversity of reproductive systems in *Leptogenys* makes the genus an excellent model system for understanding the evolution of flightlessness in queens, the loss of reproductive ability in workers, and the loss of the queen caste (Villet *et al.*, 1991). While *Leptogenys* is almost certainly descended from an ancestor with winged queens, the almost complete absence of winged queens in extant *Leptogenys* implies that ergatoid queens are plesiomorphic within the genus. The phylogenetic placement of *L. langi* (which has alate queens) and *L. ergatogyna* (with queens intermediate between alates and ergatoids) are unknown but are of particular interest as these species may represent a sister group (or groups) to the rest of the genus. Alternatively, they may represent reversals from ancestors with ergatoid queens. Also of great interest are the phylogenetic placements of species with gamergates or sterile workers.

Virtually nothing is known about *Leptogenys* mating behavior, but since queens of most *Leptogenys* species are flightless, mating may occur in the natal nest of the unmated queen, with the males finding the nest through chemical means. Alternatively, males may locate emigrating colonies and mate en route. Hölldobler & Engel-Siegel (1982) examined the abdominal glands of *L. diminuta* males and discovered that they have a huge sternal gland. They speculated that the secretions of this gland might mimic queen pheromones, enabling the males to enter foreign nests and thus mate with virgin queens. In *L. processionalis* and *L. chinensis*, males fly from their natal nest and then land and search for recruitment trails laid by conspecific workers. Once located, the males follow these trails, and could mate with ergatoid queens on the trails (Maschwitz & Mühlenberg, 1975; Maschwitz & Schonegge, 1983; Peeters, 1991a). Maschwitz *et al.* (1989) reported that males of an undescribed species closely related to *L. mutabilis* are carried by workers during emigrations.

As is true for most ponerines, the myrmecophile fauna associated with *Leptogenys* is virtually unknown, perhaps reflecting a true scarcity of such associations. In this regard *L. distinguenda* is exceptional, as it has a rich assemblage of myrmecophiles, including mites, isopods, bristletails, silverfish, phorid flies, springtails, spiders, various beetles, and even the only known myrmecophilous gastropod (Ferrara *et al.*, 1987; Witte *et al.*, 1999, 2002; Kistner *et al.*, 2003). It is probably not a coincidence that the other ponerine species with a rich myrmecophile fauna (*Megaponera analis*) also has relatively large colonies.

**Phylogenetic and taxonomic considerations.** *Leptogenys* was erected by Roger (1861) to house three newly described species as well as *Ponera maxillosa* F. Smith. Bingham (1903) later designated the first of these new species, *L. falcigera*, as the type species of the genus. Subsequent authors placed *Leptogenys* variously in Ponerini (*e.g.*, Emery, 1895d) or in its own tribe, Leptogenyini (starting with Forel, 1893a; also called Leptogenysii by some authors). Emery (1911) retained *Leptogenys* in Leptogenyini based on the shape of the mandibles, the gaster, and the pectination of the tarsal claws. Brown (1963) argued that the pectination of the tarsal claws (which isn't even universal in *Leptogenys*) was a weak character to base a tribe on, and moved *Leptogenys* into Ponerini. Schmidt's (2013) molecular phylogeny of the Ponerinae confirms that *Leptogenys* is indeed nested within Ponerini.

The genus-level taxonomy of *Leptogenys* has also been complex, due to its numerous junior synonyms. Mayr (1862) erected the genus *Lobopelta* and noted its close similarity to *Leptogenys*, basing his generic distinction mainly on differences in the mandibular and clypeal structure. Most subsequent authors considered *Lobopelta* a valid genus, though some treated it as a subgenus or junior synonym of *Leptogenys* (*e.g.*, Forel, 1892, Emery, 1896). *Lobopelta* eventually came to hold the majority of the species now included in *Leptogenys*. Schmidt's (2013) molecular phylogeny of the Ponerinae includes several species formerly placed in *Lobopelta* (including its type species, *L. diminuta*), as well as the type species of *Leptogenys*, *L. falcigera*, which clearly emerges from within a non-monophyletic *Lobopelta*. We are therefore retaining *Lobopelta* as a junior synonym of *Leptogenys*.

Emery (1895a) erected the genus *Prionogenys* based on its unusually long mandibles. Taylor (1988) convincingly argued for the junior synonymy of *Prionogenys* under *Leptogenys*, pointing out that derived mandibular structure (and other cephalic characters) is a common occurrence in *Leptogenys*, presumably related to

adaptation to different types of prey. He also suggested that the species formerly placed in *Prionogenys* may not be sisters, rather that their unusually long mandibles may be convergently derived. Though Schmidt (2013) did not sample either species in his molecular phylogeny, we are maintaining *Prionogenys* as a junior synonym of *Leptogenys* given the lack of any compelling morphological evidence that they are distinct.

Emery (1911) erected *Machaerogenys* as a subgenus of *Leptogenys*, again based on supposed differences in the mandibles and clypeus. Brown (1973) and Bolton (1975a) provisionally synonymized *Machaerogenys* under *Leptogenys*, without any explanation. Though Schmidt (2013) did not sample any former *Machaerogenys* species in his molecular phylogeny, we do not see any argument for resurrecting it as a valid subgeneric name, and in fact it appears to us to be very closely related to *L. falcigera*, the type species of *Leptogenys*. Emery (1911) also created the subgenus *Odontopelta*, which he differentiated from typical *Leptogenys* based on the mandibles, clypeus, and the petiole. As with *Machaerogenys*, we have seen no evidence to suggest that it is nothing more than a derived *Leptogenys*, and we follow Brown (1973) in treating it as a junior synonym of *Leptogenys*.

The most unusual junior synonym of *Leptogenys* is *Dorylozelus* (Forel, 1915b). The single species originally in this genus, *D. mjobergi* (now *Leptogenys tricola*), is morphologically interesting in that it superficially resembles a cross between a ponerine and the army ant genus *Dorylus* (hence the genus name; Forel, 1915b; Brown, 1960). It is apparently adapted to a hypogeic lifestyle, with greatly reduced eyes, flattened scapes, a very smooth cuticle, and short robust legs (Taylor, 1969). The taxonomic placement of this species was unclear for decades after its description, with authors variously placing it in Ponerini (Forel, 1917), its own tribe Dorylozelini (also spelled Dorylozeli; Wheeler, 1922b; Donisthorpe, 1943b), or even *incertae sedis* in Amblyoponini (Brown, 1960). Taylor (1969) re-examined the type specimen (the only specimen of the species ever collected) and deduced that it was in fact a *Leptogenys*, given its pectinate tarsal claws. He also suggested that *L. tricola* (as he renamed it) is likely a member of the *L. processionalis* species group, a hypothesis that we find plausible, as the relatively broad head and wide mandibles of *L. tricola* are reminiscent of that group. If true, this would suggest the possibility of a hypogeic army ant lifestyle similar to many *Dorylus*, perhaps explaining the superficial morphological convergence between these taxa. An alternative hypothesis is that *Dorylozelus* is closely related to the *bequaerti* species group of *Centromyrmex*, with which it bears a remarkable superficial resemblance. The large number of significant morphological differences between them makes it more likely that this is a simple case of convergence, but without corroborating molecular evidence the possibility remains that *Dorylozelus* is in fact close to *Centromyrmex*.

The final junior synonym of *Leptogenys* is *Microbolbos*, which Donisthorpe (1948) described to house a single species, *M. testaceus* (now *Leptogenys testacea*). Wilson (1955b) re-examined the holotype and concluded that it was in fact a member of *Leptogenys*. The species is morphologically unusual in that its tarsal claws are simple and it has multiple mandibular teeth, but Wilson (1955b) points out that other *Leptogenys* species have these characters. We see no reason to disagree with his assessment that *Microbolbos* is a junior synonym of *Leptogenys*.

*Leptogenys* is a member of the *Odontomachus* group, and along with its probable sister group *Myopias* (and possibly *Mesoponera*) it apparently forms the sister group to the rest of the *Odontomachus* group (Schmidt, 2013). *Leptogenys* is morphologically most similar to *Myopias*, with both genera typically having linear or at least subtriangular mandibles, round propodeal spiracles, a nodiform petiole, a strong constriction between A3 and A4, a prominent sting, and relatively smooth and shiny cuticle. Of these, the only character that is likely to be truly synapomorphic for these genera is the non-triangular mandible shape, and possibly the prominent sting, with most of the other characters likely to be plesiomorphies. Round propodeal spiracles are lacking in most other members of the *Odontomachus* group except *Brachyponera* and many *Mesoponera*, but the plesiomorphic condition in the group is uncertain.

Except for the small sampling of species in Schmidt's (2013) molecular phylogeny of the Ponerinae, nothing is known about the internal phylogeny of *Leptogenys*. Schmidt's phylogeny suggests an early split between the *L. processionalis* species group and the remainder of the genus. Given this fact, as well as their divergent morphological structures and behavior, the *L. processionalis* group could arguably be split off into a separate genus, though we are not going to take that step. The *L. falcigera* group (*Leptogenys sensu stricto*), with its very thin and curved mandibles, has clearly emerged from within a non-monophyletic "*Lobopelta*". The historical biogeography of *Leptogenys* is likely to be complex, with much migration between Africa and Asia/Australia (Bolton, 1975a) and probably at least two separate invasions of the New World (including once by relatives of *L. falcigera*). Given the potential utility of *Leptogenys* as a model system for studying the evolution of foraging and



reproductive behavior, as well as historical biogeography, a detailed species-level phylogeny of *Leptogenys* would be extremely valuable. In fact, there is probably no better target for such work within the Ponerinae, and it should be made a priority for near-term study.

### Species of *Leptogenys*

Wilson (1958b) gives a key to Melanesian *Leptogenys* species, Bolton (1975a) provides keys to the African and Malagasy *Leptogenys* species, Xu (2000) gives a key to Chinese *Leptogenys* species, and Lattke (2011) has revised the New World taxa.

*L. acutangula* Emery, 1914: New Caledonia  
*L. acutirostris* Santschi, 1912: Madagascar  
*L. adlerzi* Forel, 1900: Australia  
*L. alluaudi* Emery, 1895: Madagascar  
*L. amazonica* Borgmeier, 1930: Brazil  
*L. amon* Bolton, 1975: Cameroon  
*L. amu* Lattke, 2011: Colombia  
*L. angusta* (Forel, 1892): Madagascar  
*L. angustinoda* Clark, 1934: Australia  
*L. anitae* Forel, 1915: Australia  
*L. ankhesa* Bolton, 1975: DRC  
*L. antillana* Wheeler, W.M. & Mann, 1914: Haiti  
*L. antongilensis* Emery, 1899: Madagascar  
*L. arcistrostris* Santschi, 1926: Madagascar  
*L. arcuata* Roger, 1861: Suriname  
*L. arnoldi* Forel, 1913: Zimbabwe  
*L. aspera* (André, 1889): Vietnam  
*L. assamensis* Forel, 1900: India  
*L. attenuata* (Smith, F., 1858): South Africa  
*L. australis* (Emery, 1888): Argentina  
*L. bellii* Emery, 1901: Ethiopia  
*L. bidentata* Forel, 1900: Australia  
*L. bifida* Lattke, 2011: Honduras  
*L. binghamii* Forel, 1900: Myanmar  
*L. birmana* Forel, 1900: Myanmar  
*L. bituberculata* Emery, 1901: New Guinea  
*L. bohlsi* Emery, 1896: Paraguay  
*L. borneensis* Wheeler, W.M., 1919: Borneo  
*L. breviceps* Viehmeyer, 1914: New Guinea  
*L. bubastis* Bolton, 1975: Cameroon  
*L. buyssoni* Forel, 1907: Ethiopia  
*L. caeciliae* Viehmeyer, 1912: New Guinea  
*L. camerunensis* Stitz, 1910: Cameroon  
*L. carbonaria* Lattke, 2011: Colombia  
*L. carinata* Donisthorpe, 1943: India  
*L. castanea* (Mayr, 1862): South Africa  
*L. centralis* Wheeler, W.M., 1915: Australia  
*L. chalybaea* (Emery, 1887): Borneo  
*L. chamela* Lattke, 2011: Mexico  
*L. chelifera* (Santschi, 1928): Australia  
*L. chinensis* (Mayr, 1870): China  
*L. ciliata* Lattke, 2011: Ecuador

*L. clarki* Wheeler, W.M., 1933: Australia  
*L. coerulescens* Emery, 1895: Madagascar  
*L. confucii* Forel, 1912: Taiwan  
*L. conigera* (Mayr, 1876): Australia  
*L. conradti* Forel, 1913: Cameroon  
*L. consanguinea* Wheeler, W.M., 1909: Mexico  
*L. cordoba* Lattke, 2011: Mexico  
*L. corniculans* Lattke, 2011: Brazil  
*L. cracens* Lattke, 2011: Mexico  
*L. crassicornis* Emery, 1895: Myanmar  
*L. crassinoda* Arnold, 1926: South Africa  
*L. crudelis* (Smith, F., 1858): Brazil  
*L. crustosa* Santschi, 1914: Guinea  
*L. cryptica* Bolton, 1975: Ghana  
*L. cuneata* Lattke, 2011: Ecuador  
*L. dalyi* Forel, 1900: India  
*L. darlingtoni* Wheeler, W.M., 1933: Australia  
*L. davydovi* Karavaiev, 1935: Vietnam  
*L. deborae* Lattke, 2011: Venezuela  
*L. dentilobis* Forel, 1900: India  
*L. diatra* Bolton, 1975: Cameroon  
*L. diminuta* (Smith, F., 1857): Borneo  
*L. diminuta deceptrix* Forel, 1901: India  
*L. diminuta diminutolaeviceps* Forel, 1900: India  
*L. diminuta fruhstorferi* Emery, 1896: Indonesia (Java)  
*L. diminuta laeviceps* (Smith, F. 1857): Borneo  
*L. diminuta nongnongi* Karavaiev, 1925: Indonesia (Java)  
*L. diminuta opacinodis* (Emery, 1887): Indonesia (Sumatra)  
*L. diminuta palliseri* Forel, 1900: India  
*L. diminuta sarasinorum* Forel, 1900: Sri Lanka  
*L. diminuta striatula* Emery, 1895: Myanmar  
*L. diminuta tjibodana* Karavaiev, 1926: Indonesia (Java)  
*L. diminuta woodmasoni* (Forel, 1886): India  
*L. donisthorpei* Mann, 1922: Honduras  
*L. drepanon* Wilson, 1958: New Guinea  
*L. ebenina* Forel, 1915: Australia  
*L. elegans* Bolton, 1975: Nigeria  
*L. elongata* (Buckley, 1866): United States  
*L. emeryi* Forel, 1901: New Britain  
*L. emiliae* Forel, 1902: India  
*L. ergatogyna* Wheeler, W.M., 1922: DRC  
*L. erugata* Lattke, 2011: Venezuela  
*L. erythraea* Emery, 1902: Ethiopia  
*L. excellens* Bolton, 1975: DRC  
*L. excisa* (Mayr, 1876): Australia  
*L. exigua* Crawley, 1921: Australia  
*L. exudans* (Walker, 1859): Sri Lanka  
*L. falcigera* Roger, 1861: Sri Lanka  
*L. fallax* (Mayr, 1876): Australia  
*L. famelica* Emery, 1896: Costa Rica  
*L. ferrarii* Forel, 1913: Zimbabwe  
*L. foraminosa* Lattke, 2011: Costa Rica

*L. foreli* Mann, 1919: Solomon Islands  
*L. fortior* Forel, 1900: Australia  
*L. foveonates* Lattke, 2011: Venezuela  
*L. foveopunctata* Mann, 1921: Fiji Islands  
*L. fugax* Mann, 1921: Fiji Islands  
*L. furtiva* Arnold, 1926: Zimbabwe  
*L. gagates* Mann, 1922: Honduras  
*L. gaigei* Wheeler, W.M., 1923: Guyana  
*L. gatu* Lattke, 2011: Panama  
*L. glabra* Lattke, 2011: Colombia  
*L. gorgona* Lattke, 2011: Colombia  
*L. gracilis* emery, 1899: Madagascar  
*L. grandidieri* Forel, 1910: Madagascar  
*L. guianensis* Wheeler, W.M., 1923: Guyana  
*L. guineensis* Santschi, 1914: Guinea  
*L. hackeri* Clark, 1934: Australia  
*L. harmsi* Donisthorpe, 1935: Christmas Island  
*L. havilandi* Forel, 1901: South Africa  
*L. hebrideana* Wilson, 1958: Vanuatu  
*L. hemioptica* Forel, 1901: Indonesia (Sumatra)  
*L. hezhouensis* Zhou, 2001: China  
*L. hodgsoni* Forel, 1900: Myanmar  
*L. honduriana* Mann, 1922: Honduras  
*L. honoria* Bolton, 1975: Cameroon  
*L. huangdii* Xu, 2000: China  
*L. huapingensis* Zhou, 2001: China  
*L. humiliata* Mann, 1921: Fiji Islands  
*L. hysterica* Forel, 1900: Sri Lanka  
*L. iheringi* Forel, 1911: Brazil  
*L. imperatrix* Mann, 1922: Honduras  
*L. incisa* Forel, 1891: Madagascar  
*L. indigatrix* Wilson, 1958: New Guinea  
*L. ingens* Mayr, 1866: Colombia  
*L. intermedia* Emery, 1902: South Africa  
*L. intricata* Viehmeyer, 1924: Australia  
*L. iridescent* (Smith, F., 1857): Borneo  
*L. iridescent currens* Forel, 1901: Borneo  
*L. iridipennis* (Smith, F., 1858): India  
*L. ixta* Lattke, 2011: Mexico  
*L. jeanettei* Tiwari, 2000: India  
*L. jeanneli* Santschi, 1914: Tanzania  
*L. josephi* MacKay & MacKay, 2004: Costa Rica  
*L. karawaiewi* Santschi, 1928: Java  
*L. keyssei* Viehmeyer, 1914: New Guinea  
*L. khammouanensis* Roncin & Deharveng, 2003: Laos  
*L. khaura* Bolton, 1975: Nigeria  
*L. kiche* Lattke, 2011: Guatemala  
*L. kitteli* (Mayr, 1870): India  
*L. kitteli altisquamis* Forel, 1900: Myanmar  
*L. kitteli laevis* (Mayr, 1879): Indonesia (Java)  
*L. kitteli minor* Forel, 1900: India  
*L. kitteli siemsseni* Viehmeyer, 1922: China



*L. kitteli transiens* Forel, 1911: Borneo  
*L. kraepelini baccha* Santschi, 1919: Vietnam  
*L. kraepelini esae* Forel, 1912: Indonesia (Java)  
*L. kraepelini* Forel, 1905: Java  
*L. kraepelini nero* Forel, 1913: Indonesia (Java)  
*L. laeviterga* Zhou *et al.*, 2012, China  
*L. langi* Wheeler, W.M., 1923: Guyana  
*L. laozii* Xu, 2000: China  
*L. lattkei* Bharti & Wachkoo, 2013: India  
*L. leiothorax* Prins, 1965: Mozambique  
*L. letilae* Mann, 1921: Fiji Islands  
*L. linda* Lattke, 2011: Colombia  
*L. linearis* (Smith, F., 1858): Brazil  
*L. longensis* Forel, 1915: Australia  
*L. longiceps* Santschi, 1914: Senegal  
*L. longiscapa* Donisthorpe, 1943: India  
*L. lucidula* Emery, 1895: Myanmar  
*L. luederwaldti* Forel, 1913: Brazil  
*L. mactans* Bolton, 1975: South Africa  
*L. magna* Forel, 1900: Australia  
*L. manni* Wheeler, W.M., 1923: United States  
*L. mastax* Bolton, 1975: Ghana  
*L. mavaca* Lattke, 2011: Venezuela  
*L. maxillosa* (Smith, F., 1858): Mauritius  
*L. maya* Lattke, 2011: Mexico  
*L. melena* Lattke, 2011: Venezuela  
*L. melzeri* Borgmeier, 1930: Brazil  
*L. mengzii* Xu, 2000: China  
*L. meritans* (Walker, 1859): Sri Lanka  
*L. microps* Bolton, 1975: Ivory Coast  
*L. minchinii* Forel, 1900: India  
*L. minima* Lattke, 2011: Brazil  
*L. mjobergi* Forel, 1915: Australia  
*L. modiglianii* Emery, 1900: Indonesia (Engano Island)  
*L. moelleri* (Bingham, 1903): India  
*L. montuosa* Lattke, 2011: Panama  
*L. mucronata columbica* Forel, 1901: Colombia  
*L. mucronata* Forel, 1893: Antilles Islands  
*L. mutabilis* (Smith, F., 1861): Sulawesi  
*L. myops* (Emery, 1887): Java  
*L. navua* Mann, 1921: Fiji Islands  
*L. nebra* Bolton, 1975: Cameroon  
*L. neutralis* Forel, 1907: Australia  
*L. nigricans* Lattke, 2011: Brazil  
*L. nitens* Donisthorpe, 1943: New Guinea  
*L. nuserra* Bolton, 1975: Ghana  
*L. oaxaca* Lattke, 2011: Mexico  
*L. occidentalis* Bernard, 1953: Guinea  
*L. optica* Viehmeyer, 1914: New Guinea  
*L. orchidioides* Lattke, 2011: Guatemala  
*L. oreshia* Wilson, 1958: Solomon Islands  
*L. oswaldi* (Forel, 1891): Madagascar

*L. pangui* Xu, 2000: China  
*L. panops* Lattke, 2011: French Guiana  
*L. papuana* Emery, 1897: New Guinea  
*L. paraense* Lattke, 2011: Brazil  
*L. parvula* Emery, 1900: Indonesia (Sumatra)  
*L. pavesii* Emery, 1892: Somalia  
*L. peninsularis* Mann, 1926: Mexico  
*L. peringueyi* Forel, 1913: South Africa  
*L. peruana* Lattke, 2011: Peru  
*L. peugueti* (André, 1887): Vietnam  
*L. phylloba* Lattke, 2011: Colombia  
*L. pinna* Lattke, 2011: Costa Rica  
*L. piroskae* Forel, 1910: Ethiopia  
*L. pittieri* Lattke, 2011: Venezuela  
*L. podenzenai* (Emery, 1895): Australia  
*L. pompilioides* (Smith, F., 1857): Borneo  
*L. princeps* Bolton, 1975: Ghana  
*L. processionalis* (Jerdon, 1851): India  
*L. processionalis distinguenda* (Emery, 1887): Borneo  
*L. pruinosa* Forel, 1900: Sri Lanka  
*L. pubiceps cubaensis* Santschi, 1930: Cuba  
*L. pubiceps* Emery, 1890: Venezuela  
*L. pubiceps vincentensis* Forel, 1901: Antilles  
*L. pucuna* Lattke, 2011: Ecuador  
*L. punctata* Emery, 1914: New Caledonia  
*L. punctaticeps* Emery, 1890: Costa Rica  
*L. punctiventris* (Mayr, 1879): India  
*L. purpurea* (Emery, 1887): New Guinea  
*L. pusilla* (Emery, 1890): Costa Rica  
*L. quadrata* Lattke, 2011: Colombia  
*L. quiriguana* Wheeler, W.M., 1923: Guatemala  
*L. quirozi* Lattke, 2011: Mexico  
*L. rasila* Lattke, 2011: Ecuador  
*L. ravida* Bolton, 1975: DRC  
*L. reggae* Lattke, 2011: Jamaica  
*L. regis* Bolton, 1975: Kenya  
*L. ridens* Forel, 1910: Madagascar  
*L. ritae* Forel, 1899: Panama  
*L. roberti coonoorensis* Forel, 1900: India  
*L. roberti* Forel, 1900: India  
*L. rouxi* (Emery, 1914): New Caledonia  
*L. rufa* Mann, 1922: Honduras  
*L. rufida* Zhou *et al.*, 2012, China  
*L. rugosopunctata* Karavaiev, 1925: Java  
*L. sagaris* Wilson, 1958: New Caledonia  
*L. santacruzii* Lattke, 2011: Ecuador  
*L. saussurei* (Forel, 1891): Madagascar  
*L. schwabi* Forel, 1913: Zimbabwe  
*L. serrata* Lattke, 2011: Panama  
*L. sianka* Lattke, 2011: Mexico  
*L. sjostedti* Forel, 1915: Australia  
*L. socorda* Lattke, 2011: Colombia

*L. sonora* Lattke, 2011: Mexico  
*L. spandax* Bolton, 1975: Ghana  
*L. stenocheilos* (Jerdon, 1851): India  
*L. sterops* Bolton, 1975: Ivory Coast  
*L. strator* Bolton, 1975: DRC  
*L. strenna* Zhou, 2001: China  
*L. striatidens* Bolton, 1975: Cameroon  
*L. stuhlmanni* Mayr, 1893: Mozambique  
*L. stygia* Bolton, 1975: Nigeria  
*L. sulcinoda* (André, 1892): Gabon  
*L. tama* Lattke, 2011: Colombia  
*L. terroni* Bolton, 1975: Cameroon  
*L. testacea* (Donisthorpe, 1948): Ghana  
*L. tiobil* Lattke, 2011: Venezuela  
*L. titan* Bolton, 1975: Cameroon  
*L. toxeres* Lattke, 2011: Costa Rica  
*L. transitionis* Bharti & Wachkoo, 2013: India  
*L. tricola* Taylor, 1969: Australia  
*L. triloba* Emery, 1901: New Guinea  
*L. trilobata* Santschi, 1924: DRC  
*L. truncata* Mann, 1919: Solomon Islands  
*L. truncatirostris* Forel, 1897: Madagascar  
*L. turneri* Forel, 1900, Australia  
*L. turneri* Forel, 1900: Australia  
*L. unistimulosa* Roger, 1863: Brazil  
*L. vericosa* Stitz, 1925: Philippines  
*L. vindicis* Bolton, 1975: Cameroon  
*L. violacea* Donisthorpe, 1942: New Guinea  
*L. vitiensis* Mann, 1921: Fiji Islands  
*L. voeltzkowi* Forel, 1897: Madagascar  
*L. vogeli* Borgmeier, 1933: Brazil  
*L. volcanica* Lattke, 2011: Costa Rica  
*L. watsoni* Forel, 1900: Myanmar  
*L. wheeleri* Forel, 1901: Mexico  
*L. yerburyi* Forel, 1900: Sri Lanka  
*L. yocota* Lattke, 2011: Honduras  
*L. zapyxis* Bolton, 1975: Ghana  
*L. zhuangzii* Xu, 2000: China

*Incertae sedis* (fossil species)

† *L. lacerata* Zhang, 1989: China

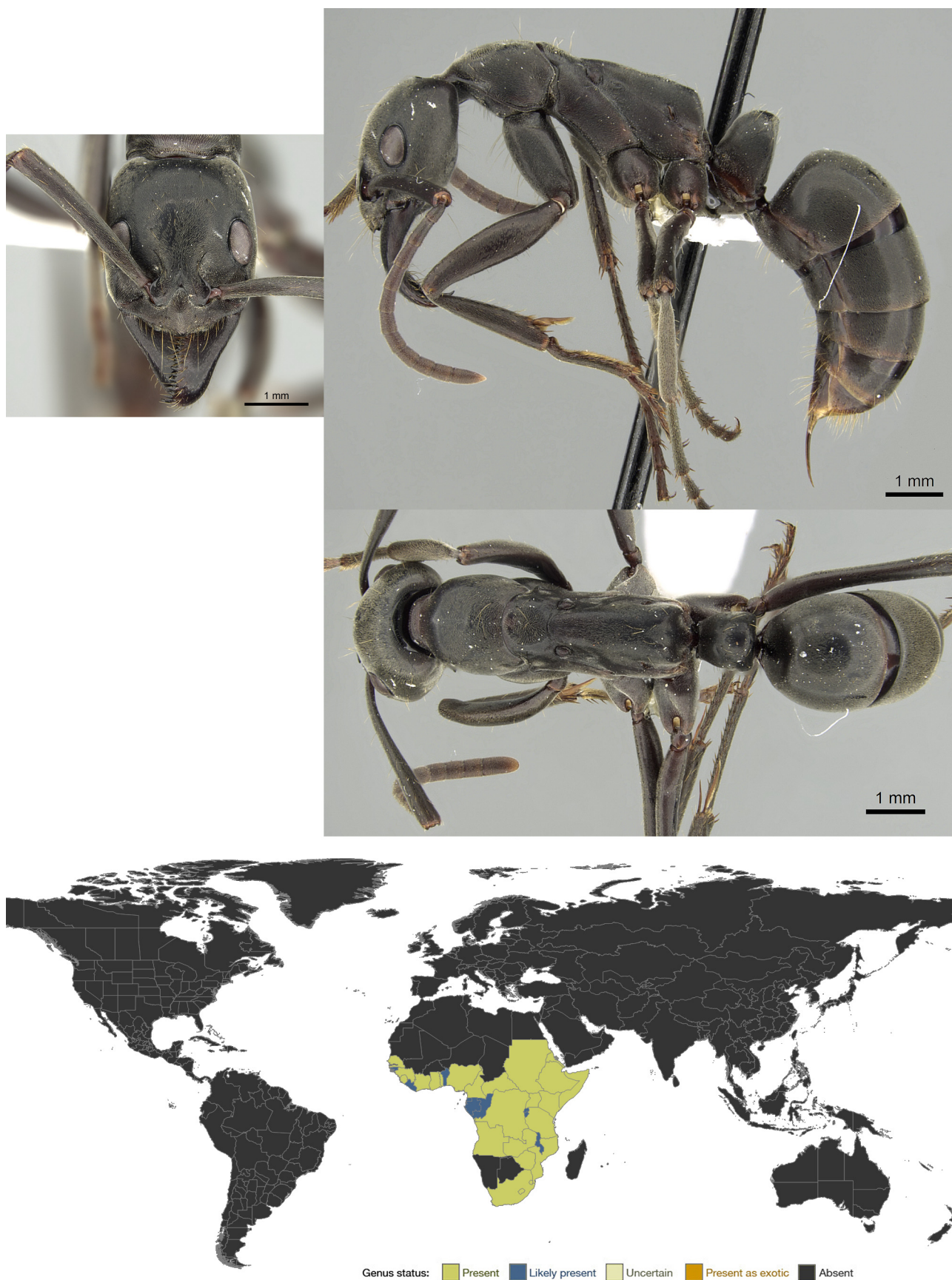
## ***Megaponera* Mayr**

Fig. 16

*Megaponera* Mayr, 1862: 714 (as genus in Ponerinae [Poneridae]). Type-species: *Formica foetens* Fabricius, 1793: 354 (junior primary homonym in *Formica*, replaced by *Formica analis* Latreille, 1802a: 282); by monotypy. **Gen. rev.**  
*Megaloponera* Roger, 1863b: 17 (incorrect subsequent spelling of *Megaponera*).

*Megaponera* is a monotypic genus (with an additional five subspecies) widespread in Sub-Saharan Africa. It is notable for its ergatoid queens, polymorphic workers, obligate group foraging, and specialized termite predation.





**FIGURE 16.** Worker caste of *Megaponera analis*: lateral and dorsal view of body and full-face view of head (CASENT0249196, Estella Ortega and [www.antweb.org](http://www.antweb.org)); world distribution of *Megaponera*.

**Diagnosis.** Diagnostic morphological apomorphies of *Megaponera* workers include the presence of preocular carinae and size polymorphism, which do not occur in combination in any other ponerine. Preocular carinae occur in *Odontoponera* and many *Neoponera* species, but *Megaponera* lacks *Odontoponera*'s striate sculpturing and denticulate clypeus, and *Neoponera*'s prominent white projecting arolia, simple tarsal claws and U-shaped cuticular lip posterior to the metapleural gland orifice.

**Synoptic description.** *Worker.* Large to very large (TL 9–18 mm) ants with the standard characters of Ponerini. Workers polymorphic, varying principally in size and pubescence. Mandibles triangular. Eyes large, located near head midline, with distinct preocular carinae. Frontal lobes widely separated anteriorly and appearing flattened in frontal view. Scapes flattened, with distinct anterior margins. Metanotal groove shallow. Propodeum moderately narrowed dorsally. Propodeal spiracles slit-shaped. Tarsal claws with a preapical tooth. Metatibial spur formula (1s, 1p). Petiole nodiform. Constriction between pre- and postsclerites of A4 indistinct. Stridulitrum present on pretergite of A4. Head and body finely punctate, with scattered pilosity and dense pubescence (sparse in minor workers). Color black.

*Queen.* Wingless, similar to a major worker but larger (TL 18.5 mm), with more extensive sculpturing, denser pilosity, a deeper metanotal groove, an anteriorly slanting squamiform petiole, and a more expansive gaster. (Adapted from Arnold, 1915.)

*Male.* See descriptions in Emery (1897b), Arnold (1915), and Wheeler (1922b).

*Larva.* Described by Wheeler & Wheeler (1952).

**Geographic distribution.** *Megaponera* is widespread in tropical Sub-Saharan Africa. Wheeler (1922b) shows the range as encompassing the African continent from roughly 10° N latitude to 30° S latitude. We have seen two specimens of *Megaponera* in the USNM labelled as coming from India (with no additional collection information), but this is almost certainly in error as we know of no other collections of this genus from outside Africa.

**Ecology and behavior.** *Megaponera analis* has an unusual suite of ecological, behavioral, and social adaptations relative to most ponerines. The typical ponerine species has small colonies (usually fewer than 100 individuals), alate queens, and monomorphic workers which forage singly. *Megaponera* has diverged significantly from this basic pattern, having relatively large colonies, flightless queens, and polymorphic workers which are specialized mass raiders of termites.

*Megaponera* nests in the ground, in deserted termite mounds, or even partially in rotting logs (Lévieux, 1976B; Longhurst & Howse, 1979a), and has relatively large colonies by ponerine standards, with from 500 to 2,000 workers (Peeters, 1991b; Hölldobler *et al.*, 1994). The nests are host to a diverse assemblage of myrmecophiles (Arnold, reprinted in Wheeler, 1922b). Colonies have a single highly fecund ergatoid queen, which in most respects resembles a large major worker but is endowed with a rich array of glands for chemical communication with the workers (Peeters, 1991b; Hölldobler *et al.*, 1994). Males locate virgin queens by following the recruitment trails of workers back to their nests (Longhurst & Howse, 1979b). Workers retain spermathecae and ovarioles, but do not appear to mate and do not produce viable haploid eggs (Villet, 1990a; Villet & Duncan, 1992). Workers are continuously polymorphic for size (Longhurst & Howse, 1979a; Crewe *et al.*, 1984), though they are often referred to as “majors”, “medias” and “minors”. They are known to emit a strong odor, to stridulate loudly when disturbed, and to have a very painful sting (Arnold, 1915).

*Megaponera* are specialized mass raiders of termites (Wheeler, 1922b, 1936; Weber, 1964; Lévieux, 1966). Longhurst & Howse (1979a) studied their foraging behavior in detail and described the sequence of events in a typical raid (see also the account by Weber, 1964). Raids begin when a solitary major worker locates foraging termites. This scout returns directly to its nest, laying a trail of poison gland-derived pheromones exuded through its sting (Longhurst *et al.*, 1979A), and recruits up to several hundred of its nestmates (Corbara & Déjean, 2000). They proceed as a column to the termites' protected foraging tunnels, which the major workers tear open. Minor workers then haul out termites. When this process is complete, the major workers stack the termites in their mandibles and the ants return as a column to their nest. Corbara & Déjean (2000) compared the behavior of minor and major workers during prey capture and found that though they are generally similar, major workers are more likely to attack termite soldiers than are minor workers. Longhurst & Howse (1979a) reviewed the literature on *Megaponera* foraging behavior and found significant regional variation in how raids are conducted. Taylor (2008) hints that this variation supports his hypothesis of multiple species within *Megaponera*.

Hölldobler & Wilson (1990; see also Wilson, 1958a) hypothesized that the *Megaponera* style of foraging, in which scouts lead columns of workers on raids of other social insects, could be the first step in the evolution of true

legionary behavior, such as that of the dorylines (see also Oster & Wilson, 1978). Of the hallmarks of legionary behavior identified by Brady (2003), *Megaponera* exhibits obligate collective foraging and a weak form of nomadism, by which colonies frequently emigrate to new nest sites. This latter behavior was described in detail by Arnold (reprinted in Wheeler, 1922b) and Longhurst & Howse (1979a). Wheeler (1922b) also discussed the adaptations of *Megaponera* brood to emigration. The reasons for these frequent emigrations are unknown, but Longhurst & Howse (1979a) argue that they are not likely caused by prey shortages and may be a response to predation by *Dorylus* driver ants. In an interesting observation, Beck & Kunz (2007) found cooperative altruistic defensive actions among *Megaponera* workers under attack by *Dorylus*.

**Phylogenetic and taxonomic considerations.** The genus *Megaponera* was erected by Mayr (1862) to hold the single species *Formica analis* Latreille. The original specific epithet “*foetens*” was a junior primary homonym but has been used incorrectly in much of the extensive literature on this species. *Megaponera* experienced relative taxonomic stability until W. L. Brown (in Bolton, 1994) synonymized it under *Pachycondyla* without phylogenetic justification.

We are reviving *Megaponera* to full genus status based on both morphological and molecular evidence. Schmidt's (2013) molecular phylogeny of the Ponerinae places *Megaponera* with strong support within the *Odontomachus* group as sister to *Ophthalmopone*, and not at all close to *Pachycondyla*. A sister group relationship with *Ophthalmopone* is also strongly supported by morphology. Workers of the two genera are remarkably similar, differing significantly only in *Megaponera*'s preocular carinae and size polymorphism and *Ophthalmopone*'s slender build, huge posteriorly set eyes, and armed hypopygium.

These genera also share derived ecological and behavioral attributes. Both are specialist termite predators, with *Megaponera* and some *Ophthalmopone* species raiding termites in large groups. It is possible that the common ancestor of these genera was a mass raider of termites, with a reversal to solitary foraging being favored in some *Ophthalmopone* species. Alternatively, mass raiding may have evolved independently in *Megaponera* and *Ophthalmopone*. Both genera also lack a winged queen caste, though reproduction in *Megaponera* is performed by ergatoid queens and in *Ophthalmopone* it is performed by gamergate workers. The reproductive caste in the ancestor of these genera could conceivably have been either ergatoid or gamergate (or neither). The close relationship of these taxa make them excellent models for studying the selective forces driving the evolution of alternative reproductive strategies in ants, as well as the evolution of mass foraging.

While *Megaponera* and *Ophthalmopone* could arguably be synonymized, the age of their divergence is consistent with that of other ponerine genera (Schmidt, 2013) and we feel that their morphological and behavioral distinctiveness warrant separate generic status. The sister group of *Megaponera* + *Ophthalmopone* is still unknown, but a close relationship with *Hagensia* is plausible (see discussion under that genus).

## Species of *Megaponera*

*M. analis* (Latreille, 1802): Guinea (**comb. rev.**)

*M. analis amazon* Santschi, 1935: Ethiopia

*M. analis crassicornis* (Gerstcker, 1859): Mozambique

*M. analis rapax* Santschi, 1914b: Tanzania

*M. analis subpilosa* Santschi, 1937: Angola

*M. analis termitivora* Santschi, 1930: DRC

## *Mesoponera* Emery

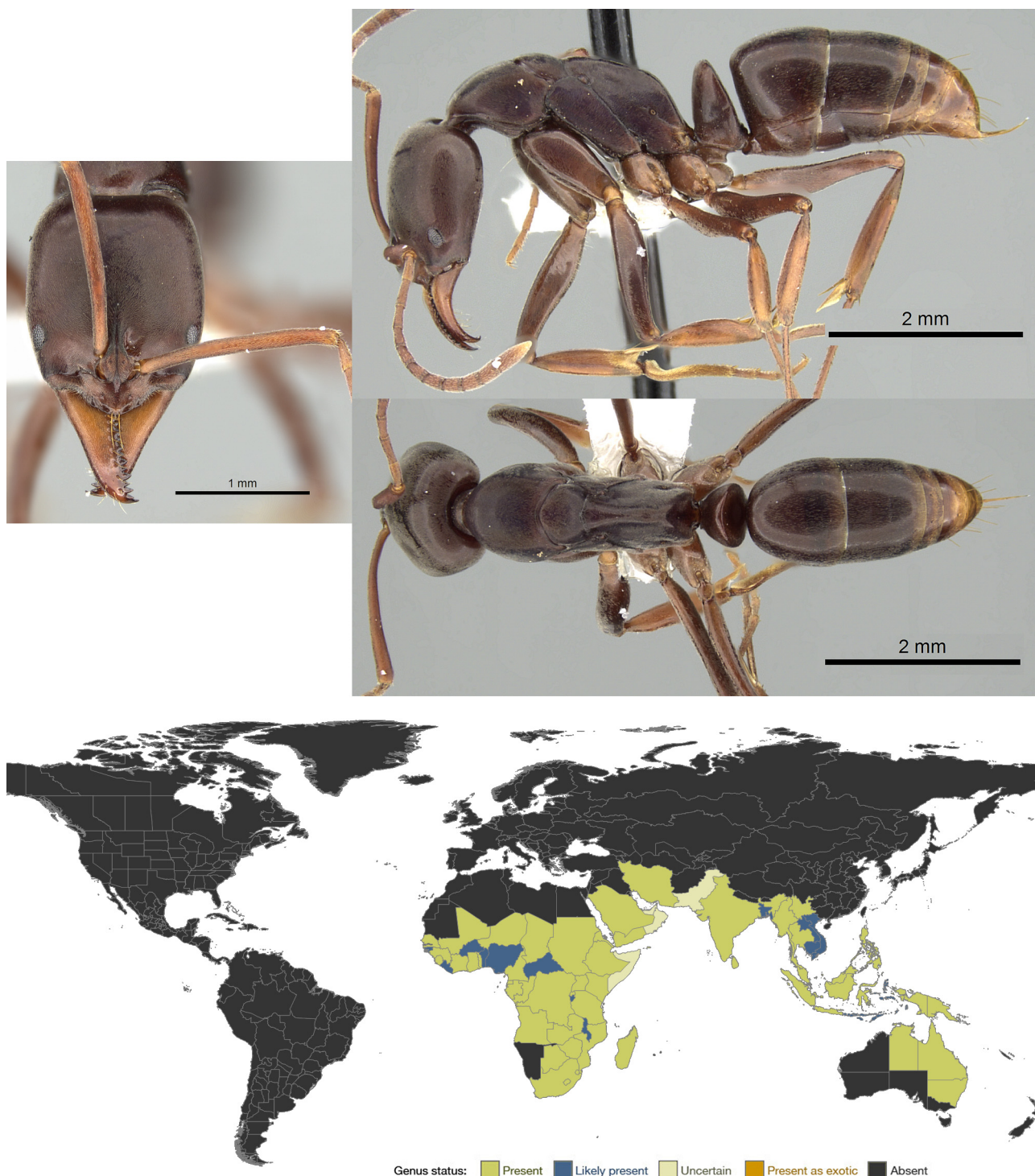
Fig. 17

*Mesoponera* Emery, 1900b: 668 (as subgenus of *Euponera*). Type-species: *Ponera melanaria* Emery, 1893b: 260; by monotypy. **Gen. rev.**

*Xiphopelta* Forel, 1913a: 108 (as subgenus of *Ponera*). Type-species: *Ponera (Xiphopelta) arnoldi* Forel, 1913a: 108 (junior synonym of *Ponera elisae* var. *rotundata* Emery, 1895c: 20); by monotypy. **Syn. nov.**

*Mesoponera* is a moderately sized genus, with 28 described species and subspecies, restricted to the Old World tropics from Sub-Saharan Africa to Australia and the Solomon Islands.





**FIGURE 17.** Worker caste of *Mesoponera melanaria*: lateral and dorsal view of body and full-face view of head (CASENT0249169, Ryan Perry and [www.antweb.org](http://www.antweb.org)); world distribution of *Mesoponera*.

**Diagnosis.** *Mesoponera* workers are perhaps the least derived of any ponerine genus, as they lack any obvious apomorphies. *Mesoponera* bears superficial resemblance to a number of other relatively plesiomorphic genera, especially *Fisheropone*, *Neoponera*, *Mayaponera*, *Pseudoponera*, and *Hypoconera*, and to a lesser degree genera such as *Hagensia*, *Megaponera*, and *Paltothyreus*. *Mesoponera* can be separated from these genera by the following combination of characters (most of which are probably plesiomorphic): mandibles without a basal groove, frontal lobes very small and closely approximated, eyes relatively small and placed anterior of head midline, preocular carinae absent, pronotum without sharp lateral margins, metanotal groove shallow to moderately

deep (in *M. subiridescens* and “*Xiphopelta*” species), propodeum narrowed dorsally, metapleural gland orifice without a U-shaped posterior lip, metatibia with a large pectinate spur and a smaller simple spur, petiole surmounted by a simple scale which lacks sharp lateral margins, gaster with only a moderate constriction between A3 and A4, metatibiae with two spurs, arolia not prominent, and head and body only weakly sculptured with sparse pilosity but dense pubescence.

**Synoptic description.** *Worker.* Medium (TL 5–9.5 mm) slender ants with the standard characters of Ponerini. Mandibles triangular, relatively long; mandibles crossed when closed in the *M. melanaria* group. Eyes small, placed anterior of head midline; absent or reduced to a small pigmented spot in a few species. Frontal lobes very small and closely approximated. Mesopleuron usually not divided by a transverse groove. Metanotal groove shallow to moderately deep (in “*Xiphopelta*” species). Propodeum narrowed dorsally. Propodeal spiracles small and round in most *M. melanaria* group species, but slit-like in the *M. ingesta* group. Metatibial spur formula (1s, 1p). Petiole squamiform. Gaster with only a weak girdling constriction between pre- and postsclerites of A4. Stridulitrum sometimes present on pretergite of A4. Head and body finely punctate, with sparse pilosity but a dense fine pubescence. Color variable. (Note: This description excludes *M. subiridescens*, which we place within *Mesoponera* only tentatively. *M. subiridescens* differs from the above description by its shining cuticle, relatively large eyes, mesopleuron divided by a transverse groove, deep metanotal groove, and long narrow toothless mandibles which have distinct basal grooves and basal margins that are not concealed by the clypeus when closed.)

*Queen.* Similar to worker, but winged and with the other differences typical for alate ponerine queens.

*Male.* See descriptions in Arnold (1915) and Donisthorpe (1942).

*Larva.* Described by Wheeler & Wheeler (1971b).

**Geographic distribution.** Members of this genus are found throughout Sub-Saharan Africa (including Madagascar) extending to Yemen (*M. flavopilosa*, Collingwood & van Harten, 2005) and the Seychelles (*M. melanaria macra*), with a second set of species occurring from Sri Lanka eastward to northern Australia and the Solomon Islands.

**Ecology and behavior.** Almost nothing is known about the ecology or behavior of most *Mesoponera* species, especially members of the *M. melanaria* and *M. subiridescens* groups. Donisthorpe (1941) and Wilson (1958c) note that *M. papuana* nests in rotting wood and forages diurnally in leaf litter, and that *M. manni* nests in rotting wood or soil, but otherwise reports of their habits are scarce.

Most species in the *M. ingesta* group are similarly unstudied, but *M. cafferaria* has received a fair bit of attention. This species is a predator of insects and also collects sugary liquids. It is locally abundant (Lévieux, 1983) and colonies are fairly small (roughly 60 to 120 workers; Agbogba, 1992, 1994). Nesting occurs in the ground (Villet, 1990b) or in active or abandoned termitaries (Agbogba, 1992; Déjean *et al.*, 1996, 1997), and colony founding is semiclaustral (Villet, 1990b). Queens inhibit reproduction by workers, but orphaned workers lay fertile eggs (Villet & Duncan, 1992). The division of labor of *M. cafferaria* workers has been well studied and is unusual. Rather than displaying a typical age-dependent polyethism, individual workers show a remarkable degree of task specialization, which is determined at an early age (Agbogba, 1992, 1994). Apparently only a low rate of role change occurs after this initial specialization (Bonavita & Poveda, 1970; Agbogba, 1992). Roughly two-thirds of workers specialize on intra-nest activities (studied by Agbogba, 1991), while the remainder specialize on foraging (Bonavita & Poveda, 1970). Foragers further specialize on the collection of sugary liquids or on either the stinging or retrieval of insect prey. When hunting termites, the behavior of *M. cafferaria* foragers varies depending on the species and caste of the termites encountered (Agbogba, 1985). Interestingly, large groups of *M. cafferaria* foragers will attack termite nests, and the entire ant colony will then emigrate into the nest, at least temporarily (Agbogba, 1990, 1992). Both the recruitment of foragers and the movement of the colony are coordinated through tandem running, using both visual and chemical cues (Agbogba, 1984 and 1992). Masson (1970a, 1970b, 1972) studied the neuroanatomy and neurodevelopment of *M. cafferaria*, Bonavita & Lemasne (1970) studied food exchange between *M. cafferaria* workers, and Bonavita & Poveda (1972) examined intestinal structure in *M. cafferaria* larvae.

**Phylogenetic and taxonomic considerations.** *Mesoponera* was erected by Emery (1900b) as a subgenus of *Euponera* to house the single species *Ponera melanaria* Emery. He caused confusion the next year (Emery, 1901) by redescribing the genus as new and making *Ponera cafferaria* F. Smith the type species. Most subsequent authors treated *M. cafferaria* as the type species, until Bolton (2003) reconfirmed the status of *M. melanaria* as the type species. Most authors also continued to treat *Mesoponera* as a subgenus of *Euponera* (except Bingham, 1903) until

Wilson (1958c) raised it to full genus status. Brown (1973) and most subsequent authors have treated *Mesoponera* as a junior synonym of *Pachycondyla*. Forel (1917) moved *Xiphopelta* from being a subgenus of *Ponera* to being a subgenus of *Euponera* but this was short lived, with Wheeler (1922) synonymizing *Xiphopelta* with *Mesoponera*, a treatment that we support and follow here.

*Mesoponera* acted as a repository for ponerine species which exhibited a suite of characters that are clearly either plesiomorphic or convergently derived. Emery (1911) gave the following basic worker diagnosis for *Mesoponera* (at the time a subgenus of *Euponera*): mandibles elongate and armed with many teeth, maxillary palp with four segments, first funicular segment shorter or the same length as the second, mesonotum an oval disk surrounded by distinct sutures, and mesotarsi without stiff spines dorsally. Species placed in *Mesoponera* also have tended to share weak sculpturing, a squamiform petiole, and relatively small eyes. All or most of these characters are likely plesiomorphic within the Ponerini, making it highly likely that *Mesoponera* would prove to be non-monophyletic. Schmidt's (2013) molecular phylogeny confirms this expectation. Schmidt (2013) sequenced five species formerly considered to be in *Mesoponera*, and they turned out to be widely scattered across the phylogeny of Ponerini, in *Pseudoponera*, *Neoponera*, the new genus *Mayaponera*, and *Mesoponera* itself (which is probably still not monophyletic; see below).

We are reviving *Mesoponera* to full genus status based on both morphological and molecular evidence. Morphologically, *Mesoponera* as we have defined it lacks any clear autapomorphies and this makes diagnosis difficult. It certainly lacks those combinations of characters diagnostic of other ponerine genera. Additional justification for full genus status for *Mesoponera* comes from Schmidt's (2013) molecular phylogeny, which places both the *M. melanaria* and *M. ingesta* groups within the *Odontomachus* group (*M. subiridescens* was not sampled), but without a clear sister group for either one. They are certainly not closely related to *Pachycondyla*. The monophyly of *Mesoponera* as we have defined it is not strongly supported by Schmidt's phylogeny. Additionally, recent preliminary data from P.S. Ward (pers. comm.) found that an Asian species (*M. melanaria*) did not group with an African species (*M. ambigua*), both of which we place within *Mesoponera*. These results suggest that *Mesoponera* as conceived here is not monophyletic.

Based on the available molecular evidence as well as the morphological diversity within *Mesoponera* we explored the possibility of erecting several closely related genera for the species placed here. For example, species related to *M. melanaria* have a round propodeal spiracle (spiracle elongate in other species), those related to *M. ingesta* have relatively short mandibles (elongate in others) while *M. subiridescens* has the mesopleuron strongly divided and the metanotal groove well developed. However, when examining species from across the genus the propodeal spiracle shape shows considerable variation, with all shapes from round to elongate being present, and a divided mesopleuron can be found in species with both round and elongate propodeal spiracles. Thus it became impossible to develop clear diagnoses for groups of species based around these apparently informative characters. Additionally, Schmidt's (2013) molecular data for the *M. melanaria* group species (*M. rubra*) and Ward's data are incomplete, making robust conclusions hard to draw. Given these uncertainties, we are choosing to be conservative in keeping these groups together within *Mesoponera* until additional data can be collected, with anticipation that the genus as conceived here will need to be modified in the future.

### Species of *Mesoponera*

- M. ambigua* (André, 1890): Sierra Leone (**comb. nov.**)
- M. australis* (Forel, 1900): Australia (**comb. rev.**)
- M. caffraria* (Smith, 1858): South Africa (**comb. rev.**)
- M. caffraria affinis* (Santschi, 1935): Congo (**comb. nov.**)
- M. caffraria caffra* (Santschi, 1935): Guinea (**comb. nov.**)
- M. elisae* (Forel, 1891): Madagascar (**comb. nov.**)
- M. elisae divaricata* (Emery, 1915): Ethiopia (**comb. nov.**)
- M. elisae redbankensis* (Forel, 1913): Zimbabwe (**comb. nov.**)
- M. elisae rotundata* (Emery, 1895): South Africa (**comb. nov.**)
- M. escherichi* (Forel, 1910): Ethiopia (**comb. nov.**)
- M. flavopilosa* (Weber, 1942): Sudan (**comb. nov.**)
- M. ingesta* (Wheeler, W.M., 1922): DRC (**comb. nov.**)



*M. manni* (Viehmeyer, 1924): Solomon Is. (**comb. rev.**)  
*M. melanaria* (Emery, 1893): Sri Lanka (**comb. rev.**)  
*M. melanaria macra* (Emery, 1894): Seychelles Islands (**comb. nov.**)  
*M. nimba* (Bernard, 1953): Guinea (**comb. nov.**)  
*M. novemdentata* (Bernard, 1953): Guinea (**comb. nov.**)  
*M. papuana* (Viehmeyer, 1914): New Guinea (**comb. rev.**)  
*M. picea* (Bernard, 1953): Guinea (**comb. nov.**)  
*M. rubra* (Smith, F., 1857): Singapore (**comb. nov.**)  
*M. rubra javana* (Forel, 1905): Indonesia (Java) (**comb. nov.**)  
*M. scolopax* (Emery, 1899): Cameroon (**comb. nov.**)  
*M. senegalensis* (Santschi, 1914): Senegal (**comb. nov.**)  
*M. subiridescens* (Wheeler, 1922): DRC (**comb. nov.**)  
*M. testacea* (Bernard, 1953): Guinea (**comb. nov.**)  
*M. villiersi* (Bernard, 1953): Guinea (**comb. nov.**)  
*M. weberi* (Bernard, 1953): Guinea (**comb. nov.**)

## **Myopias Roger**

Fig. 18

*Myopias* Roger, 1861: 39 (as genus). Type-species: *Myopias amblyops* Roger, 1861: 39; by monotypy.

*Trapeziopelta* Mayr, 1862: 715 (as genus in Ponerinae [Poneridae]). Type-species: *Ponera maligna* Smith, F., 1861: 44; by monotypy. Willey & Brown, 1983: 249 (*Trapeziopelta* as junior synonym of *Myopias*).

*Bradyponera* Mayr, 1886: 362 (as genus). Type-species: *Ponera nitida* Smith, F., 1861: 45 (junior primary homonym in *Ponera*, replaced by *Myopias mayri* [Donisthorpe, 1932]); by monotypy. Willey & Brown, 1983: 249 (*Bradyponera* as junior synonym of *Myopias*).

*Myopias* is a moderately large genus (35 described species) restricted to Southeast Asia and Australia. Relatively little is known about its habits, but at least some are specialist predators of millipedes.

**Diagnosis.** Workers of *Myopias* are distinctive and unlikely to be mistaken for any other genus. Diagnostic characters of the genus (in combination) include: linear mandibles, blunt medial clypeal projection (absent in some species), round propodeal spiracles, nodiform petiole, strong gastral constriction, and simple tarsal claws. The clypeal projection and simple tarsal claws separate *Myopias* from *Leptogenys*, the morphologically most similar (and phylogenetically closest) genus. *Buniapone* and *Paltothyreus* also have blunt medial clypeal projections, but they differ in many other characters and are unlikely to be confused with *Myopias*.

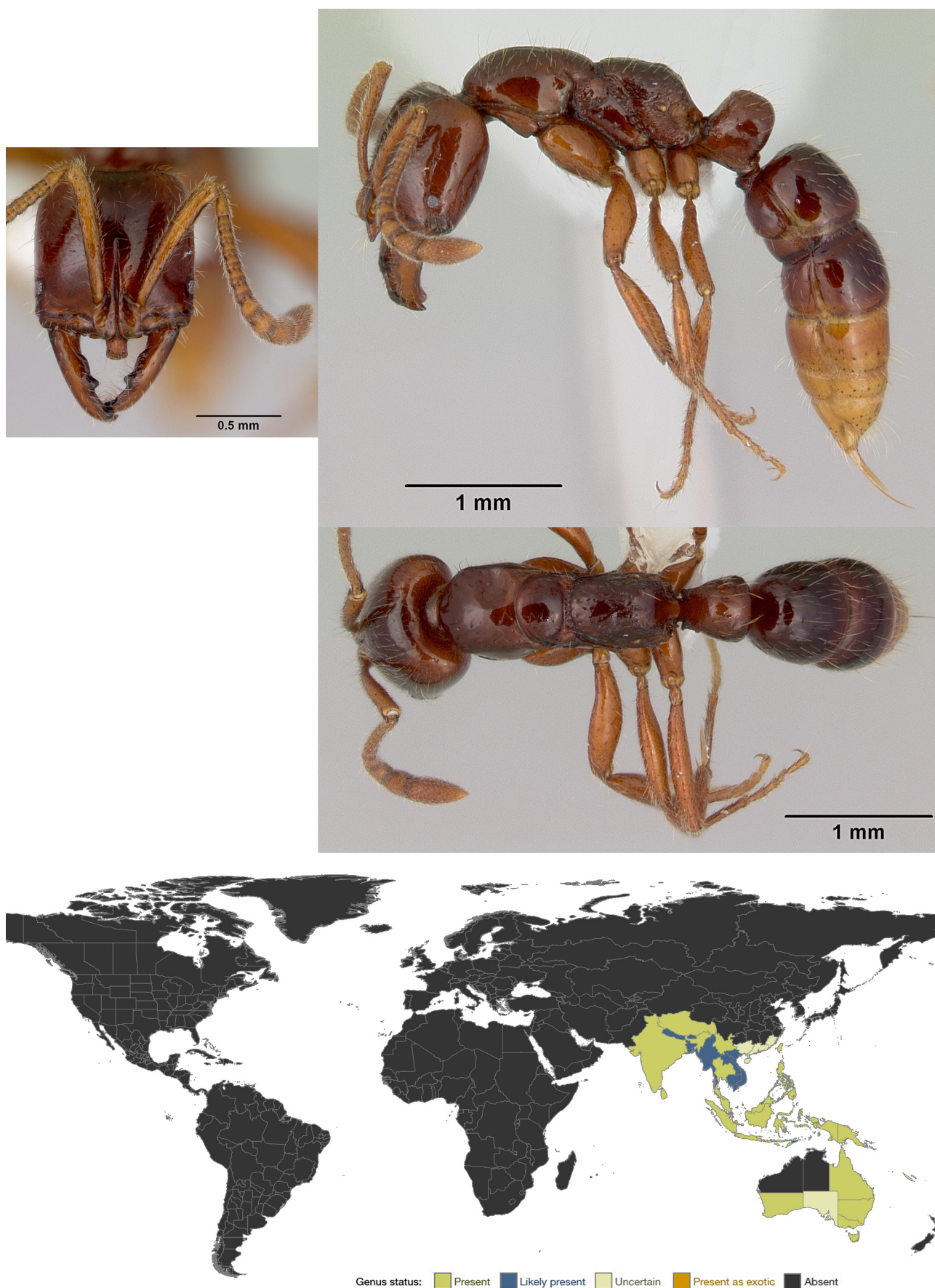
**Synoptic description.** *Worker.* Small to large (TL 2.8–16.9 mm) ants with the standard characters of Ponerini. Mandibles usually narrow and moderately curved (triangular in *M. delta*), with only a few teeth, often without a distinct basal angle, and with a strong basal groove. Clypeus very shallow, the frontal lobes reaching or surpassing the anterior clypeal margin, which usually has a small blunt anterior projection. Eyes very small to moderate in size (rarely absent), located far anterior of the head midline. Mesopleuron not divided by a transverse groove (though sometimes with a row of foveae giving the impression of a groove). Metanotal groove shallow to deep. Propodeum broad dorsally. Propodeal spiracles small and round. Metatibial spur formula (1s, 1p). Petiole nodiform, widening posteriorly and dorsally. Gaster with a strong girdling constriction between pre- and postsclerites of A4. Presence of stridulitrum on pretergite of A4 variable. Head and body foveolate or smooth and shining, sometimes with lateral striations on the mesosoma. Head and body with scattered pilosity and little to no pubescence. Color variable, yellow to black.

*Queen.* Similar to worker but usually slightly larger (sometimes smaller, as in *M. chapmani*), alate and with the other caste differences typical for ponerines (Willey & Brown, 1983). Ergatoid queens occur in at least some species.

*Male.* Undescribed and apparently unknown.

*Larva.* Larvae of some *Myopias* species have been described by Wheeler & Wheeler (1964, 1976).

**Geographic distribution.** The range of *Myopias* extends from Sri Lanka in the west and China in the north to Australia and Tasmania, with the greatest species diversity in Indonesia and New Guinea (Willey & Brown, 1983).



**FIGURE 18.** Worker caste of *Myopias chapmani*: lateral and dorsal view of body and full-face view of head (CASENT0172093, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Myopias*.

**Ecology and behavior.** *Myopias* is a poorly known genus, probably due to its cryptic nesting and foraging habits. Most of what is known about its ecology and behavior comes from anecdotal observations. Nests are generally constructed in rotting wood, though some species are subterranean nesters (Wheeler, 1923b; Willey & Brown, 1983). Reported colony sizes are typically less than 100 workers, and often much less (Wilson, 1959a; Willey & Brown, 1983; Gobin *et al.*, 2006). At least some species are polygynous, and ergatoid queens (in conjunction with normal dealate queens) occur in at least two species (*M. concava* and an undescribed Indonesian species; Willey & Brown, 1983; Gobin *et al.*, 2006). Workers of *M. emeryi* are obligately sterile (Gobin *et al.*, 2006). Males have apparently never been reported for any *Myopias* species, which could simply be a reflection of the paucity of observations of any kind for this genus, or may suggest an unusual reproductive strategy. The feeding habits of most species are unknown, but some species are specialist predators of millipedes (Wilson, 1959a; Willey & Brown, 1983) and *M. delta* is a specialist predator of ants (especially myrmicines but also other ponerines). Gobin *et al.* (2003b) identified subepithelial glands in *M. emeryi* and *M. maligna* which may function in hydrocarbon production. Abdominal glands within a number of *Myopias* species were examined by Billen *et al.* (2013), leading to the discovery of several glands which were previously unknown in ants.

**Phylogenetic and taxonomic considerations.** *Myopias* was erected by Roger (1861) to house his newly described species *M. amblyops*. Except for a brief provisional synonymy under *Pachycondyla* (Brown, 1973; Snelling, 1981), *Myopias* has always been treated as a distinct genus. Emery (1911) placed the genus in his subtribe Plectroctenini, based on very weak characters (sculpturing, pubescence, and the presence of a pectinate spur on the meso- and metatibiae). Willey & Brown (1983) synonymized the genus *Trapeziopelta* and its junior synonym *Bradypонера* under *Myopias*.

We continue to treat *Myopias* as a distinct genus, based on both molecular and morphological data. Schmidt's (2013) molecular phylogeny of Ponerinae places *Myopias* with strong support in the *Odontomachus* group, probably as sister to *Leptogenys*, though sister relationships to *Mesoponera* (s.s.) or *Leptogenys* + *Mesoponera* cannot be rejected.

Emery (1911) separated *Myopias* and *Trapeziopelta* based on characters of the clypeus (in *Trapeziopelta* the clypeus has a medial blunt anterior projection, which is lacking in *Myopias* s.s.) and mandibular teeth. *Myopias* (s.s.) was restricted to a few small hypogeic species, while *Trapeziopelta* was considered to include most of the taxa now included in *Myopias*. Though Schmidt (2013) did not have molecular data for any species of *Myopias* s.s., we tentatively agree with the synonymy of these genera by Willey & Brown (1983). It seems likely that either *Trapeziopelta* represents a distinct clade within *Myopias* (with the clypeal projection being an apomorphy of this group), or that the presence of the clypeal projection is plesiomorphic and was subsequently lost in a handful of species which evolved more cryptic habits (perhaps several times independently). It will be necessary to obtain molecular data for *M. amblyops* or another member of *Myopias* (s.s.) in order to test these hypotheses. It is also possible that *Myopias* and *Trapeziopelta* will prove to be unrelated lineages, though we do not think this is likely.

### Species of *Myopias*

See Willey & Brown (1983) for a key to Australian species of *Myopias*.

- M. amblyops* Roger, 1861: Sri Lanka
- M. bidens* (Emery, 1900): Indonesia (Sumatra)
- M. bidens polita* (Stitz, 1925): Philippines
- M. breviloba* (Wheeler, W.M., 1919): Borneo
- M. castaneicola* (Donisthorpe, 1938): New Guinea
- M. chapmani* Willey & Brown, 1983: Australia
- M. concava* Willey & Brown, 1983: New Guinea
- M. conicara* Xu, 1998: China
- M. crawleyi* (Donisthorpe, 1941): Indonesia (Sumatra)
- M. cribriceps* Emery, 1901: New Guinea
- M. delta* Willey & Brown, 1983: New Guinea
- M. densesticta* Willey & Brown, 1983: Australia
- M. emeryi* (Forel, 1913): Indonesia (Java)



*M. gigas* Willey & Brown, 1983: New Guinea  
*M. hollandi* (Forel, 1901): Indonesia (Sumatra)  
*M. julivora* Willey & Brown, 1983: New Guinea  
*M. kuehni* (Forel, 1902): Indonesia (Key Island)  
*M. latinoda* (Emery, 1897): New Guinea  
*M. levigata* (Emery, 1901): New Guinea  
*M. lobosa* Willey & Brown, 1983: Philippines  
*M. lorlai* (Emery, 1897): New Guinea  
*M. maligna* (Smith, F., 1861): Indonesia (Sulawesi)  
*M. maligna punctigera* (Emery, 1900): Indonesia (Mentawai I.)  
*M. mandibularis* (Crawley, 1924): Indonesia (Sumatra)  
*M. mayri* (Donisthorpe, 1932): Indonesia (Sulawesi)  
*M. media* Willey & Brown, 1983: New Guinea  
*M. modiglianii* (Emery, 1900): Indonesia (Sumatra)  
*M. nops* Willey & Brown, 1983: Taiwan  
*M. papua* Snelling, 2008: New Guinea  
*M. philippinensis* (Menozzi, 1925): Philippines  
*M. ruthae* Willey & Brown, 1983: New Guinea  
*M. santschii* (Viehmeyer, 1914): New Guinea  
*M. tasmaniensis* Wheeler, W.M., 1923: Tasmania  
*M. tenuis* (Emery, 1900): New Guinea  
*M. trumani* (Donisthorpe, 1949): New Guinea  
*M. xiphias* (Emery, 1900): New Guinea

## ***Odontomachus* Latreille**

Fig. 19

*Odontomachus* Latreille, 1804: 179 (as genus). Type-species: *Formica haematoda* Linnaeus, 1758: 582; by monotypy.

*Pedetes* Bernstein, 1861: 7. Type-species: *Pedetes macrorhynchus* Bernstein, 1861: 8; by monotypy. Dalla Torre, 1893: 51 (*Pedetes* as junior synonym of *Odontomachus*).

*Champsomyrmex* Emery, 1892: 558. Type-species: *Odontomachus coquereli* Roger, 1861: 30; by monotypy. Brown, 1976: 96 (*Champsomyrmex* as junior synonym of *Odontomachus*).

*Thempsomyrmex* Forel, 1893a: 163 (incorrect subsequent spelling of *Champsomyrmex*).

*Myrtoteris* Matsumura, 1912: 191. Type-species: *Myrtoteris kuroiwae* Matsumura, 1912: 192 (junior synonym of *Odontomachus monticola* Emery, 1892). Brown, 1976: 96 (*Myrtoteris* as junior synonym of *Odontomachus*).

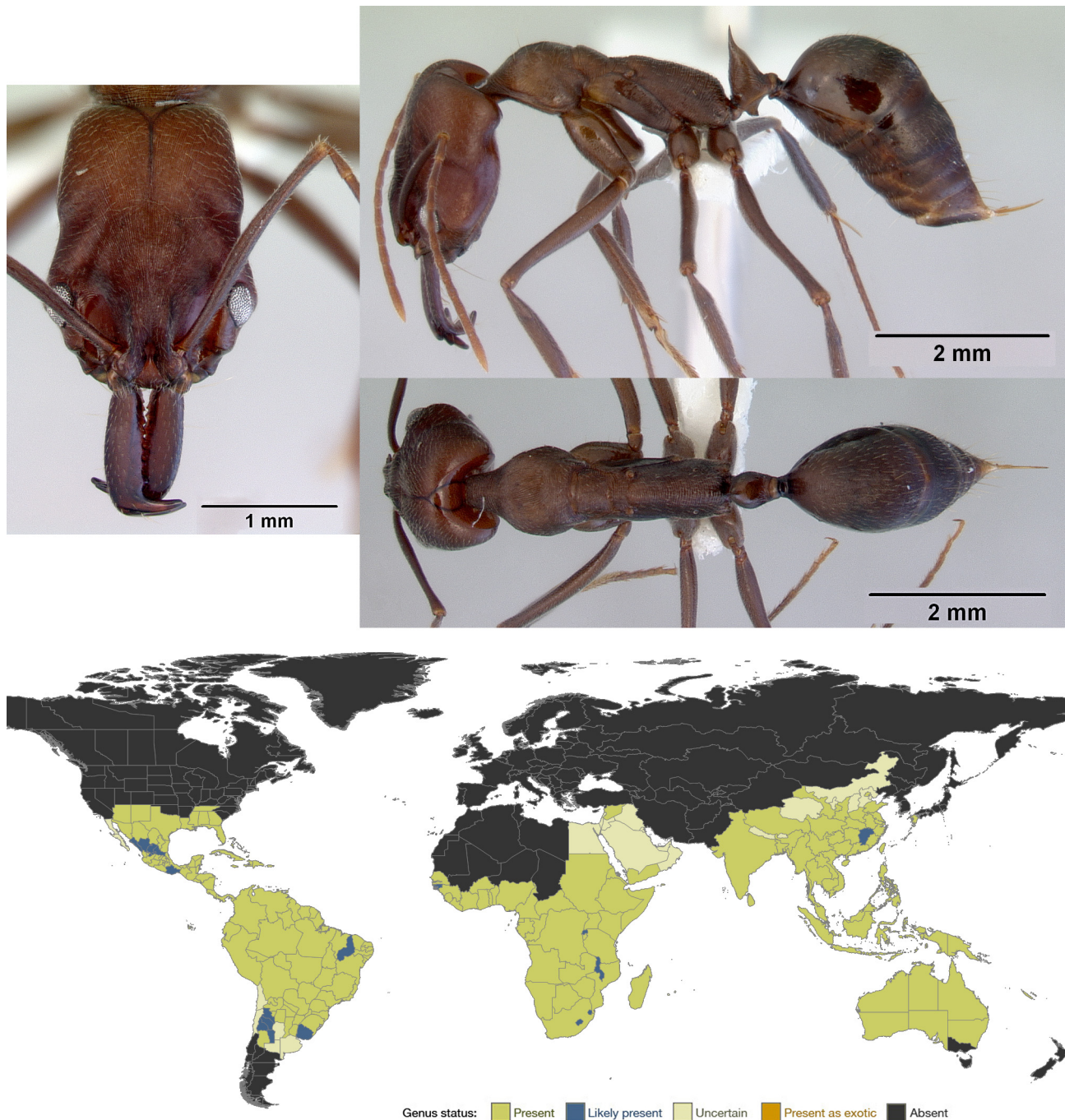
*Odontomachus* is a large genus (63 described extant species) widespread and abundant in the tropics and subtropics of the world, with a few species extending into temperate regions. Like its sister genus *Anochetus*, *Odontomachus* is notable for its remarkable trap mandibles. The closure of *Odontomachus* mandibles is the fastest movement ever recorded in any animal.

**Diagnosis.** Workers of *Odontomachus* are so distinctive that they are difficult to confuse with those of any other genus except *Anochetus*, the sister genus of *Odontomachus*. The unusual trap mandibles and head shape of *Odontomachus* are synapomorphic with *Anochetus*, but the genera are readily differentiated by examination of the posterior face of the head. In *Odontomachus* the nuchal carina is V-shaped medially, and the posterior surface of the head has a pair of dark converging apophyseal lines. In *Anochetus* the nuchal carina is continuously curved and the posterior surface of the head lacks visible apophyseal lines. These genera also tend to differ in size (*Anochetus* are generally smaller, though there is some overlap), propodeal teeth (absent in *Odontomachus* but usually present in *Anochetus*), and petiole shape (always coniform in *Odontomachus*, but variable in *Anochetus*).

**Synoptic description.** *Worker.* Medium to large (TL 6–20 mm; Brown, 1976) slender ants with the standard characters of Ponerini. Mandibles straight and narrow, articulating with the head medially, capable of being held open at 180°, and with a trio of large apical teeth and often a row of smaller teeth along the masticatory margin. Head with a pair of long trigger setae below the mandibles. Clypeus truncate laterally and anteriorly. Frontal lobes

small and relatively widely spaced. Head strangely shaped: much longer than wide, with a distinct constriction behind the eyes and then often a gradual broadening posteriorly, the posterior margin of the head straight or mildly concave, the nuchal carina V-shaped medially, the posterior surface of the head with a pair of dark converging apophyseal lines. Eyes fairly large, located anterior of head midline on temporal prominences. Metanotal groove shallowly to deeply impressed. Propodeum broadly rounded dorsally, as broad as mesonotum but narrower than pronotum. Propodeal spiracles small, circular to ovoid. Metatibial spur formula (1s, 1p). Petiole surmounted by a conical node, topped by a posteriorly-directed spine of variable length. Gaster without a girdling constriction between pre- and postsclerites of A4. Stridulitrum almost always present on pretergite of A4. Head and body shiny to lightly striate, with very sparse pilosity and pubescence. Color variable, orange to black.

*Queen.* Similar to worker but slightly larger, alate and with the other caste differences typical for ponerines (Brown, 1976). Queens of *O. coquereli* are ergatoid (Molet *et al.*, 2007).



**FIGURE 19.** Worker caste of *Odontomachus turneri*: lateral and dorsal view of body and full-face view of head (CASENT0172405, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Odontomachus*.

*Male.* See descriptions in Brown (1976) and Yoshimura & Fisher (2007).

*Larva.* Larvae of various *Odontomachus* species have been described by Wheeler (1918), Wheeler & Wheeler (1952, 1964, 1971a, 1980), Brown (1976), and Petralia & Vinson (1980).

**Geographic distribution.** *Odontomachus* is abundant in the tropical and subtropical regions of the world, though it is most diverse in the Asian tropics and the Neotropics. Australia boasts a handful of species, while Africa has two species (*O. assiniensis* and *O. troglodytes*) and the Malagasy region has three species (*O. coquereli*, *O. troglodytes*, and *O. simillimus*, the latter apparently introduced to the Seychelles; Fisher & Smith, 2008). A few species extend into temperate regions, notably in the southwestern United States, northeastern China, central Argentina, and southwestern Australia (reviewed in Brown, 1976).

**Ecology and behavior.** In most respects *Odontomachus* are fairly typical ponerines. The nesting habits of many species have been observed, and most of these nest in soil or rotting wood (e.g., *O. affinis*: Brandão, 1983; *O. bauri*: Ehmer & Hölldobler, 1995; *O. brunneus*, *O. clarus*, *O. relictus*, and *O. ruginodis*: Deyrup & Cover, 2004; *O. cephalotes*: Wilson, 1959b; *O. chelifer*: Fowler, 1980; Passos & Oliveira, 2004; *O. coquereli*: Molet *et al.*, 2007; *O. erythrocephalus*: Longino, 2013; *O. opaciventris*: de la Mora *et al.*, 2007; *O. rixosus*: Ito *et al.*, 1996; *O. simillimus*: Wilson, 1959b; van Walsum *et al.*, 1998; *O. tyrannicus*: Wilson, 1959b), though some species will nest in more unusual locations such as in abandoned termite nests (Déjean *et al.*, 1996, 1997) or arboreally (e.g., *O. troglodytes*: Colombel, 1972; *O. brunneus*, *O. hastatus*, and *O. mayi*: Brown, 1976; *O. bauri* and *O. hastatus*: Longino, 2013). The nests of *O. bauri* are apparently polydomous (Ehmer & Hölldobler, 1995). *Odontomachus* workers are monomorphic and are epigeic foragers, and some species are at least partially arboreal in their habits (Brown, 1976; Longino, 2013). Most species are generalist predators of arthropods, though many species partially specialize on certain types of prey, especially termites (e.g., Fowler, 1980; Léveux, 1982; Ehmer & Hölldobler, 1995). At least some species will also tend honeydew-secreting insects or visit extrafloral nectaries (e.g., *O. affinis*: Borgmeier, 1920; *O. bauri*, *O. hastatus*, and *O. panamensis*: Schemske, 1982; Longino, 2013; *O. troglodytes*: Evans & Leston, 1971; Lachaud & Déjean, 1991a), and the Neotropical species *O. chelifer* is known to eat fruit and the arils of certain seeds, which the ants ultimately disperse (Pizo & Oliveira, 1998; Passos & Oliveira, 2002, 2004). *O. laticeps* and *O. meinerti* (as *O. minutus*) also collect seeds with nutritious arils (Horvitz & Beattie, 1980; Horvitz, 1981). *O. malignus* is notable for its habit of foraging among corals at low tide (Wilson, 1959b). Foraging workers of *O. bauri* navigate using visual cues from the forest canopy overhead as well as chemical cues (Oliveira & Hölldobler, 1989). Recruitment of nestmates via tandem running was observed in *O. troglodytes* (Lachaud & Déjean, 1991a).

Colony size is highly variable across the genus, ranging from an average of only 18 workers in *O. coquereli* (Molet *et al.*, 2007) to as many as 10,000 workers in *O. opaciventris* (de la Mora *et al.*, 2007). Most species seem to have colony sizes of several hundred workers: *O. chelifer* colonies average between 100 to 650 workers (Fowler, 1980; Passos & Oliveira, 2004), colonies of *O. rixosus* had an average of 142 workers (Ito *et al.*, 1996), and *O. bauri* is reported to have up to 300 workers per colony (Jaffe & Marcuse, 1983), though *O. troglodytes* colonies can have over 1,000 workers (Colombel, 1970a).

Most species of *Odontomachus* have typical winged queens and semi-claustral nest founding (Brown, 1976), though *O. coquereli* has wingless ergatoid queens and colonies apparently reproduce by division (Molet *et al.*, 2007). An undescribed species from Malaysia is also reported to have ergatoid queens (Gobin *et al.*, 2006), and colony reproduction by fission is suspected to occur in some other species (Brown, 1976). While some *Odontomachus* species are likely to be monogynous, many species are polygynous (e.g., *O. assiniensis*: Ledoux, 1952; *O. cephalotes*: Peeters, 1987; *O. chelifer*: Medeiros *et al.*, 1992; *O. rixosus*: Ito *et al.*, 1996; *O. troglodytes*: Ledoux, 1952). Queens of *O. rixosus* perform many of the tasks more typical of the worker caste, including foraging outside the nest (Ito *et al.*, 1996). In the most detailed series of studies on a single *Odontomachus* species, Colombel examined various aspects of the behavior of *O. troglodytes*, including caste determination (Colombel, 1978), egg development (Colombel, 1974) reproduction by workers (Colombel, 1972), ecology, nest structure, demographics and population dynamics (Colombel, 1970a), egg-laying by queens (Colombel, 1970b), and alarm pheromones (Colombel, 1968). The laying of haploid eggs by workers has also been observed in *O. chelifer* (Medeiros *et al.*, 1992), *O. rixosus* (Ito *et al.*, 1996), and *O. simillimus* (van Walsum *et al.*, 1998). Wheeler *et al.* (1999) examined the egg proteins of *O. chelifer* and *O. clarus*.

Only a handful of papers have been published on the social behavior of *Odontomachus*. Polyethism in *O. troglodytes* was studied by Déjean & Lachaud (1991), while division of labor in *O. affinis* was examined by



Brandão (1983). Powell & Tschinkel (1999) discovered that the workers of *O. brunneus* organize themselves into a social hierarchy via ritualized dominance interactions, with repercussions for task specialization within the nest. Whether similar hierarchies exist among workers in other *Odontomachus* species is unknown, though dominance hierarchies exist among queens in colonies of the polygynous species *O. chelifera* (Medeiros *et al.*, 1992). Jaffe & Marcuse (1983) observed both nestmate recognition and territorial aggression in *O. bauri*. Aspects of the mating behavior of *O. assiniensis*, the other African *Odontomachus* species, were studied by Ledoux (1952).

Wheeler & Blum (1973) identified the mandibular glands as the source of alarm pheromones in *O. brunneus*, *O. clarus* and *O. hastatus*. Morgan *et al.* (1999) examined the mandibular gland secretions of *O. bauri*, while Longhurst *et al.* (1978) studied the mandibular gland secretions of *O. troglodytes* and the response of males to these secretions. Oliveira & Hölldobler (1989) identified the roles of pygidial, mandibular and poison gland secretions in *O. bauri* for recruitment, alarm and attack behaviors. Alarmed *Odontomachus* workers can also stridulate (*e.g.* Carlin & Gladstein, 1989).

The trap mandibles and associated behaviors of *Odontomachus* (and *Anochetus*) rank among the most specialized of any ponerine. When hunting, *Odontomachus* workers hold their highly modified mandibles open at 180° and shut them with extreme force and speed on their prey. In fact, this is the fastest movement ever measured in any animal (Patek *et al.*, 2006; Spagna *et al.*, 2008). The contact of trigger setae (located beneath the mandibles) with the prey triggers the mandibular closure. The morphological, physiological and neurological characteristics of trap mandibles (and associated structures and behaviors) have been extensively studied (*e.g.*, Gronenberg *et al.*, 1993; Gronenberg & Tautz, 1994; Gronenberg, 1995a, 1995b; Ehmer & Gronenberg, 1997; Just & Gronenberg, 1999; Paul & Gronenberg, 1999; Spagna *et al.*, 2008). Kinematic data indicate that the force of jaw closure in *Odontomachus* scales positively with body size, while acceleration scales inversely with body size (Spagna *et al.*, 2008). The significance of these scaling relationships for the optimal foraging strategy in a given species is unknown.

The sequence of actions taken during prey capture by a hunting *Odontomachus* worker was summarized by de la Mora *et al.* (2007). Upon detection of a suitable prey item, the worker antennates it, then withdraws the antennae and snaps its mandibles shut on the prey. Generally the prey are held in the mandibles, lifted off the substrate, stung, and then transported back to the nest, though sometimes stinging is not necessary (Brown, 1976). The exact behavioral sequence used during prey capture varies somewhat depending on the *Odontomachus* species and the identity of the prey. For example, multiple mandibular strikes may be used to stun or dismember the prey. *Odontomachus* workers are often cautious during prey capture, especially with potentially dangerous prey such as termites. De la Mora *et al.* (2007) describe the predatory behavior of *O. opaciventris* in detail; the foraging behaviors of several other *Odontomachus* species have been described by other authors (*e.g.*, *O. assiniensis*: Ledoux, 1952; *O. bauri*: Jaffe & Marcuse, 1983; *O. chelifera*: Fowler, 1980; *O. troglodytes*: Déjean, 1982?, 1987; Déjean & Bashingwa, 1985). Déjean (1987) found that workers of *O. troglodytes* learn to avoid noxious prey.

Rapid mandibular strikes are used by *Odontomachus* to perform a variety of specialized tasks in addition to prey capture. Patek *et al.* (2006) found that workers of *O. bauri* utilize the force of their mandible strikes to bounce to safety (or to bounce onto intruders), and also to eject intruders away. This latter behavior (the “bouncer defense”) was studied in detail in *O. ruginodis* by Carlin & Gladstein (1989). In addition to these highly specialized tasks, the mandibles of *Odontomachus* remain functional for more typical activities such as nest construction and brood care (Just & Gronenberg, 1999).

**Phylogenetic and taxonomic considerations.** *Odontomachus* was erected by Latreille (1804) to house the single species *Formica haematoda* Linnaeus, and it has experienced relative taxonomic stability at the genus level since then, except for the recognition of several junior synonyms: *Pedetes* (Bernstein, 1861), *Champsomyrmex* (Emery, 1892), and *Myrtoteras* (Matsumura, 1912). *Odontomachus* has had a somewhat more unsettled taxonomic history at the tribe and family level. Initially placed in Ponerites (Lepeletier de Saint-Fargeau, 1835), then Poneridae (Smith, 1857), *Odontomachus* (and its sister genus *Anochetus*) spent most of the latter half of the 19<sup>th</sup> century and most of the 20<sup>th</sup> century in a state of flux, variously placed in its own family Odontomachidae (*e.g.*, Smith, 1871), in a separate subfamily within Formicidae (Odontomachidae or Odontomachinae; *e.g.*, Mayr, 1862), in tribe Odontomachini of Ponerinae (*e.g.*, Forel, 1893a; sometimes also spelled Odontomachii, as in Forel, 1893a), in Ponerini subtribe Odontomachiti (Brown, 1976), or simply in Ponerini (*e.g.*, Emery & Forel, 1879, and most recent authors). This taxonomic chaos was the result of the highly derived mandible and head structure of *Odontomachus*, which led many authors to believe that it was unrelated to the more typical genera in Ponerinae.

Schmidt's (2013) molecular phylogeny of the Ponerinae confirms that *Odontomachus* is a member of tribe Ponerini, and that its sister is *Anochetus*, a result supported unequivocally by morphological synapomorphies of their head and mandibles (among other characters). The phylogeny is equivocal about the monophyly of *Odontomachus* (*O. coquereli* is resolved as either sister to the other *Odontomachus* species or as sister to *Anochetus*, with approximately equal probability), and it is possible that *Odontomachus* and *Anochetus* will prove to not be mutually monophyletic (as suggested by Brown, 1976). On the other hand, a species level phylogeny for these genera, which includes additional taxa and genes, strongly supports their reciprocal monophyly, though some phylogenetically critical *Anochetus* taxa were not sampled (C. Schmidt, unpublished data). This is consistent with the findings of Santos *et al.* (2010), who examined the chromosomes of both genera. We are therefore retaining *Anochetus* and *Odontomachus* as distinct genera. Additional taxon sampling may reveal that one or the other of these genera is non-monophyletic, in which case *Anochetus* would likely be synonymized under *Odontomachus*. The sister group of *Odontomachus* + *Anochetus* is still unresolved.

### Species of *Odontomachus*

Brown (1976) revised the species-level taxonomy of *Odontomachus*. His keys to *Odontomachus* species are slightly outdated but are still the most complete for the world fauna.

*O. aciculatus* Smith, F., 1863: Indonesia  
*O. affinis* Guérin-Méneville, 1844: Brazil  
*O. alius* Sorger & Zettel, 2011: Philippines (Cebu I.).  
*O. allolabis* Kempf, 1974: Brazil  
*O. angulatus* Mayr, 1866: Fiji Islands  
*O. animosus* Smith, F., 1860: New Guinea  
*O. assiniensis* Emery, 1892: Ivory Coast  
*O. banksi* Forel, 1910: Philippines  
*O. bauri* Emery, 1892: Galapagos Islands  
*O. biolleyi* Forel, 1908: Costa Rica  
*O. biumbonatus* Brown, 1976: Ecuador  
*O. bradleyi* Brown, 1976: Peru  
*O. brunneus* (Patton, 1894): United States  
*O. caelatus* Brown, 1976: Brazil  
*O. cephalotes* Smith, F., 1863: Indonesia  
*O. chelifera* (Latreille, 1802): South America  
*O. circulus* Wang, 1993: China  
*O. clarus* Roger, 1861: United States  
*O. coquereli* Roger, 1861: Madagascar  
*O. cornutus* Stitz, 1933: Ecuador  
*O. erythrocephalus* Emery, 1890: Costa Rica  
*O. floresensis* Brown, 1976: Indonesia (Flores Island)  
*O. fulgidus* Wang, 1993: China  
*O. granatus* Wang, 1993: China  
*O. haematodus* (Linnaeus, 1758): America meridionali  
*O. hastatus* (Fabricius, 1804): Central America  
*O. imperator* Emery, 1887: New Guinea  
*O. infandus* Smith, F., 1858: Philippines  
*O. insularis* Guérin-Méneville, 1844: Cuba  
*O. kuroiwae* (Matsumura, 1912): Japan  
*O. laticeps* Roger, 1861: Mexico  
*O. latidens* Mayr, 1867: Indonesia (Java)  
*O. latissimus* Viehmeyer, 1914: New Guinea  
*O. macrorhynchus* (Bernstein, 1861): Indonesia

*O. malignus* Smith, F., 1859: New Guinea  
*O. mayri* Roger, 1861: Brazil  
*O. meinerti* Mann, 1912: Brazil  
*O. montanus* Stitz, 1925: New Guinea  
*O. monticola* Emery, 1892: Myanmar  
*O. mormo* Brown, 1976: Ecuador  
*O. nigriceps* Smith, F., 1860: New Guinea  
*O. opaciventris* Forel, 1899: Mexico  
*O. opaculus* Viehmeyer, 1912: New Guinea  
*O. panamensis* Forel, 1899: Panama  
*O. papuanus* Emery, 1887: New Guinea  
*O. peruanus* Stitz, 1933: Peru  
*O. philippinus* Emery, 1893: Philippines  
*O. relictus* Deyrup & Cover, 2004: United States  
*O. rixosus* Smith, F., 1857: Singapore  
*O. ruficeps* Smith, F., 1858: Australia  
*O. rufithorax* Emery, 1911: New Guinea  
*O. ruginodis* Smith, M.R., 1937: Bahamas  
*O. saevissimus* Smith, F., 1858: Indonesia  
*O. scalptus* Brown, 1978: Ecuador  
*O. schoedli* Sorger & Zettel, 2011: Philippines (Luzon I.)  
*O. scifictus* Sorger & Zettel, 2011: Philippines (Camiguin I.)  
*O. silvestrii* Wheeler, W.M., 1927: Vietnam  
*O. simillimus* Smith, F., 1858: Fiji Islands  
*O. spissus* Kempf, 1962: Brazil  
*O. sumbensis* Brown, 1976: Indonesia  
*O. tensus* Wang, 1993: China  
*O. testaceus* Emery, 1897: New Guinea  
*O. troglodytes* Santschi, 1914: Kenya  
*O. turneri* Forel, 1900: Australia  
*O. tyrannicus* Smith, F., 1859: Indonesia (Aru Island)  
*O. unispinosa* (Fabricius, 1793): Guadelupe Island  
*O. xizangensis* Wang, 1993: China  
*O. yucatecus* Brown, 1976: Mexico

Fossil species

† *O. pseudobauri* De Andrade, 1994: Dominican Amber

† *O. spinifer* De Andrade, 1994: Dominican Amber

### ***Odontoponera* Mayr**

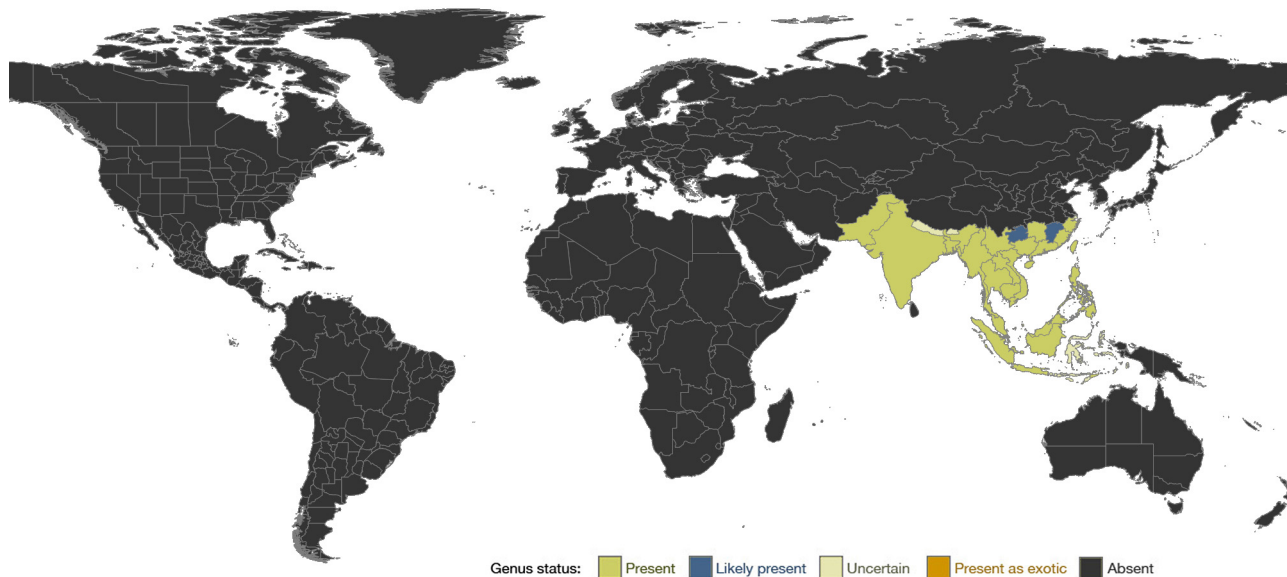
Fig. 20

*Odontoponera* Mayr, 1862: 713, 717 (as genus in Ponerinae [Poneridae]). Type-species: *Ponera denticulata* Smith, F., 1858: 91; by monotypy.

*Odontoponera* is a small genus with two species and 3 subspecies restricted to Southeast Asia, where it is one of the most commonly observed ants.

**Diagnosis.** Workers of *Odontoponera* are easily differentiated from other ponerines by their denticulate anterior clypeal margin, toothed pronotal margins, denticulate-emarginate petiolar scale and a small, ventrally-directed tooth at the apex of the hypopygium, all of which are autapomorphic within Ponerinae. The strong striate sculpturing of *Odontoponera* is also characteristic, though *Diacamma*, *Ectomomyrmex* and *Paltothyreus* also have striate sculpturing (these genera lack the other diagnostic characters of *Odontoponera*).





**FIGURE 20.** Worker caste of *Odontoponera transversa*: lateral and dorsal view of body and full-face view of head (CASENT0249126, Ryan Perry and [www.antweb.org](http://www.antweb.org)); world distribution of *Odontoponera*.

**Synoptic description.** *Worker.* Medium-sized (TL 9–12 mm; Bingham, 1903) ants with the standard characters of Ponerini. Mandibles short, triangular and massive, with a basal groove. Clypeus with a denticulate anterior margin. Eyes fairly small, placed anterior of head midline, with a subtle preocular carina (often difficult to distinguish from the striate sculpturing of the head). Pronotum with a short spine at each anterodorsal corner. Metanotal groove very shallowly impressed or reduced to a simple suture. Propodeum narrowed dorsally, the posterior margins with shallow denticulate ridges. Propodeal spiracle ovoid. Metatibial spur formula (1s, 1p).

Petiole squamiform, with a sharp denticulate and emarginate dorsal margin. Gaster with only a weak girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and mesosoma deeply striate, the gaster only lightly punctate. Head and body with scattered pilosity and only light pubescence. Color ferrugineous to black.

*Queen.* Similar to worker but larger (TL 11–13 mm; Bingham, 1903) and winged.

*Male.* See description in Smith (1858).

*Larva.* Described by Wheeler & Wheeler (1952).

**Geographic distribution.** *Odontoponera* is restricted to Southeast Asia, where its range stretches from India to the Philippines and from southern China to the Lesser Sunda Islands of southern Indonesia (Creighton, 1929).

**Ecology and behavior.** Virtually nothing is known about the social behavior of *Odontoponera*, but the genus has received some attention from ecologists due to its abundance. For example, Wheeler & Chapman (1925) noted the abundance of *Odontoponera* at a site in the Philippines, and it was common in a Bornean rainforest (Berghoff *et al.*, 2003), was one of the dominant ants in a study in Vietnam (Eguchi *et al.*, 2004), was the dominant ground-nesting ant in a study in Thailand (Sitthicharoenchai & Chantarasawat, 2006), was one of the most abundant ants in a forest in southern China (Zhou *et al.*, 2007), and one of us (CAS) frequently observed it in a rainforest in peninsular Malaysia. Levy (1996) reported a density of 3,000 nest entrances per hectare in a Bornean rainforest. Colonies have over 100 workers, and the polydomous subterranean nests are linked by interconnecting tunnels (Berghoff *et al.*, 2003).

*Odontoponera* workers are predominantly epigeic foragers and are generalist predators and scavengers (Levy, 1996; Hashimoto *et al.*, 1997; Berghoff *et al.*, 2003; Pfeiffer *et al.*, 2006; Zhou *et al.*, 2007). Wheeler & Chapman (1925) noted that, in the Philippines, *Odontoponera* “is especially fond of termites and is often seen raiding their colonies.” Remarkably, Berghoff *et al.* (2003) observed that *Odontoponera* workers are effective at guarding their nest entrances from marauding *Dorylus* army ants and that the *Odontoponera* workers actually prey on the *Dorylus*. Ants and termites made up nearly half of the food items collected by *O. transversa* workers in the study by Levy (1996). Workers only forage within about a meter from the nest entrances (Eguchi *et al.*, 2004).

Morgan *et al.* (1999, 2003) studied the mandibular gland and abdominal gland secretions of *Odontoponera*, and Leluk *et al.* (1989) examined the protein composition of *Odontoponera* venom.

**Phylogenetic and taxonomic considerations.** *Odontoponera* was erected by Mayr (1862) to house the single species *Ponera denticulata* F. Smith (now a junior synonym of *O. transversa*). The genus has experienced complete taxonomic stability at the genus level, as all subsequent authors have continued to treat it as a distinct genus.

We also consider *Odontoponera* to be distinct from other genera. Schmidt's (2013) molecular phylogeny of Ponerinae places *Odontoponera* with strong support within the *Odontomachus* group, but its sister group is unresolved. Morphologically, *Odontoponera* has several autapomorphies (denticulate clypeal margin, pronotal spines, and denticulate-emarginate petiolar scale) which readily distinguish it from other ponerines. Its deep striate sculpturing is also unique within the *Odontomachus* group (*Paltothyreus* has only shallow striate sculpturing), though *Diacamma* and *Ectomomyrmex* in the *Ponera* group have both convergently evolved deep striate sculpturing. In short, there are no morphological characters suggesting a close relationship with any other particular genus. *Odontoponera* is apparently yet another product of the early explosive radiation of the *Odontomachus* group.

### Species of *Odontoponera*

*Odontoponera* currently contains two species, one of which has three subspecies (Yamane, 2009). However, the status of the species has been questioned and Yamane (2009) suggests that at least one of them should be treated as a junior synonym. A full revision of the group will be required to determine the true taxonomic status of these taxa.

***O. denticulata*** (Smith, F., 1858): Singapore

***O. transversa*** (Smith, F., 1857): Singapore

***O. transversa biconcentrica*** Wheeler, W.M. & Chapman, 1925: Philippines

***O. transversa infusata*** Creighton, 1929: Indonesia (Java).

***O. transversa nitens*** Creighton, 1929: Borneo

## *Ophthalmopone* Forel

Fig. 21

*Ophthalmopone* Forel, 1890: cxi (as genus). Type-species: *Ophthalmopone berthoudi* Forel, 1890: cxiii; by monotypy. **Gen. rev.**

*Ophthalmopone* Arnold, 1915: 49 (incorrect subsequent spelling of *Ophthalmopone*).

*Ophthalmopone* is a small genus (five described species) restricted to Sub-Saharan Africa. It is notable for its polydomous colonies, specialized termite predation, and reproduction by gamergate workers.

**Diagnosis.** Diagnostic morphological apomorphies of *Ophthalmopone* workers include very large eyes located at or posterior to the head midline and a hypopygium armed with stout spines. This combination of characters is unique to *Ophthalmopone*. *Ophthalmopone* is similar to *Megaponera* but lacks the preocular carinae of that genus. Large eyes also occur in *Harpegnathos*, but those of *Harpegnathos* are even larger and located at the extreme anterior end of the head, rather than at or posterior to the head midline. Stout hypopygial spines occur in several other ponerine genera, but these groups lack *Ophthalmopone*'s combination of slender build, dense pubescence, large eyes, nodiform petiole, and obsolete gastral constriction.

**Synoptic description.** *Worker.* Large (TL 8–13.5 mm; Emery, 1886, 1902) slender ants with the standard characters of Ponerini. Mandibles triangular and long. Eyes very large, located at or posterior to the head midline. Frontal lobes small, widely separated anteriorly by a triangular extension of the clypeus. Metanotal groove shallowly impressed. Propodeum moderately narrowed dorsally. Propodeal spiracle slit-shaped. Metatibial spurs formula (1s, 1p). Tarsal claws unarmed or armed with a single preapical tooth. Petiole nodiform. Gaster without a girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Hypopygium armed with a row of stout setae on either side of the sting. Head and body finely punctate, largely devoid of pilosity but with a dense pubescence. Color black.

*Queen.* Unknown and apparently absent.

*Male.* See descriptions in Emery (1911) and Arnold (1915).

*Larva.* Larvae of *O. berthoudi* were described by Wheeler & Wheeler (1971a).

**Geographic distribution.** *Ophthalmopone* is restricted to Sub-Saharan Africa. *O. berthoudi* has the widest range of any member of the genus, occurring from Sudan to South Africa (Weber, 1942; Prins, 1978). Other species are restricted to southern Africa (*O. hottentota*), south-central Africa (*O. depilis* and *O. mocquerysi*), or eastern Africa (*O. ilgii*).

**Ecology and behavior.** Due to its unusual suite of characteristics, *Ophthalmopone* has drawn considerable attention from ecologists and ethologists. *O. berthoudi* is by far the best studied species in the genus, and most of what is known about *Ophthalmopone* ecology and behavior derives from observations of that species.

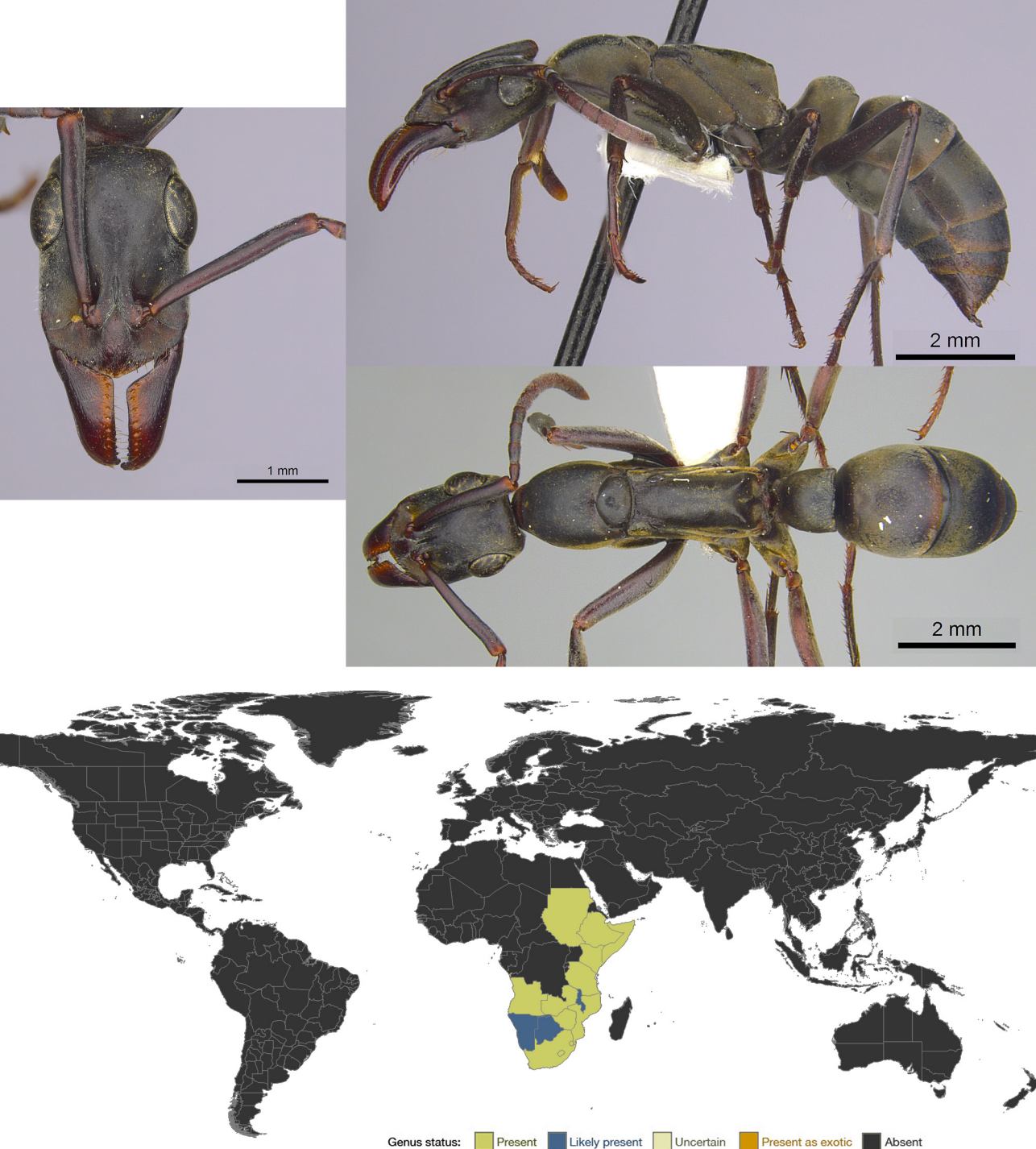
*O. berthoudi* colonies are polydomous, with from two to seven nests located up to 75 m apart under stones, in open ground or in abandoned termitaria (Arnold, 1915; Peeters, 1985; Peeters & Crewe, 1987). *O. hottentota* nests are also located under stones or in open ground (Dean, 1989). Workers regularly transport brood, other workers, and even males between the nests (Peeters, 1985; Peeters & Crewe, 1987; Sledge *et al.*, 1996). Nests of *O. berthoudi* have from 20 to 800 workers (mean = 186 workers; Peeters & Crewe, 1987; mean = 89 workers for four excavated nests of *O. hottentota*; Peeters & Crewe, 1985b; Dean, 1989). A highly variable proportion of workers in each nest are mated (1.4–66% for *O. berthoudi*; Peeters & Crewe, 1985a; Sledge *et al.*, 1996 and 2001), and these gamergate workers perform all reproduction for the colony.

Males enter foreign colonies and mate preferentially with the younger workers (Peeters & Crewe, 1986a). There is apparently no social regulation over which or how many workers mate. Sledge *et al.* (2001) found no evidence of aggressive dominance interactions among gamergates or between gamergates and unmated workers in *O. berthoudi*, though they found clear evidence that gamergates chemically suppress haploid egg production in virgin workers. The fecundity of gamergates is low (fewer than one egg per gamergate per day; Peeters & Crewe, 1985a), which is offset by the presence of multiple reproductives per colony. Sledge *et al.* (1999) studied the division of labor in *O. berthoudi* colonies and found that as the percentage of gamergates in a colony decreases over a season, the fecundity of the gamergates increases and their range of activities becomes more restricted. Gamergates are never found outside the nest except during nest transfers (Peeters & Crewe, 1985a).

Like workers of their sister genus *Megaponera*, *Ophthalmopone* workers are specialist termite predators, though they are not polymorphic as in *Megaponera*. It appears that the workers of some species forage in organized



raids, like *Megaponera*, while others forage singly. Arnold (1915) observed “irregular columns” of the exceptionally fast-running foragers of *O. berthoudi*, and Forel (1928) reported foraging columns of *O. ilgii*. On the other hand, more recent studies of foraging behavior in *O. berthoudi* (Peeters & Crewe, 1987) and *O. hottentota* (Dean, 1989) failed to observe group foraging in these species. Neither study found any evidence of recruitment or of chemical trails, as the workers of both species hunted termites singly. Dean (1989) observed caches of hundreds of paralyzed termites in nests of *O. hottentota*; prey caching has not been observed in *O. berthoudi*. Foragers of both species return repeatedly to harvest a single termite source.



**FIGURE 21.** Worker caste of *Ophthalmopone berthoudi*: lateral and dorsal view of body and full-face view of head (CASENT0249198, Will Ericson and [www.antweb.org](http://www.antweb.org)); world distribution of *Ophthalmopone*.

Duncan (2001) discussed the energetic challenges facing an *Ophthalmopone* colony, which depends on an unpredictable and scattered food source (foraging termites), and the paradoxical observation that only a small percentage of workers in a colony forage (Peeters, 1985). She found that foraging workers of *O. berthoudi* are exceptionally energy efficient, and hypothesized that this, along with the polydomous nature of the colonies, resolves the apparent paradox.

**Phylogenetic and taxonomic considerations.** Forel (1890) erected *Ophthalmopone* as a genus along with his description of the type species, *O. berthoudi*. He correctly recognized the distinctiveness of the taxon, as did all subsequent authors until W. L. Brown (in Bolton, 1994) synonymized it under *Pachycondyla* without phylogenetic justification.

We are reviving *Ophthalmopone* to full genus status, based on both molecular and morphological evidence. Schmidt's (2013) molecular phylogeny of the Ponerinae places *O. berthoudi* with strong support within the *Odontomachus* group as sister to *Megaponera*, and not at all close to *Pachycondyla*. A sister group relationship with *Megaponera* is also supported by morphology, the workers of the two genera being remarkably similar. These genera also share the ecological and behavioral synapomorphies of specialist predation on termites and an absence of winged queens. See the discussion under *Megaponera* for more details on the similarities and differences between these sister genera.

Apparent apomorphies of the genus include very large eyes set at or posterior to the midline of the head, stout hypopygeal spines on either side of the sting, specialized termite predation, and reproduction by gamergates. Species-level relationships within *Ophthalmopone* are unstudied and would provide an interesting opportunity to explore the evolution of mass foraging, given the variability within the genus.

### Species of *Ophthalmopone*

*O. berthoudi* Forel, 1890: South Africa (**comb. rev.**)

*O. berthoudi pubescens* Weber, 1942: Sudan (**comb. rev.**)

*O. depilis* Emery, 1902: São Tomé Is. (**comb. rev.**)

*O. hottentota* (Emery, 1886): South Africa (**comb. rev.**)

*O. ilgii* Forel, 1894: Ethiopia (**comb. rev.**)

*O. mocquersyi* Emery, 1902: São Tomé Is. (**comb. rev.**)

### *Paltothyreus* Mayr

Fig. 22

*Paltothyreus* Mayr, 1862: 714, 735 (as genus). Type-species: *Formica tarsata* Fabricius, 1798: 280; by monotypy. **Gen. rev.**

*Paltothyreus* is a monotypic genus (with five subspecies) widespread in Sub-Saharan Africa. It is sister to *Buniapone* and is notable for its huge nests, noxious alarm pheromones, chemical recruitment, and prey transfer behavior.

**Diagnosis.** Diagnostic morphological apomorphies of *Paltothyreus* workers include their striate sculpturing, blunt clypeal projection, complex metapleural gland orifice (with both anterior and posterior cuticular flanges), and hypopygium armed with stout setae. This combination of characters does not occur in any other ponerine genus. Striate sculpturing and an armed hypopygium occur in several other ponerine genera, but never together, and never in combination with a blunt clypeal projection or complex metapleural gland orifice. The apomorphies of the clypeus and metapleural gland orifice are shared with *Buniapone*, but that genus lacks striate sculpturing and an armed hypopygium.

**Synoptic description.** *Worker.* Very large (TL 17-20 mm; Arnold, 1915) ants with the standard characters of Ponerini. Mandibles triangular and long, with a distinct basal groove. Clypeus with a blunt squarish anteromedial projection. Frontal lobes widely separated anteriorly by an extension of the clypeus. Eyes large, located anterior to head midline. Ocelli sometimes present in workers. Metanotal groove at most present as a faint suture. Propodeum broad dorsally. Propodeal spiracle ovoid. Metapleural gland orifice complex, with a broad cuticular flange posteriorly and a small cuticular flange anteriorly, together forming a deep transverse groove. Metatibial spur



formula (1s, 1p). Tarsal claws with a single preapical tooth. Petiole surmounted by a thick scale. Subpetiolar process a deep keel. Sternite of A3 with a large keel-like anteroventral process. Tergite of A3 with blunt dorsolateral angles. Gaster with a moderate girdling constriction between pre- and post-tergites of A4. Hypopygium armed with a row of stout setae on either side of the sting. Head and body striate, with scattered to abundant pilosity and moderate pubescence. Color black.



**FIGURE 22.** Worker caste of *Paltothyreus tarsatus*: lateral and dorsal view of body and full-face view of head (CASENT0172430, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Paltothyreus*.



*Queen*. Similar to worker but larger (TL 23 mm; Arnold, 1915) and winged.

*Male*. See descriptions in Emery (1911), Arnold (1915), and Wheeler (1922b).

*Larva*. Not described.

**Geographic distribution.** *Paltothyreus* is widespread and common in Sub-Saharan Africa, though it is patchily distributed (Arnold, 1915; Wheeler, 1922b). Wheeler (1922b) gives its range as encompassing all of Africa south of roughly 15° N latitude. Emery (1911) includes Madagascar in the range of the genus, but this has not been reported elsewhere and is presumably in error.

**Ecology and behavior.** *Paltothyreus*, the African stink ant, is so called because its workers produce powerfully smelly sulfur-containing alarm pheromones in their mandibular glands (Casnati *et al.*, 1967; Crewe & Fletcher, 1974; Crewe & Ross, 1975a, 1975b). *Paltothyreus* occurs mainly in forests and forest-savannah transition zones. Colonies are relatively large, with as many as 2,500 workers (mean = 926 workers; Braun *et al.*, 1994) but only a single queen. Nests are constructed in the ground or in abandoned termite nests (Kalule-Sabiti, 1980; Déjean *et al.*, 1996, 1997) and are of exceptional size, encompassing surface areas of as much as 1,200 m<sup>2</sup>, with multiple entrance holes and extensive tunnel systems (Braun *et al.*, 1994). Some colonies inhabit multiple distantly-separated nests connected by underground tunnels, which Braun *et al.* (1994) characterize as a form of polydomy. The tunnels and multiple nest entrances allow workers to access a large foraging area with minimal time spent in the open. During nest relocations, workers employ a pygidial gland-derived pheromone to recruit nestmates for tandem running (Hölldobler, 1984; Braun *et al.*, 1994). Hölldobler (1980) discovered that *Paltothyreus* foragers visually navigate through their forest environments by memorizing the canopy overhead.

*Paltothyreus* are largely termite predators, though they do hunt or scavenge a broad range of other invertebrates, including other ants (Lévieux, 1977; Kalule-Sabiti, 1980; Déjean *et al.*, 1993a, 1993b, 1999). Workers primarily forage singly, but will recruit nestmates to large prey or concentrated termite sources, using a trail pheromone produced by sternal glands (Hölldobler, 1984; Déjean *et al.*, 1993a). Workers often sting their prey upon capture, and when collecting termites will stack multiple individuals between the mandibles for one return trip to the nest (Déjean *et al.*, 1993b; López *et al.*, 2000). *Paltothyreus* foragers often employ a unique form of group prey retrieval, termed “prey chain transfer behavior” (López *et al.*, 2000), by which successful foragers (“finders”) returning to the nest will transfer their termite prey to other workers (“receivers”) at locations between the prey capture site and the nest. The finders then go back to capture more termites, while the receivers head to the nest, sometimes transferring the prey to yet other workers. López *et al.* (2000) hypothesize that this behavior increases the efficiency of prey capture and also serves as a simple form of recruitment.

The mating and dispersal behavior of *Paltothyreus* were studied by Villet *et al.* (1989). The abdominal glands of *Paltothyreus* males were studied by Hölldobler & Engel-Siegel (1982). Queens apparently chemically suppress the production of eggs by workers (Braun *et al.*, 1994).

**Phylogenetic and taxonomic considerations.** *Paltothyreus* was described by Mayr (1862) to hold the single species *Formica tarsata* Fabricius. The genus experienced relative taxonomic stability until W. L. Brown (in Bolton, 1994) synonymized it under *Pachycondyla* without phylogenetic justification.

We are reviving *Paltothyreus* to full genus status based on both morphological and molecular evidence. Schmidt's (2013) molecular phylogeny of the Ponerinae places *Paltothyreus* with strong support within the *Odontomachus* group as sister to *Buniapone*, and not at all close to *Pachycondyla*.

A sister group relationship between *Paltothyreus* and *Buniapone* is initially a surprising and suspect result. Superficially, these taxa are remarkably different. Whereas *Paltothyreus* is a very large epigeic African ant with triangular mandibles and large eyes, *Buniapone* is a fairly small hypogeic ant restricted to Southeast Asia, with subtriangular mandibles and extremely reduced eyes. *Paltothyreus* would seem to most closely resemble other large African ponerines like *Megaponera*, *Ophthalmopone* or *Hagensia*. *Buniapone*, on the other hand, superficially bears a closer resemblance to *Centromyrmex* or *Cryptopone*.

A closer examination of the morphological structures of these taxa strongly supports a close relationship, however, as they share several apomorphies: a blunt squarish anteromedial clypeal projection, a nearly or completely obsolete metanotal suture, ovoid propodeal spiracles, a complex metapleural gland orifice with both posterior and anterior cuticular flanges, and a squamiform petiole with a large keel-like ventral process. The unusual metapleural gland orifice in particular is a strong synapomorphy for the two genera. See the discussion under *Buniapone* for more on the evolutionary implications of their close relationship.

## Species of *Paltothyreus*

*Paltothyreus* is currently considered to be monotypic, though *P. tarsatus* has a large number of junior synonyms and subspecies, suggesting significant morphological variation within the species. A careful study of the variation in *P. tarsatus* could reveal it to be a species complex.

*P. tarsatus* (Fabricius, 1798): Senegal (**comb. rev.**)

*P. tarsatus delagoensis* Emery, 1899: Mozambique (**comb. rev.**)

*P. tarsatus mediana* Santschi, 1919: Congo (**comb. rev.**)

*P. tarsatus robusta* Santschi, 1919: Somalia (**comb. rev.**)

*P. tarsatus striatidens* Santschi, 1919: Kenya (**comb. rev.**)

*P. tarsatus striatus* Santschi, 1930: Benin (**comb. rev.**)

*P. tarsatus subopaca* Santschi, 1919: Gabon (**comb. rev.**)

## *Phrynoponera* Wheeler

Fig. 23

*Phrynoponera* Wheeler, W.M., 1920: 52 (as genus). Type-species: *Bothroponera gabonensis* André, 1892: 50; by original designation.

*Phrynoponera* is a small genus (five described species) restricted to the African tropics. Its sister group is unresolved and very little is known about its habits.

**Diagnosis.** Diagnostic morphological apomorphies of *Phrynoponera* workers include their posterodorsal propodeal spines and their squamiform, sweeping five-spined petiolar node. Propodeal spines or teeth also occur in *Streblognathus*, *Pseudoneoponera bispinosa*, and some species of *Anochetus* and *Platythyrea*, but these taxa all lack the unusual petiolar node of *Phrynoponera*, which is autapomorphic within Formicidae. Superficially, *Phrynoponera* most resembles *Bothroponera* (s.s.) and *Pseudoneoponera*, but it is readily separated from these genera by the combination of propodeal spines, unusual petiole structure, and weak gastral constriction. Bolton & Fisher (2008b) discuss additional diagnostic characters of the petiolar sternite and prora of *Phrynoponera*.

**Synoptic description.** *Worker.* Medium to large (TL 5–12 mm; Bolton & Fisher, 2008b) robust ants with the standard characters of Ponerini. Mandibles subtriangular, with a basal groove. Frontal lobes large. Eyes moderately large and placed anterior of head midline. Metanotal groove obsolete or vestigial dorsally. Propodeum broad dorsally, with a pair of sharp teeth on the posterodorsal margin. Propodeal spiracle a short slit. Metatibial spur formula (1s, 1p). Petiole squamiform, the scale curving posteriorly and armed with five sharp teeth posterodorsally. Gaster without a distinct girdling constriction between pre- and postsclerites of A4. Head and body coarsely sculptured, with abundant pilosity and no pubescence. Color variable. See Bolton & Fisher (2008b) for a more detailed description of these and other characters.

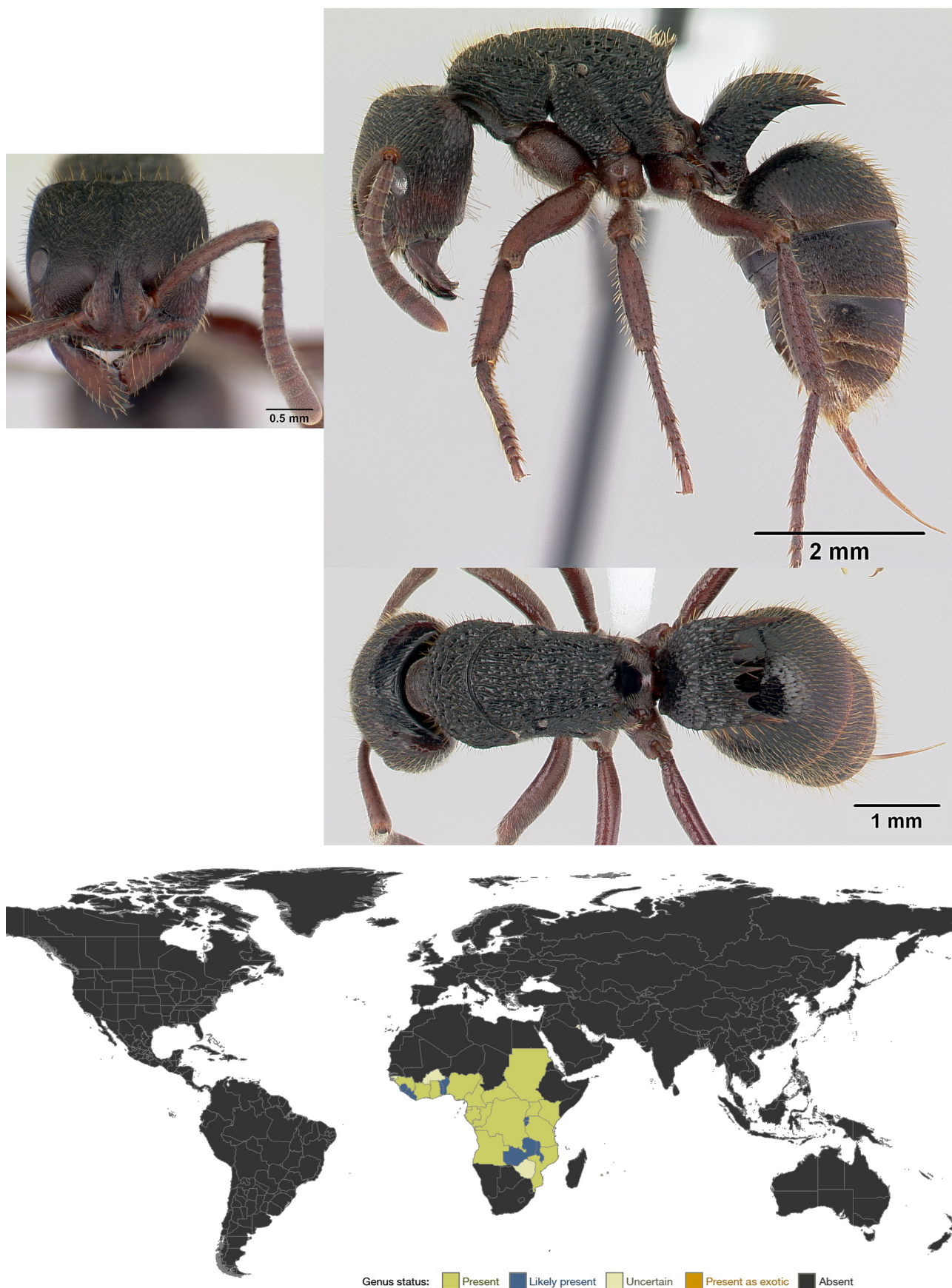
*Queen.* Similar to workers but alate, with three ocelli on the head and a transverse sulcus on the mesopleuron (Bolton & Fisher, 2008b).

*Male.* See description in Bolton & Fisher (2008b).

*Larva.* Not described.

**Geographic distribution.** *Phrynoponera* occurs in the forests of tropical Africa, with most species restricted to central Africa. *P. gabonensis* has the widest range, occurring from Ivory Coast to Kenya and from Sudan to Angola. *P. pulchella*, likely the sister to the rest of the genus, is known only from Kenya (Bolton & Fisher, 2008b).

**Ecology and behavior.** Bolton & Fisher (2008b) summarized what little is known about the ecology and behavior of *Phrynoponera*. These ants inhabit forests and nest in rotten wood, soil (Bolton & Fisher, 2008b), or in termite mounds (Déjean *et al.*, 1996, 1997). They are infrequently collected in the leaf litter (Belshaw & Bolton, 1994) and are apparently generalist predators (Déjean *et al.*, 1999). The unusual petiole structure of *Phrynoponera* presumably evolved for defensive purposes, but the identity of the predator(s) involved is unknown. Many specimens examined by Wheeler (1922b) were extracted from the stomachs of toads.



**FIGURE 23.** Worker caste of *Phrynoponera gabonensis*: lateral and dorsal view of body and full-face view of head (CASENT0178229, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Phrynoponera*.



**Phylogenetic and taxonomic considerations.** Wheeler (1920, 1922b) erected *Phrynoponera* to house *Bothroponera gabonensis* André and several new species. He believed that these taxa were distinct from *Bothroponera* (including *Pseudoneoponera*, which we consider to be a separate genus) based on a number of characters. He noted that *Pseudoneoponera bispinosa* and *Ps. rufipes* each have a morphological character that is reminiscent of the condition in *Phrynoponera* (propodeal spines in the former and a denticulate squamiform petiole in the latter), but believed that these characters were independently derived. In their recent revision of *Phrynoponera*, Bolton & Fisher (2008b) agreed with this assessment, and noted an additional morphological similarity between *Phrynoponera* and both *Asphinctopone* and *Brachyponera*, a similarity that they believed was also convergently derived. Brown (1973) provisionally synonymized *Phrynoponera* with *Pachycondyla*, but Bolton (1994) revived it to full genus status.

We continue to treat *Phrynoponera* as a distinct genus. Morphologically it is quite different from all other genera, with several autapomorphies in both sexes. *Phrynoponera* workers superficially resemble those of *Bothroponera* (s.s.) and *Pseudoneoponera*, as all three are characterized by a robust build, strong sculpturing, an obsolete metanotal groove, and a broad propodeal dorsum. On the other hand, all of these characters have evolved independently in other ponerines on multiple occasions, so they are not likely to be good phylogenetic markers. Schmidt's (2013) molecular phylogeny places *Phrynoponera* with strong support within the *Odontomachus* group, but does not resolve its sister group. *Phrynoponera* is certainly not closely related to *Pachycondyla*, but a sister relationship with either *Bothroponera* or *Pseudoneoponera* cannot be rejected at this time. Interestingly, the best supported sister group of *Phrynoponera* is *Anochetus* and *Odontomachus*, though it is difficult to identify any morphological synapomorphies linking these genera.

### Species of *Phrynoponera*

Bolton & Fisher (2008b) revised the genus. They suggested that *P. pulchella* is probably sister to the rest of the genus, based on synapomorphies of the other species, and we concur. For synonyms and a key to species see Bolton & Fisher (2008b).

*P. bequaerti* Wheeler, W.M., 1922: DRC

*P. gabonensis* (André, 1892): Gabon

*P. pulchella* Bolton & Fisher, 2008b: Kenya

*P. sveni* (Forel, 1916): DRC

*P. transversa* Bolton & Fisher, 2008b: Gabon

### *Promyopias Santschi*

Fig. 24

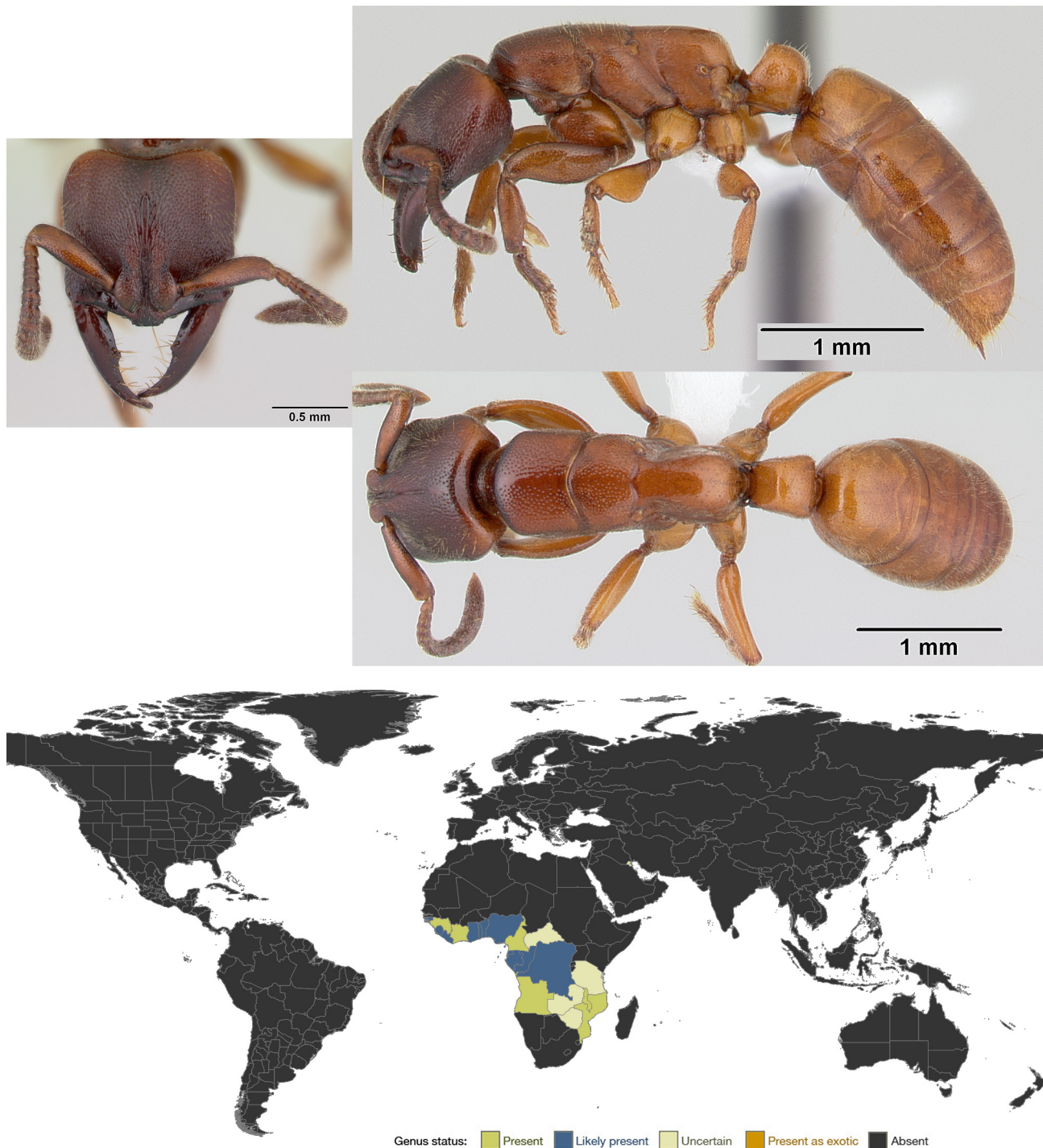
*Promyopias* Santschi, 1914: 323 (as subgenus of *Myopias*). Type-species: *Myopias (Promyopias) silvestrii* Santschi, 1914: 324; by monotypy. Bolton & Fisher, 2008c: 28 (*Promyopias* revived status as genus).

*Promyopias* is a monotypic genus restricted to western Africa. Nothing definite is known about its habits, but it is presumably hypogeic and may be a termite specialist.

**Diagnosis.** Workers of *Promyopias* can be identified by the following unique combination of characters: mandibles narrow and curved, anterior margin of clypeus with a blunt medial projection, eyes absent, metapleural gland orifice shielded laterally by a cuticular flap, traction setae present on mesotibiae and meso-/metabasitarsi, and petiole articulating near the midheight of the first gastral segment. The flap lateral to the metapleural gland orifice is autapomorphic. *Promyopias* workers may be confused with those of *Centromyrmex*, *Buniapone*, or *Feroponera*, as all four genera share traction setae on the legs, a relatively high helcium, and absent or tiny (in *Buniapone*) eyes. None of these other genera have similarly narrow and curved mandibles, however, and only *Buniapone* has a medial clypeal projection. *Promyopias* may also be confused with *Myopias*, but *Myopias* lacks traction setae on the legs, usually has eyes, and has a low helcium (among many other differences).

**Synoptic description.** *Worker.* Medium-sized (TL 6.0–6.3 mm) ants with the standard characters of Ponerini. Mandibles long and narrow, with at most a few small teeth and with a faint basal groove. Anterior margin of

clypeus with a short blunt medial projection. Frontal lobes moderately large. Sapes moderately flattened. Eyes absent. Metanotal groove absent to distinct dorsally. Propodeum moderately narrowed dorsally. Propodeal spiracles ovoid. Metapleural gland orifice shielded laterally by a cuticular flap. Mesotibiae and meso-/metabasitarsi armed with stout traction setae. Metatibial spur formula (1s, 1p). Petiole nodiform, becoming wider posteriorly. Helcium projecting from near midheight of anterior face of A3. Gaster with a slight girdling constriction between A3 and A4. Head and body lightly sculptured (variously punctate, striate or smooth), with scattered pilosity and pubescence. Color dark orange. See Bolton & Fisher (2008c) for a more detailed description of worker structure, including a description of the lone autapomorphy of the genus: the unique shape of the prora.



**FIGURE 24.** Worker caste of *Promyopias silvestrii*: lateral and dorsal view of body and full-face view of head (CASENT0178751, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Promyopias*.

*Queen*. Similar to worker but slightly larger, winged and with compound eyes and ocelli (Bolton & Fisher, 2008c).

*Male*. Unknown.

*Larva*. Not described.

**Geographic distribution.** *Promyopias* is known only from a handful of collections from western Africa (Bolton & Fisher, 2008c).

**Ecology and behavior.** Nothing is known about the habits of *Promyopias*, though based on its morphological characteristics it is undoubtedly hypogeic. Bolton & Fisher (2008c) suggest that it most likely feeds on termites, though this has never been observed. Their hypothesis is apparently based on a presumed close relationship with *Centromyrmex*, which is a termite specialist. However, the mandibular and clypeal structure of *Promyopias* is much more similar to that of *Myopias*, *Plectroctena*, *Leptogenys*, and *Psalidomyrmex*, which are to large degrees specialist predators of millipedes (*Myopias*, *Plectroctena*), isopods (*Leptogenys*), or earthworms (*Psalidomyrmex*). Long curved mandibles and medial clypeal projections are apparently favored for the capture of round prey (Déjean et al, 2001), and we hypothesize that *Promyopias* likewise feeds on some kind of hard round prey, most likely millipedes. On the other hand, both *Plectroctena* and *Leptogenys* include species known to feed on termites, so termite predation by *Promyopias* is not improbable.

**Phylogenetic and taxonomic considerations.** *Promyopias* was originally described by Santschi (1914) as a subgenus of *Myopias*, based on similar mandibular and clypeal structure. Since that time the genus has had a complicated taxonomic history. Emery (1915) gave *Promyopias* full generic status, but Wheeler (1922b) considered it a subgenus of *Pseudoponera*. Wheeler's association of *Promyopias* with *Pseudoponera* was apparently based on similarities in the mandibles and legs, though true *Pseudoponera* lacks the characters referred to by Wheeler, and we can only presume that he was referencing *Pseudoponera amblyops* (now *Buniapone amblyops*). Santschi (1924) revived *Promyopias* to full genus status and placed it in subtribe Plectroctenini, but it was later synonymized under *Centromyrmex* due to the shared presence of spinose setae on the legs (Brown, 1973; Bolton & Fisher, 2008c).

In their revision of African *Centromyrmex*, Bolton & Fisher (2008c) revived *Promyopias* once again to generic status, based on the unique structure of its helcium and the absence of the apomorphic metapleural gland orifice structure characteristic of *Centromyrmex*. Bolton & Fisher did note the multiple similarities between the genera, such as the eyeless condition of the workers, the spinose legs, and the high helcium, and suggested that these characters may be synapomorphic for these genera (along with *Feroponera*).

However, recent preliminary molecular results (P.S. Ward, pers. comm.) suggest that *Promyopias* belongs to the *Odontomachus* group and is only distantly related to *Centromyrmex*. These results suggest that the similarities noted above are convergent rather than being apomorphic. Additional study will be required to clarify the placement of this genus within the subfamily Ponerinae.

Wheeler (1922b) apparently believed that *Promyopias* was closely related to *Buniapone amblyops*. These taxa share a number of morphological apomorphies, including narrowed mandibles (though the details of mandibular structure differ between them), a median clypeal projection, moderately large frontal lobes, basally flattened scapes, absent or reduced eyes, reduced or vestigial metanotal groove, ovoid propodeal spiracle, a high helcium, and spinose setae on the mesotibiae and meso-/metabasitarsi. Most of these morphological apomorphies are adaptations to a hypogeic lifestyle, and may have been convergently evolved by these genera. Both genera also have cuticular flaps at the metapleural gland orifice, though the details of this character differ between the genera: in *Buniapone* the metapleural gland orifice has two flaps, one anterior and one posterior to the orifice, while in *Promyopias* the flap is lateral and shields the orifice (B. Bolton, pers. comm.).

### Species of *Promyopias*

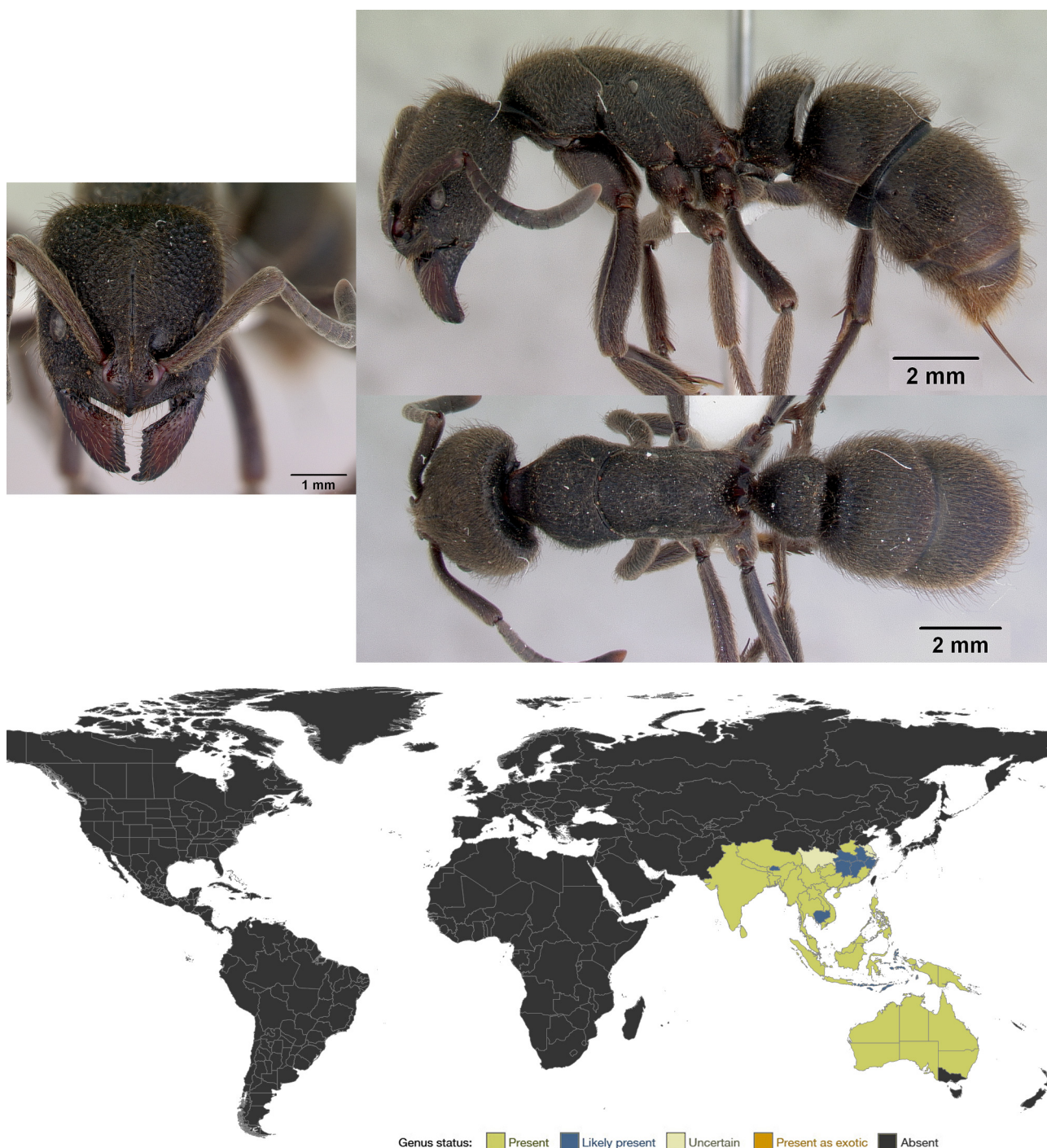
*P. silvestrii* (Santschi, 1914): Guinea

### *Pseudoneoponera* Donisthorpe

Fig. 25

*Pseudoneoponera* Donisthorpe, 1943a: 439 (as genus). Type-species: *Pseudoneoponera verecundae* Donisthorpe, 1943a: 439; by original designation. **Gen. rev.**





**FIGURE 25.** Worker caste of *Pseudoneoponera oculata*: lateral and dorsal view of body and full-face view of head (CASENT0172433, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Pseudoneoponera*.

*Pseudoneoponera* is a moderately large genus, with 18 described species, and ranges from India to Australia. Its sister group is unresolved. *Pseudoneoponera* is notable for the unusual foamy defensive secretions its workers exude from the sting, for its small colonies, and for its unusual social systems, including the frequent occurrence of gamergates.

**Diagnosis.** Workers of *Pseudoneoponera* are distinguished from other ponerines by their combination of robust build, coarse sculpturing, shaggy pilosity, obsolete metanotal groove, a nodiform petiole which is semicircular in dorsal view and often has a denticulate posterodorsal margin, longitudinally striate tergite A3 (rarely otherwise sculptured), and strong gastral constriction between A3 and A4. *Pseudoneoponera* most closely resembles *Bothroponera* and *Phrynoponera*, and to a lesser extent *Ectomomyrmex*, but these genera lack the

shaggy pilosity, semicircular denticulate petiole, and longitudinally striate tergite A3 of *Pseudoneoponera*, and *Pseudoneoponera* lacks the spinose propodeum (except *Ps. bispinosa*), five-spined petiolar node, and unconstricted gaster of *Phrynoponera*, and the small eyes, angular sides of the head, divided mesopleuron (except in a few species), and weakly constricted gaster of *Ectomomyrmex*.

**Synoptic description.** *Worker.* Medium to large (TL 9–18 mm) robust ants with the standard characters of Ponerini. Mandibles triangular and usually with a distinct basal groove. Eyes moderate to large in size, placed anterior of head midline. Mesopleuron usually not divided by a transverse groove. Metanotal groove absent. Propodeum broad dorsally, the posterodorsal margin usually unarmed (bispinose in *P. bispinosa*). Propodeal spiracle slit-shaped. Metatibial spur formula (1s, 1p). Petiole surmounted by a wide node, which is roughly semicircular in dorsal view (the anterior face convex and the posterior face flat or concave), the posterodorsal margin often denticulate (rarely medially incised or trispinose). Gaster with a strong girdling constriction between pre- and postsclerites of A4. Head and body coarsely sculptured, the tergite of A3 usually deeply longitudinally striate. Head and body shaggy, clothed in dense pilosity, which is often reddish in color. Color ferruginous to black.

*Queen.* Queens have been formally described only for *P. sandakana* (Wheeler, 1919), for which the worker caste is still undescribed. Queens have also been noted to occur in *P. tridentata* (Sommer & Hölldobler, 1992) and an undescribed species from Java (Ito, 1993). Gamergates are common in the genus, and the queen caste has apparently been completely lost in many species. From the description of *P. sandakana*, it appears that queens, when they exist, are similar to workers but are alate and have the typical modifications of the head and thorax found in other alate ponerine queens.

*Male.* See descriptions in Forel, 1900a, Wheeler (1919), and Donisthorpe (1943a).

*Larva.* Described by Wheeler & Wheeler (1971b, 1976).

**Geographic distribution.** *Pseudoneoponera* occurs from India through Southeast Asia to Australia, where it reaches its greatest species diversity. At least one species, *P. rufipes*, ranges all the way from India to Australia.

**Ecology and behavior.** *Pseudoneoponera* has received a fair bit of attention from researchers due to its unusual reproductive and social strategies. While most species have not been carefully surveyed, the queen caste has apparently been found in only a few species, while gamergates have been found in several species (Monnin & Peeters, 2008). In at least two species, both queens and gamergates may cohabit a single colony (see below). Just how widespread reproduction by gamergates is in *Pseudoneoponera* is unknown, but it may be characteristic of much or most of the genus. Interestingly, queens are unknown from all Australian *Pseudoneoponera* species, having only been found in some Indonesian species. It is tempting to think that the complete loss of the queen caste may be synapomorphic for the Australian species, but too little is known about relationships within the genus to test this hypothesis.

*Pseudoneoponera* species studied to date all have very small colonies (roughly 10 to 20 workers; Ito, 1993; Peeters *et al.*, 1991; Ito & Higashi, 1991; Higashi *et al.*, 1994; Sommer *et al.*, 1994). Peeters *et al.* (1991) report that *P. sublaevis* workers forage individually and prey on insects, and Shivashankar *et al.* (1995) report that *P. rufipes* feeds on a wide diversity of arthropods and other invertebrates, but otherwise few direct observations of *Pseudoneoponera* feeding have been published. Presumably these ants are generalist predators and scavengers, like most ponerines.

An unusual characteristic of this genus is that workers produce a foamy thread-like defensive excretion from their venom glands. This has been observed in at least *P. bispinosa*, *P. insularis*, *P. rufipes*, *P. sublaevis*, and *P. tridentata* (Bingham, 1903; Maschwitz *et al.*, 1981; Peeters *et al.*, 1991; Sommer *et al.*, 1994). The foaming is made possible by the atrophication of the Dufour's gland and the resulting mixing of venom gland proteins with air (Maschwitz *et al.*, 1981; Buschinger & Maschwitz, 1984). The report by Bingham (1903) that *P. bispinosa* and *P. rufipes* release the foam from their mouths is almost certainly a misinterpretation of the phenomenon, as suggested by Maschwitz *et al.* (1981); indeed, one of us (CS) personally witnessed a *P. rufipes* worker emit foam from the tip of its abdomen. Maschwitz *et al.* (1981) report that *P. insularis* and *P. tridentata* retain a normal sting response, in addition to the foaming mechanism, and that their sting is painful. They hypothesize (and provide supporting experimental evidence) that the foaming mechanism is more effective than the sting against small fast moving enemies such as other ants. The foam apparently acts as a physical obstacle requiring active cleaning rather than as a neurotoxin (Buschinger & Maschwitz, 1984). A similar foamy secretion has been independently evolved by at least one species of *Pachycondyla* (*P. harpax*; Overal, 1987).

*P. tridentata* has an unusual social system in which colonies can have both multiple dealate queens and multiple gamergates, which compete with each other for reproductive dominance (Sommer & Hölldobler, 1992). Some colonies lack queens, in which case reproduction is performed solely by gamergates. A large proportion of both queens and workers in a colony are mated (47–100% and 81–100%, respectively; Sommer *et al.*, 1994), and multiple individuals can be reproductively active. Since so many individuals in a colony are mated, reproduction seems to be correlated with age and behavioral dominance rather than with mating status. Workers apparently mate with males produced by their own colony, while queens do not (Sommer *et al.*, 1994). Colony founding in *P. tridentata* may occur via several different mechanisms, including pleiometrosis and fission (Hölldobler *et al.*, 1992; Sommer *et al.*, 1994). Tandem recruitment is used during nest emigration (Maschwitz *et al.*, 1981). Workers of *P. tridentata* forage individually at night, and nesting generally occurs in the ground, though nests have also been found in trees (Maschwitz *et al.*, 1981; Sommer *et al.*, 1994). Jessen & Maschwitz (1983) found that *P. tridentata* is endowed with a large number of abdominal glands whose functions are unknown.

Ito (1993, 1999) studied the reproductive strategy of an undescribed *Pseudoneoponera* species in Java. This species is unusual in that multiple mated workers may be present in a colony, but only the top-ranked worker is a gamergate (Ito 1993). Queens do occur, but most colonies are apparently queenless and have around 10 workers, of which one or more are mated (Ito 1993). The workers in a colony are ranked in a dominance hierarchy structured via frequent antagonistic interactions; low-ranking workers are the principal foragers (Ito, 1993). Males attempt to mate with their nestmates but are usually rejected; mating only occurs with foreign males, and only when a gamergate is absent (Ito, 1999).

*P. sublaevis* also reproduces via gamergates, but in yet another variation on the theme, only a single worker in the colony is mated and performs all reproduction for the colony (Ito & Higashi, 1991; Peeters *et al.*, 1991). The members of a colony are organized in a strict linear hierarchy determined by age and by ritualized dominance displays, and queens are apparently absent (Higashi *et al.*, 1994). This species occurs in Australian *Eucalyptus* forests, and nests in the ground (Peeters *et al.*, 1991). Gamergates are also known to occur in *P. porcata* (Peeters, 1993), but the details of its mating system are unknown.

**Phylogenetic and taxonomic considerations.** *Pseudoneoponera* was erected by Donisthorpe (1943a) to house his new species *P. verecundae*, known from a single male specimen. He believed it to be closely related to *Neoponera*, based on “various characters,” though he didn’t explain how or why he came to this conclusion in any additional detail, and he noted numerous differences between the genera. Donisthorpe also erected a new section of Ponerinae, Exeuponerinae, to house *Pseudoneoponera*, as its males have retractile genitalia and do not correspond to any of the sections erected by Emery (1911) based on male and larval characters. Wilson (1958c) found that the *P. verecundae* type was extremely similar to males tentatively associated with *P. tridentata* (then *Bothroponera tridentata*), and synonymized *Pseudoneoponera* with *Bothroponera*. *Pseudoneoponera* later became a junior synonym of *Pachycondyla* along with *Bothroponera* (Brown, 1973).

Based on Wilson’s comparison of the *P. verecundae* type to males of “*Bothroponera*” *tridentata*, we believe that *P. verecundae* is a member of a cluster of species formerly considered to be in *Bothroponera*. These taxa, which form a geographically compact group, are characterized by their robust builds, coarse sculpturing, shaggy pilosity, obsolete metanotal groove, semicircular petiolar node, and longitudinally striate tergite A3. Based on both molecular and morphological evidence, we are removing this group of species to its own genus. As the type species of *Bothroponera* (*B. pumicosa*) does not belong to this cluster of species, *Pseudoneoponera* becomes the only available name.

Schmidt’s (2013) molecular phylogeny places *P. rufipes* with strong support within the *Odontomachus* group but does not resolve its sister group. It is certainly not closely related to *Pachycondyla* or *Neoponera* (to which Donisthorpe thought it was related), but a sister relationship with *Bothroponera* or *Phrynoponera* cannot be rejected. Morphologically, *Pseudoneoponera* most closely resembles *Bothroponera* and *Phrynoponera*, and to a lesser extent *Streblognathus*, though there are no obvious synapomorphies linking these genera (see the discussions under *Bothroponera* and *Phrynoponera* for more). Even if *Pseudoneoponera* is found to be the sister to one or more of these genera, they are morphologically and behaviorally distinct enough and phylogenetically old enough to warrant separate generic status.



## Species of *Pseudoneoponera*

- P. barbata* (Stitz, 1911): Australia (**comb. nov.**)  
*P. bispinosa* (Smith, F., 1858): India (**comb. nov.**)  
*P. denticulata* (Kirby, 1896): Australia (**comb. nov.**)  
*P. dubitata* (Forel, 1900): Australia (**comb. nov.**)  
*P. excavata* (Emery, 1893): Australia (**comb. nov.**)  
*P. excavata acuticostata* (Forel, 1900): Australia (**comb. nov.**)  
*P. havilandi* (Forel, 1901): Singapore (**comb. nov.**)  
*P. incisa* (Emery, 1911): New Guinea (**comb. nov.**)  
*P. insularis* (Emery, 1889): Java (**comb. nov.**)  
*P. insularis brevior* (Forel, 1901): Borneo (**comb. nov.**)  
*P. mayri* (Emery, 1887): Australia (**comb. nov.**)  
*P. obesa* (Emery, 1897): New Guinea (**comb. nov.**)  
*P. oculata* (Smith, F., 1858): Australia (**comb. nov.**)  
*P. piliventris* (Smith, F., 1858): Australia (**comb. nov.**)  
*P. piliventris intermedia* (Forel, 1900): Australia (**comb. nov.**)  
*P. piliventris regularis* (Forel, 1907): Australia (**comb. nov.**)  
*P. porcata* (Emery, 1897): Australia (**comb. nov.**)  
*P. rufipes* (Jerdon, 1851): Australia (**comb. nov.**)  
*P. rufipes ceylonensis* (Forel, 1911): Sri Lanka (**comb. nov.**)  
*P. sandakana* (Wheeler, 1919): Borneo (**comb. nov.**)  
*P. sublaevis* (Emery, 1887): Australia (**comb. nov.**)  
*P. sublaevis kurandensis* (Forel, 1910): Australia (**comb. nov.**)  
*P. sublaevis murina* (Forel, 1910): Australia (**comb. nov.**)  
*P. sublaevis reticulata* (Forel, 1900): Australia (**comb. nov.**)  
*P. sublaevis rubicunda* (Emery, 1893): Australia (**comb. nov.**)  
*P. tridentata* (Smith, F., 1858): Borneo (**comb. nov.**)  
*P. tridentata debilior* (Forel, 1901): Borneo (**comb. nov.**)  
*P. tridentata exasperans* (Forel, 1911): West Malaysia (**comb. nov.**)  
*P. verecundae* Donisthorpe, 1943: New Guinea (**comb. rev.**)

## *Streblognathus* Mayr

Fig. 26

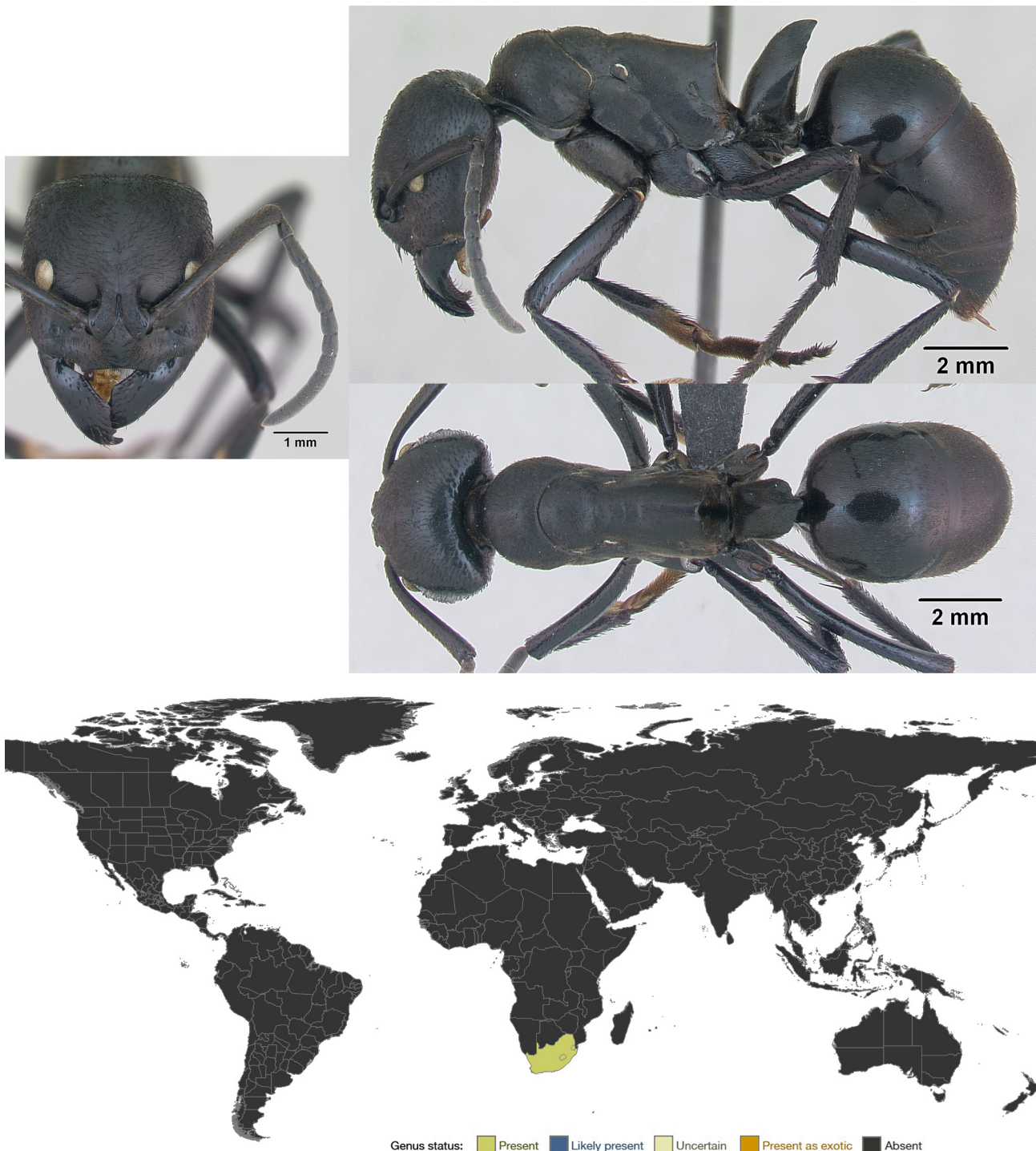
*Streblognathus* Mayr, 1862: 716 (as genus in Ponerinae [Poneridae]). Type-species: *Ponera aethiopica* Smith, F., 1858: 91; by monotypy.

*Streblognathus* is a small genus (two described species) restricted to southern Africa. It is notable for the large size of its workers and for its reproduction by gamergates.

**Diagnosis.** Diagnostic morphological apomorphies of *Streblognathus* workers include their subtriangular mandibles, paired teeth on the anterior clypeal margin, small paired propodeal teeth, broad cuticular flange posterior to the metapleural gland orifice, and tall fin-like petiole. This combination of characters does not occur in any other ponerine genus, and indeed the shape of the petiole is unique among ants. Subtriangular mandibles occur in several other ponerine genera, paired clypeal teeth occur in *Dinoponera*, propodeal spines or teeth occur in a handful of other genera, and a cuticular flange behind the metapleural gland orifice occurs in *Paltothyreus*, but none of these genera has all the apomorphies of *Streblognathus* in combination, and none of them has a similar petiole. *Streblognathus* workers are the largest of any African ponerine, exceeded globally only by those of *Dinoponera*.

**Synoptic description.** *Worker.* Very large (TL 25 mm; Robertson, 2002) ants with the standard characters of Ponerini. Mandibles subtriangular, with relatively short masticatory margins and a weak basal groove. Anterior margin of clypeus straight or with a broad concavity, bounded on each side by a short tooth. Frontal lobes widely

separated anteriorly by an extension of the clypeus. Eyes of moderate size, located just anterior of head midline and somewhat medially. Metanotal groove very shallowly impressed. Propodeal dorsum narrowed, with a shallow longitudinal depression and a pair of small teeth at the posterodorsal margin. Propodeal spiracle slit-shaped. Metapleural gland orifice with a broad shallow cuticular flange posteriorly. Metatibial spur formula (1s, 1p). Petiole fin-shaped, in profile with a convex anterior face and a concave posterior face, tapering to a sharp point dorsally, with sharp lateral and anterior margins on the dorsal third; petiole taller than the mesosoma and gaster. Gaster squat, without a girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and body sparsely punctate, with generally sparse pilosity except for scattered short decumbent black hairs on the head and pronotum; pubescence of moderate density. Color black.



**FIGURE 26.** Worker caste of *Streblognathus peetersi*: lateral and dorsal view of body and full-face view of head (CASENT0173636, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Streblognathus*.

*Queen*. Unknown and apparently absent.

*Male*. See description in Robertson (2002).

*Larva*. The larvae of *S. "aethiopicus"* were described by Wheeler & Wheeler (1989), though given their collection locality they were probably actually larvae of *S. peetersi* (described later by Robertson, 2002).

**Geographic distribution.** *Streblognathus* is restricted to Lesotho, Swaziland and South Africa (Robertson, 2002).

**Ecology and behavior.** Relatively little is known about most aspects of *Streblognathus* ecology. They occur in arid thorn scrub and grasslands in extreme southeastern Africa, and apparently are specialist predators of tenebrionid beetles (Brown, 2000; Robertson, 2002). Workers stridulate when disturbed (Ware, 1994) and are able to differentiate nestmates from non-nestmates (Schlüns *et al.*, 1996).

In contrast, a fair bit is known about the reproductive and social behavior of the genus. Colonies are small, with usually around 100 workers or fewer (mean = 35 for *S. aethiopicus*; mean = 95 for *S. peetersi*; Ware *et al.*, 1990; Peeters, 1993). The queen caste is entirely absent, with reproduction instead being performed by a single mated gamergate worker. This gamergate, or "alpha" worker, is morphologically indistinguishable from the other workers but differs from them in its ovarian development (Ware *et al.*, 1990), hormone levels (Brent *et al.*, 2006), neurochemistry (Cuvillier-Hot & Lenoir, 2006), cuticular hydrocarbons (Cuvillier-Hot *et al.*, 2005), and relative proportions of mandibular gland secretions (Jones *et al.*, 1998). Within a colony, workers are behaviorally differentiated into foragers, nest workers and the sole reproductive gamergate (Ware *et al.*, 1990).

A dominance hierarchy exists among the workers in a colony, with high-ranking workers subordinate to the alpha but dominant over the low-ranking individuals. Gamergates inhibit reproduction by subordinate workers through chemical signaling (Cuvillier-Hot *et al.*, 2004b). The reproductive division of labor within the colony is further maintained by the low-ranking workers, who identify the alpha worker and aggressively prevent sub-alpha workers from ascending to dominance unless the alpha senesces. In such instances, high-ranking workers aggressively compete until a single alpha ascends to dominance; this is usually the previous "beta," or second ranked, worker (Cuvillier-Hot *et al.*, 2004a, 2004b).

**Phylogenetic and taxonomic considerations.** *Streblognathus* was erected by Mayr (1862) to house the species *Ponera aethiopica* F. Smith. All subsequent authors have maintained distinct generic status for this taxon. Robertson (2002) revised the genus and divided *S. aethiopicus* into two species. We continue to treat *Streblognathus* as a distinct genus on both morphological and molecular grounds. Schmidt's (2013) molecular phylogeny of the Ponerinae places *Streblognathus* solidly within the *Odontomachus* group, though its sister group is unresolved.

Carpenter (1930), in describing the fossil ponerine genus *Archiponera*, argued for a close relationship between *Streblognathus* and *Dinoponera*, even going so far as to suggest that they be considered a supergenus. He apparently based this hypothesized relationship on the relatively medial placement of the eyes, the presence of paired teeth on the anterior margin of the clypeus, and presumably their large size; to this list of similarities could be added the loss of a queen caste. This purported relationship has been repeated in much of the subsequent literature on *Streblognathus* and *Dinoponera* (e.g., Haskins, 1970; Haskins & Zahl, 1971), but is clearly false. The similarities between *Streblognathus* and *Dinoponera* are apparently the result of convergence, as morphological and molecular evidence otherwise argue against a sister relationship between these genera. *Archiponera*, which Carpenter believed was close to both *Dinoponera* and *Streblognathus*, has uncertain affinities but is unlikely to actually represent an ancestor or sister group to either of these extant genera (see further discussion under *Dinoponera*). The true sister group of *Streblognathus* is still unresolved.

### Species of *Streblognathus*

Robertson (2002) revised *Streblognathus* and provided a key to the species.

*S. aethiopicus* (Smith, F., 1858): South Africa

*S. peetersi* Robertson, 2002: South Africa



## ***Pachycondyla* genus group**

The *Pachycondyla* genus group arose from a Neotropical radiation into mostly epigeic predator niches. It is one of the most morphologically, ecologically and behaviorally diverse ponerine genus groups.

**Discussion.** The monophyly of the *Pachycondyla* genus group as defined here is somewhat uncertain. Though it is supported with a BPP of 0.99 in the phylogeny of Schmidt (2013), a thorough assessment of the phylogenetic results indicated significant uncertainty about the grouping of *Simopelta* and/or *Thaumatomyrmex* with the rest of the genus group. The group is supported by a potential synapomorphy: a U-shaped cuticular lip posterior to the metapleural gland orifice. A similar cuticular lip also occurs in *Diacamma* (as well as *Bothroponera* s.s.), however, meaning that it may be a synapomorphy for the *Pachycondyla* and *Ponera* groups together (subsequently lost in most members of the *Ponera* group).

Generic relationships within the group are generally very well supported, except at the base, where the relationships are unresolved. *Simopelta* is most often reconstructed as sister to the rest of the group, but this is not strongly supported (Schmidt, 2013). Among the remaining genera in the group, *Mayaponera* is strongly inferred as sister to a clade consisting of *Dinoponera*, *Pachycondyla* and *Neoponera*, with *Dinoponera* and *Pachycondyla* forming sister groups. *Belonopelta*, *Simopelta* and *Thaumatomyrmex* appear to be closely related and may form the sister group to the remaining genera (P.S. Ward, pers. comm.; Schmidt, 2013).

## ***Belonopelta* Mayr**

Fig. 27

*Belonopelta* Mayr, 1870: 394 (as genus). Type-species: *Belonopelta attenuata* Mayr, 1870: 395; by monotypy.

*Leiopelta* Baroni Urbani, 1975: 309 (as genus). Type-species: *Belonopelta deletrix* Mann, 1922: 9; by original designation.

Hölldobler & Wilson, 1990: 10 (*Leiopelta* as junior synonym of *Belonopelta*).

*Belonopelta* is a small genus (two described species) restricted to the Neotropics. Little is known about their habits, but they are apparently cryptobiotic predators of diplurans and other soft-bodied arthropods.

**Diagnosis.** *Belonopelta* workers are easily differentiated from those of most other ponerine genera by their narrow curved mandibles, which have several long teeth. *Emeryopone* is quite similar to *Belonopelta*, but they can be separated by their frontal lobes (very small and closely approximated in *Belonopelta*, medium sized and mildly separated anteriorly in *Emeryopone*) and by their body sculpturing and pilosity (pruinose and without upright pilosity in *Belonopelta*, foveolate with abundant pilosity in *Emeryopone*). *Thaumatomyrmex* also has curved mandibles with an attenuated apical tooth, but its teeth are much longer than in *Belonopelta* and it has much more widely spaced frontal lobes and larger eyes.

**Synoptic description.** *Worker.* Small (TL 4–5 mm) ants with the standard characters of Ponerini. Mandibles narrow and curved, with five or six teeth, the apical tooth greatly attenuated, without a distinct basal margin or basal groove. Anterior clypeal margin triangular, sometimes with a prominent tooth medially. Frontal lobes very small and closely approximated. Eyes very small, located anterior of head midline. Metanotal groove shallow or reduced to a simple suture. Propodeum mildly narrowed dorsally. Propodeal spiracles round. Metatibial spur formula (1p). Petiole nodiform, wider than long. Subpetiolar process sometimes with an anterior fenestra. Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and body shining to pruinose, with scattered small foveae or punctations, very sparse pilosity and a dense short pubescence. Color reddish-brown to nearly black.

*Queen.* Described for *B. deletrix* by Wilson (1955a): similar to worker but slightly larger, alate, with ocelli, larger compound eyes, and the modifications of the thorax typical for alate ponerine queens.

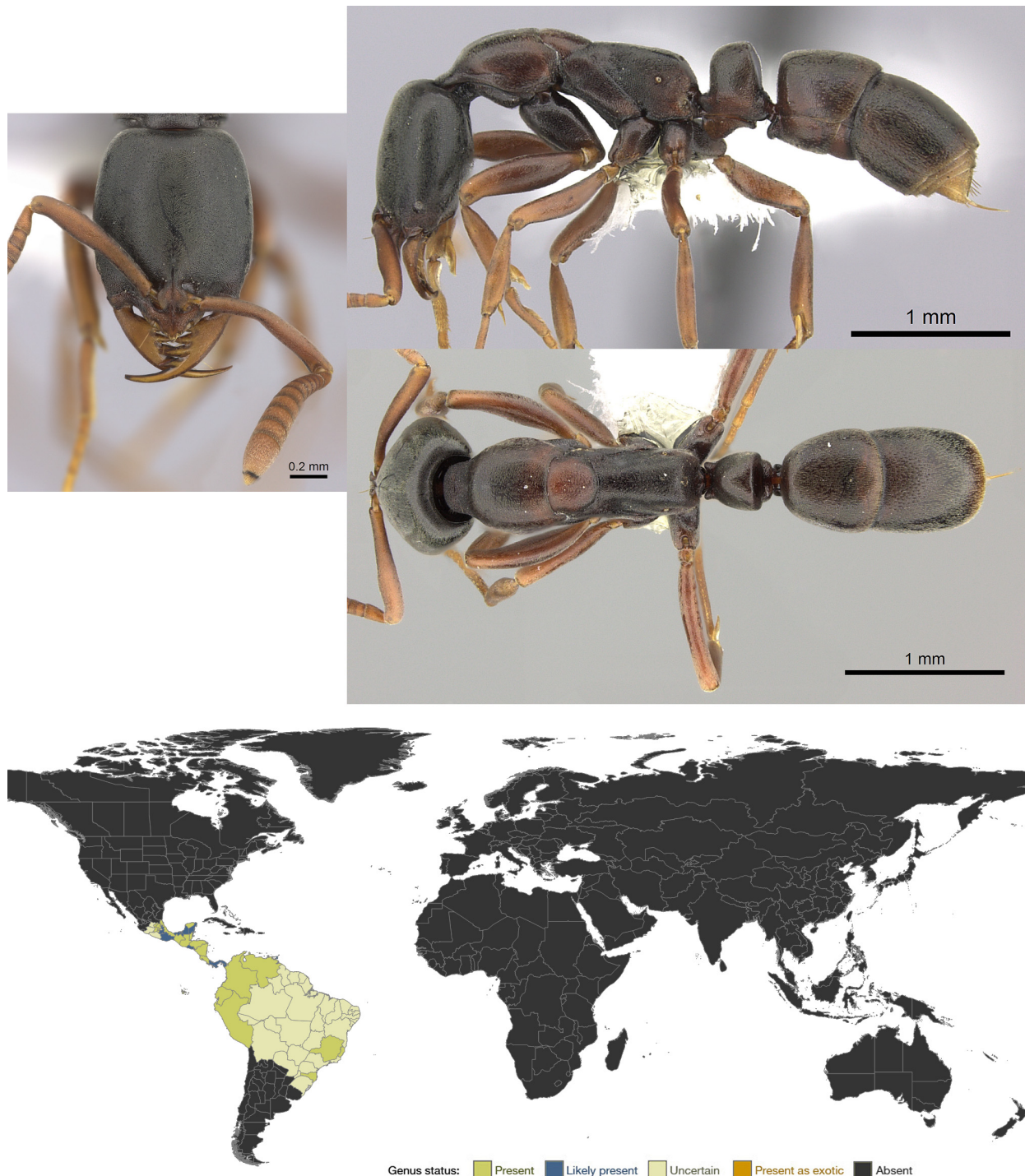
*Male.* Not described.

*Larva.* Described for *B. deletrix* by Wheeler & Wheeler (1964).

**Geographic distribution.** *Belonopelta* is restricted to the Neotropics, ranging from southern Mexico to Colombia (Wilson, 1955a; Baroni Urbani, 1975).

**Ecology and behavior.** Very little is known about the habits of *Belonopelta*, as they are rarely collected (Wheeler, 1935). Their vestigial eyes are suggestive of a cryptobiotic lifestyle, and field observations confirm this, as individual workers are found among leaf litter, under logs or in soil (Mann, 1922; Brown, 1950; Longino, 2013),

and nests are constructed in rotting wood (Wilson, 1955a). Colonies are small, with roughly 16 or fewer workers and a single dealate queen (Wilson, 1955a; W. L. Brown, pers. comm. cited in Longino, 2013). Records of *Belonopelta* food preferences are scant, but Wilson (1955a) observed that *B. deletrix* workers in captivity readily preyed on diplurans, small geophilid centipedes, and a small cicadellid, but largely ignored large centipedes, termites, beetles (both larvae and adults), moth larvae, isopods, and millipedes. Wilson hypothesized that in nature *B. deletrix* is largely a specialist predator of diplurans, and observed that the method of prey capture by *B. deletrix* is typical for ponerines despite their highly specialized mandibular structure. Wilson (1955a) also observed that *B. deletrix* workers are very timid and readily flee from non-prey arthropods. The degree to which Wilson's observations of *B. deletrix* apply also to *B. attenuata* is uncertain.



**FIGURE 27.** Worker caste of *Belonopelta deletrix*: lateral and dorsal view of body and full-face view of head (CASENT0260514, Shannon Hartman and [www.antweb.org](http://www.antweb.org)); world distribution of *Belonopelta*.

**Phylogenetic and taxonomic considerations.** *Belonopelta* has had a complicated taxonomic history. Mayr (1870) erected the genus for the single species *B. attenuata* and noted the general similarity between *Belonopelta* and *Ponera*, citing the medial clypeal tooth and highly derived mandibles of *B. attenuata* as major distinguishing features. Subsequently, the genus *Simopelta* was at times considered a subgenus (Mann, 1922) or junior synonym (Baroni Urbani, 1975) of *Belonopelta*. Baroni Urbani (1975) revised *Belonopelta* and made *Emeryopone* a junior synonym of *Belonopelta*, at the same time removing *B. deletrix* to the separate genus *Leiopelta*. None of Baroni Urbani's (1975) genus-level taxonomic changes withstood scrutiny by subsequent authors, as Hölldobler & Wilson (1990) synonymized *Leiopelta* under *Belonopelta* and moved *Simopelta* back to full genus status, and Bolton (1994) moved *Emeryopone* back to full genus status. See the discussion under *Simopelta* for more on the phylogenetic position of that genus.

Recently, P. S. Ward (pers. comm.) examined a number of primarily African ponerines using molecular data and found *Belonopelta* to be closely related to *Thaumatomyrmex*. Combined with Schmidt's (2013) demonstration that *Thaumatomyrmex* is close to *Simopelta*, it appears that these three genera form a clade or basal grade. As these three genera belong to the *Pachycondyla* group and *Emeryopone* is in the *Ponera* group, Baroni Urbani's (1975) belief that *B. attenuata* and *Emeryopone* are congeneric (with *B. deletrix* excluded) is not supported. We are here retaining *Belonopelta* as a separate genus from *Emeryopone* as the available data suggest that they are unrelated.

### Species of *Belonopelta*

*B. attenuata* Mayr, 1870: Colombia

*B. deletrix* Mann, 1922: Honduras

### *Dinoponera* Roger

Fig. 28

*Dinoponera* Roger, 1861: 37 (as genus). Type-species: *Ponera grandis* Guérin-Ménéville, 1838: 206 (junior synonym of *Ponera gigantea* Perty, 1833: 135); by monotypy.

*Dinoponera* is a small genus (ten described species and subspecies) found in rainforests to savannahs from southern Colombia south to Argentina and Uruguay. It boasts the world's largest monomorphic ant workers (up to 40 mm or more). The genus is also notable for reproducing via gamergates (with the loss of the queen caste).

**Diagnosis.** *Dinoponera* workers are unmistakable due to their enormous size. Other diagnostic characters (in combination) include: subtriangular mandibles, clypeal teeth, complex metapleural gland orifice, toothed tarsal claws, and stout hypopygial spines. Some of these characters are synapomorphic with *Pachycondyla*, which is sister to *Dinoponera* and the most similar genus morphologically. *Pachycondyla* lacks the huge size, subtriangular mandibles, clypeal teeth, and toothed tarsal claws of *Dinoponera*. *Streblognathus* bears some resemblance to *Dinoponera*, given its large size, subtriangular mandibles, clypeal teeth, and forward facing eyes, but *Streblognathus* has a novel fin-shaped petiole and lacks the complex metapleural gland orifice, toothed tarsal claws, and hypopygial spines of *Dinoponera*, and is somewhat smaller.

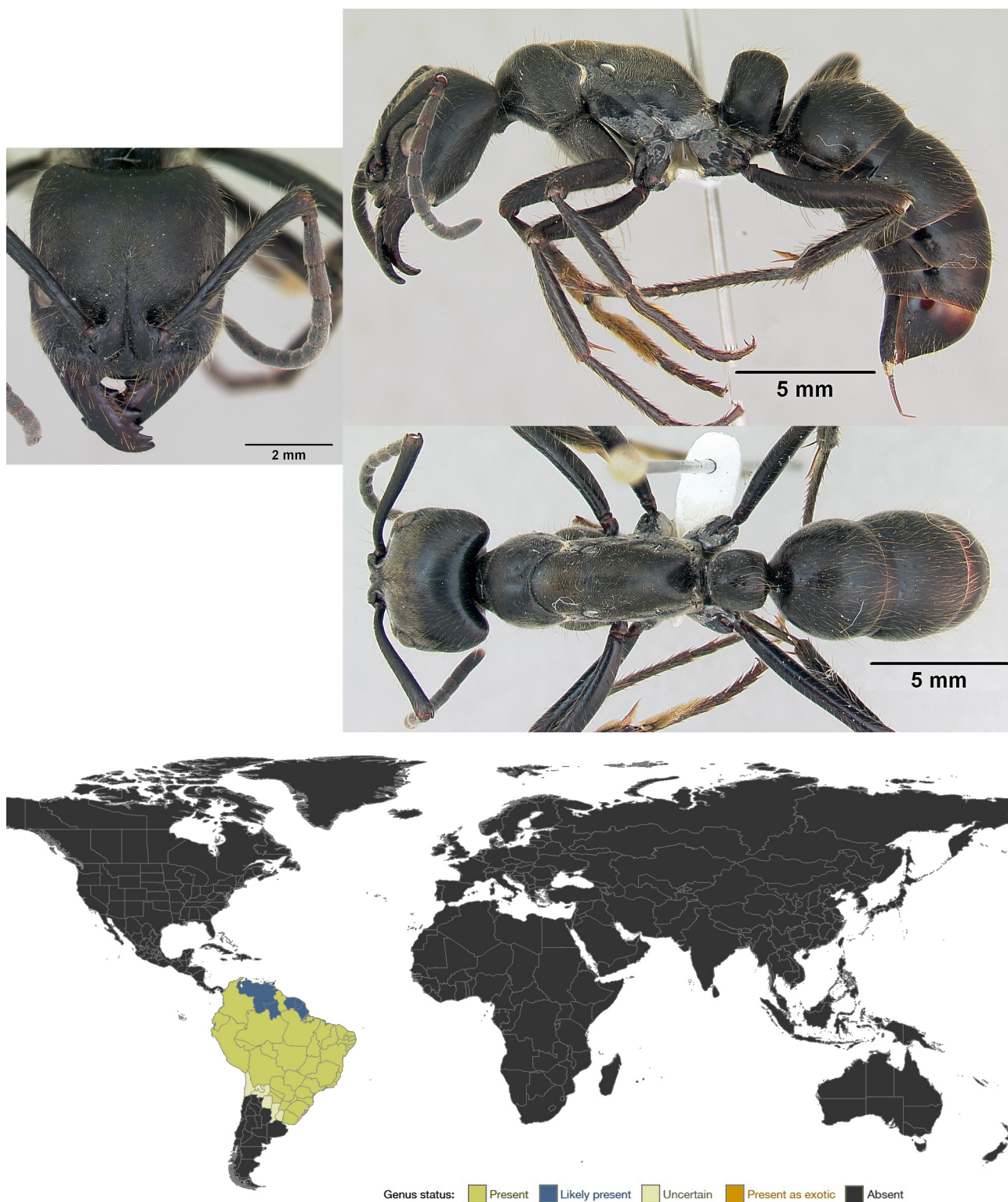
**Synoptic description.** *Worker.* Huge (TL 25–40 mm; Kempf, 1971; Paiva & Brandão, 1995) ants with the standard characters of Ponerini. Mandibles subtriangular, with roughly five teeth and without a distinct basal angle or basal groove. Anterior margin of clypeus with a pair of long anteriorly-directed teeth. Frontal lobes moderately large. Eyes moderately large, located anterior of head midline and relatively forward-facing. Posterolateral corners of head prominent. Metanotal groove reduced to a subtle suture. Propodeum broad dorsally. Propodeal spiracles slit-like. Metapleural gland orifice with a posterior U-shaped cuticular lip and a lateral groove. Tarsal claws with a single tooth. Metatibial spur formula (1s, 1p). Petiole nodiform, with a blunt dorsal longitudinal ridge. Gaster with a strong girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Hypopygium with a row of stout spines on either side of the sting. Head and body smooth to sparsely punctate, with sparse to abundant pilosity and patchy pubescence. Color black. See also description in Lenhart *et al.* (2013).

*Queen.* Absent, reproduction instead being performed by gamergates.

*Male.* See description in Lenhart *et al.* (2013).

*Larva.* Described for *D. gigantea* by Wheeler & Wheeler (1986a).





**FIGURE 28.** Worker caste of *Dinoponera australis*: lateral and dorsal view of body and full-face view of head (CASENT0173381, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Dinoponera australis*.

**Geographic distribution.** *Dinoponera* is a strictly South American genus, found from montane rainforests on the eastern slope of the Andes in Perú, Ecuador and Colombia to savannah and lowland rainforest in Brazil, Guyana, south through Bolivia, Paraguay and Argentina (Lenhart *et al.*, 2013). Lenhart *et al.* also provide maps showing the distribution of each *Dinoponera* species.

**Ecology and behavior.** *Dinoponera* is one of the best studied ponerine genera, due to its interesting social

behaviors and large body size, which makes it relatively easy to work with. In particular, the papers by Monnin and colleagues document in unprecedented detail the social and reproductive behaviors of *Dinoponera*, especially of *D. quadricaps* (e.g., Monnin *et al.*, 1998, 2002, 2003; Monnin & Peeters, 1997, 1998, 1999; Monnin & Ratnieks, 1999, 2001; Peeters *et al.*, 1999; Hart & Monnin, 2006; also Hart & Ratnieks, 2005). We will only briefly summarize their results here, with the caveat that much of this information stems from studies of *D. quadricaps* alone, and its general applicability to the entire genus is in some cases uncertain.

*Dinoponera* colonies generally contain fewer than 100 workers, though colony size varies among species (Fowler, 1985; Paiva & Brandão, 1995; Fourcassie & Oliveira, 2002; Vasconcellos *et al.*, 2004; Monnin & Peeters, 2008). *Dinoponera* has completely lost the queen caste and reproduction in each colony is instead performed by a single mated gamergate worker who is the top (alpha) individual in a ranked dominance hierarchy (Haskins & Zahl, 1971; Monnin *et al.*, 2003). Below her in the hierarchy are three to five subordinate workers who vie with one another for the opportunity to succeed the alpha once she dies (Monnin *et al.*, 2002; Peixoto *et al.*, 2008). These “hopeful reproductives” perform little work in the colony and represent a drain on the colony’s resources (Monnin & Ratnieks, 1999, 2001; Monnin *et al.*, 2003; Hart & Monnin, 2006). The remaining workers perform most of the work for the colony and also police the colony, punishing high-ranking workers who attempt to prematurely overthrow the alpha (Monnin & Ratnieks, 2001; Monnin *et al.*, 2002). This policing is quite effective, as early replacement of the alpha is apparently rare (Hart & Monnin, 2006).

A newly anointed alpha worker briefly leaves the colony and mates with a single male (Monnin & Peeters, 1998). Subordinate workers do not mate, but sometimes lay haploid eggs which will develop into males if the alpha does not discover and cannibalize them (Dantas de Araujo *et al.*, 1990; Monnin & Ratnieks, 2001). Alpha workers have a different cuticular hydrocarbon profile from other workers, and this profile is transferred to their eggs, allowing them to identify the eggs of subordinates (Monnin & Peeters, 1997; Peeters *et al.*, 1999). The hydrocarbon profile is apparently related to ovarian activity, and allows workers to assess the rank and reproductive status of each member of the colony (Monnin *et al.*, 1998; Monnin & Peeters, 1999; Peeters *et al.*, 1999; Monnin & Ratnieks, 2001).

As with most ponerines lacking winged queens, colony reproduction in *Dinoponera* occurs via fission, with workers carrying brood and males to new nest sites and recruiting other workers via tandem running, with apparently no chemical trail (*D. australis*: Fowler, 1985; *D. gigantea*: Overal, 1980). Nests are built into the soil, can be quite extensive, and house diverse communities of myrmecophiles including inquiline *Pheidole* species (Zahl, 1957; Hermann *et al.*, 1994; Paiva & Brandão, 1995; Vasconcellos *et al.*, 2004). Workers are not generally aggressive but can deliver a painful sting if provoked (Allard, 1951; Zahl, 1957; Hermann *et al.*, 1994). *Dinoponera* workers forage diurnally or crepuscularly on the ground, and are generalist predators of insects and opportunistic scavengers of fruits and other food sources (Oldham *et al.*, 1994; Hermann *et al.*, 1994; Paiva & Brandão, 1995; Fourcassie & Oliveira, 2002; Monnin *et al.*, 2003; Araújo & Rodrigues, 2006). Workers always forage individually (Zahl, 1957; Haskins & Zahl, 1971; Fowler, 1985; Fourcassie & Oliveira, 2002; Araújo & Rodrigues, 2006). Orientation and navigation by foraging *D. gigantea* workers were studied by Fourcassie *et al.* (1999).

The large size and interesting behaviors of *Dinoponera* have made them attractive model systems for histological and biochemical research, including studies of the mandibular gland (Oldham & Morgan, 1993; Oldham *et al.*, 1994; Hermann *et al.*, 1994), Dufour’s gland (Hermann *et al.*, 1994; Morgan *et al.*, 2003), sting apparatus and venom gland (Hermann *et al.*, 1994; Morgan *et al.*, 2003), convoluted gland (inside venom reservoir; Schoeters & Billen, 1995), post-pharyngeal gland (Schoeters & Billen, 1997), and antennal sensillae and glands (Marques-Silva *et al.*, 2006). Interestingly, *D. lucida* has the highest number of chromosomes known for any hymenopteran ( $2n=120$ ), though the total number ranges from  $2n=106$  to  $2n=120$  and the significance or cause of this large number and variation is unknown (Mariano *et al.*, 2004; Barros *et al.*, 2009).

**Phylogenetic and taxonomic considerations.** *Dinoponera* was erected by Mayr (1861) as a monotypic genus to house *Ponera grandis* Guérin-Méneville (now *Dinoponera gigantea*). The enormous size and other morphological apomorphies of *Dinoponera* led to a stable taxonomic history for the genus. Schmidt’s (2013) molecular phylogeny strongly indicates that *Dinoponera* is a close sister genus to *Pachycondyla*. *Dinoponera* and *Pachycondyla* are morphologically quite similar, and the presence of a row of stout spines on either side of the hypopygium is a strong synapomorphy linking the two genera. Ironically, though W. L. Brown (in Bolton, 1995) synonymized numerous unrelated ponerine genera under *Pachycondyla*, he failed to include *Dinoponera*, which is

the only ponerine genus closely related enough to *Pachycondyla* to actually justify synonymy. Given the numerous morphological apomorphies of *Dinoponera* (including their huge body size, subtriangular mandibles, clypeal teeth, and toothed tarsal claws) and their highly derived social behaviors, we are retaining *Dinoponera* as a separate genus from *Pachycondyla*.

*Dinoponera* has at times been considered closely related to *Streblognathus* (see discussion under that genus), but neither morphological or molecular evidence supports this hypothesis. The fossil genus *Archiponera* was also considered by Carpenter (1930) to be closely related to *Dinoponera* and *Streblognathus*. While *Archiponera* does bear some superficial resemblance to these genera, and especially to *Dinoponera*, the purported age of this fossil genus makes it unlikely to represent an ancestor or sister group to either *Streblognathus* or *Dinoponera*.

### Species of *Dinoponera*

Lenhart *et al.* (2013) revised the genus and provided a key to species.

*D. australis* Emery, 1901: Paraguay

*D. australis bucki* Borgmeier, 1937: Brazil

*D. australis nigricolor* Borgmeier, 1937: Brazil

*D. gigantea* (Perty, 1833): Brazil

*D. hispida* Lenhart, Dash & Mackay, 2013: Brazil

*D. longipes* Emery, 1901: Peru

*D. lucida* Emery, 1901: Brazil

*D. mutica* Emery, 1901: Brazil

*D. quadriceps* Kempf, 1971: Brazil

*D. snellingi* Lenhart, Dash & Mackay, 2013: Brazil

### *Mayaponera* gen. nov.

Fig. 29

Type-species: *Ponera constricta* Mayr, 1884: 31; by monotypy.

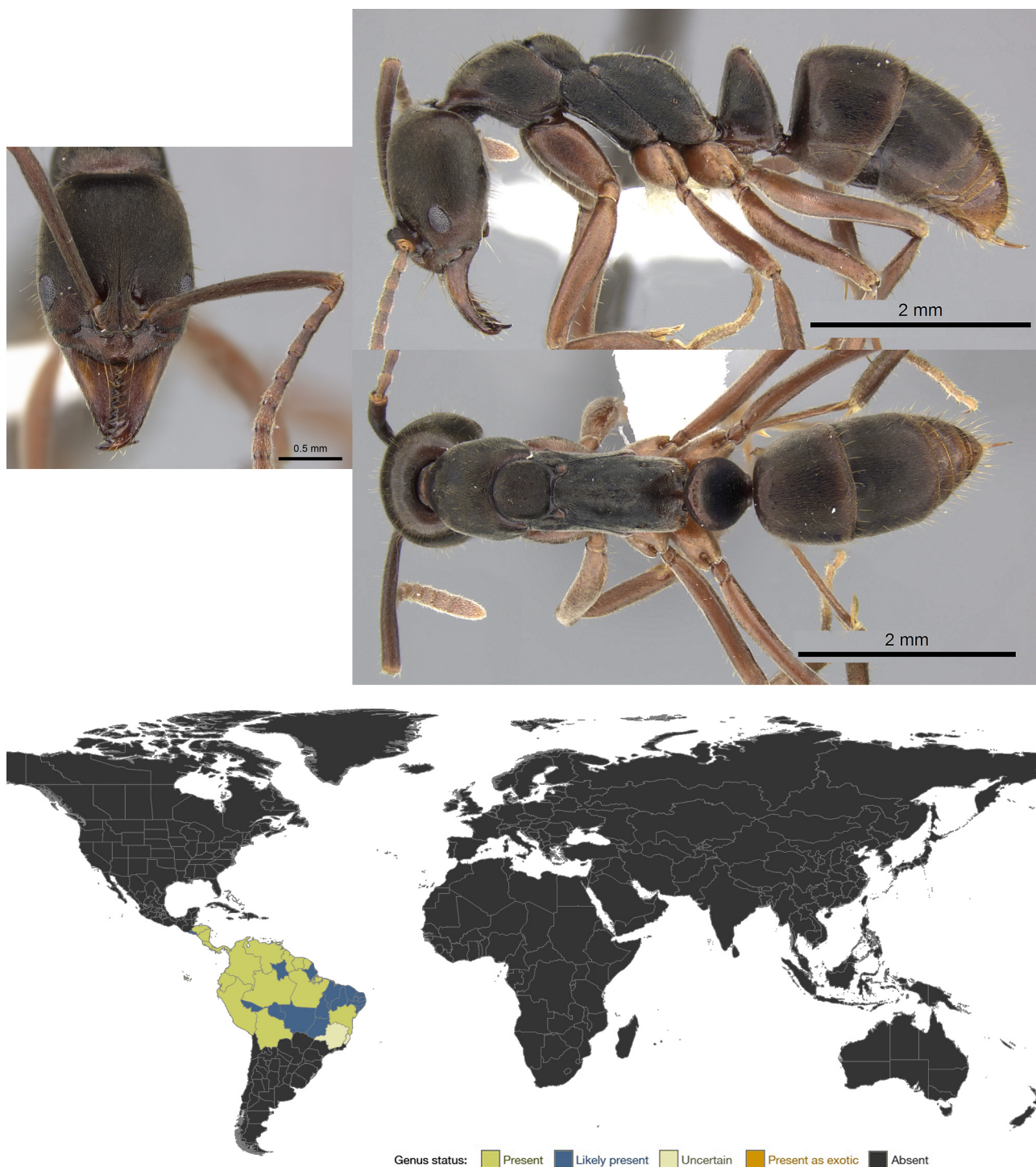
*Mayaponera* is a monotypic genus widespread in Central and South America. It is found in wide range of natural and farming habitats.

**Etymology.** *Mayaponera* is named in memory of the first author's daughter Maya and for the Maya peoples of southern Mexico and northern Central America, included in the range of the genus. The suffix *-ponera* is derived from the subfamily name Ponerinae.

**Diagnosis.** *Mayaponera* workers lack any obvious autapomorphies and superficially have a very generalized appearance. They are most likely to be confused with some *Neoponera* and *Mesoponera*, but *Mayaponera* differs from *Neoponera* in its round propodeal spiracles, deeply impressed metanotal groove (at most only slightly impressed in *Neoponera*), and strongly narrowed propodeum with a dorsal longitudinal groove. It can be separated from the handful of *Neoponera* species in which the propodeal spiracle is round (some members of the *N. emiliae* group) by the presence of narrow and fang-like metasternal processes (the processes are triangular-shaped in *Neoponera*). *Mayaponera* differs from *Mesoponera* in having a complex metapleural gland orifice and prominent arolia.

**Synoptic description.** *Worker.* Medium-sized (TL 6–7.5 mm) slender ants with the standard characters of Ponerini. Mandibles triangular, with about a dozen teeth on the masticatory margin. Clypeus with a broadly convex anterior margin and a subtle median emargination. Frontal lobes of moderate size. Eyes of moderate size, placed anterior of head midline. Metanotal groove deeply impressed. Propodeal dorsum strongly narrowed and with a longitudinal groove. Propodeal spiracles round. Metapleural gland orifice complex, with a posterior U-shaped cuticular lip and a shallow lateral groove. Metatibial spur formula (1s, 1p). Arolia prominent. Petiole a thick scale. Gaster with only a weak girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and body finely punctate, with scattered pilosity and dense pubescence. Color dark brownish gray. See also Mackay & Mackay (2010).





**FIGURE 29.** Worker caste of *Mayaponera constricta*: lateral and dorsal view of body and full-face view of head (CASENT0249137, Ryan Perry and [www.antweb.org](http://www.antweb.org)); world distribution of *Mayaponera*.

*Queen.* Both alate and ergatoid queens are known for *M. constricta*. Ergatoids lack a deeply impressed metanotal groove and have a bulkier mesosoma than workers (Longino, 2013). See also Mackay & Mackay (2010).

*Male.* See description in Forel (1908) and Mackay & Mackay (2010).

*Larva.* Described by Wheeler & Wheeler (1952, 1976).

**Geographic distribution.** *Mayaponera constricta* is widespread in the Neotropics from Central America to Bolivia and southern Brazil (Mackay & Mackay, 2010).

**Ecology and behavior.** Very little is known about the habits of *Mayaponera*. Mackay & Mackay (2010) reviewed *M. constricta* as part of their study of New World "*Pachycondyla*" while Longino (2013) and Baena

(1993) summarized their observations on the species in Costa Rica and Colombia, respectively. The genus is common in a range of habitats from mature rainforests to cocoa plantations and other farm habitats, where it is frequently collected in leaf litter samples (Longino, 2013) and pitfall traps (Mackay & Mackay, 2010). Nests usually occur in rotting wood but can also be found directly in soil (often under stones), and workers forage predominantly at night on and among leaf litter (Baena, 1993; Longino, 2013; Mackay & Mackay, 2010). *M. constricta* apparently uses tandem running to recruit nestmates to food sources (S. Levings, pers. comm. cited in Hölldobler & Wilson, 1990). Both alate and ergatoid queens occur (Longino, 2013), and reported colony sizes are small (up to 29 workers; Baena, 1993) though nothing else is known about their reproductive or social behavior. Orivel & Déjean (2001) measured the toxicity of *M. constricta* venom. Given that it holds a critical phylogenetic position in the midst of several taxa with highly derived characteristics, additional observations on the ecological and behavioral traits of *Mayaponera* would be of great assistance in reconstructing character evolution in the *Pachycondyla* group.

**Phylogenetic and taxonomic considerations.** *Mayaponera constricta* (originally *Ponera constricta* Mayr) has traditionally been associated with the genus *Mesoponera*, in all of its iterations as a subgenus of *Euponera* (Emery, 1901), a full genus (Kempf, 1972), or a junior synonym of *Pachycondyla* (W. L. Brown, in Bolton, 1995). This has presumably been based on the generalized structure and superficial similarities of *M. constricta* and *Mesoponera*. These taxa lack obvious autapomorphies and exhibit a suite of largely plesiomorphic characters, including weak sculpturing, moderate pilosity, triangular mandibles, medium-sized frontal lobes and eyes, a distinct metanotal groove, two metatibial spurs, and a squamiform petiole. Schmidt's (2013) molecular phylogeny clearly distances *M. constricta* from *Mesoponera*, instead reconstructing it as a novel lineage within the *Pachycondyla* group and sister to *Dinoponera*, *Pachycondyla* and *Neoponera*. This result is also supported by morphology, as *M. constricta* has the complex metapleural gland orifice and prominent arolia typical of the *Pachycondyla* group, but has round propodeal spiracles in contrast to the apparently derived slit-shaped spiracles of the *Dinoponera* + *Pachycondyla* + *Neoponera* clade. Given the strength of this molecular and morphological evidence, we are erecting a new genus, *Mayaponera*, to house this species.

### Species of *Mayaponera*

*M. constricta* (Mayr, 1884): French Guiana (**comb. nov.**)

### *Neoponera* Emery

Fig. 30

*Neoponera* Emery, 1901: 43 (as genus). Type-species: *Formica villosa* Fabricius, 1804: 409; by original designation. **Gen. rev.** *Eumecopone* Forel, 1901b: 335 (as subgenus of *Neoponera*). Type-species: *Neoponera (Eumecopone) agilis* Forel, 1901b: 336; by monotypy. Brown, 1973: 180 (*Eumecopone* as provisional junior synonym of *Neoponera*).

*Termitopone* Wheeler, W.M., 1936: 159 (as genus). Type-species: *Ponera laevigata* Smith, F., 1858: 98; by original designation. *Termitopone* as junior synonym of *Neoponera*: **Syn. nov.**

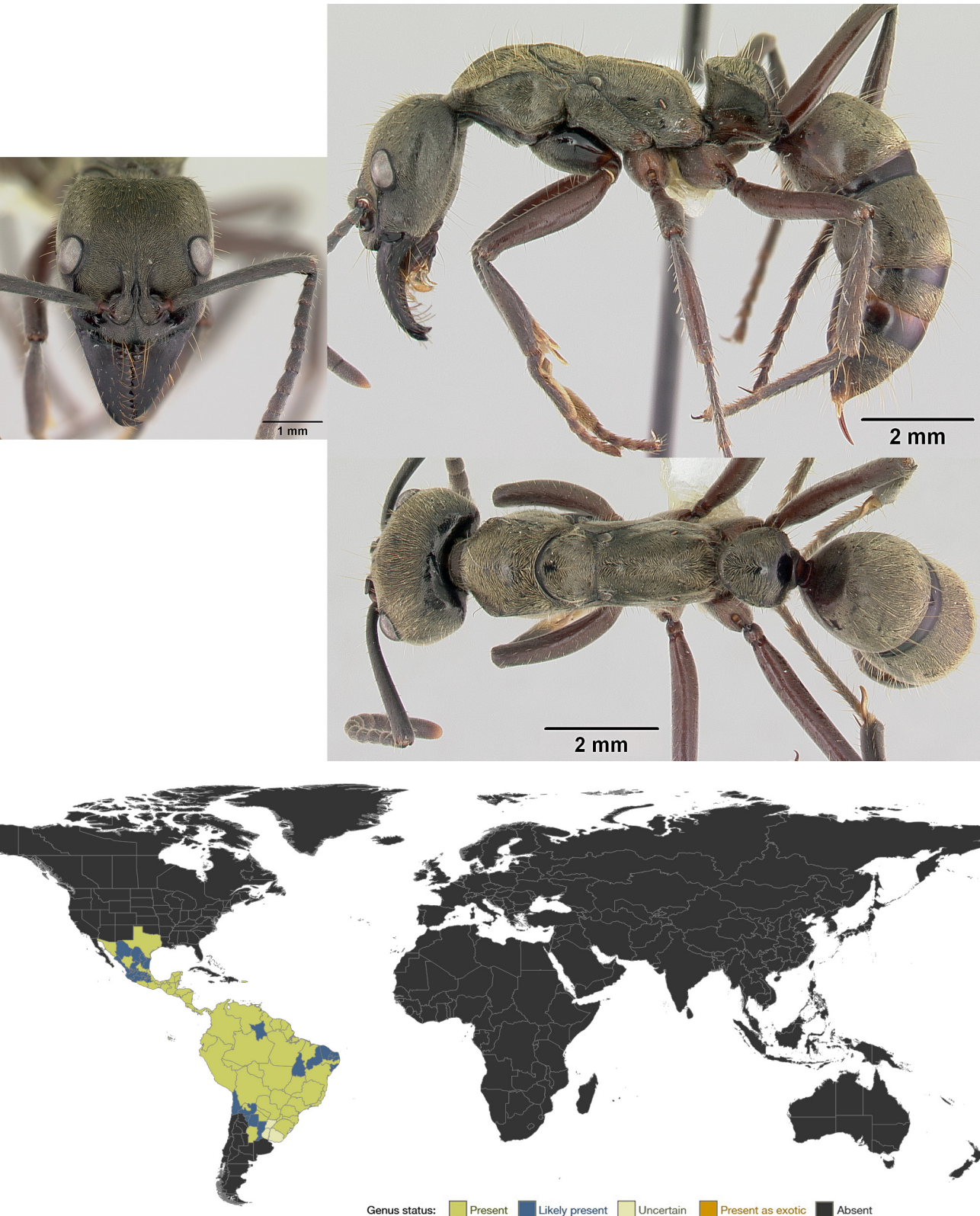
*Syntermitopone* Wheeler, W.M., 1936: 169 (as subgenus of *Termitopone*). Type-species: *Ponera commutata* Roger, 1860: 311; by original designation. *Syntermitopone* as junior synonym of *Neoponera*: **Syn. nov.**

*Neoponera* is a large (54 described species) Neotropical genus, and is one of the most morphologically and behaviorally diverse of all ponerine genera. Many *Neoponera* are arboreal, and some species are specialized mass raiders of termites.

**Diagnosis.** *Neoponera* is morphologically diverse. Its workers can be most readily identified by the following combination of characters: eyes relatively large and located at or near the midline of the head, metapleural gland orifice with a U-shaped posterior cuticular lip and lateral groove, arolia prominent, stridulitrum present on pretergite of A4, and hypopygium without a row of stout spines on either side of the sting. Many *Neoponera* also have distinct preocular carinae. Members of *Neoponera* are superficially most similar to *Pachycondyla*, *Mayaponera*, *Mesoponera*, and perhaps *Megaponera*. *Neoponera* workers differ most obviously from those of *Pachycondyla* in having prominent arolia, a stridulitrum on the pretergite of A4, and an unarmed hypopygium, and differ from those of *Mayaponera* in having slit-shaped propodeal spiracles and at most only a shallowly impressed



metanotal groove. *Neoponera* species with round propodeal spiracles (some members of the *N. emiliae* group) can be separated from *Mayaponera* by the triangular-shaped metasternal processes (the processes are narrow and fang-like in *Mayaponera*). Both *Mesoponera* and *Megaponera* lack the complex metapleural gland orifice and prominent arolia of *Neoponera*.



**FIGURE 30.** Worker caste of *Neoponera villosa*: lateral and dorsal view of body and full-face view of head (CASENT0178188, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Neoponera*.



**Synoptic description.** *Worker.* Medium to large (TL 6.5–19 mm) slender ants with the standard characters of Ponerini. Usually monomorphic, but size polymorphic in *N. laevigata*, *N. marginata*, and *N. luteola*. Mandibles triangular, with numerous teeth on the masticatory margins and often with a faint basal groove. Anterior clypeal margin convex, sometimes emarginate or coming to a point medially. Frontal lobes of moderate size. Preocular carinae present (*Neoponera s.s.*) or absent (“*Termitopone*” and relatives). Eyes large to very large, placed at or anterior to head midline. Pronotum often with sharp humeral margins (rounded in “*Termitopone*” and relatives). Mesopleuron often divided by a transverse groove, but sometimes undivided. Metanotal groove sometimes shallowly impressed but usually reduced to a simple suture. Propodeum moderately narrowed dorsally and often with shallowly ridged posterior margins. Propodeal spiracles slit-shaped in most species, round in a few (*P. concava*, *P. emiliae*, *P. schultzi*, *P. venusta*). Metapleural gland orifice with a U-shaped posterior cuticular lip and a lateral groove. Metatibial spur formula (1s, 1p). Arolia prominent. Petiole nodiform but highly variable, in *Neoponera s.s.* the node usually with a vertical or sloped anterior face and a sloping posterodorsal face, the two faces meeting along a sharp edge; the node is more rounded in “*Termitopone*” and its relatives. Gaster with a strong to moderate girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Head and body usually finely punctate, sometimes striate, pruinose, or smooth and shiny (“*Termitopone*”). Head and body with sparse to scattered pilosity, and with absent (“*Termitopone*”) to abundant pubescence. Color variable, orange to black.

*Queen.* Very similar to worker but winged, slightly larger, and with ocelli and the modifications of the mesosoma typical of alate ponerine queens.

*Male.* See descriptions for individual species in Forel (1899), Santschi (1921, 1923), Wheeler (1925, 1936), Borgmeier (1959) and Mackay & Mackay (2010).

*Larva.* Described for individual species by Wheeler & Wheeler (1952, 1971a, 1974), Petralia & Vinson (1980) and Mackay & Mackay (2010).

**Geographic distribution.** *Neoponera* is a strictly Neotropical genus and ranges from southern Texas and northern Mexico to northern Argentina and southern Brazil, with some species spanning virtually that entire range and others with more restricted distributions (Emery, 1911; Longino, 2013; Mackay & Mackay, 2010).

**Ecology and behavior.** *Neoponera* is among the most behaviorally diverse of all ponerine genera. While relatively little is known about most members of the genus, certain species groups (especially the *N. apicalis*, *N. laevigata*, and *N. villosa* groups) have been heavily studied and have become model systems for studies of social and foraging behavior.

Phylogenetic evidence suggests that the ancestral *Neoponera* was an epigeic generalist predator and scavenger that foraged on the ground (see discussion of phylogenetic relationships within *Neoponera*, below). This is still apparently the pattern followed by those *Neoponera* species formerly placed in *Mesoponera* (such as *N. aenescens*; Longino, 2013), as well as members of the *N. apicalis* species group (see below). From this ancestral condition two major deviations occurred: the ancestor of the *N. laevigata* group became a specialized mass raider of termites, while the ancestor of most members of *Neoponera (s.s.)* took the unusual step among ponerines of becoming arboreal.

Colonies of most *Neoponera* species are small, with typically fewer than 200 workers (e.g., *N. carinulata*, *N. crenata*, *N. lineaticeps*, and *N. unidentata*; Longino, 2013; *N. apicalis* species group: Fresneau, 1985; Fresneau & Dupuy, 1988; Düsselmann *et al.*, 1996; Gobin *et al.*, 2003a; *N. villosa* species group: D’Ettorre *et al.*, 2006). Exceptions include *N. goeldii*, whose colonies can have at least 500 workers (Denis *et al.*, 2007), the *N. laevigata* species group, which have colony sizes of up to at least 1,800 workers (Leal & Oliveira, 1995; Longino, 2013), and *N. luteola*, which reportedly has colonies with tens or hundreds of thousands of workers (Yu & Davidson, 1997). An interesting behavior observed in some *Neoponera* species is the collection of drops of water or honeydew between the mandibles (e.g., in *N. apicalis*: Fresneau & Dupuy, 1988). *N. villosa* workers collect drops of liquid between their mandibles and act as “social buckets” by distributing the liquid to their nestmates (Déjean & Corbara, 1990b; Hölldobler & Wilson, 1990; Paul & Roces, 2003); some of the liquid may be used to control nest humidity (Hölldobler & Wilson, 1990). The ants use their mandibles as an external crop, to compensate for their lack of proper structures for internal liquid storage.

Among those *Neoponera* species that are terrestrial generalist predators and scavengers, only the members of the *N. apicalis* species group (*N. apicalis*, *N. obscuricornis*, and *N. verenae*) have been heavily studied, though they are behaviorally quite derived and should not necessarily be considered typical of terrestrial generalist *Neoponera*.

The *N. apicalis* species group was revised by Wild (2005), who provided a good summary of the habits of these species and noted that most published studies on *N. obscuricornis* actually involved *N. verenae*. Individual workers forage diurnally among leaf litter or on low vegetation for live and dead insects, vertebrate carcasses, fruit, and nectar sources, and look and behave similarly to pompilid wasps (Fresneau, 1985; Fresneau & Dupuy, 1988; Wild, 2002; Sujii *et al.*, 2004; Longino, 2013). The foraging behavior of *N. apicalis* was studied in detail by Fresneau (1985), and modeled by Goss *et al.* (1989). Computer scientists have used models of *N. apicalis* foraging behavior to develop highly efficient search algorithms for complex problems in computer science (e.g. Monmarché *et al.*, 2000; Wang & Ip, 2005; Admane *et al.*, 2006; Luh & Lin, 2008). Duelli & Duelli-Klein (1976) found that workers of *P. verenae* can navigate using patterns of polarization of sunlight. Members of the *N. apicalis* species group construct small nests in rotting wood or soil (Traniello & Hölldobler, 1984; Fresneau & Dupuy, 1988; Pezon *et al.*, 2005; Wild, 2002, 2005). Colonies emigrate frequently to new nest sites via tandem running (Fresneau, 1985; Pezon *et al.*, 2005), which is mediated by a pheromone produced in the pygidial gland (studied in *N. verenae*: Traniello & Hölldobler, 1984).

The reproductive and social behaviors of the *N. apicalis* group have been extensively studied. Colonies are facultatively polygynous (*N. apicalis*: Fresneau & Dupuy, 1988; *N. verenae*: Traniello & Hölldobler, 1984) and may include intercaste queens which both mate and lay eggs (*N. verenae*: Düssman *et al.*, 1996). Workers apparently are unable to mate and in queenright colonies will usually only lay trophic eggs (queens largely suppress worker reproduction), but in queenless nests workers will lay haploid eggs (Düssman *et al.*, 1996; Dietemann & Peeters, 2000). Workers form dominance hierarchies in both queenright and queenless colonies, with the highest ranked individuals dominating the egg laying (Oliveira & Hölldobler, 1990, 1991; Düssman *et al.*, 1996; Gobin *et al.*, 2003a). Gobin *et al.* (2003a) found that such dominance interactions impose a significant energetic cost on the colony. Ovarian development in *N. verenae* workers and queens is related to their social status (Fresneau, 1984). The division of labor among *N. apicalis* workers is similar to that of most ants, with the exception that queens engage in colony work to an unusually high degree (Fresneau & Dupuy, 1988).

Several studies have examined the structure and secretions of glands in members of the *N. apicalis* species group, including the labial glands (*N. verenae*: Lommelen *et al.*, 2002, 2003), Dufour's and venom glands (*N. apicalis*: Schmidt *et al.*, 1984; Lopez & Morgan, 1997; *N. verenae*: Morgan *et al.*, 2003), metapleural gland (Hölldobler & Engel-Siegel, 1994), postpharyngeal gland and cuticular hydrocarbons (*N. apicalis* Soroker *et al.*, 1998, 2003; Hefetz *et al.*, 2001), and mandibular gland (*N. verenae*: Morgan *et al.*, 1999). Giovannotti (1996) and Pavan *et al.* (1997) studied the structure and acoustics of the stridulatory organ in *N. apicalis*.

Species related to *N. apicalis* were used to explore the role of acoustics in the speciation process. Ferreira *et al.* (2010) found that what had been considered to be a single species actually consisted of several distinct but cryptic species. A close examination of the stridulatory organ, both morphologically and acoustically, revealed that each of the identified morphs within "*N. apicalis*" possessed a distinct morphology and that all sympatric morphs made distinctive sounds. The differentiation observed in the stridulatory organs were the result of both worker size and intrinsic features of the organ and the distinct acoustic signals produced were the result of differences in both organ morphology and the behaviour of the ants. Ferreira *et al.* (2010) also found that divergence in acoustic signals only occurred among sympatric morphs and that in cases where morphs were allopatric their signals were similar. They conclude that the acoustic signals may be the result of inter-specific competitive interactions and that this character system is a useful tool in identifying and diagnosing complexes of closely related species.

Excepting the *N. apicalis* group, most species of *Neoponera* (s.s.) are arboreal, nesting in dead branches, stem internodes, among epiphytes, or in other suitable microhabitats in trees, and primarily foraging arboreally (e.g., *N. crenata*: Wild, 2002; Longino, 2013; *N. foetida*, *N. lineaticeps*, *N. striatinodis*, *N. theresiae*, *N. unidentata*: Longino, 2013; *N. goeldii*: see below; *N. luteola*: Davidson & Fisher, 1991; Yu & Davidson, 1997; *N. villosa*: Déjean, 1990; Heinze *et al.*, 1996; Déjean & Olmsted, 1997; Trunzer *et al.*, 1999; Wild, 2002; D'Ettorre & Heinze, 2005; Longino, 2013; multiple species frequently collected in trees: Morini *et al.*, 2006). In at least some cases, the relationships between arboreal *Neoponera* species and their host trees seem to be mutualistic, with the ants effectively defending their hosts from herbivores and the ants in return receiving nest sites and food from extrafloral nectaries and Müllerian bodies (e.g., *N. luteola* in *Cecropia* sp.: Davidson & Fisher, 1991; Yu & Davidson, 1997; *N. villosa* in various host species: Déjean & Corbara, 1990a; Déjean *et al.*, 1992; Longino, 2013).

*N. goeldii* is an interesting arboreal species which colonizes disturbed areas, encourages the growth of certain epiphytes, and then nests in the resulting ant-gardens (Orivel & Déjean, 1999; Marini, 1999; Déjean *et al.*, 2000;

Orivel & Déjean, 2000; Denis *et al.*, 2006a). A single monogynous colony will occupy several such gardens, clustered within a small area (Denis *et al.*, 2006a). Workers occupying queenless nests form dominance hierarchies and have increased ovarian activity relative to those in queenright nests (Denis *et al.*, 2006b, 2008). As with most or all *Neoponera*, workers of *N. goeldii* lack spermathecae and can only lay haploid eggs (Denis *et al.*, 2007). Worker reproductive status is conveyed by their cuticular hydrocarbon profile (Denis *et al.*, 2006b). *N. goeldii* workers are aggressive toward members of other colonies (Denis *et al.*, 2006b). The hunting strategies employed by *N. goeldii* (a generalist predator) were reported by Orivel *et al.* (2000). Orivel *et al.* (2001) discovered that the venom of *N. goeldii* contains a suite of novel anti-bacterial and anti-insecticidal compounds, which they named “ponericins.”

Orivel & Déjean (2001) measured the toxicity of venom from several *Neoponera* species and found that their venom tended to be much more potent than that of measured *Mayaponera*, *Brachyponera*, *Pseudoponera*, *Bothroponera*, and *Pachycondyla* species. Their study suffered from a lack of phylogenetic consideration (they treated all tested species as congeners in *Pachycondyla*, with no underlying phylogeny), but they hypothesized that the high venom toxicity of some *Neoponera* species is an adaptation to hunting prey in an arboreal environment. Their hypothesis may very well be correct, but a phylogenetically-corrected analysis of their data would likely lack the power to find statistical significance.

The most thoroughly studied arboreal *Neoponera* species are *N. villosa* and its close relative *N. inversa* (Lucas *et al.*, 2002), whose social behaviors have attracted a great deal of attention. Colonies of *N. villosa* and *N. inversa* are often co-founded by multiple queens, who organize themselves into dominance hierarchies and stay together even after the first workers eclose, in a rare example of stable primary polygyny (Trunzer *et al.*, 1998; Kolmer & Heinze, 2000; Tentschert *et al.*, 2001; Kolmer *et al.*, 2002; D’Ettorre *et al.*, 2005). In such polygynous colonies, subordinate queens forage and dominant queens stay in the nest and guard the brood, though they all lay eggs at the same rate. Queens of these species are unusual in that they often (or usually) mate with more than one male (Kolmer *et al.*, 2002; Kellner *et al.*, 2007). Colonies of *N. villosa* have from one to five queens, with two-queen colonies being the most common and the most stable (Trunzer *et al.*, 1998; D’Ettorre *et al.*, 2005), while single queen colonies are most common in *N. inversa* (D’Ettorre *et al.*, 2006). Queens can distinguish between individual nestmate queens using chemical cues, and at least in *N. inversa* can remember them for at least 24 hours (D’Ettorre & Heinze, 2005; Dreier *et al.*, 2007).

Queens of *N. inversa* suppress worker reproduction, as workers separated from the queens will begin to lay eggs (van Zweden *et al.*, 2007). Workers police each other through aggression and by eating worker-derived eggs, which have a distinct chemical profile from queen-derived eggs (Heinze *et al.*, 1996; D’Ettorre *et al.*, 2004a, 2006; van Zweden *et al.*, 2007). Some workers seem to be behaviorally specialized for policing (van Zweden *et al.*, 2007). Workers of a species near *N. inversa* lack spermathecae and do not mate, but in orphaned colonies will form linear dominance hierarchies and begin laying haploid eggs (Heinze *et al.*, 2002). Similarly, workers in orphaned colonies of *N. villosa* aggressively compete through biting and antennal boxing, forming linear dominance hierarchies in which dominant individuals lay eggs (Heinze *et al.*, 1996; Trunzer *et al.*, 1999). Workers in *N. villosa* can also lay trophic eggs (Mathias & Caetano, 1995a). The fertility and rank of both queens and workers is communicated by their cuticular hydrocarbon profiles (Tentschert *et al.*, 2001; Heinze *et al.*, 2003; D’Ettorre *et al.*, 2004b). The role of cuticular hydrocarbons in nestmate recognition has been studied in *N. villosa* (Lucas *et al.*, 2004). Foraging workers of *N. villosa* exhibit great flexibility in predatory behaviors depending on the type and status of prey encountered (Déjean *et al.*, 1990; Déjean & Corbara, 1990a, 1998). Morphological and ultrastructural studies have examined *N. villosa* larval fat body cells (Zara *et al.*, 2003), larvae (Zara & Caetano, 2001), oocytes (Mathias & Caetano, 1998; Caperucci & Mathias, 2006), corpora alata (Mathias & Caetano, 1995b), ovarioles (Mathias & Caetano, 1996), and mandibular glands (Duffield & Blum, 1973; Mathias *et al.*, 1991). Trindl *et al.* (2004) isolated several microsatellite loci for *N. inversa*.

The three *Neoponera* species formerly placed in the genus *Termitopone* (*N. commutata*, *N. laevigata* and *N. marginata*) are mass-raiding termite specialists. The prey preferences of these species correlate with their body size, as *N. commutata* (which is far larger than the other two species) preys exclusively on the very large termites of the genus *Syntermes*, while *N. laevigata* and *N. marginata* prey on a variety of smaller termites (Wheeler, 1936; Mill, 1984). Wheeler (1936) reported that workers of *N. laevigata* and *N. marginata* are dimorphic for size, but Longino (2013) states that workers of *N. laevigata* in Costa Rica are continuously polymorphic.

Raids by *N. marginata* occur infrequently (every two to three weeks) and may last for over 24 hours (Leal &



Oliveira, 1995; Hölldobler *et al.*, 1996a), and though the number of workers employed in raids of this species is unreported, raiding parties of *N. laevigata* contain hundreds of workers (Wheeler, 1936). *N. marginata* raids termite nests, while *N. commutata* raids only surface columns of *Syntermes* (Mill, 1984). Raids are often, but not always, initiated by scouts who locate potential prey and then return to their nest to recruit nestmates (Mill, 1982a, 1984). Colonies of *N. marginata* contain roughly 500 to 1,600 workers and usually multiple dealate queens (Leal & Oliveira, 1995; Hölldobler *et al.*, 1996a), and colonies of *N. laevigata* are reported to be of roughly similar size (Longino, 2013). Nests are constructed in the ground under logs or leaf litter (Wheeler, 1936; Hölldobler & Traniello, 1980; Mill, 1984), and emigrations are infrequent, occurring on average every 150 days in *N. marginata* (Leal & Oliveira, 1995). In *N. marginata*, emigrations to new nest sites are initiated by scouts who recruit nestmates with a trail pheromone from their pygidial gland (Hölldobler & Traniello, 1980; Hölldobler *et al.*, 1996a). Recruitment rates are enhanced by a rapid shaking motion of the body by the scouts or other workers (Hölldobler, 1999; Hölldobler *et al.*, 1996a). Trail pheromones from the pygidial gland are also used during raids (Hölldobler *et al.*, 1996a). Mill (1982b) described in detail an emigration by *N. commutata*. Blum (1966) reported that the hindgut was the source of trail pheromones in *N. laevigata*. Workers of *N. marginata* have specialized magnetic organs in their bodies (especially in their antennae) which provide them with a sense of direction and help orient them during emigrations (Acosta-Avalos *et al.*, 1999, 2001; Wajnberg *et al.*, 2000; Esquivel *et al.*, 2004; Wajnberg *et al.*, 2004). Colony reproduction in *N. marginata* occurs by budding or by either haplometrotic or (more commonly) pleiometrotic foundation (Leal & Oliveira, 1995).

**Phylogenetic and taxonomic considerations.** *Neoponera* has had a fairly complex taxonomic history. Emery (1901) erected the genus to hold those New World “*Pachycondyla*” species with preocular carinae and eyes located laterally near the midline of the head. Subsequent authors continued to treat *Neoponera* as a distinct genus until Brown (1973; also in Bolton, 1994) synonymized it under *Pachycondyla* without justification.

Forel (1901b) erected the subgenus *Eumecopone* to hold two species (now *N. agilis* and *N. rostrata*) which differ from typical *Neoponera* in having extremely long mandibles (Emery, 1911). Wheeler (1936) created a new genus, *Termitopone*, in which he placed three termitophagous species (now *N. commutata*, *N. laevigata*, and *N. marginata*). Wheeler also erected a monotypic subgenus of *Termitopone*, *Syntermitopone*, for *N. commutata*; Borgmeier (1959) later made *Syntermitopone* a junior synonym of *Termitopone*. Brown (1973) eventually synonymized *Eumecopone*, *Termitopone*, and *Syntermitopone* under *Pachycondyla* along with *Neoponera* and several other ponerine genera.

Based on strong molecular and morphological evidence, we are reviving *Neoponera* as a distinct genus, retaining *Eumecopone* as its junior synonym, designating *Termitopone* and *Syntermitopone* as new junior synonyms, and combining within it several “*Pachycondyla*” species formerly considered members of *Mesoponera*. Schmidt's (2013) molecular phylogeny of the Ponerinae lends strong support to a clade consisting of (among sampled species) the type species of *Neoponera*, *N. villosa*, three other species traditionally placed in *Neoponera* (*N. apicalis*, *N. carinulata*, and *N. unidentata*), two members of the former genus *Termitopone* (*N. commutata* and *N. marginata*), and two species formerly considered *Mesoponera* (*N. aenescens* and *N. fauveli*). This clade is inferred to be sister to *Dinoponera* plus *Pachycondyla*, but the split between *Neoponera* and these other genera is old enough, and the morphological and behavioral differences significant enough, to warrant separate generic status.

Morphological evidence also supports the new synonymizations and combinations described above. *Neoponera* as defined here is characterized by several apomorphies: moderately large eyes which are located laterally at or near the midline of the head, prominent arolia, and a stridulitrum on the pretergite of A4. Members of *Neoponera* (s.s.) are also characterized by the presence of distinct preocular carinae (*N. commutata* also has preocular carinae, though these were apparently independently evolved). *Neoponera* (s.s.) forms one half of the basal split in the genus, with “*Termitopone*” and the “*Mesoponera*” species forming the other half (at least among species sampled by Schmidt (2013)). All of these taxa are very closely related, however, and a separate genus is not justified for the “*Termitopone/Mesoponera*” clade. Though Schmidt (2013) did not sample either “*Eumecopone*” species in his molecular phylogeny, their morphological traits strongly suggest that they are simply *Neoponera* with unusually long mandibles.

## Species of *Neoponera*

- N. aenescens* (Mayr, 1870): Colombia (**comb. nov.**)  
*N. agilis* Forel, 1901: United States (error) (**comb. rev.**)  
*N. antecurvata* (Mackay & Mackay, 2010): Costa Rica (**comb. nov.**)  
*N. apicalis* (Latreille, 1802): South America (**comb. rev.**)  
*N. battronica* (Fernandes, De Oliveira & Delabie, 2014): Brazil (**comb. nov.**)  
*N. billemma* (Fernandes, De Oliveira & Delabie, 2014): Brazil (**comb. nov.**)  
*N. bucki* (Borgmeier, 1927): Brazil (**comb. nov.**)  
*N. bugabensis* (Forel, 1899): Panama (**comb. rev.**)  
*N. carbonaria* (Smith, F., 1858): Ecuador (**comb. nov.**)  
*N. carinulata* (Roger, 1861): Guyana (**comb. rev.**)  
*N. cavinodis* (Mann, 1916): Brazil (**comb. rev.**)  
*N. chyzeri* (Forel, 1907): Colombia (**comb. nov.**)  
*N. commutata* (Roger, 1860): S. America (**comb. rev.**)  
*N. concava* (Mackay & Mackay, 2010): Brazil (**comb. nov.**)  
*N. cooki* (Mackay & Mackay, 2010): Brazil (**comb. nov.**)  
*N. coveri* (Mackay & Mackay, 2010): Peru (**comb. nov.**)  
*N. crenata* (Roger, 1861): Brazil (**comb. rev.**)  
*N. curvinodis* (Forel, 1899): Guatemala (**comb. rev.**)  
*N. dismarginata* (Mackay & Mackay, 2010): Costa Rica (**comb. nov.**)  
*N. donosoi* (Mackay & Mackay, 2010): Ecuador (**comb. nov.**)  
*N. eleonorae* (Forel, 1921): Ecuador (**comb. nov.**)  
*N. emiliae* Forel, 1901: Venezuela (**comb. rev.**)  
*N. fauveli* Emery, 1896: Bolivia (**comb. nov.**)  
*N. fiebrigi* Forel, 1912: Panama (**comb. rev.**)  
*N. fisheri* (Mackay & Mackay, 2010): Panama (**comb. nov.**)  
*N. foetida* (Linnaeus, 1758): “America meridionali” (**comb. rev.**)  
*N. fusca* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)  
*N. globularia* (Mackay & Mackay, 2010): Bolivia (**comb. nov.**)  
*N. goeldii* Forel, 1912: Brazil (**comb. rev.**)  
*N. hispida* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)  
*N. holcotyle* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)  
*N. insignis* (Mackay & Mackay, 2010): Costa Rica (**comb. nov.**)  
*N. inversa* (Smith, 1858): South America (**comb. rev.**)  
*N. laevigata* (Smith, F., 1858): Brazil (**comb. nov.**)  
*N. latinoda* (Mackay & Mackay, 2010): Brazil (**comb. nov.**)  
*N. lineaticeps* (Mayr, 1866): Mexico (**comb. rev.**)  
*N. luteola* (Roger, 1861): Brazil (**comb. rev.**)  
*N. magnifica* Borgmeier, 1929: Brazil (**comb. nov.**)  
*N. marginata* (Roger, 1861): Brazil (**comb. nov.**)  
*N. metanotalis* (Luederwaldt, 1928): Brazil (**comb. nov.**)  
*N. moesta* (Mayr, 1870): Colombia (**comb. rev.**)  
*N. oberthueri* (Emery, 1890): Brazil (**comb. rev.**)  
*N. obscuricornis* (Emery, 1890): Brazil (**comb. rev.**)  
*N. procidua* Emery, 1890: Suriname (**comb. nov.**)  
*N. recava* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)  
*N. rostrata* (Emery, 1890): Venezuela (**comb. rev.**)  
*N. rugosula* Emery, 1902: Peru (**comb. rev.**)  
*N. schoedli* (Mackay & Mackay, 2006): Ecuador (**comb. nov.**)  
*N. schultzi* (Mackay & Mackay, 2010): Brazil (**comb. nov.**)  
*N. solisi* (Mackay & Mackay, 2010): Costa Rica (**comb. nov.**)

*N. striatinodis* (Emery, 1890): Costa Rica (**comb. rev.**)  
*N. theresiae* (Forel, 1899): Panama (**comb. rev.**)  
*N. unidentata* (Mayr, 1862): Brazil (**comb. rev.**)  
*N. venusta* (Forel, 1912): Brazil (**comb. nov.**)  
*N. verenae* Forel, 1922: Panama (**comb. rev.**)  
*N. villosa* (Fabricius, 1804): Central America (**comb. rev.**)  
*N. zuparkoi* (Mackay & Mackay, 2010): Peru (**comb. nov.**)

### ***Pachycondyla* Smith, F.**

Fig. 31

*Pachycondyla* Smith, F., 1858: 105 (as genus in Poneridae). Type-species: *Ponera crassinoda* Latreille, 1802b: 198; by subsequent designation of Emery, 1901: 42.

*Pachycondyla* has been the focus of the greatest taxonomic confusion within Ponerinae, and was previously considered the senior synonym of numerous genera which are here considered distinct. *Pachycondyla* is in reality a small Neotropical genus (11 described species) that is closely related to *Dinoponera*. Relatively little is known about its habits.

**Diagnosis.** *Pachycondyla* workers are fairly generalized and lack any obvious autapomorphies, making their diagnosis more complicated than for most ponerine genera. They can most easily be identified by the following combination of characters: mandibles triangular, anterior clypeal margin without projecting teeth, metanotal groove at most present as a faint suture, propodeal spiracles slit-shaped, metapleural gland orifice with a posterior U-shaped cuticular lip, arolia not prominent, tarsal claws unarmed, petiole a thick block-like node, stridulitrum absent from pretergite of A4, and hypopygium with a row of stout spines on either side of the sting. *Pachycondyla* is most likely to be confused with *Dinoponera*, *Neoponera*, *Ectomomyrmex*, or *Bothroponera*, but *Pachycondyla* differs from *Dinoponera* in its smaller size, triangular mandibles, unarmed clypeal margin and tarsal claws, and block-like petiole; from *Neoponera* in its lack of a stridulitrum on the pretergite of A4 and by its hypopygial spines; from *Ectomomyrmex* in its complex metapleural gland orifice and hypopygial spines; and from *Bothroponera* in its hypopygial spines.

**Synoptic description.** *Worker.* Medium to large (TL 7–20 mm) robust ants with the standard characters of Ponerini. Mandibles triangular, sometimes with a faint basal groove. Anterior margin of clypeus convex and often medially emarginate. Frontal lobes moderately large. Eyes of moderate size and located anterior of head midline. Pronotum often with sharp lateral margins. Mesopleuron variable: fully, partially, or not at all divided by a transverse groove. Metanotal groove absent or at most present as a faint suture. Propodeum broad dorsally. Propodeal spiracles slit-shaped. Metapleural gland orifice with a posterior U-shaped cuticular lip and a lateral depression. Metatibial spur formula (1s, 1p). Petiole with a thick block-like node which widens posteriorly. Gaster with only a weak girdling constriction between pre- and postsclerites of A4. Hypopygium with a row of stout spines on either side of the sting. Head and body densely punctate to striate (rugoreticulate in at least one population of *P. harpax*), with abundant pilosity and dense pubescence. Color dark brown to black.

*Queen.* Winged, with ocelli and the other modifications typical of ponerine queens, and slightly larger than the worker, but otherwise very similar to that caste.

*Male.* See descriptions for individual species in Smith (1858) and Santschi (1921).

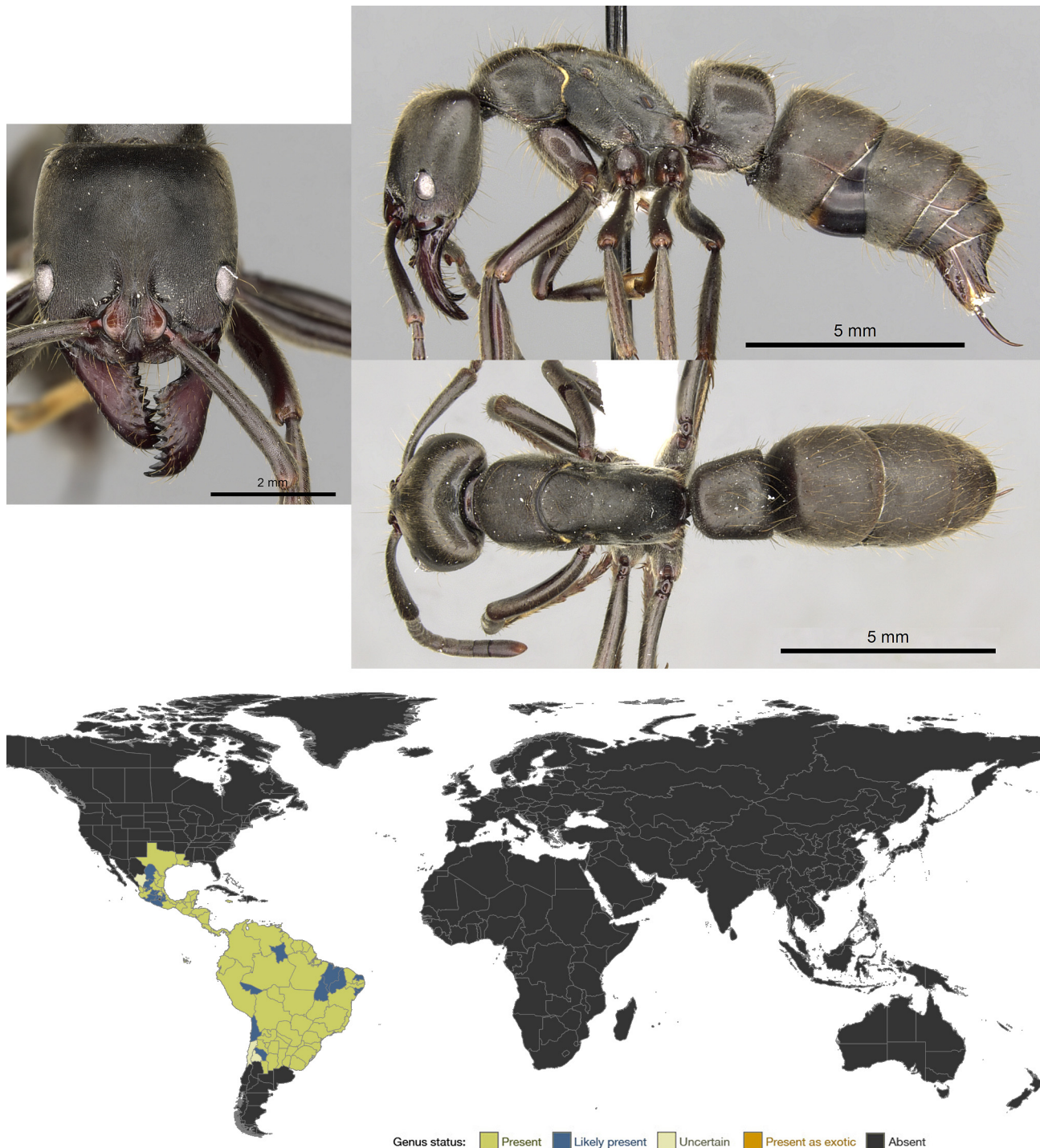
*Larva.* Described for individual species by Wheeler & Wheeler (1952).

**Geographic distribution.** The range of *Pachycondyla* extends from the southern United States (Louisiana and Texas) to northern Argentina, and includes some islands of the Caribbean (Kempf, 1961). *P. harpax* covers most of the range of the genus, but most other *Pachycondyla* species have a much more restricted range.

**Ecology and behavior.** Relatively little is known about the ecology and behavior of *Pachycondyla*. Longino (2013) reports that *P. harpax* and *P. impressa* forage on the forest floor and are never observed foraging arboreally. They are presumably generalist predators and scavengers, though published accounts of their food preferences are scant. Wheeler (1900b) reported that *P. harpax* workers in captivity would feed on egg yolk and sugar but ignored termites. Overal (1987) stated that *P. harpax* eats soft-bodied insects (including termites) and myriapods, and García-Pérez *et al.* (1997) observed *P. harpax* preying predominantly on termites. *P. striata* will readily harvest and



consume fruits and the arils of seeds from the forest floor, though it is unknown if this behavior occurs in other members of the genus (Pizo & Oliveira, 1998, 2001; Passos & Oliveira, 2002, 2003, 2004; Raimundo *et al.*, 2004). Nestmates are apparently recruited to food sources via tandem running (observed in *P. harpax* and *P. impressa*; S. Levings, pers. comm. cited in Hölldobler & Wilson, 1990).



**FIGURE 31.** Worker caste of *Pachycondyla crassinoda*: lateral and dorsal view of body and full-face view of head (CASENT0249138, Ryan Perry and [www.antweb.org](http://www.antweb.org)); world distribution of *Pachycondyla*.

When reported, nests are constructed in the ground (*P. harpax* and *P. impressa*; Wheeler, 1900b; Overall, 1987; Longino, 2013) or in soil collected in the crowns of palms (*P. harpax*; Overall, 1987). Mating occurs via typical nuptial flights (*P. harpax*: Longino, 2013; *P. impressa*: Ortiús & Lechner, 1997). Wheeler (1900b) reported on egg production by workers of *P. harpax*, which he interpreted as being ergatoid queens but which are more likely just normal workers laying haploid eggs, as is common in Ponerinae. The mandibular, Dufour's and venom gland

secretions of *P. striata* were studied by Morgan *et al.* (1999, 2003; the mandibular gland of this species was also studied by Tomotake *et al.*, 1992, and Mathias *et al.*, 1995), the ovaries and corpora allata of *P. striata* queens and workers were compared by Thiele & Mathias (1999) and Figueira & Mathias (2002), respectively, the fat body of *P. striata* queens was studied by Thiele & Mathias (2003), and the structure of the venom gland in *P. striata* was described by Ortiz & Mathias (2003, 2006). Overall (1987) observed that *P. harpax* produces a foamy defensive secretion from the tip of the abdomen, similar to the behavior exhibited by *Pseudoneoponera* (see the description under that genus). *P. harpax* also injects venom from the sting, and Orivel & Déjean (2001) measured the toxicity of this species' venom.

**Phylogenetic and taxonomic considerations.** The taxonomic status of *Pachycondyla* and its putative synonyms has been one of the central problems in ponerine systematics for many years. In fact, the taxonomic chaos represented by *Pachycondyla* was the initial motivation for this revision of the Ponerinae. From the very first description of *Pachycondyla* (Smith, 1858), and continuing until the present day, the true boundaries of this genus have been obscured by excessive synonymy and a lack of serious phylogenetic consideration. We will briefly review the taxonomic history of *Pachycondyla* before discussing the results of Schmidt's (2013) molecular phylogenetic analyses and our morphological observations as they relate to *Pachycondyla*.

Smith (1858) erected *Pachycondyla* based on a suite of morphological traits now shown to be of dubious phylogenetic value, including a subquadrate head, a convex anterior clypeal margin, large denticulate mandibles, clavate antennae (this character is mysterious, as the species that Smith included in *Pachycondyla* have more or less filiform antennae), medium-sized eyes that are located anteriorly on the sides of the head, four-segmented labial and maxillary palps, pectinate tibial spurs (presumably he meant only the larger spur), a thick and wide petiolar node, and an elongate abdomen. While this long list of characters may seem to be a reasonable basis for defining a genus, most or all of these characters are probably plesiomorphic within the Ponerini. The species originally included in *Pachycondyla* by Smith are now dispersed into several distinct genera: *Pachycondyla*, *Pseudoneoponera*, *Ectomomyrmex*, *Paltothyreus*, and even *Platythyrea*.

Smith did not designate a type species for *Pachycondyla*, but Emery (1901) later designated *P. crassinoda* as the type, presumably because it was the first species listed by Smith under *Pachycondyla*. Latreille (1804) had previously designated *P. crassinoda* as the type species of *Ponera*, but Westwood (1840) subsequently designated *Ponera coarctata* as the type species of *Ponera*. We continue to recognize the traditional application of the generic names *Ponera* and *Pachycondyla*, which has been nearly universal since Emery's designation of *P. crassinoda* as the type species of *Pachycondyla*. See Taylor (1967) for more on this controversy.

After Smith's original description, *Pachycondyla* experienced more than a century of relative taxonomic stability, with the most significant change being Emery's (1901) designation of *Bothroponera*, *Ectomomyrmex*, and *Pseudoponera* as subgenera of *Pachycondyla*. Emery (1911) later removed *Pseudoponera* from the genus and rediagnosed *Pachycondyla* by a presence of "subtriangular" toothed mandibles, convex anterior clypeal margin, the location of the eyes, a lack of preocular carinae, an obsolete metanotal groove, and a thick petiole. Subsequent authors variously treated *Bothroponera* and *Ectomomyrmex* as valid genera or as subgenera of *Pachycondyla* (see Bolton, 2006).

W. L. Brown worked for decades on a broad revision of *Pachycondyla*, and though he died before publishing his formal revision, his planned taxonomic changes became entrenched in the myrmecology community through various publications (principally Brown, 1973; Snelling, 1981; Hölldobler & Wilson, 1990; Bolton, 1994, 1995, 2003, 2006). These changes amounted to a broad synonymization of no fewer than 18 distinct generic names under *Pachycondyla*, without phylogenetic justification: *Bothroponera*, *Brachyponera*, *Ectomomyrmex*, *Eumecopone*, *Euponera*, *Hagensia*, *Megaponera*, *Mesoponera*, *Neoponera*, *Ophthalmopone*, *Paltothyreus*, *Pseudoneoponera*, *Pseudoponera*, *Syntermitopone*, *Termitopone*, *Trachymesopus*, *Wadeura*, and *Xiphopelta*. Brown apparently included in *Pachycondyla* any ponerine species whose workers have triangular mandibles, eyes, two metatibial spurs, and the absence of any apomorphies extreme enough to justify a separate genus. These characters are almost certainly plesiomorphic, rendering them uninformative about the monophyly of the group as thus defined. Given its extensive morphological diversity and the apparent close relationship between some of its species and other recognized genera, *Pachycondyla* (*sensu* Brown) was almost certainly bound to be non-monophyletic based on morphological evidence alone.

Schmidt's (2013) molecular phylogeny of the Ponerinae confirms the vast non-monophyly of *Pachycondyla*. Schmidt (2013) sampled representatives from nearly all junior synonyms of *Pachycondyla*, and none of them are

inferred to even be the sister group of true *Pachycondyla*, which is represented in the phylogeny by *P. crassinoda*, *P. harpax* and *P. impressa*. From morphology we are also confident that those junior synonyms which Schmidt (2013) did not sample (*Wadeura* and *Xiphopelta*) are also not closely related to *Pachycondyla*. The actual sister group of *Pachycondyla* is *Dinoponera*, which ironically has never been considered its junior synonym. Their close relationship is supported by strong molecular and morphological evidence (see the discussion under *Dinoponera* for more on their morphological synapomorphies). True *Pachycondyla* is a small Neotropical genus consisting of the type species *P. crassinoda* and its close relatives. *Pachycondyla* workers are united morphologically by their combination of triangular mandibles, unadorned anterior clypeal margin, medium-sized eyes, unarmed tarsal claws, block-like petiole, absence of a stridulitrum from the pretergite of A4, and a row of stout spines on the hypopygium on either side of the sting.

### Species of *Pachycondyla*

Kempf (1961) came closest to providing a revision for true *Pachycondyla*. His revision and keys deal ostensibly with the Brazilian *Pachycondyla* fauna, but this includes all species we associate with the genus except *P. lenkoi*, which he described soon afterward, and also includes *Neoponera magnifica* and *N. metanotalis*, which Kempf included in *Pachycondyla* but which we have transferred to *Neoponera*.

*P. constricticeps* Mackay & Mackay, 2010: Argentina

*P. crassinoda* (Latreille, 1802): Suriname

*P. fuscoatra* (Roger, 1861): Colombia

*P. harpax* (Fabricius, 1804): “South America”

*P. impressa* (Roger, 1861): Colombia

*P. inca* Emery, 1901: Peru

*P. lattkei* Mackay & Mackay, 2010: Venezuela

*P. lenis* Kempf, 1961: Brazil

*P. lenkoi* Kempf, 1962: Brazil

*P. purpurascens* Forel, 1899: Costa Rica

*P. striata* Smith, F., 1858: Brazil

We have not managed to discern the proper taxonomic placement for a handful of ponerine species previously associated with *Pachycondyla*. In some cases this uncertainty stems from our failure to examine specimens of the species in question (especially when the original descriptions are ambiguous), while in other cases the morphological traits of the species leave doubts about its affinities. We leave these species as *incertae sedis* within *Pachycondyla* while acknowledging this placement is undoubtedly incorrect. Exact placement will require detailed examination of relevant material of these taxa.

### *Incertae sedis*

*P. curiosa* Mackay & Mackay, 2010: Brazil

*P. jonesii* Forel, 1891: Madagascar

*P. solitaria* Smith, F., 1860: Indonesia

*P. unicolor* Smith, F., 1860: Indonesia

*P. vidua* Smith, F., 1857: Borneo

*P. vieirai* Mackay & Mackay, 2010: Ecuador

### Fossil species (*incertae sedis*)

† *P. baltica* Dlussky, 2002: Baltic Amber

† *P. calcarea* (Théobald, 1937): France (Oligocene)

† *P. conservata* Dlussky, 2009: Rovno Amber

† *P. crawleyi* (Donisthorpe, 1920): Great Britain (Oligocene)

† *P. dubia* (Théobald, 1937): France (Oligocene)

† *P. eocenica* Dlussky & Wedmann, 2012: Germany (Eocene)



- † *P. globiventris* (Théobald, 1937): France (Oligocene)
- † *P. gracilicornis* (Mayr, 1868): Baltic Amber
- † *P. labandeirai* (Dlussky & Rasnitsyn, 2002): U.S.A. (Eocene)
- † *P. lutzi* Dlussky & Wedmann, 2012: Germany (Eocene)
- † *P. messeliana* Dlussky & Wedmann, 2012: Germany (Eocene)
- † *P. minuta* Dlussky & Wedmann, 2012: Germany (Eocene)
- † *P. minutansata* (Zhang, 1989): China (Miocene)
- † *P. nubeculata* (Zhang, 1989): China (Miocene)
- † *P. petiolosa* Dlussky & Wedmann, 2012: Germany (Eocene)
- † *P. petrosa* Dlussky & Wedmann, 2012: Germany (Eocene)
- † *P. succinea* (Mayr, 1868): Baltic Amber
- † *P. tristis* (Dlussky, 2009): Bitterfeld Amber

## ***Simopelta* Mann**

Fig. 32

*Simopelta* Mann, 1922: 10 (as subgenus of *Belonopelta*). Type-species: *Belonopelta (Simopelta) jeckylli* Mann, 1916: 415; by original designation.

*Simopelta* is a moderate-sized genus (21 described species) restricted to the Neotropics. These ants are notable for their army ant-like lifestyles, including apparently obligate group predation on other ants, reproduction by dichthadiiform queens, and nomadism.

**Diagnosis.** *Simopelta* workers can be readily diagnosed by the following combination of characters: subtriangular mandibles, raised clypeal rostrum, eyes small and often consisting of only a single enlarged ommatidium, metapleural gland orifice with a posterior U-shaped lip, usually an absence of stout traction setae on the middle and hind legs, and presence of prominent arolia. The clypeal rostrum is autapomorphic within Ponerini. Some *Simopelta* species (*S. pergandei* and its relatives) superficially resemble *Feraponera* and some *Cryptopone*, but differ from them in lacking traction setae on the legs, among other differences.

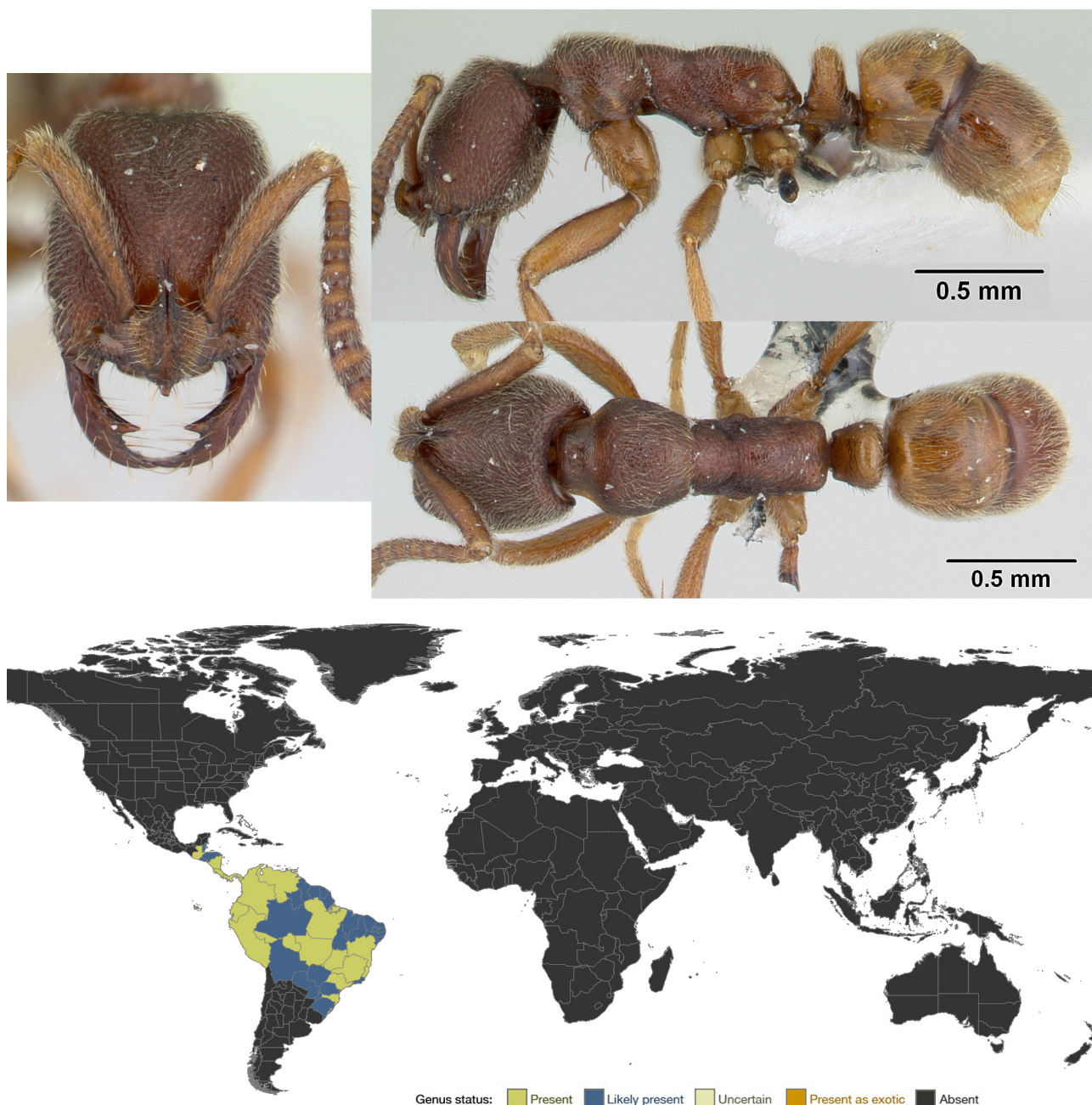
**Synoptic description.** *Worker.* Small (TL 2.1–4.9 mm) slender ants with the standard characters of Ponerini. Mandibles subtriangular, with a weak basal angle, a pair of apical teeth and variable dentition proximally, and no basal groove. Median portion of clypeus forming a raised triangular rostrum which projects past the anterior margin of the clypeus, sometimes with a short medial tooth. Frontal lobes small and closely approximated. Eyes small, often reduced to a single enlarged ommatidium, located on the sides of the head anterior of the head midline. Metanotal groove usually only shallowly impressed, though the mesosomal profile is often distinctly discontinuous due to a gradual posterior depression of the mesonotum. Mesonotum and propodeum much narrower than the pronotum, but the propodeum itself not narrowing significantly dorsally. Propodeal spiracles small and round. Metapleural gland orifice with a posterior U-shaped cuticular lip and a lateral groove. Metatibial spur formula (1p). Arolia prominent. Petiole nodiform to nearly squamiform. Gaster with a weak to strong girdling constriction between pre- and postsclerites of A4. Head, mesosoma and petiole usually heavily punctate, striate, or rugoreticulate, the gaster shiny or lightly punctate. Head and body with sparse to scattered pilosity and fairly light pubescence. Color variable, orange to black. Note: An undescribed hypogeic *Simopelta* species from Costa Rica (Longino, 2013) differs from this general description in its testaceous coloration, clubbed antennae, presence of stout traction setae on the mesotibiae, and complete absence of eyes.

*Queen.* Wingless and dichthadiiform, generally morphologically simplified relative to conspecific workers but with an enlarged petiole and gaster. See more detailed descriptions in Borgmeier (1950) and Gotwald & Brown (1967).

*Male.* Unknown.

*Larva.* Described by Borgmeier (1950), Wheeler & Wheeler (1957, 1986b), and Gotwald & Brown (1967). Wheeler & Wheeler (1957) describe the young larvae of *Simopelta* as among the most unusual of any ant.

**Geographic distribution.** *Simopelta* is restricted to central and northern South America, including Guatemala, Costa Rica, Brazil, Peru, and Ecuador (Gotwald & Brown, 1967; Longino, 2013). It primarily inhabits mid-elevation moist forests (Longino, 2013).



**FIGURE 32.** Worker caste of *Simopelta pergandei*: lateral and dorsal view of body and full-face view of head (CASENT0178701, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Simopelta*.

**Ecology and behavior.** Little to no focused research has been performed on the habits of *Simopelta*, but based on morphology and on anecdotal observations it appears that *Simopelta* has converged extensively on a true army ant lifestyle, much more so than have the mass termite raiders *Megaponera*, the *Leptogenys processionalis* species group, and the *Neoponera laevigata* species group. Morphologically, the reduced eyes of the workers and the dichthadiiform queens (wingless and with greatly distended gasters) are both convergent with ecitonine army ants, and the behavior of individual workers is reportedly much like that of army ants (Gotwald & Brown, 1967).

The additional similarities between *Simopelta* and army ants are striking. *Simopelta* colonies are fairly large by ponerine standards, with estimates of 1,000 to 2,000 workers (Gotwald & Brown, 1967). Foraging occurs during the day, usually on the ground and arboreally (Longino, 2013), though the morphological structure of a newly discovered Costa Rican species suggests that it is purely hypogeic (Longino, 2013). *Simopelta* workers form large raiding columns of up to several hundred individuals, at least, and these raiding workers apparently follow an odor trail (Gotwald & Brown, 1967). Anecdotal accounts suggest that they are specialist predators of both the adults and

brood of other ants, particularly *Pheidole* (Gotwald & Brown, 1967; Longino, 2013). *Simopelta* construct both temporary nests and long-term nests, which together with the dichthadiiform nature of the queens, the uniform age of the brood (indicating pulses of reproduction), and observations of colony emigrations suggest a nomadic lifestyle with an alternation between migratory and stationary colony phases, as in army ants (Borgmeier, 1950; Gotwald & Brown, 1967; Brady, 2003; Longino, 2013). Colony reproduction apparently occurs via budding, as in army ants (Gotwald & Brown, 1967). Interestingly, males have never been observed, suggesting the possibility that these ants may be parthenogenetic (Longino, 2013). Longino (2013) provides numerous interesting field accounts of *Simopelta* in Costa Rica.

**Phylogenetic and taxonomic considerations.** *Simopelta* was erected by Mann (1922) as a subgenus of *Belonopelta*, and since then it has variously been considered a subgenus or junior synonym of *Belonopelta* (e.g., Donisthorpe, 1943c; Baroni Urbani, 1975) or a separate genus (e.g., Wheeler, 1935; Gotwald & Brown, 1967; Bolton, 2003). On the one hand the morphological argument for a close relationship between *Simopelta* and *Belonopelta* is a weak one, as they are quite distinct and their similarities seem to be of the sort that are frequently evolved by small or cryptobiotic ponerines. On the other hand, though Schmidt (2013) did not sample *Belonopelta* in his molecular phylogeny of the Ponerinae, P.S. Ward (pers. comm.) found that *Belonopelta* is closely related to *Thaumatomyrmex*, and Schmidt found *Thaumatomyrmex* to be close to *Simopelta*. These findings support the close relationship of these three genera, although their exact relationships will require further study.

Schmidt's (2013) phylogeny places *Simopelta* with strong support as a member of the *Pachycondyla* group, and resolves it as sister to the remainder of that group, though other possible placements receive some support from Bayesian analyses, including sister relationships with *Thaumatomyrmex* and the *Ponera* group. *Simopelta*, *Belonopelta* and *Thaumatomyrmex* both differ from other members of the *Pachycondyla* group in having only a single metatibial spur. This could be a synapomorphy for these genera, could be independently evolved, or could represent the plesiomorphic condition within the *Pachycondyla* genus group, though the latter hypothesis is unlikely because it implies the re-evolution of a second spur. For now, the molecular data suggest most strongly that *Simopelta* is sister to the rest of the *Pachycondyla* group and closely related to *Belonopelta* and *Thaumatomyrmex*.

### Species of *Simopelta*

Mackay & Mackay (2008) revised the genus and provide a key to species, while Longino (2013) provides a key to Costa Rican species, including many that are undescribed. The large number of new *Simopelta* species from Costa Rica alone suggests that the true species diversity of the genus is much greater than presently known.

*S. andersoni* Mackay & Mackay, 2008: Costa Rica  
*S. bicolor* Borgmeier, 1950: Brazil  
*S. breviscapa* Mackay & Mackay, 2008: Panama  
*S. curvata* (Mayr, 1887): Brazil  
*S. fernandezi* Mackay & Mackay, 2008: Colombia  
*S. jeckylli* (Mann, 1916): Brazil  
*S. laevigata* Mackay & Mackay, 2008: Colombia  
*S. laticeps* Gotwald & Brown, 1967: Peru  
*S. longinoda* Mackay & Mackay, 2008: Costa Rica  
*S. longirostris* Mackay & Mackay, 2008: Colombia  
*S. manni* Wheeler, W.M., 1935: Ecuador  
*S. mayri* Mackay & Mackay, 2008: Colombia  
*S. minima* (Brandão, 1989): Brazil  
*S. oculata* Gotwald & Brown, 1967: Costa Rica  
*S. paeminosa* Snelling, 1971: Costa Rica  
*S. pentadentata* Mackay & Mackay, 2008: Costa Rica  
*S. pergandei* (Forel, 1909): Guatemala  
*S. quadridentata* Mackay & Mackay, 2008: Costa Rica  
*S. transversa* Mackay & Mackay, 2008: Colombia



*S. vieirai* Mackay & Mackay, 2008: Ecuador

*S. williamsi* Wheeler, W.M., 1935: Ecuador

### ***Thaumatomyrmex* Mayr**

Fig. 33

*Thaumatomyrmex* Mayr, 1887: 530 (as genus). Type-species: *Thaumatomyrmex mutilatus* Mayr, 1887: 531; by monotypy.

*Thaumatomyrmex* is a small (12 described species) Neotropical ponerine genus. These ants are notable for their pitchfork-like mandibles and other unusual cephalic characters and their specialized predation on polyxenid millipedes. Formerly considered a tribe separate from Ponerini, we confirm here their phylogenetic placement within the *Pachycondyla* group of Ponerini.

**Diagnosis.** *Thaumatomyrmex* workers are among the most morphologically derived of all ponerines, and would be difficult to confuse with those of any other genus. Their pitchfork-like mandibles and widely separated frontal lobes are autapomorphic within Ponerini and immediately identify them as *Thaumatomyrmex*. *Belonopelta* and *Emeryopone* also have mandibles with long attenuated teeth, but their teeth are shorter than those of *Thaumatomyrmex* and their frontal lobes are closely approximated as is typical for Ponerini.

**Synoptic description.** *Worker.* Small (TL 3.3–5.0 mm; Kempf, 1975) ants with the standard characters of Ponerini except that the antennal sockets are very widely separated by a broad posterior extension of the clypeus. Mandibles pitchfork-like with three very long and attenuated teeth, the mandibular articulations located on narrow anterolateral projections of the head. Clypeus generally greatly reduced except for a broad posterior extension. Frontal lobes of moderate size, semi-vertical, reaching or surpassing the anterior clypeal margin. Eyes large and very convex, located anterior of head midline. Metanotal groove absent to shallowly impressed. Propodeal dorsum moderately narrowed but rounded. Propodeal spiracles round. Metapleural gland orifice with a U-shaped cuticular flange posteriorly and a shallow groove laterally. Metatibial spur formula (1p). Petiole ranging from a thick broad scale with sharp lateral margins to a cuboidal node. Gaster with only a weak constriction between pre- and postsclerites of A4. Pretergite of A4 with a distinct stridulitrum. Head and body with variable sculpturing, ranging from smooth and shiny to finely shagreened to finely punctate and rugulose. Head and body with scattered pilosity and no pubescence. Color black.

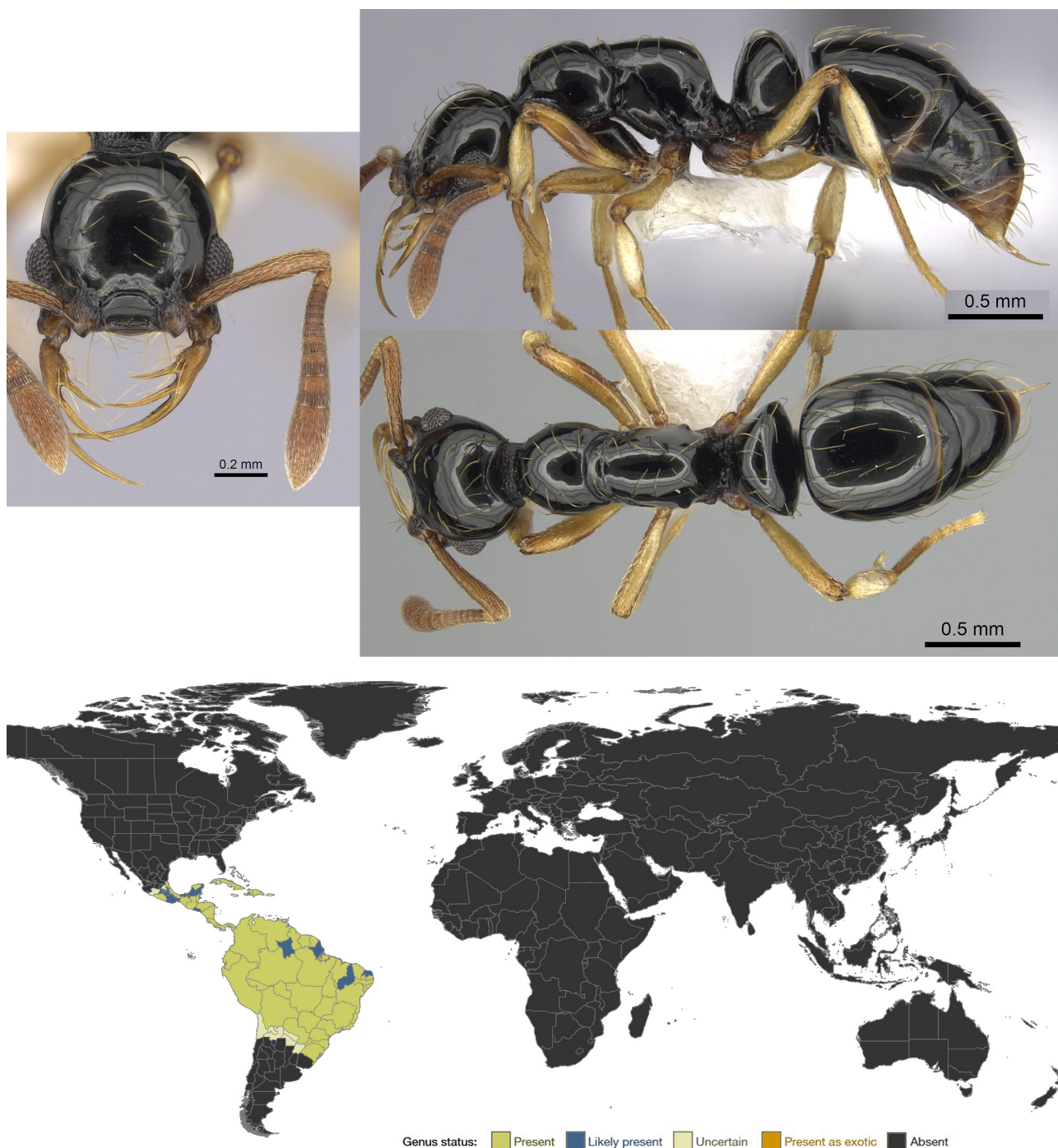
*Queen.* Kempf (1975) mentioned the existence of an alate queen of *T. zeteki* (= *T. atrox*), but it has neither been described nor confirmed. Gamergates occur in at least two species (Jahyny *et al.*, 2002).

*Male.* See description by Kempf (1975).

*Larva.* Discussed in Kempf (1975) and described for *T. mutilatus* by Kempf (1954) and Wheeler & Wheeler (1964).

**Geographic distribution.** *Thaumatomyrmex* is a strictly Neotropical genus whose known range extends from Mexico to Brazil on the mainland and also includes some islands of the Caribbean (Kempf, 1975).

**Ecology and behavior.** *Thaumatomyrmex* displays an unusual suite of morphological, ecological and behavioral traits. Brandão *et al.* (1991) examined the feeding habits of *T. atrox* and *T. contumax* and found that they are highly specialized predators of polyxenid millipedes (confirmed by Delabie *et al.*, 2000; see also the account in Hölldobler & Wilson, 1995). Polyxenids are covered with protective hooked setae which hunting *Thaumatomyrmex* workers must deal with before consuming their prey. The ants deal with the polyxenids by grasping them with their pitchfork mandibles, stinging them (presumably to minimize defensive struggles), and finally scraping off the defensive setae using their modified front tarsi, rendering the millipedes palatable (Brandão *et al.*, 1991). Given the highly specialized mandibular structure present in all *Thaumatomyrmex* species and the observation of millipede predation in two different species groups, polyxenid predation is probably universal in the genus. *Thaumatomyrmex* workers forage individually in leaf litter and feign death when disturbed (Brandão *et al.*, 1991). Though *Thaumatomyrmex* were long considered to be rare (Longino, 1988), improved sampling methods have demonstrated that their colony density can be very high (Delabie *et al.*, 2000). Given the cryptobiotic foraging habits of *Thaumatomyrmex*, the function of the large well-developed eyes in the workers is a mystery (Baroni Urbani & de Andrade, 2003).



**FIGURE 33.** Worker caste of *Thaumatomyrmex ferox*: lateral and dorsal view of body and full-face view of head (CASENT0249251, Shannon Hartman and [www.antweb.org](http://www.antweb.org)); world distribution of *Thaumatomyrmex*.

*Thaumatomyrmex* nests have been observed under bark, in rotting wood, under leaves, and in abandoned wasp nests (Kempf, 1975; Brandão *et al.*, 1991; Delabie *et al.*, 2000). Jahyny *et al.* (2002) studied the reproductive system of two species, *T. atrox* and *T. contumax*, and found that they reproduce via gamergates and that their colonies are exceptionally small (fewer than five workers, on average, and never more than nine). Kempf (1975) also reported a small colony size for *T. mutilatus* and the existence of an alate queen of *T. zeteki* (= *T. atrox*). Delabie *et al.* (2000) documented aggressive interactions between a putative gamergate and her nestmates in a colony of *T. contumax*.

**Phylogenetic and taxonomic considerations.** Mayr (1888) erected *Thaumatomyrmex* to house the single species *T. mutilatus* Mayr. Several additional species were subsequently described. Given the bizarre

morphological traits of these ants, there has never been any doubt that *Thaumatomyrmex* constitutes a valid genus. There has been uncertainty, however, about its higher taxonomic placement, with authors variously placing it in Ectatommini (e.g., Emery, 1895d), Ponerini (e.g., Forel, 1895), *Cylindromyrmecini* (Ashmead, 1905), or most commonly and most recently in its own tribe, *Thaumatomyrmecini* (e.g., Emery, 1901; also sometimes spelled *Thaumatomyrmii*). Its close relationship with Ponerini was confirmed by the discovery of the first male specimen (Kempf, 1954), which had vestigial mandibles as in members of Ponerini. Bolton (2003) continued to treat it as a tribe separate from Ponerini, given its lack of supposed apomorphies of Ponerini, though he suggested that the vestigial male mandibles were likely synapomorphic for the two tribes.

In the molecular phylogeny of Formicidae published by Brady *et al.* (2006), *Thaumatomyrmex* was inferred to be nested within a non-monophyletic Ponerini. Schmidt's (2013) molecular phylogeny of Ponerinae confirms this placement, with *Thaumatomyrmex* resolved as sister either to *Simopelta* or more likely to the remainder of the *Pachycondyla* group minus *Simopelta*; a sister relationship to Ponerini was statistically rejected. These results show that *Thaumatomyrmex* is simply a highly aberrant member of tribe Ponerini. The placement of the genus in its own tribe outside Ponerini (e.g., Bolton, 2003) was always suspect, as the apomorphies of Ponerini which are absent in *Thaumatomyrmex* (close approximation of the frontal lobes and hence only a narrow posterior extension of the clypeus) are some of the very characters which are so highly derived in *Thaumatomyrmex* (along with the mandibles, which are poor phylogenetic markers). In all other respects these ants are morphologically fairly typical for Ponerini. Given the unequivocal results from molecular phylogenetic analyses and the above morphological consideration, we are synonymizing *Thaumatomyrmecini* under Ponerini.

### Species of *Thaumatomyrmex*

For some time there was uncertainty about the species-level taxonomy of *Thaumatomyrmex*, given the apparent lack of sympatry among any two species and the shortage of discrete character differences among them. Longino (1988) suggested the possibility that *Thaumatomyrmex* may be a single species with many divergent localized populations. Brandão *et al.* (1991) discovered the first case of sympatry in the genus, which indicates that there are at least two distinct species, while Jahyny *et al.* (2008) discuss the four species known from Colombia and include a key and extensive biological notes. The supposed rarity of sympatry is probably an artifact from the rarity of collections for this genus (which likely underestimates the ranges of most species), and which is itself probably the result of inadequate collecting methods (Delabie *et al.*, 2000; Baroni Urbani & de Andrade, 2003).

- T. atrox* Weber, 1939: Guyana
- T. bariay* Fontenla, 1995: Cuba
- T. cochlearis* Creighton, 1928: Cuba
- T. contumax* Kempf, 1975: Brazil
- T. ferox* Mann, 1922: Honduras
- T. mandibularis* Baroni Urbani & de Andrade, 2003: Cuba
- T. manni* Weber, 1939: Bolivia
- T. mutilatus* Mayr, 1887: Brazil
- T. nageli* Baroni Urbani & de Andrade, 2003: Cuba
- T. paludis* Weber, 1942: Venezuela
- T. soesilae* Makhan, 2007: Surinam
- T. zeteki* Smith, M.R. 1944: Panama

### *Plectroctena* Genus Group

The *Plectroctena* genus group is apparently the result of a gradual radiation into hypogeic niches in the African tropics, with the frequent evolution of prey specialization. Among the group's members, only a few *Centromyrmex* species occur outside of Africa (in the Neotropics and Southeast Asia).

**Discussion.** The monophyly of the *Plectroctena* genus group is strongly supported by molecular data (Schmidt, 2013), with the exceptions of *Dolioponera* and *Feraponera*, for which molecular data are lacking and for



which placement in the *Plectroctena* group are tentative. An apparent synapomorphy of the group (excluding *Feroponera*; see below) is the lateral opening of the metapleural gland orifice, which among ponerines is otherwise only found in *Harpegnathos* and *Platythyrea*. It should be stressed that due to uncertainty in relationships among ponerine genus groups, a laterally opening metapleural gland orifice may be plesiomorphic within Ponerini.

*Centromyrmex* forms the sister group of a clade consisting of *Psolidomyrmex* + (*Plectroctena* + *Loboponera*). These relationships are unequivocally supported by molecular data (Schmidt, 2013) and are also supported by morphological evidence. Among these four genera, *Psolidomyrmex*, *Plectroctena* and *Loboponera* are supported as a clade by the derived shape of the anteroventral articulatory surface of the petiole (Bolton & Brown, 2002). *Plectroctena* and *Loboponera* are united by the presence of longitudinal grooves on their meso- and metafemora and by the division of the mesopleuron, with the anepisternum appearing fused to the mesonotum and metapleuron.

*Boloponera* is almost certainly very closely related to *Plectroctena* and *Loboponera*, as it also has longitudinal grooves on its metafemora (but not mesofemora) and has the same division and fusion of the mesopleuron. In his original description of *Boloponera*, Fisher (2006) hypothesized that it was outside the clade of *Psolidomyrmex* + *Loboponera* + *Plectroctena* (the *Plectroctena* genus group *sensu* Bolton & Brown, 2002), due to its apparent lack of a similarly modified petiole articulatory surface. From consideration of the totality of morphological evidence, however, we reach a different conclusion. As noted above, *Boloponera* shares with *Loboponera* and *Plectroctena* the presence of a longitudinal groove on the metafemora as well as characters of the mesopleuron. In addition, *Boloponera* has several potential synapomorphies with *Plectroctena* (as Fisher noted): linear mandibles, anteriorly projecting frontal lobes, and propodeal lamellae. *Boloponera* lacks the semicircular clypeal excavations and dorsal mandibular groove of *Plectroctena*, however. Finally, in our evaluation the structure of the anteroventral petiolar articulatory surface in *Boloponera* is not different enough from that in *Psolidomyrmex*, *Plectroctena* and *Loboponera* to warrant its exclusion from that clade. If anything, the shape of the median depression in the petiolar articulatory surface of *Boloponera* is more similar to that of *Plectroctena* than is the shape in *Loboponera*. At best, this character is ambiguous about relationships among these genera.

In conclusion, the morphological evidence strongly suggests a close relationship between *Boloponera*, *Plectroctena* and *Loboponera*. The exact nature of the relationships among them is uncertain and depends on the assumptions made about the ancestral character states. The absence of a longitudinal groove in the mesofemora of *Boloponera* supports the monophyly of *Loboponera* + *Plectroctena*, but the linear mandibles and projecting frontal lobes of *Boloponera* suggest a sister relationship between it and *Plectroctena*. *Boloponera* could also be sister to *Loboponera* or even nested within *Plectroctena*.

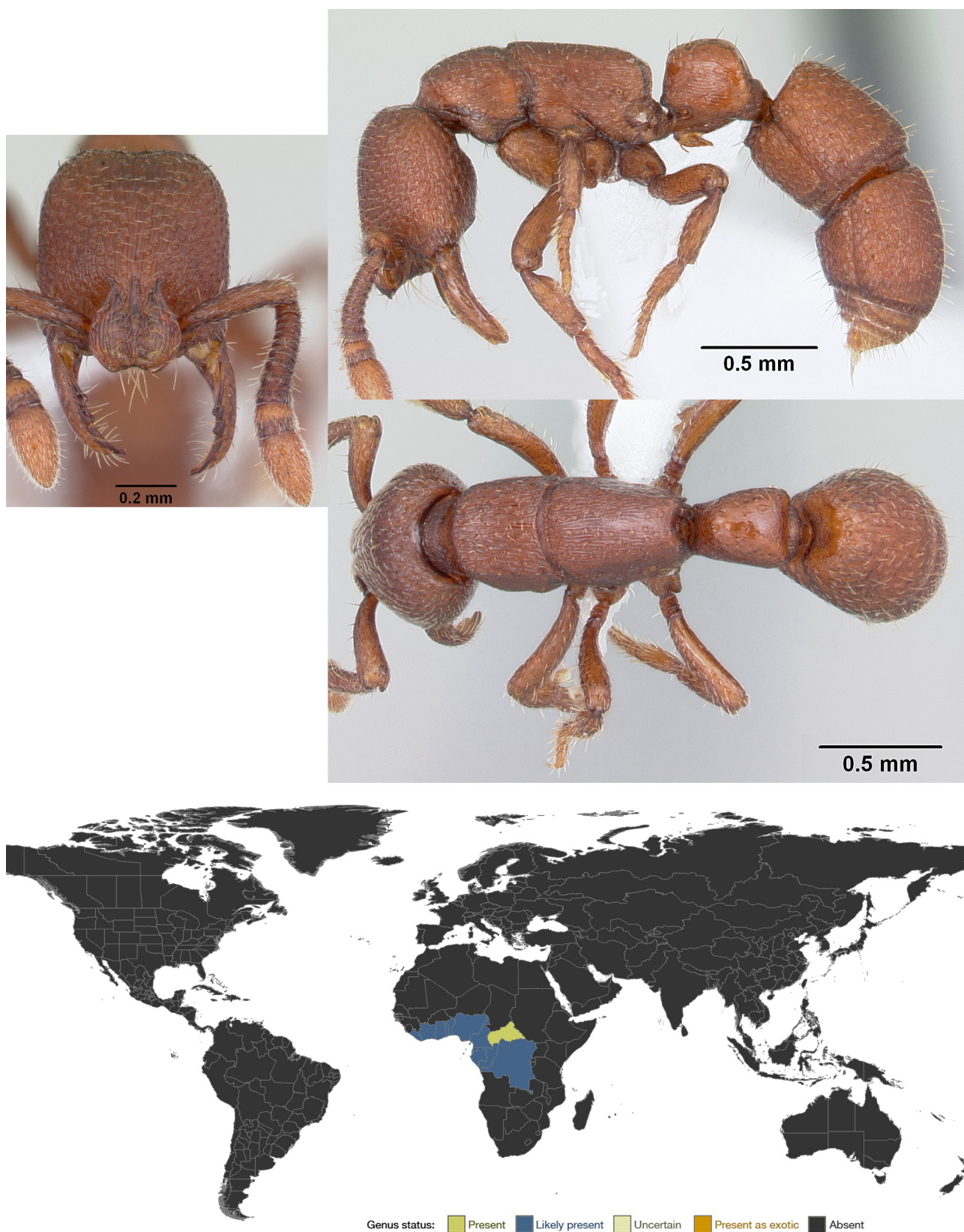
The inclusion of *Dolioponera* and *Feroponera* in the *Plectroctena* genus group is less certain. In overall gestalt *Dolioponera* bears some resemblance to *Psolidomyrmex*, *Plectroctena*, *Loboponera*, *Boloponera*, and it shares with the latter three genera an apparent fusion of the mesopleuron to the mesonotum (though the mesopleuron in *Dolioponera* is undivided). The shape of the petiolar articulatory surface in *Dolioponera* is dissimilar to that in these four genera, but *Dolioponera* has a laterally opening metapleural gland orifice that is similar to that in members of the *Plectroctena* genus group (B. Bolton, pers. comm.). Given these observations, we consider the most likely phylogenetic placement of *Dolioponera* to be as sister to the *Psolidomyrmex* + *Plectroctena* + *Loboponera* + *Boloponera* clade. Its geographic range (central Africa) is also consistent with this view.

The phylogenetic placement of *Feroponera* is highly uncertain, though Bolton & Fisher (2008c) hypothesized that it may form a clade with *Centromyrmex*, given the shared lack of eyes, presence of tibial traction setae, and relatively high helcium. All of these characters occur elsewhere within Ponerini, however, so we do not consider them strong evidence of monophyly for these genera. Arguing against such a clade are the posteriorly opening metapleural gland orifice in *Feroponera*, which differs from the apparent synapomorphic condition for the *Plectroctena* genus group. In the absence of stronger evidence about its phylogenetic relationships, however, we are tentatively including *Feroponera* within the *Plectroctena* group.

### ***Boloponera* Fisher**

Fig. 34

*Boloponera* Fisher, 2006: 112 (as genus in Ponerini). Type-species: *Boloponera vicans* Fisher, 2006: 113; by original designation.



**FIGURE 34.** Worker caste of *Boloponera vicans*: lateral and dorsal view of body and full-face view of head (CASENT0401737, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Boloponera*.

*Boloponera* is a monotypic genus known from only a single specimen collected in leaf litter in the Central African Republic. Nothing is known about its habits.

**Diagnosis.** *Boloponera* can be most easily diagnosed by the following unique combination of characters: mandibles linear, frontal lobes hypertrophied, eyes absent, head without posteroventral lamellae, propodeum with posterior lamellae, metafemora with longitudinal groove, mesotibiae and meso-/metabasitarsi without stout traction setae, relatively high helcium, and tergite A4 not arched. It bears significant similarity to *Loboponera*, *Plectroctena*, and *Feroponera*, but the characters above serve to differentiate it from all of these genera. *Boloponera* differs from *Loboponera* in having linear mandibles, loss of eyes, no posteroventral lamellae on the head, and a tubular tergite A4. It differs from *Plectroctena* in lacking a dorsal longitudinal groove on the mandibles, lacking excavations in the clypeus at the mandibular articulations, and lacking eyes. *Boloponera* can be separated from *Feroponera* by its linear mandibles, metafemoral grooves, and absence of traction setae on the middle and hind legs.

**Synoptic description.** *Worker.* Small (TL 3.3 mm) robust ponerine ants with the standard characters of Ponerini. Mandibles linear, with two small teeth and a basal groove. Frontal lobes hypertrophied and projecting beyond the anterior clypeal margin. Antennae with two-segmented club. Eyes absent. Mesopleuron divided by a transverse groove, the anepisternum appearing fused to the mesonotum and metapleuron. Metanotal groove absent. Propodeum broad dorsally, the posterolateral margins drawn out posteriorly into cuticular lamellae. Propodeal spiracles round. Metafemora with dorsal longitudinal groove. Metatibial spur formula (1p). Petiole nodiform, the subpetiolar process a posteriorly-directed tooth. Helcium projecting from near midheight on the anterior surface of A3. Strong constriction between pre- and postsclerites of A4 apparent. Head and body foveate and longitudinally striate, with abundant short pilosity and no pubescence. Color orange.

*Queen.* Unknown.

*Male.* Unknown.

*Larva.* Undescribed.

**Geographic distribution.** *Boloponera* is known from a single specimen collected in the Central African Republic (Fisher, 2006).

**Ecology and behavior.** Nothing is known about the habits of *Boloponera*. The single known specimen was collected from leaf litter (Fisher, 2006), and in combination with its morphological characteristics (*e.g.*, lack of eyes) suggests that it is cryptobiotic. The identity of its prey is unknown but its linear mandibles are suggestive of prey specialization.

**Phylogenetic and taxonomic considerations.** *Boloponera* was described by Fisher (2006) as a distinct genus based on the absence of autapomorphies of members of the *Plectroctena* genus group (*sensu* Bolton & Brown, 2002). He noted similarities between *Boloponera* and *Plectroctena*, including linear mandibles, hypertrophied anteriorly-projecting frontal lobes, propodeal lamellae, and metafemoral grooves. The latter three characters also occur in *Loboponera*. Despite these clear similarities, and the overwhelming similarity of their overall gestalt, Fisher insisted that *Boloponera* was not a member of the *Plectroctena* genus group (*Plectroctena* + *Loboponera* + *Psalidomyrmex*) based on the structure of its anteroventral petiolar articulation. We respectfully disagree with this assessment, and believe that *Boloponera* is in fact sister to *Plectroctena*, *Loboponera*, or to these two genera together. See the previous discussion of generic relationships within the *Plectroctena* group for more on the possible phylogenetic positions of *Boloponera*.

### Species of *Boloponera*

*B. vicans* Fisher, 2006: Central African Republic

### *Centromyrmex* Mayr

Fig. 35

*Centromyrmex* Mayr, 1866: 894 (as genus in Poneridae). Type-species: *Centromyrmex bohemani* Mayr, 1866: 895 (junior synonym of *Centromyrmex brachycola* (Roger, 1861)); by monotypy.

*Spalacomyrmex* Emery, 1889: 489 (as genus). Type-species: *Spalacomyrmex feae* Emery, 1889: 491; by monotypy. Emery, 1890: 40 (*Spalacomyrmex* as junior synonym of *Centromyrmex*).



*Glyphopone* Forel, 1913b: 308 (as genus). Type-species: *Glyphopone bequaerti* Forel, 1913b: 308; by monotypy. Brown, 1963: 9 (*Glyphopone* as junior synonym of *Centromyrmex*).

*Leptopone* Arnold, 1916: 163 (as subgenus of *Glyphopone*, in Ponerinae, Ponerini). Type-species: *Glyphopone (Leptopone) rufigaster* Arnold, 1916: 163 (junior synonym of *Centromyrmex bequaerti* Forel, 1913); by original designation. Brown, 1963: 9 (*Leptopone* as junior synonym of *Centromyrmex*).

*Typhloteras* Karavaiev, 1925: 128 (as genus). Type-species: *Typhloteras hamulatum* Karavaiev, 1925: 129; by monotypy. Brown, 1953a: 8 (*Typhloteras* as junior synonym of *Centromyrmex*).

*Centromyrmex* is a moderately sized genus (15 described species) distributed in the Neotropics, Afrotropics, and Asian tropics. They are superbly adapted to life underground and are specialist termite predators.

**Diagnosis.** Despite significant morphological heterogeneity within the genus, *Centromyrmex* workers are readily diagnosed by their relatively smooth cuticle, lack of eyes, strongly flattened scapes, obsolete metanotal grooves, laterally-opening metapleural gland orifices situated just below the propodeal spiracle, relatively high helcium (located near the midheight of the first gastral segment), and spiniform setae on mesotibiae and meso-/metabasitarsi. Of these characters, only the location of the metapleural gland orifice is truly autapomorphic for *Centromyrmex*. *Centromyrmex* bears some morphological resemblance to *Promyopias*, *Feroponera*, *Buniapone*, and *Cryptopone*, all of which are also adapted to a cryptic lifestyle. In addition to differences in the locations of their metapleural gland orifices, these genera are easily differentiated from *Centromyrmex* as follows. *Promyopias* has linear mandibles and a blunt medial clypeal projection. *Feroponera* has a pair of teeth projecting from the anterior clypeal margin, closely approximated frontal lobes which overhang the anterior clypeal margin, and strongly clubbed antennae. *Buniapone* has vestigial eyes, a blunt medial clypeal projection, a complex metapleural gland orifice, a squamiform petiole, and lacks spiniform setae on the mesotibiae and meso-/metabasitarsi. *Cryptopone* lacks the smooth and relatively hairless cuticle of *Centromyrmex* and spiniform setae on the meso- and metabasitarsi (though they are present on the mesotibiae), has basal mandibular pits (in most species), small closely approximated frontal lobes, eyes, a distinct metanotal groove, and a narrowed propodeal dorsum.

**Synoptic description.** *Worker.* Small to large (TL 3.5–13 mm) robust ants with the standard characters of Ponerini. Usually monomorphic, but polymorphic in the *C. bequaerti* species group. Mandibles triangular to subtriangular with variable dentition and a faint basal groove. Frontal lobes moderately large. Scapes strongly flattened basally and with a sharp anterior edge. Eyes absent. Pronotum usually with rounded lateral margins, but with sharp lateral margins in the *C. feae* species group. Mesopleuron sometimes divided by a transverse groove. Metanotal groove almost always obsolete. Mesosomal profile usually continuous but with a distinct depression in the propodeum in the *C. feae* species group. Propodeal spiracles slit-shaped or ovoid. Metapleural gland orifice opening laterally just below the propodeal spiracle. Mesotibiae and meso-/metabasitarsi armed with stout traction setae. Metatibial spur formula (1p) or (1s, 1p). Petiole nodiform, becoming wider dorsally and posteriorly. Helcium projecting from near midheight of anterior face of A3. Gaster with a weak to strong constriction between pre- and postsclerites of A4. Head and body shining, sometimes sparsely punctate, with sparse to scattered pilosity and no pubescence. Color testaceous to ferrugineous. See Bolton & Fisher (2008c) for a detailed description of *Centromyrmex* structure.

*Queen.* Similar to worker but winged and with compound eyes and ocelli (Bolton & Fisher, 2008c); generally only slightly larger than conspecific workers, but much larger in *C. bequaerti* (Déjean & Fénéron, 1996; Bolton & Fisher, 2008c).

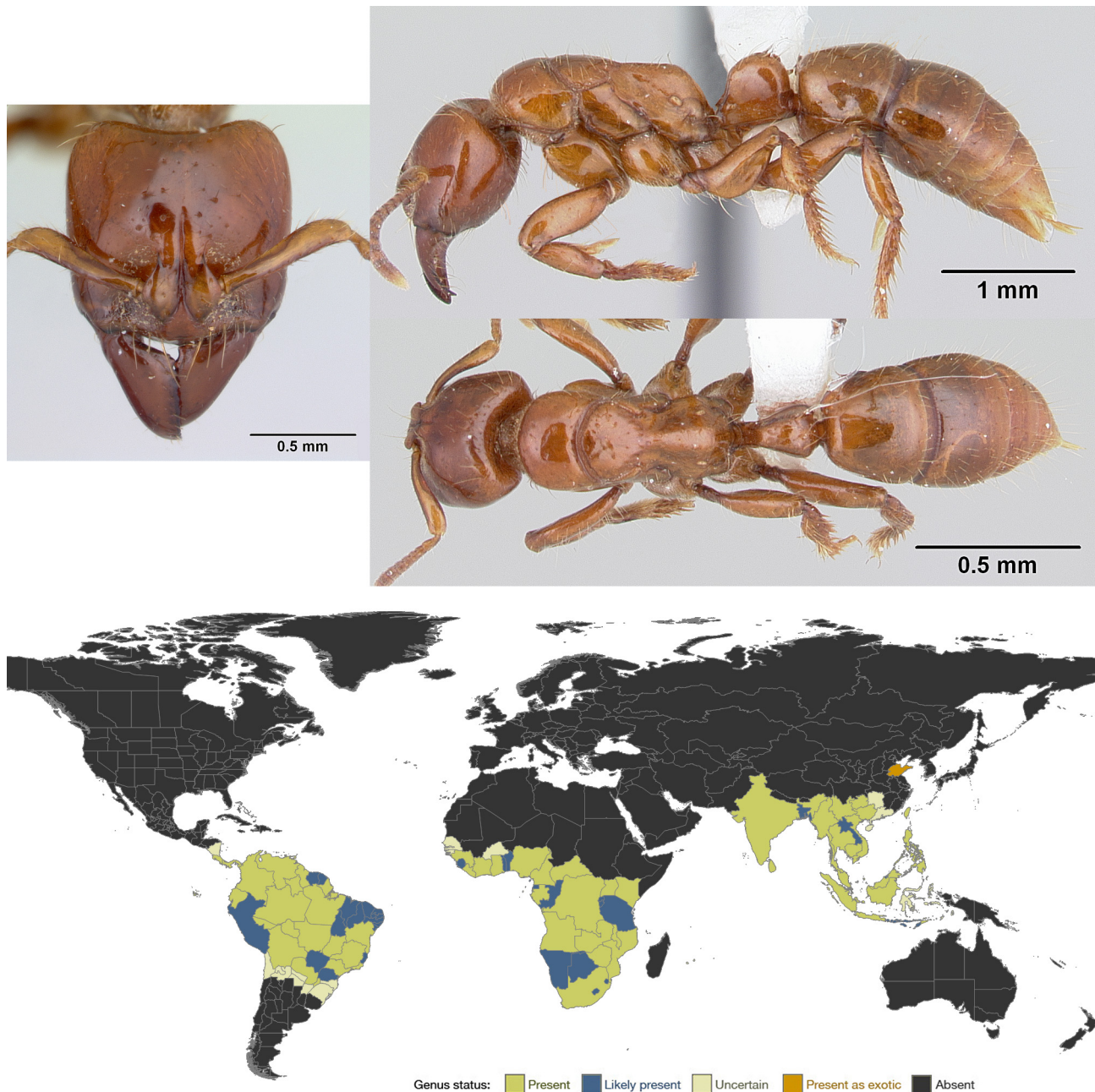
*Male.* See description in Bolton & Fisher (2008c).

*Larva.* Described for two species by Wheeler & Wheeler (1952, 1976).

**Geographic distribution.** *Centromyrmex* is widespread in the tropics except the Malagasy and Australasian regions. Three species are known from the Neotropics (all in the *C. brachycola* species group), and two species in the *C. feae* and *C. hamulatus* species groups occur in the Asian tropics. There are almost certainly undescribed species from these regions (Bolton & Fisher, 2008c). The Afrotropical fauna was recently revised (Bolton & Fisher, 2008c) and consists of 10 known species in the *C. bequaerti* and *C. feae* groups.

**Ecology and behavior.** Very little is known about the ecology and behavior of *Centromyrmex*, with virtually all information on the genus stemming from anecdotal observations, with the exception of *C. bequaerti* (see below). *Centromyrmex* are clearly well adapted to a hypogeic and fossorial lifestyle (confirmed by direct field observations), as their relatively smooth cuticles, low pigmentation, lack of eyes, flattened scapes, and short thick legs with traction setae are all features commonly found in other hypogeic or fossorial ants. Workers are found in

termitaries, upper soil layers, beneath leaf litter, or in rotten logs (Weber, 1949; Bolton & Fisher, 2008c). Nesting sites are usually in close proximity to termitaries or even inside the termitaries themselves (e.g., *C. alfaroi*: Delabie, 1995; *C. bequaerti*: Déjean *et al.*, 1996, 1997; Déjean & Fénéron, 1999; *C. brachycola*: Mann, 1934; *C. feae*: Wheeler, 1936; *C. gigas*: Luederwaldt, 1926; Delabie, 1995; *C. sellaris*: Lévieux, 1976, 1983; Déjean & Fénéron, 1996; Déjean *et al.*, 1996, 1997; but see Arnold, 1915). All *Centromyrmex* species for which there are ecological data appear to be obligate termite specialists (Luederwaldt, 1926; Mann, 1934; Wheeler, 1936; Lévieux, 1983; Delabie, 1995; Déjean & Fénéron, 1996, 1999; Bolton & Fisher, 2008c). Some *Centromyrmex* species are known to prey on a wide range of termite species; other species may be even more specialized.



**FIGURE 35.** Worker caste of *Centromyrmex brachycola*: lateral and dorsal view of body and full-face view of head (CASENT0178344, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Centromyrmex*.

The details of *Centromyrmex* social organization and foraging behavior are generally unstudied except for two African species representing distinct species groups: *C. sellaris*, whose nest architecture was studied by Lévieux (1976); and *C. bequaerti*, whose social organization and foraging behavior were examined by Déjean & Fénéron (1996, 1999). Nests of *C. sellaris* consist of 10 or more small chambers distributed in the soil across an area of

about 8 m<sup>2</sup> and connected to each other by narrow tunnels (Lévieux, 1976). The single colony examined had over 400 workers and a single queen. Workers apparently always travel in the soil when foraging and can range up to 20 m from the nest. *C. sellaris* is known to prey on termites, but no additional details of its foraging behavior are known.

*C. bequaerti* exhibits a rather different suite of behaviors, which are unusual among ponerines but similar to those displayed by some termitolestic myrmicines (Déjean & Féneron, 1996, 1999). This species nests inside the termitaries of a wide range of termite species and preys exclusively on its hosts. Colonies are polygynous and relatively large, with up to 13 queens and several hundred workers, and they inhabit multiple cavities within host termitaries. The worker caste displays strong size polymorphism, and queens are substantially larger than even the major workers. The size ratio (4x) of *C. bequaerti* queens and minor workers is the largest known within the Ponerinae. Major workers principally act as guards, while smaller workers perform most of the hunting and basic nest activities, though there is overlap in these tasks. When a *C. bequaerti* scout detects a termite gallery, it attacks and paralyzes several termites, then returns to its nest to recruit a small number of nestmates, which it leads to the termites using chemical trails (Déjean & Féneron, 1999). Workers might also recruit nestmates by tapping their heads on the substrate, though the actual function of this behavior has not been determined. Once they arrive at the termite gallery, the ants attack and paralyze large numbers of termites and stack them into piles before transporting them back to their nest. The response of a *C. bequaerti* worker to a termite depends on the caste of the termite: workers are seized and then stung, while soldiers are stung first, presumably to minimize the risk of a damaging counterattack. Déjean & Féneron (1999) found that the gaster of *C. bequaerti* workers is shaped such that the mandibles of termite soldiers slip off without causing injury.

**Phylogenetic and taxonomic considerations.** *Centromyrmex* was erected by Mayr (1866) to house the single species *C. bohemanni* (now *C. brachycola*). The morphological diversity within the genus (as presently defined) led to the creation of several other genera which were gradually synonymized under *Centromyrmex*: *Spalacomyrmex* (Emery, 1889; synonymy by Emery, 1890), *Glyphopone* (Forel, 1913b; synonymy by Brown, 1963), *Promyopias* (Santschi, 1914; synonymy by Brown, 1973), *Leptopone* (Arnold, 1916; synonymy by Brown, 1963), and *Typhloteras* (Karavaiev, 1925; synonymy by Brown, 1953a).

Bolton & Fisher (2008c), in their recent revision of *Centromyrmex*, revived *Promyopias* as a distinct genus but retained the other synonymies. They arranged the species of *Centromyrmex* into several species groups: the *C. bequaerti* group, which corresponds to *Glyphopone* and *Leptopone*; the *C. feae* group, which corresponds to *Spalacomyrmex*; the *C. hamulatus* group, which corresponds to *Typhloteras*; and the *C. brachycola* group, which is poorly defined morphologically and may not be monophyletic. *C. brachycola* itself is the type species and represents *Centromyrmex* (s.s.). Schmidt's (2013) molecular phylogeny of the Ponerinae includes three *Centromyrmex* species: *C. brachycola*, *C. hamulatus*, and *C. sellaris*. These taxa form a tight clade, confirming the synonymy of *Spalacomyrmex* and *Typhloteras* under *Centromyrmex*. The *C. bequaerti* group is morphologically quite distinctive from the other species groups, but they do have the sole autapomorphy of the genus, the unusual location of the metapleural gland orifice (Bolton & Fisher, 2008c). In the absence of any contradictory molecular evidence, it therefore seems prudent to retain *Glyphopone* and *Leptopone* as junior synonyms of *Centromyrmex*.

Emery (1911) placed *Centromyrmex* in its own subtribe within Ponerini, Centromyrmecini. Brown (1953a; also Bolton, 2003) synonymized Centromyrmecini under Ponerini, but Bernard (1953) considered it worthy of full tribal status. Schmidt's (2013) molecular phylogeny of the Ponerinae clearly places *Centromyrmex* within Ponerini, and among the taxa included in the phylogeny *Centromyrmex* is resolved as sister to *Psalidomyrmex* + *Loboponera* + *Plectroctena*. The actual sister group of *Centromyrmex* may be *Feraponera*, though molecular data for these taxa are currently lacking, and some morphological evidence argues against this relationship. See the previous discussion of phylogenetic relationships within the *Plectroctena* group for more on the possible sister of *Centromyrmex*.

### Species of *Centromyrmex*

Bolton & Fisher (2008c) provide lists of synonyms, subspecies, and keys to world species groups and Afrotropical species. Kempf (1967) provides a key to Neotropical species.

*C. alfaroi* Emery, 1890: Costa Rica

*C. angolensis* Santschi, 1937: Angola



*C. bequaerti* (Forel, 1913): DRC  
*C. brachycola* (Roger, 1861): Brazil  
*C. decessor* Bolton & Fisher, 2008c: Gabon  
*C. ereptor* Bolton & Fisher, 2008c: Central African Rep.  
*C. feae* (Emery, 1889): Myanmar  
*C. feae ceylonicus* Forel, 1900: Sri Lanka  
*C. feae greeni* Forel, 1901: Singapore  
*C. fugator* Bolton & Fisher, 2008c: DRC  
*C. gigas* Forel, 1911: Brazil  
*C. hamulatus* (Karavaiev, 1925): Indonesia (Sumatra)  
*C. longiventris* Santschi, 1919: Cameroon  
*C. praedator* Bolton & Fisher, 2008c: DRC  
*C. raptor* Bolton & Fisher, 2008c: Zambia  
*C. secutor* Bolton & Fisher, 2008c: Gabon  
*C. sellaris* Mayr, 1896: Cameroon

### ***Dolioponera* Brown**

Fig. 36

*Dolioponera* Brown, 1974a: 31 (as genus in Ponerinae, Ponerini). Type-species: *Dolioponera fustigera* Brown, 1974b: 32; by original designation.

*Dolioponera* is a monotypic genus known from only a few specimens collected in west and central Africa. They are apparently cryptobiotic, but nothing else is known about their habits.

**Diagnosis.** *Dolioponera* are among the most morphologically distinctive of all ponerines. Their long sinuous bodies are unmistakable, and their unusual setose mandibular teeth are also autapomorphic. Other diagnostic characters (in combination) include their blunt anteromedial clypeal projection, laterally expanded triangular frontal lobes, tiny or absent eyes, clubbed antennae, fusion of mesopleuron with the mesonotum, and relatively high helcium.

**Synoptic description.** *Worker.* Very small (TL 2.2–2.8 mm) and very slender ants with the standard characters of Ponerini. Mandibles triangular, with a rounded basal angle, a basal groove, and a series of unusual teeth on the inner surface which appear to be modified setae. Anterior margin of clypeus with a short blunt medial projection. Frontal lobes moderately expanded laterally, with broadly triangular lateral margins. Apical antennal segment enlarged. Eyes absent to very small. Mesopleuron apparently fused to the mesonotum. Metanotal groove absent. Propodeum broad dorsally. Propodeal spiracle round. Metatibial spur formula (1p). Petiole nodiform, the node long and cylindrical. Helcium projecting from near midheight on the anterior surface of A3. Gaster with a strong girdling constriction between pre- and postsclerites of A4. A4 long and cylindrical. Head and body densely punctate, with only sparse pilosity but a dense pubescence. Color orange.

*Queen.* Similar to worker except eyes present and conspicuous, moderately large and well in front of midlength of head capsule (maximum length of eye about equal to maximum width of scape; much larger than in the specimens reported by Fisher (2006)); large ocelli present. Mesosoma considerably more voluminous than in worker, and with a full complement of flight sclerites.

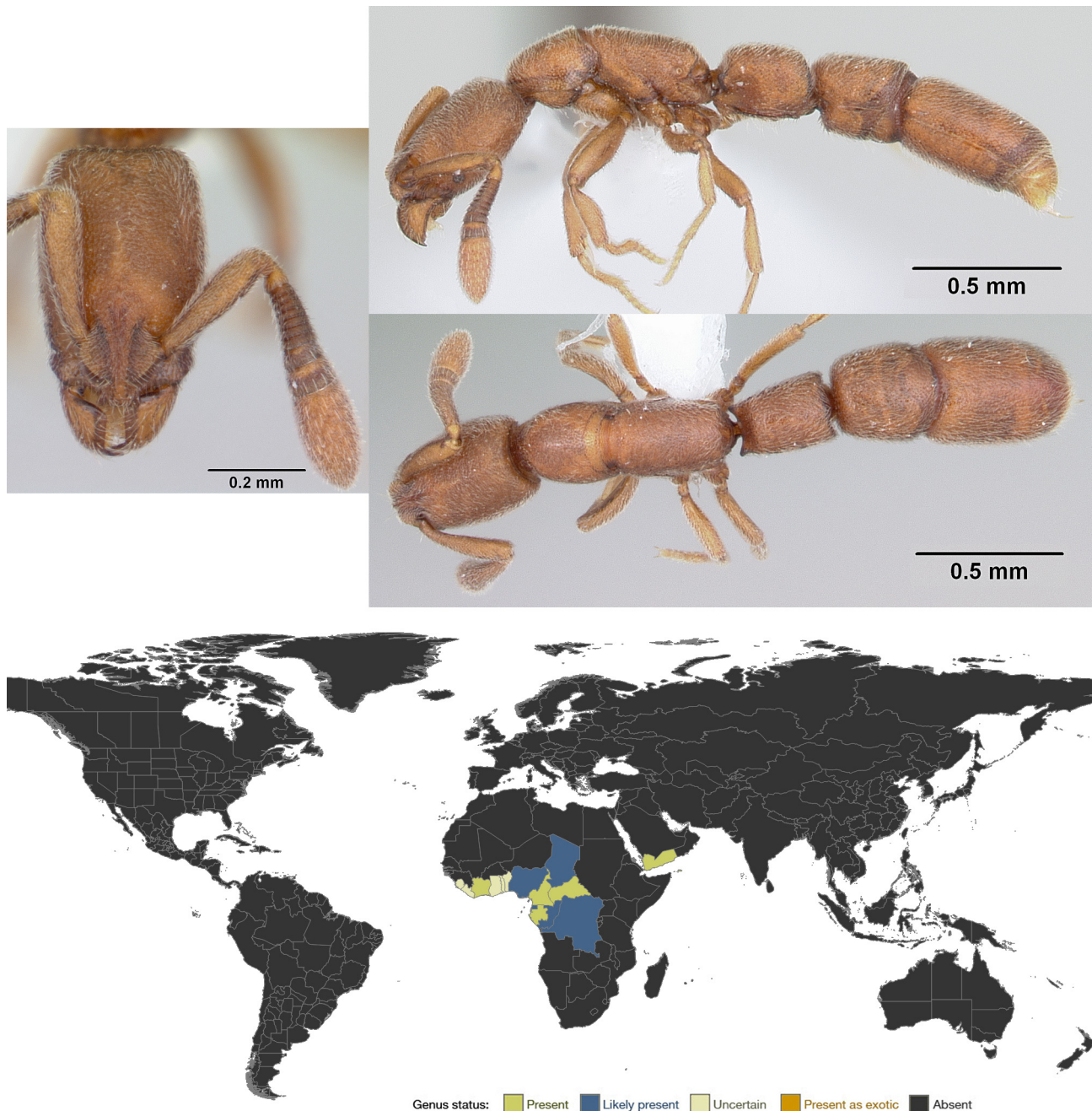
*Male.* Unknown.

*Larva.* Undescribed.

**Geographic distribution.** *Dolioponera* is known from only a few collections in Cameroon, Central African Republic and Gabon (Fisher, 2006), Ivory Coast (B. Bolton, pers. comm.) and from a single record from Yemen (Collingwood & van Harten, 2005). The true extent of its range is uncertain.

**Ecology and behavior.** Virtually nothing is known about the habits of *Dolioponera*. All known specimens were collected from soil or leaf litter, and their morphological characteristics strongly suggest a cryptobiotic lifestyle. Their tiny body size and unusual sinuous body form suggest that they inhabit and forage in very tight spaces, and their strange mandibular dentition and medial clypeal projection suggest that they are specialist predators, though the identity of their prey is unknown.

**Phylogenetic and taxonomic considerations.** Brown (1974a) described *Dolioponera* based on a single specimen from Gabon, and since then a few additional specimens have been collected (Fisher, 2006). The phylogenetic position of *Dolioponera* is unclear, as molecular data are lacking and morphological evidence is ambiguous. Bolton & Brown (2002), Fisher (2006), and Bolton & Fisher (2008c) suggest the possibility of a close relationship between *Dolioponera* and the *Plectroctena* genus group (*sensu* Bolton & Brown, 2002). We agree that this is the most probable phylogenetic placement for *Dolioponera*, and have therefore included *Dolioponera* within the *Plectroctena* group. See the earlier discussion of phylogenetic relationships within the *Plectroctena* group for more on the possible phylogenetic position of *Dolioponera*.



**FIGURE 36.** Worker caste of *Dolioponera fustigera*: lateral and dorsal view of body and full-face view of head (CASENT0411307, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Dolioponera*.

## Species of *Dolioponera*

*D. fustigera* Brown, 1974: Gabon

## *Feroponera* Bolton & Fisher

Fig. 37

*Feroponera* Bolton & Fisher, 2008c: 26 (as genus in Ponerini). Type-species: *Feroponera ferox* Bolton & Fisher, 2008c: 28; by monotypy.

*Feroponera* is a monotypic genus known only from Cameroon. It is apparently hypogeic and may be a termite specialist.

**Diagnosis.** Workers of *Feroponera* can be readily identified by their clypeal teeth, anteriorly-located and closely approximated frontal lobes, eyeless condition, clubbed antennae, and spiniform traction setae on the mesotibiae and meso-/metabasitarsi. *Feroponera* is most likely to be confused with *Centromyrmex*, *Boloponera*, and *Loboponera*. *Centromyrmex* has a uniquely located metapleural gland orifice, and while *Loboponera* does have a pair of clypeal teeth, both *Boloponera* and *Loboponera* lack traction setae on the legs, among other differences. Similar paired clypeal teeth also occur in *Dinoponera* and *Streblognathus*, but these genera are otherwise very different from *Feroponera* and are unlikely to be confused with it.

**Synoptic description.** *Worker.* Small (TL 3.5–3.8 mm) ants with the standard characters of Ponerini. Mandibles subtriangular, with five teeth and a basal groove. Anterior margin of clypeus with a pair of short projecting teeth. Frontal lobes closely approximated, of moderate size, and barely projecting past the anterior clypeal margin. Antennae terminating in a four-segmented club. Eyes absent. Pronotum anteriorly with moderately sharp lateral margins. Metanotal groove absent. Propodeum moderately narrowed dorsally. Propodeal spiracles ovoid. Mesotibiae and meso-/metabasitarsi armed with stout traction setae. Metatibial spur formula (1s, 1p). Petiole nodiform, becoming wider posteriorly. Helcium projects from near midheight on the anterior surface of A3. Gaster with a distinct girdling constriction between A3 and A4. Head and body with moderate generally rugulose sculpturing, sparse pilosity, and moderately dense pubescence. Color dark orange. See Bolton & Fisher (2008c) for a more detailed description of worker structure, including a description of some additional autapomorphies of the genus.

*Queen.* Unknown.

*Male.* Unknown.

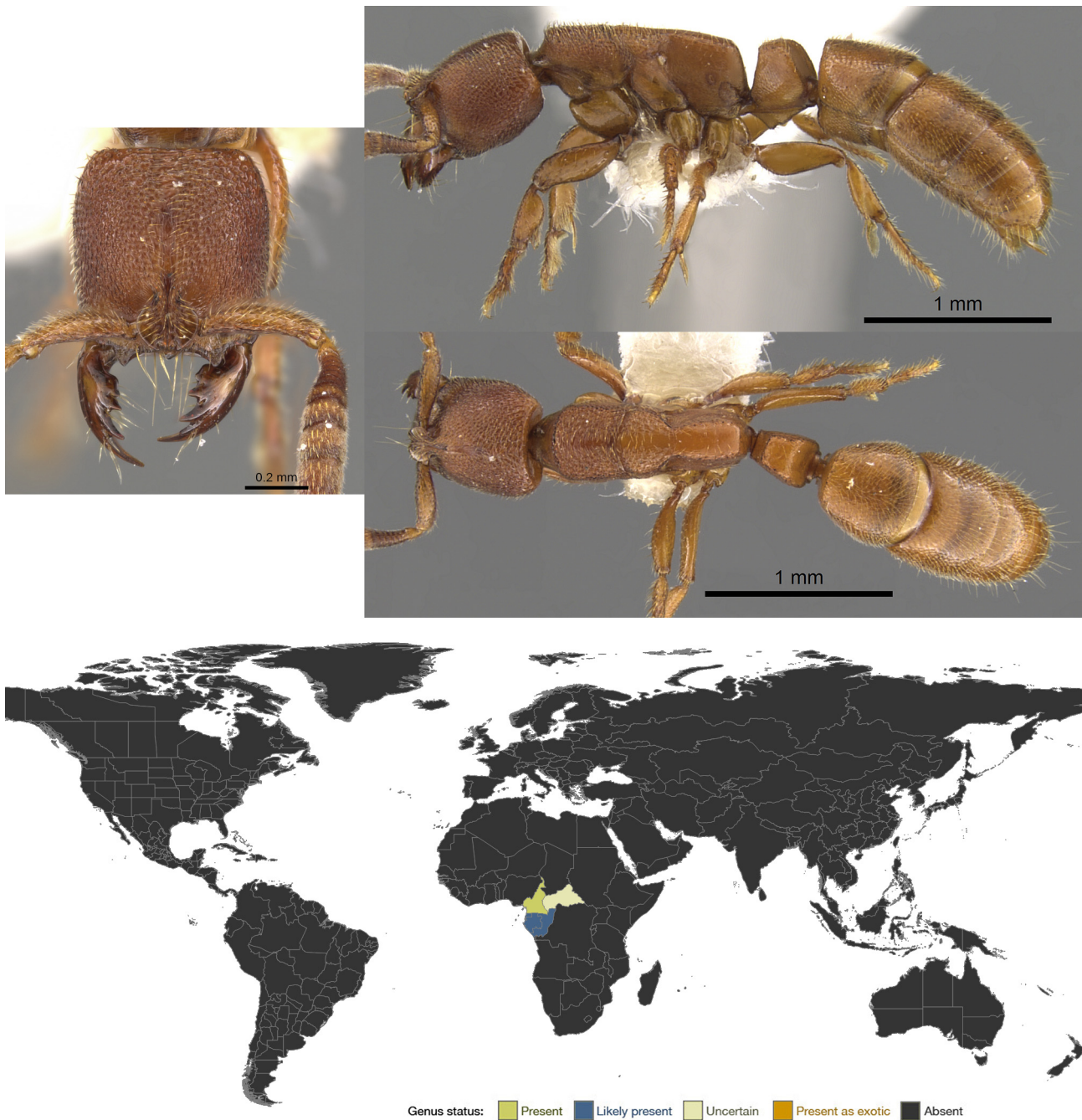
*Larva.* Not described.

**Geographic distribution.** *Feroponera* is known only from the type series collected in Cameroon (Bolton & Fisher, 2008c).

**Ecology and behavior.** Nothing is known about the habits of *Feroponera*, though based on its morphological structure it is undoubtedly hypogeic. The type series was collected from an abandoned termitary, suggesting that they may be termite specialists like *Centromyrmex*, though this has not actually been observed (Déjean *et al.*, 1996; Bolton & Fisher, 2008c).

**Phylogenetic and taxonomic considerations.** Bolton & Fisher (2008c) described the monotypic genus *Feroponera* based on a single series of workers of a new species, *F. ferox*. They noted several autapomorphies to justify their new genus: a pale patch of cuticle and unique dentition of the mandibles, a pair of teeth on the anterior clypeal margin, clubbed antennae, and an apparently glandular surface on the metatibiae. They noted several similarities between *Feroponera*, *Centromyrmex* and *Promyopias*, namely the lack of eyes in the workers, the presence of traction setae on the legs, and the relatively high helcium. These shared characters may represent synapomorphies for these genera (as suggested by Bolton & Fisher (2008c)), they could be convergently evolved, or they could represent plesiomorphies within the *Plectroctena* group. However, *Promyopias* has recently been found to belong to the *Odontomachus* group rather than the *Plectroctena* group (P.S. Ward, pers. comm.). We think it likely that *Feroponera* is either sister to *Centromyrmex* or to the remainder of the *Plectroctena* genus group. See the previous discussion of generic relationships within the *Plectroctena* group for more on the possible phylogenetic position of *Feroponera*.





**FIGURE 37.** Worker caste of *Feroponera ferox*: lateral and dorsal view of body and full-face view of head (holotype, CASENT0900369, Will Ericson and [www.antweb.org](http://www.antweb.org)); world distribution of *Feroponera*.

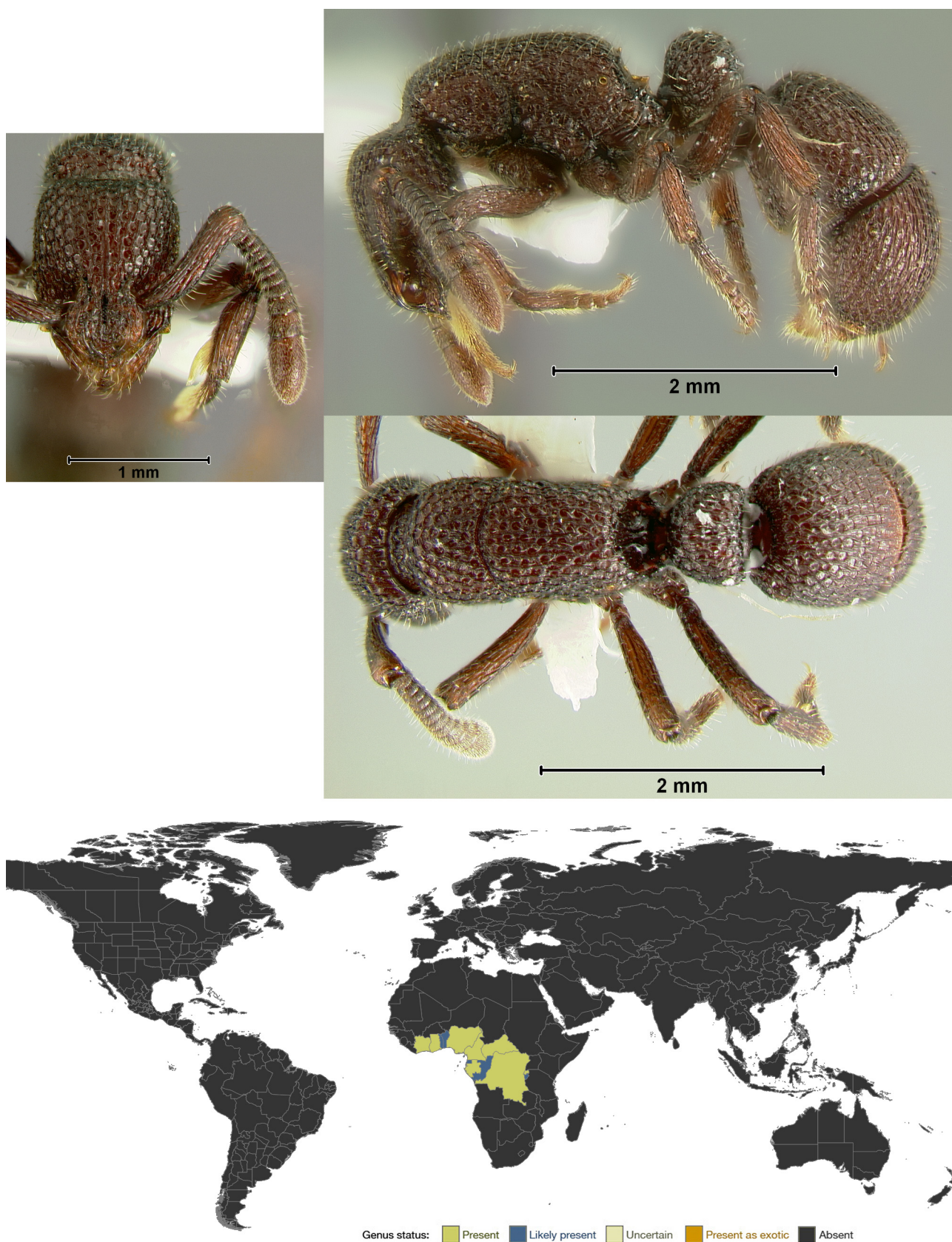
### Species of *Feroponera*

*F. ferox* Bolton & Fisher, 2008c: Cameroon

### *Loboponera* Bolton & Brown

Fig. 38

*Loboponera* Bolton & Brown, 2002: 3 (as genus in Ponerini). Type-species: *Loboponera vigilans* Bolton & Brown, 2002: 7; by original designation.



**FIGURE 38.** Worker caste of *Loboponera basalis*: lateral and dorsal view of body and full-face view of head (Ivory Coast, G.Alpert, MCZC); world distribution of *Loboponera*.



*Loboponera* is a small (nine described species) Afrotropical genus. They are cryptic nesters and foragers, but nothing else is known about their habits.

**Diagnosis.** *Loboponera* workers are readily identified by their huge frontal lobes, cuticular flanges at the posteroventral corners of the head, obsolete metanotal groove, broad propodeum, dorsal longitudinal grooves on the meso- and metafemora, and strongly arched tergite A4. *Loboponera* is most similar to *Plectroctena*, *Boloponera*, *Psalidomyrmex*, *Feroponera*, and some *Bothroponera*, but none of these other genera have posteroventral flanges on the head or a strongly vaulted gaster. *Plectroctena* has dorsal grooves on its meso- and metafemora, and *Boloponera* also has grooves on its metafemora (this is undoubtedly a synapomorphy of these three genera), but these genera both have linear mandibles, in contrast to *Loboponera*'s more triangular mandibles. *Bothroponera* has two metatibial spurs, among many other differences. *Feroponera* and *Loboponera* both have a pair of teeth on the anterior clypeal margin, but *Feroponera* has stout traction setae on its mesotibiae and meso-/metabasitarsi, and lacks eyes.

**Synoptic description.** *Worker.* Small to medium (TL 3.0–7.5 mm) robust ants with the standard characters of Ponerini. Mandibles triangular to subtriangular, with a basal groove. Anterior margin of clypeus with a blunt medial projection and laterally with a tooth projecting over each mandibular articulation. Frontal lobes greatly expanded laterally and closely approximated. Antennae moderately clubbed apically. Eyes very small, located far anterior of head midline. Posteroventral corners of head with cuticular flanges. Mesopleuron divided by a transverse groove, the anepisternum often appearing fused to the mesonotum and metapleuron. Metanotal groove absent. Propodeum broad dorsally, the posterolateral margins often forming lamellae. Propodeal spiracles round. Metapleural gland orifice opening laterally. Meso- and metafemora with a dorsal longitudinal groove. Metatibial spur formula (1p). Petiole nodiform. Anteroventral articulatory surface of petiole long and broad, with a narrow median groove. Strong girdling constriction present between pre- and postsclerite of A4. Tergite of A4 strongly vaulted and down-curved posteriorly. Head and body shining, foveolate to punctate, sometimes with some longitudinal striations on the sides of the mesosoma, and generally with sparse pilosity and pubescence. Color dark red or purple to nearly black.

*Queen.* Similar to workers but slightly larger, winged and with the characters typical of alate ponerine queens (Bolton & Brown, 2002).

*Male.* Unknown.

*Larva.* Undescribed.

**Geographic distribution.** *Loboponera* is restricted to central and western Africa, ranging from Ivory Coast to Rwanda (Bolton & Brown, 2002; Fisher, 2006).

**Ecology and behavior.** Virtually nothing is known about the ecology or behavior of *Loboponera*. Collections of this genus have come from leaf litter and rotting wood (Bolton & Brown, 2002; Fisher, 2006), which when paired with its reduced eyes and downcurved gaster (possibly an adaptation to hunting in tight spaces) strongly implies a cryptic lifestyle. Their generalized mandibular structure gives no clues to the identity of their prey.

**Phylogenetic and taxonomic considerations.** *Loboponera* was erected by Bolton & Brown (2002) to house several newly described species as well as *Pachycondyla* (*Bothroponera*) *nasica* (Santschi). Bolton & Brown linked *Loboponera* to *Plectroctena* and *Psalidomyrmex* based on the shape of the anteroventral articulatory surface of the petiole, and suggested that the presence of longitudinal grooves on the meso- and metafemora was synapomorphic for *Loboponera* and *Plectroctena*. Schmidt's (2013) molecular phylogeny of the Ponerinae confirms the sister relationship between *Loboponera* and *Plectroctena* and likewise their sister relationship to *Psalidomyrmex*, at least among the sampled taxa. We believe that *Boloponera* is probably sister to either *Loboponera* or *Plectroctena*, or to both together, in disagreement with Fisher (2006). See the earlier discussion of phylogenetic relationships within the *Plectroctena* group for more on this.

### Species of *Loboponera*

Bolton & Brown (2002) provide a key to *Loboponera* species (not including *L. nobiliae*).

*L. basalis* Bolton & Brown, 2002: Ivory Coast

*L. edentula* Bolton & Brown, 2002: Rwanda

*L. nasica* (Santschi, 1920): Gabon

*L. nobiliae* Fisher, 2006: Gabon



*L. obeliscata* Bolton & Brown, 2002: Ghana  
*L. politula* Bolton & Brown, 2002: Nigeria  
*L. subatra* Bolton & Brown, 2002: Cameroon  
*L. trica* Bolton & Brown, 2002: Ivory Coast  
*L. vigilans* Bolton & Brown, 2002: Ivory Coast

### ***Plectroctena* Smith**

Fig. 39

*Plectroctena* Smith, F., 1858: 101 (as genus in Poneridae). Type-species: *Plectroctena mandibularis* Smith, F., 1858: 101; by monotypy.

*Cacopone* Santschi, 1914: 325 (as genus). Type-species: *Cacopone hastifer* Santschi, 1914: 325; by monotypy. Bolton, 1974: 313 (*Cacopone* as junior synonym of *Plectroctena*).

*Plectroctena* is a medium sized genus (16 described species) widespread in Sub-Saharan Africa. They are cryptobiotic predators of millipedes, millipede eggs and termites.

**Diagnosis.** *Plectroctena* can be readily identified by its linear mandibles, which have dorsal longitudinal grooves, and by the anteromedial and lateral excavations of its clypeus, all of which are autapomorphic within the Ponerinae. *Plectroctena* is most similar to *Loboponera*, *Boloponera*, and *Promyopias*, which all have expanded frontal lobes and an overall similar gestalt. *Plectroctena* differs from *Loboponera* most obviously in the shape of the mandibles (triangular in *Loboponera*). *Boloponera* and *Promyopias* both have linear mandibles, but they both lack the autapomorphies of *Plectroctena* given above, among several other differences. *Plectroctena* also bears some resemblance to *Myopias*, given their linear mandibles, but *Plectroctena* lacks an anteromedial projection of the clypeus and has only a single metatibial spur.

**Synoptic description.** *Worker.* Medium to very large (TL 5.6–23.5 mm; Bolton, 1974) ants with the standard characters of Ponerini. Mandibles linear, crossing each other apically when closed, edentate or with one or two teeth, and with a dorsal longitudinal groove and a basal groove. Clypeus excavated anteromedially and with a lateral excavation near each mandibular articulation. Frontal lobes greatly expanded, closely approximated, and overhanging the anterior clypeal margin. Eyes small to absent, located far anterior on the sides of the head. Mesopleuron divided by a transverse groove, the anepisternum apparently fused to the mesonotum and metapleuron. Metanotal groove usually absent, occasionally vestigial. Propodeum broad dorsally, the posterolateral margins expanded into lamellae. Propodeal dorsum rarely with a weak longitudinal groove. Propodeal spiracles round. Metapleural gland orifice opening laterally. Meso- and metafemora with a dorsal longitudinal groove. Metatibial spur formula (1p). Anteroventral articulatory surface of petiole long and broad, with a narrow median groove. Petiole nodiform. Gaster with a strong constriction between pre- and postsclerites of A4. Head and body shining, punctate, with striations on the sides of the mesosoma, minimal pilosity, and no pubescence. Color red to black.

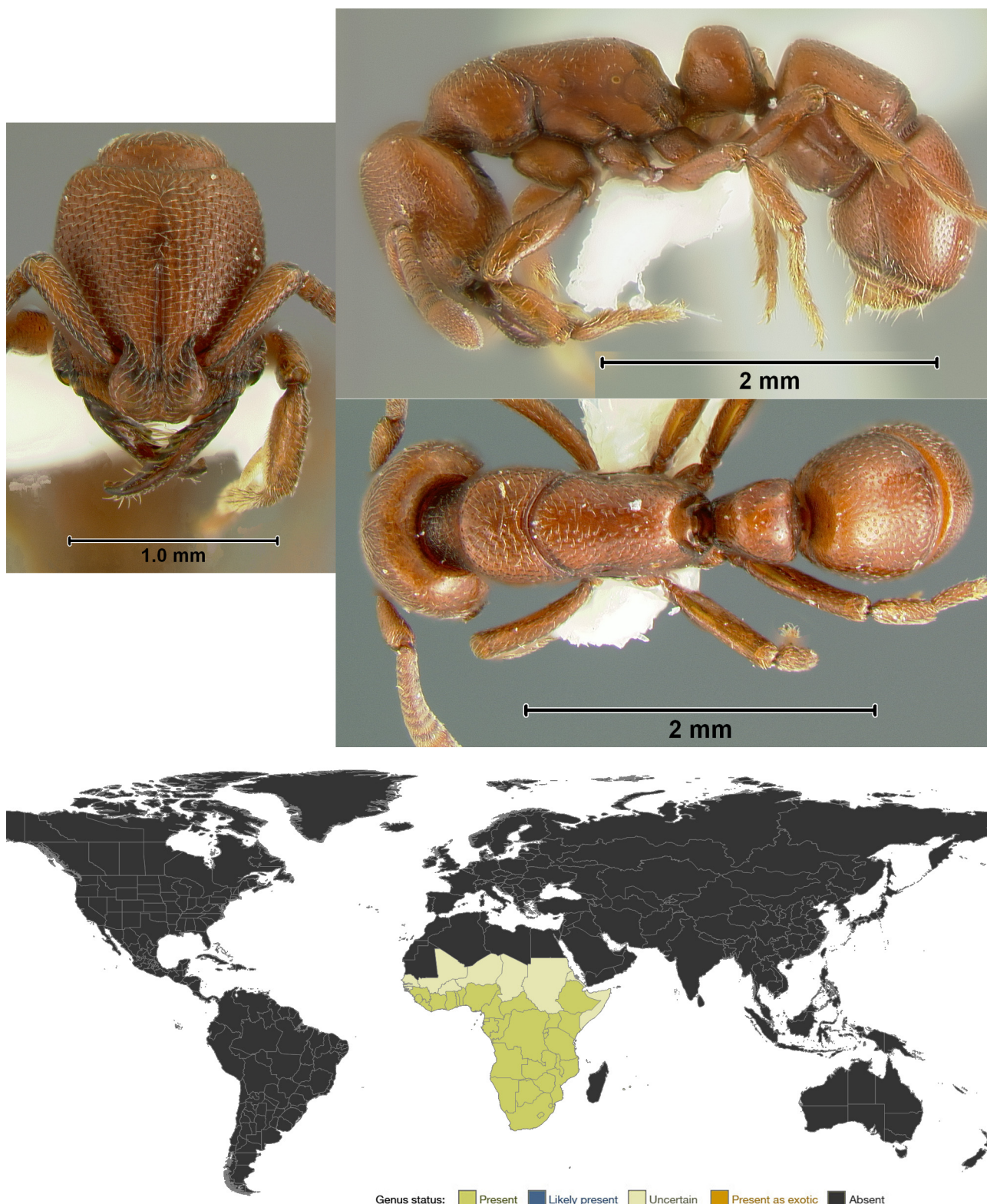
*Queen.* Usually alate, but ergatoid in some species. Alate queens are similar to workers but slightly larger, with larger eyes and with ocelli. Ergatoids are similar but at most have only vestigial ocelli (Bolton, 1974; Bolton & Brown, 2002).

*Male.* See description in Bolton (1974); also discussed in Bolton & Brown (2002).

*Larva.* Described for *P. mandibularis* by Wheeler & Wheeler (1989).

**Geographic distribution.** *Plectroctena* ranges throughout most of Sub-Saharan Africa, from Sierra Leone to Ethiopia and south to South Africa (Bolton & Brown, 2002).

**Ecology and behavior.** More is known about the habits of *Plectroctena* than of any other genus in the *Plectroctena* group, but data on most species are still scarce. Like other members of the group, *Plectroctena* are primarily cryptobiotic, nest in soil or rotting wood, and forage in these same microhabitats as well as among leaf litter (Arnold, 1915; Bolton, 1974; Bolton *et al.*, 1979; Peeters & Crewe, 1988; Bolton & Brown, 2002; Déjean *et al.*, 2002). They have also been found nesting in abandoned termitaries (Déjean *et al.*, 1996). Very little is known about the social and reproductive behavior of *Plectroctena*. Colony sizes are unknown for most species but colonies of *P. lygaria*, *P. mandibularis* and *P. minor* are reported to have about 300 or fewer workers (Bolton *et al.*, 1979; Déjean *et al.*, 2001, 2002; Wilkins *et al.*, 2006).



**FIGURE 39.** Worker caste of *Plectroctena cryptica*: lateral and dorsal view of body and full-face view of head (Ivory Coast, G.Alpert, MCZC); world distribution of *Plectroctena*.

Most *Plectroctena* species have winged queens, but at least four species have ergatoid queens (Bolton, 1974), and at least one of these (*P. mandibularis*) is facultatively polygynous (Wilkins *et al.*, 2006). In laboratory conditions, ergatoid queens of *P. mandibularis* successfully captured prey and were able to rear brood without the assistance of workers, suggesting that colony foundation in this species is semiclastral (Villet, 1991a; confirmed

in natural conditions by Villet, 1999), in contrast to most ants with ergatoid queens. Mating behavior by *P. mandibularis* is also unusual in that virgin females leave the nest and apparently call for males using a pheromone; in most ponerines with ergatoid queens, mating occurs in the natal nest of the queen (Villet, 1999). In *P. mandibularis*, ergatoid queens apparently inhibit reproduction by workers but orphaned workers of *P. mandibularis* will begin laying eggs and can successfully rear male brood (Peeters & Crewe, 1988).

*Plectroctena* are primarily specialist predators of millipedes or millipede eggs, but they also prey to a lesser extent on termites and other arthropods, including other ants (Arnold, 1915; Fletcher, 1973; Bolton *et al.*, 1979; Lévieux, 1983; Peeters & Crewe, 1988; Schatz *et al.*, 2001; Bolton & Brown, 2002; Déjean *et al.*, 2002). Workers typically forage individually but may hunt in small groups (Bolton, 1974; Peeters & Crewe, 1988), and sometimes recruit nestmates to help with large prey (see below). Foraging behavior has been extensively studied in *P. minor*, which specializes to a large degree on millipedes. In cafeteria experiments, *P. minor* workers overwhelmingly preferred millipedes, but also accepted centipedes, termites, isopods, grasshoppers, and beetle larvae (Suzzoni *et al.*, 2000; Schatz *et al.*, 2001). Queens foraging shortly after colony foundation, on the other hand, ignored large millipedes and preferred smaller, more easily captured prey such as isopods or termites (Déjean & Suzzoni, 1991; Suzzoni *et al.*, 2000). The presence of millipedes in the diet of a *P. minor* colony is required for it to produce reproductive females and significantly enhances the production of workers, but is not required for production of male brood (Suzzoni *et al.*, 2000).

Déjean & Suzzoni (1991) and Déjean *et al.* (2001) studied the capture of millipedes by *P. minor*. Workers of this species use their linear mandibles, paralyzing sting, and nestmate recruitment to capture and retrieve millipedes of a wide range of sizes, including very large individuals. Workers demonstrate significant flexibility in their foraging behavior, depending on the size and location of their prey. Their mandibles are able to grasp millipedes under 4 mm in diameter, which are stung repeatedly until paralyzed. Larger millipedes pose more of a problem and require creative strategies for capture and retrieval, including use of mandibular snapping (see below) and recruitment of two to five nestmates via use of a chemical trail. Large millipedes are either cut up or collectively transported whole, while smaller prey are retrieved by single workers. Individual *P. minor* foragers are able to retrieve millipedes weighing more than 100 times their own weight, the largest ratio of prey to worker weight known for any ant (Déjean *et al.*, 2001). Like *P. minor*, foragers of *P. mandibularis* recruit nestmates to assist in prey retrieval (Fletcher, 1973), and also lay chemical trails from the pygidial gland for individual orientation and recruitment during nest emigrations (Villet *et al.*, 1984; Wilkins *et al.*, 2006).

*Plectroctena* workers are able to snap their mandibles to stun or kill enemies or prey (Déjean and Suzzoni, 1991; Déjean *et al.* 2001, 2002). This behavior is unique among ponerines but also occurs in the ambyloponine genus *Mystrium* and some termites (Gronenberg *et al.*, 1998). The forceful snapping of the mandibles is used in territorial aggression, defense, and prey capture. In the study of Déjean *et al.* (2002), *P. minor* foragers almost always snapped their mandibles when confronted with termite soldiers (which are potentially dangerous) or large prey, while smaller prey were usually captured without snapping. Déjean *et al.* (2002) suggest that the snapping mechanism is an adaptation to hunting in tight spaces, though it is also an effective weapon against other ants and is readily employed when other ponerines (especially other *Plectroctena*) are encountered in the vicinity of the nest.

**Phylogenetic and taxonomic considerations.** *Plectroctena* was erected by F. Smith (1858) to house the species *P. mandibularis*. Emery (1911) placed it in his new subtribe Plectroctenini along with *Psalidomyrmex* and *Myopias* (and its synonym *Trapeziopelta*), based on similarities in sculpturing, pubescence, and tibial spurs.

*Plectroctena* has a single junior synonym, *Cacopone*, which was erected by Santschi (1914) to hold the single species *C. hastifer* (now *Plectroctena hastifera*). Oddly, Santschi initially stated that *Cacopone* was somehow related to *Myopias* and *Psalidomyrmex*, but did not mention *Plectroctena* despite their obvious similarities. He did make this connection in his revision of *Plectroctena*, however, but continued to separate them based on supposed differences in mandibular and clypeal structure (Santschi, 1924). Bolton (1974) synonymized *Cacopone* under *Plectroctena* after noting mistakes in Santschi's description and the discovery of a new species with mandibles intermediate between the two genera.

Schmidt's (2013) molecular phylogeny of the Ponerinae clearly places *Plectroctena* far from *Myopias*, as predicted by Bolton (1974). Among the taxa sampled in Schmidt's (2013) phylogeny, *Plectroctena* is resolved as sister to *Loboponera*, though it is possible that *Boloponera* is the true sister to *Plectroctena* (see the discussion of relationships within the *Plectroctena* genus group, above).



Bolton (1974) divided *Plectroctena* into three species groups, of which two (the *P. mandibularis* and *P. minor* groups) are included in Schmidt's (2013) phylogeny. The third species group (the *P. hastifera* group) represents *Cacopone*, and though it is not included in the phylogeny, we see no reason to withdraw it from *Plectroctena* and therefore retain it as a junior synonym of that genus.

### Species of *Plectroctena*

Bolton (1974) revised *Plectroctena*, and Bolton & Brown (2002) provided a species key (which lacks *P. thau*, described since).

*P. anops* Bolton, 1974: Ghana  
*P. cristata* Emery, 1899: Cameroon  
*P. cryptica* Bolton, 1974: Ghana  
*P. dentata* Santschi, 1912: Angola  
*P. gestroi* Menozzi, 1922: Principe Island  
*P. hastifera* (Santschi, 1914): Ghana  
*P. laevior* Santschi, 1924: Tanzania  
*P. latinodis* Santschi, 1924: DRC  
*P. lygaria* Bolton, Gotwald & Leroux, 1979: Ivory Coast  
*P. macgeei* Bolton, 1974: Nigeria  
*P. mandibularis* Smith, F., 1858: South Africa  
*P. minor* Emery, 1892: Ivory Coast  
*P. strigosa* Emery, 1899: South Africa  
*P. subterranea* Arnold, 1915: Zimbabwe  
*P. thau* Fisher, 2006: Cameroon  
*P. ugandensis* Menozzi, 1933: Uganda

### *Psalidomyrmex* André

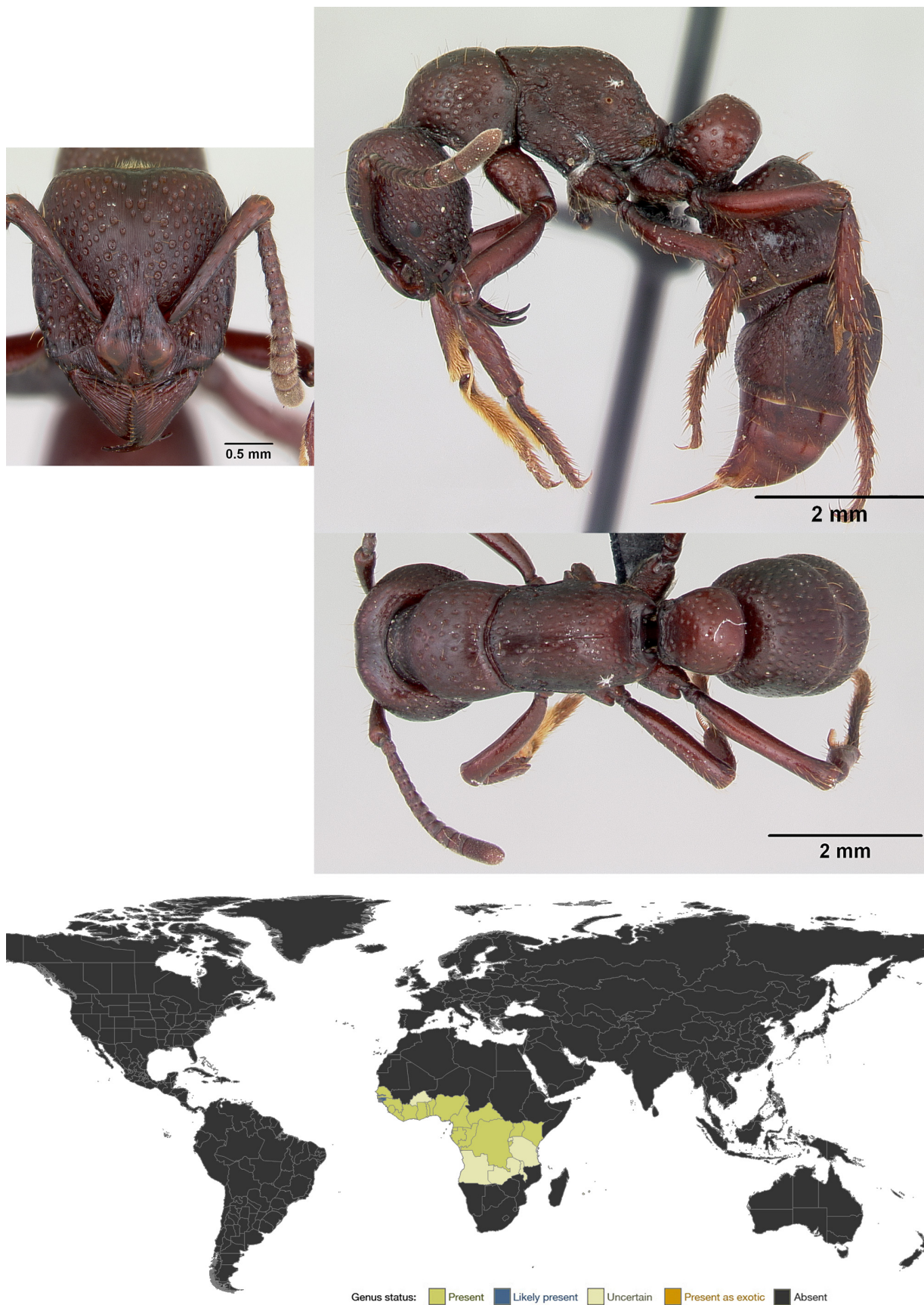
Fig. 40

*Psalidomyrmex* André, 1890: 313 (as genus). Type-species: *Psalidomyrmex foveolatus* André, 1890: 314; by monotypy.

*Psalidomyrmex* is a small genus (six described species) restricted to central and western Africa. They are cryptic foragers, and at least one species is a specialist predator of earthworms.

**Diagnosis.** *Psalidomyrmex* workers and queens are readily identified by their unique mandibular structure (mandibles falcate to subtriangular, with broadly rounded basal angles and an attenuated apical tooth) and by their projecting labral lobe, both of which are autapomorphic within the Ponerinae. Other diagnostic characters include the hypertrophied frontal lobes, longitudinal groove on the propodeal dorsum, and large lateral metapleural gland orifice. *Psalidomyrmex* is most similar to the other members of the *Plectroctena* genus group, including *Loboponera* and *Plectroctena* itself. In addition to lacking the two autapomorphies of *Psalidomyrmex* already mentioned, these genera differ from *Psalidomyrmex* in having longitudinal dorsal grooves in the meso- and metafemora and distinct propodeal lamellae.

**Synoptic description.** *Worker.* Medium to large (TL 9.0–16.0 mm; Bolton, 1975b) ants with the standard characters of Ponerini. Mandibles falcate to subtriangular, with rounded basal angles, a long apical tooth and a basal groove. Labrum projecting anteriorly beyond the anterior clypeal margin as a lobe. Frontal lobes large, expanded laterally and closely approximated. Eyes of moderate size, located anterior to head midline. Metanotal groove vestigial. Propodeum broad dorsally, with a shallow longitudinal groove dorsally. Propodeal spiracles round. Metapleural gland orifice very large, opening laterally. Metatibial spur formula (1p). Petiole nodiform. Anteroventral articulatory surface of petiole long and broad, with a narrow median V-shaped longitudinal groove. Gaster with a strong constriction between A3 and A4. Head and body with moderate sculpturing (variously punctate, foveolate or striate), with very sparse pilosity and no pubescence. Color reddish brown to black.



**FIGURE 40.** Worker caste of *Psalidomyrmex procerus*: lateral and dorsal view of body and full-face view of head (CASENT0003082, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Psalidomyrmex*.

*Queen*. Similar to workers but slightly larger, alate and with ocelli.

*Male*. See description in Bolton (1975b).

*Larva*. Described for *P. procerus* by Wheeler & Wheeler (1964).

**Geographic distribution.** *Psolidomyrmex* is restricted to central and western Africa, ranging from Sierra Leone to Kenya and as far south as Gabon and the Democratic Republic of Congo (Bolton, 1975b; Bolton & Brown, 2002).

**Ecology and behavior.** Very little is known about the ecology and behavior of *Psolidomyrmex*. They nest in rotting logs, in the soil beneath rotting logs (Bolton, 1975b), or in deserted termitaries (Déjean *et al.*, 1996, 1997), and workers forage individually in rotting wood or in leaf litter (Bolton, 1975b). *P. procerus* is known to be a specialist predator of earthworms (Lévieux, 1982; Déjean *et al.*, 1992), and though the feeding habits of the other species is unknown, it seems likely that they too may feed on earthworms, given the apparently specialized mandibular structure of the genus.

**Phylogenetic and taxonomic considerations.** *Psolidomyrmex* was erected by André (1890) to house the single species *P. foveolatus*. Bolton (1975b) revised the genus, and Bolton & Brown (2002) gave an updated diagnosis.

André (1890) apparently believed that *Psolidomyrmex* was closely related to *Belonopelta*, due to supposed similarities in their mandibular structure. However, P.S. Ward (pers. comm.) found that *Belonopelta* belongs to the *Pachycondyla* group while Schmidt (2013) placed *Psolidomyrmex* in the *Plectroctena* group. The only real similarity in the mandibles of these genera is the attenuated apical tooth, which occurs in at least two other ponerine genera (*Emeryopone* and *Thaumatomyrmex*) and this similarity is clearly convergent.

*Psolidomyrmex* has been grouped with *Plectroctena* since Emery (1911) included it in his subtribe Plectroctenini, though this was based on weak evidence. Bolton (1974) argued for a close relationship between these genera based on the structure of the mesosoma, petiole and gaster, a similar reduction in palpal segments, and male morphological characteristics. Bolton & Brown (2002) found additional evidence for a close relationship between *Psolidomyrmex* and *Plectroctena* in the structure of the anterior petiolar articulatory surface (see also Fisher, 2006). Schmidt's (2013) molecular phylogeny of the Ponerinae confirms this close relationship, with *Psolidomyrmex* resolved as sister to *Loboponera* + *Plectroctena*. *Boloponera* is also probably in this sister clade.

### Species of *Psolidomyrmex*

Bolton & Brown (2002) provide a key to *Psolidomyrmex* species (see also Bolton, 1975b).

*P. feae* Menozzi, 1922: Principe Island

*P. foveolatus* André, 1890: Sierra Leone

*P. procerus* Emery, 1901: Cameroon

*P. reichenspergeri* Santschi, 1913: Cameroon

*P. sallyae* Bolton, 1975: Ghana

*P. wheeleri* Santschi, 1923: DRC

### *Ponera* genus group

The phylogeny, distribution and characteristics of the *Ponera* genus group suggest that the bulk of its phylogenetic diversity arose during a burst of diversification into cryptobiotic niches in the Asian and Australian tropics, with several subsequent dispersal events to the New World and elsewhere. The main exception to this pattern is *Diacamma*, which is epigeic.

**Discussion.** The monophyly of the *Ponera* genus group is strongly supported by molecular data (Schmidt, 2013), but morphological synapomorphies have not yet been discovered. Generic relationships within the group are somewhat unresolved, though a sister relationship between *Diacamma* and the remainder of the group is well supported. Relationships among the remaining genera are poorly supported, though *Emeryopone* is suggested as sister to the remainder of the group, with *Cryptopone* sister to *Austroponera* + *Parvaponera* + *Pseudoponera* and *Ponera* sister to *Ectomyrmex*.



Members of the *Ponera* genus group are predominantly small cryptobiotic generalist predators. *Diacamma* and some *Ectomomyrmex* species are fairly large, however, *Diacamma* has large eyes, and *Emeryopone* is apparently a specialist predator. The *Ponera* group has a primarily Asian and Australian distribution, though *Ponera* and *Cryptopone* have each individually invaded the New World and each have a single species in Europe. The exceptions are *Pseudoponera* and *Rasopone*, which are most species rich in the New World and *Parvaponera*, with several African species.

### ***Austroponera* gen. nov.**

Fig. 41

Type-species: *Euponera* (*Brachypone*) *rufonigra* Clark, 1934b: 30; by present designation.

*Austroponera* is a small genus (3 described species) which is restricted to Australia and New Zealand. While it is found in a variety of habitats it is nowhere common and is biologically little known.

**Etymology.** *Austroponera* is a combination of *austro*, Latin for “south” and referring to Australia, the region where this genus occurs, together with “ponera” from the subfamily name Ponerinae.

**Diagnosis.** Workers of this genus can be separated from other Ponerinae by the combination of the following characters: anterior clypeal margin convex, without a blunt anteromedial rectangular projection and in side view posterior to the anterior margin of head (the clypeus rounded above mandibles), mandibles triangular and relatively short, their outer margins generally flat or convex medially and lacking a basal pit or groove, the ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur, the propodeal spiracle round or ovoid, and a prora present on the anterior margin of the first gastral sternite. *Austroponera* is morphologically similar to several other ponerine genera. These include *Brachypone*, from which it can be separated by the lack of a basal mandibular pit or groove and the presence of a prora on the anterior margin of first gastral sternite; *Cryptopone*, which has stout traction setae on the dorsum of the mesotibiae (these are absent in *Austroponera*); *Pseudoponera*, which has a slit-shaped rather than round propodeal spiracle as found in *Austroponera*; and *Rasopone*, from which it can be separated by its presence of a stridulatory organ on A4 and its rounded rather than angular anterior clypeal margin. While not closely related based on the findings of Schmidt (2013), *Austroponera* is morphologically similar to some *Mesoponera* species. It differs in the shape of the clypeus (in side view the anterior clypeal margin is posterior to the anterior margin of the head, the clypeus being rounded above mandibles) and in having shorter mandibles which have their outer margins generally flat or convex medially rather than concave. While these two genera are superficially similar and the differences outlined here subtle, they are not closely related and the similarities are due to convergence rather than relatedness.

**Synoptic description.** *Worker.* Medium-sized (TL 4–5 mm) ants with the standard characters of Ponerini. Mandibles triangular, relatively short, with roughly ten teeth and no basal pit or groove. Anterior margin of clypeus broadly convex and often with a small projecting tooth medially. Frontal lobes small. Scapes not flattened basally. Eyes moderate in size, located anterior of head midline. Mesopleuron divided by a transverse groove. Metanotal groove either shallowly depressed or reduced to a suture. Propodeum dorsally broad, not narrowed anteriorly. Propodeal spiracle round. Metatibial spur formula (1s, 1p). Petiole squamiform. Subpetiolar process lacking an anterior fenestra. Helcium low on anterior face of A3. Girdling constriction between pre- and postsclerites of A4 apparent. Stridulitrum present on pretergite of A4. Head and body with scattered pilosity. Color reddish-brown to dark brown.

*Queen.* Similar to worker, but winged or ergatoid and with the other differences typical for alate ponerine queens.

*Male.* Unknown.

*Larva.* Unknown.

**Geographic distribution.** *Austroponera* is restricted to Australia and New Zealand

**Ecology and behavior.** Species of *Austroponera* are found in a diversity of habitats ranging from open situations such as roadsides, pastures and gardens to native forests (Don, 2008; Heterick, 2009). Nests are small, with tens rather than hundreds of workers, and are found in rotting wood, leaf litter, under rocks, or directly in the soil (Brown, 1958). They are predacious and attracted to sweet baits. Workers are often encountered in leaf litter

samples and pitfall traps and when disturbed are timid, retreating into their nests (Don, 2008). Both winged (in *A. castaneicolor*) and ergatoid (in *A. castanea*) queens are known to occur in the genus (Wilson & Taylor, 1967).



**FIGURE 41.** Worker caste of *Austroponera castanea*: lateral and dorsal view of body and full-face view of head (CASENT0172341, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Austroponera*.

**Phylogenetic and taxonomic considerations.** Schmidt (2013) included *A. castanea* in his phylogeny and found it to be the sister group of *Pseudoponera*, with this pair, in turn, the sister group to *Cryptopone*. The species currently included in *Austroponera* show significant variation in a number of morphological characters. For example, the Australian species *A. rufoniger* differs from the remaining species, which are both restricted to New

Zealand, in lacking the medial clypeal tooth and well developed metanotal groove. As only one of the New Zealand species was included in Schmidt's (2013) phylogeny there is limited detailed information on its relationship to the Australian species. Given the morphological differences between these species it is possible that the genus is not monophyletic. However at this time we are placing them together based on the morphological characters outlined above, along with biogeographic considerations, while noting that this conclusion may need to be modified when the results of further studies are known.

*Austroponera* is morphologically similar to *Rasopone*, a genus known only from Central and South America. They share a similar body habitus and differ primarily in *Austroponera* possessing a stridulatory organ on A4 and in having a differently configured clypeus. Based strictly on morphology, it could be argued that they should be placed together in a single genus. However, we are keeping them separate based on the characters outlined above and biogeographic considerations (*Austroponera* is restricted to the Australian region while *Rasopone* is only known from the Americas). Unfortunately no species of *Rasopone* were included in Schmidt's (2013) phylogenetic analysis and the phylogenetic relationship between these two genera is uncertain. A detailed study of the relationships among the species currently placed in these genera would be highly advisable.

### Species of *Austroponera*

*A. castanea* (Mayr, 1865): New Zealand (**comb. nov.**)

*A. castaneicolor* (Dalla Torre, 1893): New Zealand (**comb. nov.**)

*A. rufonigra* (Clark, 1934): Australia (**comb. nov.**)

### *Cryptopone* Emery

Fig. 42

*Cryptopone* Emery, 1893a: cclxxv (as genus). Type-species: *Cryptopone testacea* Emery, 1893a: cclxxv; by monotypy. **Gen. rev.**

*Wadeura* Weber, 1939: 102 (as genus). Type-species: *Wadeura guianensis* Weber, 1939: 103; by original designation. *Wadeura* as junior synonym of *Cryptopone*. **Syn. nov.**

*Cryptopone* is a moderately large genus (25 described species and subspecies) with a cosmopolitan distribution, though the species diversity is centered in Asia. *Cryptopone* workers are well-adapted to a hypogeic lifestyle, with small body size, reduced or absent eyes, flattened scapes, and traction setae on the mesotibiae.

**Diagnosis.** *Cryptopone* workers lack any obvious autapomorphic characters, but can be identified by the following characters (in combination): mandibles usually with a basal pit or fovea (absent in members of the former genus *Wadeura*, here newly synonymized with *Cryptopone*), frontal lobes small and closely approximated, scapes flattened, eyes vestigial to absent, propodeum with a distinct dorsal face which widens posteriorly, metabasitarsus with simple setae but lacking spiniform or peg-like traction setae, and mesotibiae with stout traction setae (sometimes small and reduced to a few, but always present). Workers of *Cryptopone* most closely resemble those of *Pseudoponera* (a close relative of *Cryptopone*), but differ most consistently in the presence of mesotibial traction setae. Similar traction setae occur in *Centromyrmex*, *Feroponera*, *Promyopias*, and *Buniapone*, but these genera all lack at least some portion of the diagnosis given above. Several other ponerine genera have basal mandibular pits, including *Brachyponera*, *Euponera*, and *Hagensia*, but these genera all lack mesotibial traction setae and have larger eyes, among many other differences.

**Synoptic description.** *Worker*: Very small to medium sized (TL 1.7–6.1 mm) ants with the standard characters of Ponerini. Mandibles triangular to subfalcate, usually with a small basal pit (absent in “*Wadeura*”) and without a basal groove. Anterior margin of clypeus broadly convex. Frontal lobes small and closely approximated. Scapes flattened. Apical segments of antennal funiculus often distinctly clubbed. Eyes greatly reduced or absent (in “*Wadeura*”). Metanotal groove reduced to a suture. Propodeum with a distinct dorsal face which widens posteriorly. Propodeal spiracles round to ovoid. Mesotibiae armed with stout traction setae. Metatibial spur formula (1p) or (1p, 1s). Petiole surmounted by a thick scale, its posterior face convex in dorsal view. Helcium sometimes projecting from near midheight of the anterior face of A3. Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Head and body finely punctate, with some smooth and shining areas on the sides of the

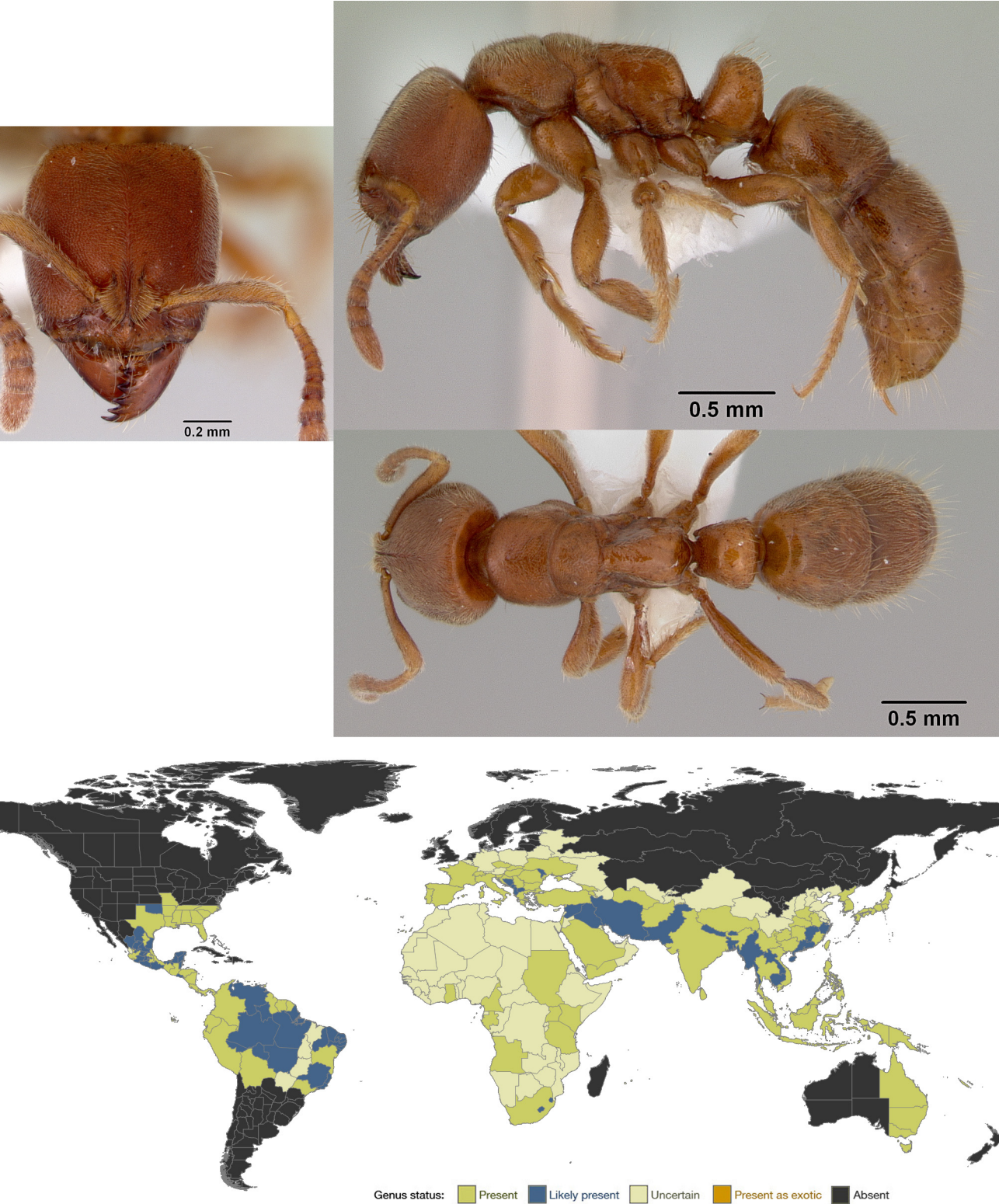


mesosoma, and with scattered to abundant short pilosity and dense pubescence. Color usually testaceous to orange, rarely black.

*Queen.* Similar to worker but slightly larger, alate, with ocelli and larger eyes, and with the other thoracic modifications typical of alate ponerine queens (Brown, 1963). See additional details in Ogata (1987).

*Male.* See descriptions by Brown (1963) and Ogata (1987).

*Larva.* Described for various species by Wheeler & Wheeler (1952, 1971a, 1986b).



**FIGURE 42.** Worker caste of *Cryptopone rotundiceps*: lateral and dorsal view of body and full-face view of head (CASENT0172100, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Cryptopone*.

**Geographic distribution.** *Cryptopone* has a virtually cosmopolitan distribution, occurring in every major biogeographic region, though the species diversity is centered in East and Southeast Asia (Brown, 1963; Bolton *et al.*, 2006).

**Ecology and behavior.** Very little is known about the habits of *Cryptopone*, but based on morphology and anecdotal observations they are clearly hypogeic (*e.g.*, Wheeler & Gaige, 1920). *Cryptopone* workers exhibit many classic characters of hypogeic ants, including small size, depigmentation, flattened scapes, vestigial eyes, and traction setae on the mesotibiae (*e.g.*, Wheeler, 1933a). Reported field observations and collection data indicate that *Cryptopone* species nest in a diversity of microhabitats including rotting wood, polypore fungi, under grass, in leaf litter, in soil, or even inside termitaria (Creighton & Tulloch, 1930; Forel, cited by Wheeler, 1933a; Smith, 1934; Weber, 1939; Wilson, 1958c; Terayama, 1999; Radchenko, 2005; Longino, 2013). Workers have been observed foraging in soil, leaf litter, and under moss or rocks (Wheeler & Gaige, 1920; Wilson, 1958c; Radchenko, 2005; Longino, 2013). Haskins (1931) observed workers of *C. gilva* in laboratory conditions foraging in exposed conditions for brief periods, suggesting that they are not strictly hypogeic. Wilson (1958c) reported that workers of *C. butteli* are timid and slow moving, and Wheeler & Gaige (1920) noted similar behavior in workers of *C. gilva* and observed that they feign death; Smith (1934) also noted sluggish behavior in *C. gilva*. *Cryptopone* are most likely generalist predators, though observations of *Cryptopone* food preferences are scant. Imai *et al.* (2003) reported that *C. sauteri* is a predator of beetle and fly larvae.

Almost nothing is known about the social organization of *Cryptopone*, but colonies are typically small (*C. butteli*: Wilson, 1958c; *C. guianensis*: Weber, 1939). Creighton & Tulloch (1930) observed a single colony of *C. gilva* with five dealate queens and stated that its colonies are small, and Smith (1934) similarly observed polygynous colonies of *C. gilva* but noted that its colonies could have as many as several hundred workers. Haskins (1931) also reported frequent polygyny in *C. gilva*. Nest emigrations are facilitated by social carrying in *C. gilva* (Haskins, 1931). Haskins (1931) gives many additional details of the habits of *C. gilva*, including the results of interesting experiments on its visual and auditory acuity.

**Phylogenetic and taxonomic considerations.** *Cryptopone* has had a somewhat complicated taxonomic history. In erecting *Cryptopone*, Emery (1893a; also 1893b) noted the similarity of its type species, *C. testacea*, to *Ponera*. He distinguished the two genera by mandibular shape (the masticatory margin is shorter in *C. testacea*) and by the relatively high articulation of the petiole with the gaster in *C. testacea*. Emery also compared *C. testacea* to *Trapeziopelta* (= *Myopias*), noting the supposedly similar mandibular shape and high helcium. The subtriangular mandibles and high helcium of *C. testacea* have proven not to be universal in *Cryptopone*, nor is a high helcium common in *Myopias*, so these characters are less informative than Emery believed. Emery also considered the four-segmented club of *C. testacea* to be of taxonomic value.

Additional species were gradually added to *Cryptopone* until Wheeler (1933a) revised the genus, splitting off two species to form the new genus *Pseudocryptopone* (which he considered to be close to *Ponera*), describing new species, and providing a revised diagnosis for the genera. Wheeler was the first to recognize the significance of the distinctive shape of the propodeum in dorsal view, of the stout mesotibial setae, and of the head shape. Based on the latter two characters, Wheeler believed that *Cryptopone* was closely related to *Trachymesopus* (= *Pseudoponera*).

Wilson (1958c) discussed the relationship between *Cryptopone* and *Trachymesopus* and believed that they could be separated by three worker characters: the metatibial spur count (one in *Cryptopone*, two in *Trachymesopus*), the shape of the mandibles (narrower and with more oblique masticatory margins in *Cryptopone*), and the presence of eyes (absent in *Cryptopone*). Brown (1963) noted the presence of stout setae on the mesotibiae and the presence of basal mandibular pits as being characteristic of the genus, recognized that *Trachymesopus* species with these traits are really *Cryptopone*, and transferred them to *Cryptopone* accordingly. More recently, Mackay & Mackay (2010) found the characters used to separate *Cryptopone* from related genera to be poor. They observed that many of these characters were too variable or difficult to see and therefore unambiguous interpretation and placement of some taxa within these genera was sometimes nearly impossible. As a result they synonymized *Cryptopone* with *Pachycondyla*. Mackay & Mackay (2010) also note that *Wadeura guianensis*, the type species of *Wadeura*, is basically a *Cryptopone* with unusual mandibles and because of this *Wadeura* does not warrant status as a full genus; they consider it to be a synonym of *Pachycondyla*.

To resolve these issues a broad range of species from across the world were examined. While some characters used to diagnose *Cryptopone* were found to be variable as noted by Mackay & Mackay (2010), we were able to develop a concise diagnosis for the genus and to produce keys which allow reliable identifications to be

undertaken. Additionally, Schmidt's (2013) molecular phylogeny of the Ponerinae places *Cryptopone* as sister to *Pseudoponera*, a relationship that Wheeler (1933a) suggested, with no close relationship indicated to true *Pachycondyla*. Based on this we treat *Cryptopone* as a valid genus with *Wadeura* as its junior synonym. It should be noted that the true boundaries of *Cryptopone* and *Pseudoponera* are somewhat unclear, but morphological evidence does support this relationship (see the discussion of the *Ponera* genus group).

Our concept of *Cryptopone* nearly mirrors that of Brown, with the exception that we consider the genus *Wadeura* to be a probable junior synonym of *Cryptopone*. *Wadeura* (described by Weber, 1939), currently considered a junior synonym of *Pachycondyla* (Brown, 1973), is a small Neotropical group of three species. Though Schmidt (2013) did not sample *Wadeura* in his molecular phylogeny, the morphological similarities between *Wadeura* and *Cryptopone* are compelling and to our surprise have apparently not been noted previously. In most respects the three species of *Wadeura* are morphologically typical of *Cryptopone*, having the same dense punctate sculpturing, dense pubescence, depigmentation, head shape, convex anterior clypeal margin, small closely approximated frontal lobes, flattened scapes, vestigial eyes (actually completely absent in *Wadeura*), anteriorly constricted propodeum and flat propodeal dorsum, round propodeal spiracles, simple posteriorly directed metapleural gland orifice, mesotibiae with stout spines, thick squamiform petiole, and the characters of the gaster. *Wadeura* differs from typical *Cryptopone* chiefly in mandibular shape (narrower and with longer teeth in *Wadeura*), in the shape of the mesonotum (bulging in *Wadeura*, with the consequent appearance of a depressed propodeum), body size (*Wadeura* is somewhat larger than most *Cryptopone*), and metatibial spur count (one in *Cryptopone*, two in *Wadeura*).

We do not consider the morphological differences between *Wadeura* and *Cryptopone* to be of genus-level significance, and interpret *Wadeura* as a lineage of *Cryptopone* (probably sister to *C. gilva* and *C. guatemalensis*) which evolved larger size and possibly prey specialization, to fill a niche left empty in the Neotropics but filled by the superficially similar *Promyopias* in Africa and *Buniapone* in Southeast Asia (as suggested by Weber, 1939). Alternatively, *Wadeura* could actually be unrelated to *Cryptopone* and represent a remarkable case of convergence, though we do not find this hypothesis very credible.

### Species of *Cryptopone*

As discussed by Bolton & Fisher (2011), *C. hartwigi* is the only species of *Cryptopone* found in tropical Africa. It possesses a basal mandibular pit and metatibial pusher setae, characteristics of *Cryptopone*, and fits the diagnosis for this genus as proposed in the present work. However, recently P.S. Ward (pers. comm.) examined a number of ponerine species using molecular methods and found that *C. hartwigi* is closely related to *Fisheropone* and only distantly related to *C. gilva* and *C. testacea*, suggesting that *C. hartwigi* is not a true *Cryptopone* and the observed similarity is due to convergence in the characters they apparently share. Unfortunately, it proved challenging to find morphological characters that would separate *C. hartwigi* from “true” *Cryptopone*. Without such characters it is impossible to determine if only *C. hartwigi* should be removed from *Cryptopone*, or if other species are also misplaced and in need of transfer to other genera (new or existing). Only a detailed study of the genus will determine the true relationships among these species. Until this can be completed we are taking a conservative approach and placing *C. hartwigi* within *Cryptopone*, acknowledging that this placement will likely need emendation as our understanding of the group improves.

*C. arabica* Collingwood & Agosti, 1996: Yemen (**comb. rev.**)

*C. butteli* Forel, 1913: Indonesia (Sumatra) (**comb. rev.**)

*C. crassicornis* (Emery, 1897): New Guinea (**comb. rev.**)

*C. fusciceps* Emery, 1900: New Guinea (**comb. rev.**)

*C. gigas* Wu & Wang, 1995: China (**comb. rev.**)

*C. gilva* (Roger, 1863): United States (**comb. rev.**)

*C. guianensis* (Weber, 1939): Guiana (**comb. nov.**)

*C. hartwigi* Arnold, 1948: South Africa (**comb. rev.**)

*C. holmgreni* (Wheeler, 1925): Peru (**comb. nov.**)

*C. jinxiuensis* Zhou, 2001: China (**comb. rev.**)

*C. mirabilis* (Mackay & Mackay, 2010): Bolivia (**comb. nov.**)



*C. motschulskyi* Donisthorpe, 1943: New Guinea (**comb. rev.**)  
*C. nicobarensis* Forel, 1905: Nicobar Islands (**comb. rev.**)  
*C. ochracea* (Mayr, 1855): Italy (**comb. rev.**)  
*C. ochracea sicula* (Emery, 1909): Italy (**comb. rev.**)  
*C. pseudogigas* Zhou & Zheng, 1997: China (**comb. rev.**)  
*C. recticlypea* Xu, 1998: China (**comb. rev.**)  
*C. rotundiceps* (Emery, 1914): New Caledonia (**comb. rev.**)  
*C. sauteri* (Wheeler, W.M., 1906): Japan (**comb. rev.**)  
*C. sinensis* Wang, 1992: China (**comb. rev.**)  
*C. subterranea* (Bharti & Wachkoo, 2013): India (**comb. rev.**)  
*C. taivanae* (Forel, 1913): Taiwan (**comb. rev.**)  
*C. tengu* Terayama, 1999: Japan (**comb. rev.**)  
*C. testacea* Emery, 1893: Sri Lanka (**comb. rev.**)  
*C. typhlos* (Karavaiev, 1935): Vietnam (**comb. rev.**)

## ***Diacamma* Mayr**

Fig. 43

*Diacamma* Mayr, 1862: 713, 718 (*Diacamma* as genus in Ponerinae [Poneridae]). Type-species: *Ponera rugosa* Le Guillou, 1842: 318; by subsequent designation of Bingham, 1903: 75.

*Diacamma* is a moderately sized (21 described species) genus which ranges from India to Australia. It is notable for its reproduction by gamergates and control of reproduction by nestmate mutilation.

**Diagnosis.** *Diacamma* workers are highly distinctive and are easily identified by the presence of deep striate sculpturing, deep pits ("gemmal pits") on the sides of the mesosoma, and a bispinose petiole. The gemmal pits are autapomorphic, but may be confused with the wing scars of dealate queens in other taxa. *Diacamma* workers lack the other characters of winged queens, however, such as ocelli and modified thoracic sclerites. The combination of deep striate sculpturing, prominent arolia, bispinose petiole, and laterally-opening metapleural gland orifice (with a posterior U-shaped cuticular lip) also differentiates *Diacamma* from the queens and workers of any other ponerine genus.

**Synoptic description.** *Worker.* Medium to large (TL 8–16 mm) ants with the standard characters of Ponerini. Mandibles triangular and usually without a basal groove. Anterior margin of clypeus convexly triangular. Frontal lobes of moderate size. Eyes large and convex, located at or just anterior of the head midline. Mesonotum very short. Large gemmal pits present laterally at the base of the mesonotum. Metanotal groove reduced to a simple suture. Propodeum moderately narrowed dorsally. Propodeal spiracles slit-shaped. Metapleural gland orifice large, opening laterally, with a posterior U-shaped cuticular lip and at most a shallow lateral depression. Metatibia with a conspicuous, depressed, usually pale glandular area on the posterior surface. Metatibial spur formula (1s, 1s) or (1s, 1p). Arolia prominent. Petiole nodiform, usually roughly cuboidal, with a pair of short spines on the posterodorsal margin. Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Head and body heavily striate, with scattered short pilosity and usually dense pubescence. Color variable, generally gray or black but often metallic. A study of thoracic structure in *D. australe* was given by Bitsch & Peeters (1991), and a detailed morphological study of workers in another *Diacamma* species was given by Okada *et al.* (2006).

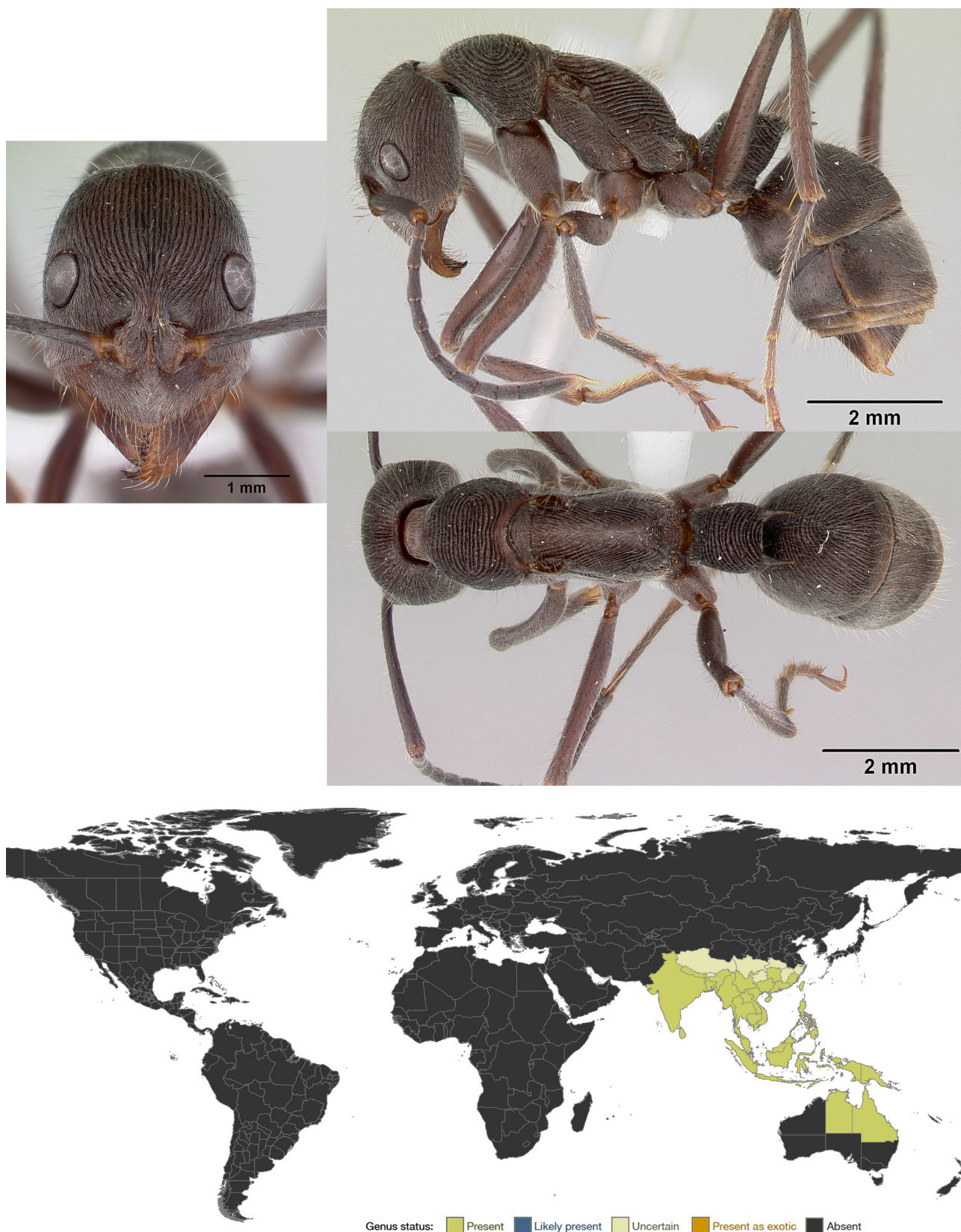
*Queen.* Absent.

*Male.* See description in Ogata (1987) and Okada *et al.* (2006).

*Larva.* Described by Wheeler & Wheeler (1952) and Baratte *et al.* (2005).

**Geographic distribution.** The range of *Diacamma* extends from India east to Japan, and from southern China to northeast Australia (Emery, 1911; Wheeler & Chapman, 1922; Suwabe *et al.*, 2007).

**Ecology and behavior.** In most respects *Diacamma* are fairly typical ponerines. The workers are monomorphic, forage individually on the ground and on low vegetation, and show a remarkable degree of directional fidelity when foraging (Abe & Uezu, 1977; Karpakakunjarum *et al.*, 2003; Eguchi *et al.*, 2004). Though the natural food preferences of *Diacamma* have been little studied, they are apparently generalist predators of arthropods (Abe & Uezu, 1977; Karpakakunjarum *et al.*, 2003). Ke *et al.* (2008) found that workers of *D. rugosum*



**FIGURE 43.** Worker caste of *Diacamma australe*: lateral and dorsal view of body and full-face view of head (CASENT0172071, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Diacamma*.

are effective predators of termites in artificial arenas, and Karpakakunjarum *et al.* (2003) observed that termites made up the majority of the diet of *D. ceylonense*. Colonies contain on average a few hundred workers or less (*e.g.*,

*D. ceylonense*: 200–300 workers; Karpakakunjarum *et al.*, 2003; Ramaswamy *et al.*, 2004; Baratte *et al.*, 2006a; *D. cyaneiventris*: 214 workers; André *et al.*, 2001; *D. indicum*: 90 workers; Viginier *et al.*, 2004; *D. rugosum*: 40–50 workers; Wheeler & Chapman, 1922; Wilson, 1959b; *Diacamma* sp. (Japan): 118 workers; Abe & Uezu, 1977; *Diacamma* sp.: 86 workers; Sommer *et al.*, 1993; *Diacamma* sp. ‘nilgiri’: 275 workers; Bocher *et al.*, 2008).

Nests are usually constructed in soil (often in the middle of clearings), rotting logs, or even in trees (Wheeler & Chapman, 1922; Abe & Uezu, 1977; Fukumoto & Abe, 1983; André *et al.*, 2001, 2006; Eguchi *et al.*, 2004; Viginier *et al.*, 2004; Allard *et al.*, 2007). The nests of many *Diacamma* species are deep and complex, allowing workers to retreat to deeper chambers in response to nest disturbance, though nests of *D. indicum* are shallow and colonies emigrate after only minor disturbances (Viginier *et al.*, 2004). *Diacamma* sp. (from Japan) also emigrates readily in response to disturbances or unfavorable environmental conditions, and utilizes both tandem running and social carrying during emigrations (Abe & Uezu, 1977; Fukumoto & Abe, 1983). Nestmate recruitment during emigration also occurs through tandem running in *D. rugosum*, with the hindgut fluid apparently acting as a long-term trail pheromone (Maschwitz *et al.*, 1986). Moffett (1986) found that colonies of *D. rugosum* in India are polydomous, with multiple shallow nests separated by a meter or more, and also discovered that these ants surround their nest entrances with feathers and ant corpses, apparently in order to collect dew (Moffett, 1985).

The reproductive behaviors of *Diacamma* are highly unusual and have been heavily studied. *Diacamma* colonies are queenless, with reproduction instead being performed by a single mated gamergate worker (Wheeler & Chapman, 1922; Peeters & Higashi, 1989). Several other ponerine lineages have similarly lost the queen caste, but the control of reproduction in *Diacamma* is unique among ants. All *Diacamma* workers eclose with a pair of novel thoracic appendages called gemmae (Tulloch, 1934). In virtually every *Diacamma* species studied (see below for the one known exception), the presence of intact gemmae causes a worker to become sexually receptive and ultimately a gamergate (Peeters & Higashi, 1989; Cuvillier-Hot *et al.*, 2002). Loss of the gemmae, however, causes an individual to become a normal worker (Allard *et al.*, 2005). The acting gamergate in a colony therefore mutilates the gemmae of newly eclosed workers and thereby maintains its reproductive dominance (Peeters, 1993). The social and reproductive conflicts in *Diacamma* colonies were reviewed by Monnin & Ratnieks (2001).

The origin of the gemmae is somewhat controversial. Based on neurological and developmental studies, Gronenberg & Peeters (1993), Gronenberg (1996), and Gotoh *et al.* (2005) suggested that the gemmae are homologous with the forewings (see also Tulloch, 1934), but Baratte *et al.* (2006b) disagree, instead arguing that the gemmae are novel organs whose development simply co-opted some of the same genes and processes as wings. Whatever their origin, the gemmae are filled with secretory cells which open to the surface (Billen & Peeters, 1991; Peeters & Billen, 1991) and play a definite role in determining the fertility of *Diacamma* workers. Though the exact mechanism of action of the gemmae have not yet been worked out, Allard *et al.* (2005) found that the mutilation of gemmae in young workers of *Diacamma* sp. (Japan) caused their bursa copulatrix and spermathecae to not develop fully, leaving them incapable of mating. Tsuji *et al.* (1998) experimentally determined that the gemmae of gamergates are not directly involved pheromonally in the suppression of worker reproduction. Bitsch & Peeters (1991) examined the structure of gemmae in *D. australe*.

In a classic study, Peeters & Higashi (1989) worked out many of the basic details of the reproductive and social behavior of *D. australe*. They found that colonies of this species contain a single gamergate, which has intact gemmae, active ovaries, and sperm-filled spermathecae, and which dominates the egg-laying in the colony. All other workers lacked gemmae and were unmated, and most of these had completely undeveloped ovaries. Only the gamergate actually mutilated the gemmae of newly eclosed workers, though other workers assisted. In experimentally orphaned colonies, some workers laid haploid eggs, and the oldest unmutilated callow worker (the future gamergate) became aggressive and began mutilating other callow workers with intact gemmae, began laying eggs, and became receptive to mating.

Subsequent research has confirmed many of these observations in other species of *Diacamma* and have filled in many additional details. In a scenario similar to that in *D. australe*, the first worker to eclose (*i.e.*, the oldest unmutilated worker) in an orphaned colony of *D. ceylonense* immediately becomes aggressive toward her nestmates, and after three weeks begins to lay haploid eggs, ceases her aggression, and becomes receptive to mating (Cuvillier-Hot *et al.*, 2002). In both *D. ceylonense* and *D. australe*, newly eclosed workers are aggressive toward other unmutilated callow workers (potential future gamergates), but do not resist their own mutilation by mature gamergates (Baratte *et al.*, 2006a).

As with other ponerines in which alate queens are absent, colony reproduction in *Diacamma* occurs through budding (Fukumoto *et al.*, 1989; André *et al.*, 2006). When this occurs, one of the colony fragments is headed by



the gamergate of the mother colony and one of them is orphaned. A colony may also be orphaned through the death of the gamergate. Succession in *Diacamma* colonies is an example of serial polygyny, as two matrilineal colonies coexist in a colony for some time after the death of the gamergate (André *et al.*, 2001). André *et al.* (2006) studied the pattern of worker and gamergate turnover in *D. cyaneiventris* and estimated that the average tenure of gamergates is about 200 days. Interestingly, gamergate turnover in this species does not significantly affect the average worker relatedness, which is very close to the expectation for a monandrous and monogynous ant colony (André *et al.*, 2001). As expected from the limited dispersal abilities of *Diacamma* queens, populations of *D. cyaneiventris* were found to be highly genetically isolated, with most gene flow occurring via male dispersal (Doums *et al.*, 2002).

In an undescribed *Diacamma* species from Japan, workers are apparently inhibited from laying haploid eggs by a non-volatile pheromone produced by the gamergate (Tsuji *et al.*, 1999). Both gamergates and non-gamergates also police reproduction by workers through aggression and egg cannibalism (Kikuta & Tsuji, 1999, Kawabata & Tsuji, 2005). Despite these obstacles, non-gamergate workers do succeed in laying a small number of eggs which are added to the colony's egg piles, especially in larger colonies (Nakata & Tsuji, 1996; Kikuta & Tsuji, 1999). In a test of the extent to which *Diacamma* workers control reproduction in the colony, Nakata (1998) observed that workers of *Diacamma* sp. (from Japan) do not differentially rear male or female brood, and therefore do not control the sex ratio of the colony's sexual brood. Peeters & Tsuji (1993) found that orphaned workers of *Diacamma* sp. (from Japan) aggressively competed with one another and formed a non-linear dominance hierarchy with a definite alpha and beta; only the alpha reproduced, and she ate the eggs of other workers. In an unidentified *Diacamma* species from Malaysia, orphaned workers also compete and form a dominance hierarchy, with only the alpha reproducing (Sommer *et al.*, 1993).

The age and reproductive status of *Diacamma* workers is communicated by their cuticular hydrocarbon profile (in *D. ceylonense*: Cuvillier-Hot *et al.*, 2001). Gamergates have a distinct hydrocarbon profile, and this seems to play a role in controlling reproduction by nestmates (Cuvillier-Hot *et al.*, 2002). Suwabe *et al.* (2007) found that workers of a *Diacamma* sp. can distinguish nestmates from non-nestmates, presumably by their cuticular hydrocarbons, and are hostile toward non-nestmates. Marukawa *et al.* (2001) and Masuda & Mori (2002) described the biochemistry of cuticular hydrocarbons in this species.

One *Diacamma* species is known in which the control of reproduction is not mediated through gemmae. In a species closely related to *D. ceylonense* (referred to as *Diacamma* sp. 'nilgiri'; Baudry *et al.*, 2003), reproduction is controlled by aggressive dominance interactions among workers (Peeters *et al.*, 1992; Bocher *et al.*, 2008), similar to the situation in other ponerines with gamergates such as *Dinoponera*. In this species, the dominant worker begins laying eggs and eventually will mate and become a fully functional gamergate (Peeters *et al.*, 1992). Ramaswamy *et al.* (2004) found that the cues for mutilation originate in the gemmae of the victim, as *D. ceylonense* callows introduced into *D. sp.* 'nilgiri' colonies are mutilated, but 'nilgiri' callows introduced into *D. ceylonense* colonies are not. Baratte *et al.* (2006a) hypothesized that the mutilation mechanism in *Diacamma* may maximize colony productivity relative to other queenless ponerines in which dominance interactions determine the dominant reproductive individual. In support of this hypothesis, Bocher *et al.* (2008) found that dominance interactions in *D. sp.* 'nilgiri' lead to reduced colony work efficiency and reduced immunocompetence in colony members. The selective conditions favoring the "dominance interaction" strategy over the "gemmae mutilation" strategy are unclear.

*Diacamma* appears to be monandrous, with single mating reported for several species (e.g., *D. cyaneiventris*: André *et al.*, 2001). In laboratory colonies of *D. australe*, foreign males encountered by foraging workers were carried into the nest, where mating occurred (Peeters & Higashi, 1989). New gamergates of *Diacamma* sp. (from Japan) wait outside the nest entrance and call to males using pheromones derived from the metatibial gland (Fukumoto *et al.*, 1989; Nakata *et al.*, 1998; the metatibial gland was described by Hölldobler *et al.*, 1996b). Peeters *et al.* (1992) also observed calling behavior by new gamergates of *Diacamma* sp. 'nilgiri'. Despite very rapid sperm transfer, copulation in *Diacamma* is exceptionally long, with males remaining attached to females for as long as two days; males actually have to be killed and forcibly removed by the gamergate and her nestmates (Allard *et al.*, 2002, 2007).

Relatively little work has been done on the division of labor in *Diacamma* colonies, other than reproductive division of labor. Nakata (1995, 1996b; also Dahbi & Jaisson, 1995) found that *Diacamma* sp. (from Japan) has a typical age-related polyethism, though workers remain behaviorally flexible. Nakata (1996a, 2000) found that smaller colonies of this species have lower temporal stability in colony productivity, and that the behavioral

flexibility of workers does not fully compensate for drops in colony productivity due to fluctuating colony demographics.

At least three cases are known of social parasitism or commensalism between *Diacamma* and other ants. Maschwitz *et al.* (2000, 2004) discovered that an undescribed *Diacamma* species acts as host to the formicine *Polyrhachis lama*, feeding and protecting the *Polyrhachis* adults and brood. A *P. lama* colony may simultaneously parasitize multiple *Diacamma* colonies (Maschwitz *et al.*, 2004). This symbiosis may have originated through mimicry of the *Diacamma* host by the *Polyrhachis* parasite. Maschwitz *et al.* (2001) observed *Diacamma* leading their *Polyrhachis* guests to new nest sites during emigrations via tandem running. Kaufmann *et al.* (2003) found two instances of compound nesting involving *Diacamma* and either *Strumigenys* or *Pheidole*, with the latter genera nesting in small chambers adjacent to the *Diacamma* nest and feeding on mites and collembolans in the *Diacamma* nest (*Strumigenys*) or on the *Diacamma* refuse piles (*Pheidole*). Eguchi *et al.* (2005) discovered myrmecophilic gastropods living with *Diacamma* sp. nr. *sculpturatum*. The gastropods probably feed on the *Diacamma* refuse piles and apparently have adaptations to ensure their spread during fissions of the host colony.

Biochemical examinations of *Diacamma* include studies of cuticular hydrocarbons and the glandular properties of the gemmae (both discussed previously), as well as the contents of the Dufour's and venom glands (Morgan *et al.*, 2003) and of the mandibular glands (Morgan *et al.*, 1999). Doums (1999) and Gopinath *et al.* (2001) identified microsatellite loci in *D. cyaneiventris* and *D. ceylonense*, respectively.

**Phylogenetic and taxonomic considerations.** *Diacamma* was erected by Mayr (1862) to house the species *D. rugosum* and *D. vagans* (now a junior synonym of *D. rugosum*). Since its original description *Diacamma* has been universally recognized as a distinct genus, presumably thanks to its unique morphological and behavioral traits, which suggest a deep split from its nearest relative. Schmidt's (2013) molecular phylogeny of the Ponerinae confirms that *Diacamma* is a deeply distinct lineage and places it with strong support as sister to the rest of the *Ponera* genus group. This phylogenetic placement is unsurprising from a biogeographic standpoint, but from morphological considerations it is unexpected (see previous discussion of relationships within the *Ponera* group). Based on strong molecular and morphological evidence we are retaining *Diacamma* as a distinct genus.

### Species of *Diacamma*

*Diacamma* is in dire need of a comprehensive species-level revision, as there are undoubtedly many additional species than are currently recognized. For example, the complex presently called *D. rugosum* almost certainly represents multiple species. Bingham (1903) provided a key to the *Diacamma* fauna of India and Sri Lanka.

*D. assamense* Emery, 1897: India

*D. australe* (Fabricius, 1775): Australia

*D. baguiense* Wheeler & Chapman, 1925: Philippines

*D. bispinosum* (Le Guillou, 1842): Indonesia

*D. ceylonense* Emery, 1897: Sri Lanka

*D. ceylonense orbiculatum* Santschi, 1932: Laos

*D. colosseense* Forel, 1915: Australia

*D. cupreum* (Smith, F., 1860): New Guinea

*D. cyaneiventris* André, 1887: India

*D. holosericeum* (Roger, 1860): Java

*D. indicum* Santschi, 1920: India

*D. intricatum* (Smith, F., 1857): Borneo

*D. intricatum kershawii* Wheeler, W.M. 1919: Borneo

*D. jacobsoni* Forel, 1912: Java

*D. leve* Crawley, 1915: Australia

*D. longitudinale* Emery, 1889: Vietnam

*D. palawanicum* Emery, 1900: Philippines

*D. palawanicum concentricum* Wheeler, W.M. & Chapman, 1925: Philippines

*D. pallidum* (Smith, F., 1858): Myanmar

*D. panayense* Wheeler & Chapman, 1925: Philippines

*D. purpureum* (Smith, F., 1863): Indonesia  
*D. rugivertex* Emery, 1902: Timor  
*D. rugosum* (Le Guillou, 1842): Borneo  
*D. rugosum anceps* Matsumura & Uchida, 1926: China  
*D. rugosum arcuatum* Karavaiev, 1925b: Indonesia (Sumatra).  
*D. rugosum balinense* Karavaiev, 1925b: Indonesia (Bali I.).  
*D. rugosum birmanum* Emery, 1887: Myanmar  
*D. rugosum celebense* Emery, 1887: Indonesia (Sulawesi)  
*D. rugosum doveri* Mukerjee, 1934: India  
*D. rugosum gibbosum* Karavaiev, 1935: Vietnam  
*D. rugosum hortense* Karavaiev, 1925: Indonesia (Java)  
*D. rugosum javanum* Emery, 1887: Indonesia (Java).  
*D. rugosum jerdoni* Forel, 1903d: India  
*D. rugosum latispinum* Karavaiev, 1925: Indonesia (Java)  
*D. rugosum lombokense* Emery, 1897: Indonesia (Lombok I.)  
*D. rugosum longiceps* Santschi, 1932: Vietnam  
*D. rugosum ovale* Karavaiev, 1935: Vietnam  
*D. rugosum rothneyi* Forel, 1900: India  
*D. rugosum sculptum* Jerdon, 1851: India  
*D. rugosum sikkimense* Forel, 1903: India  
*D. rugosum timorensis* Emery, 1887: Indonesia (Timor I.)  
*D. rugosum viridipurpureum* Emery, 1893: Philippines  
*D. scalpratum* (Smith, F., 1858): India  
*D. scalpratum violaceum* Forel, 1900d: Myanmar  
*D. schoedli* Shattuck & Barnett, 2006: Australia  
*D. sericeiventris* Stitz, 1925: Philippines  
*D. tritschleri* Emery, 1897: Indonesia (Sumatra)

### ***Ectomomyrmex* Mayr**

Fig. 44

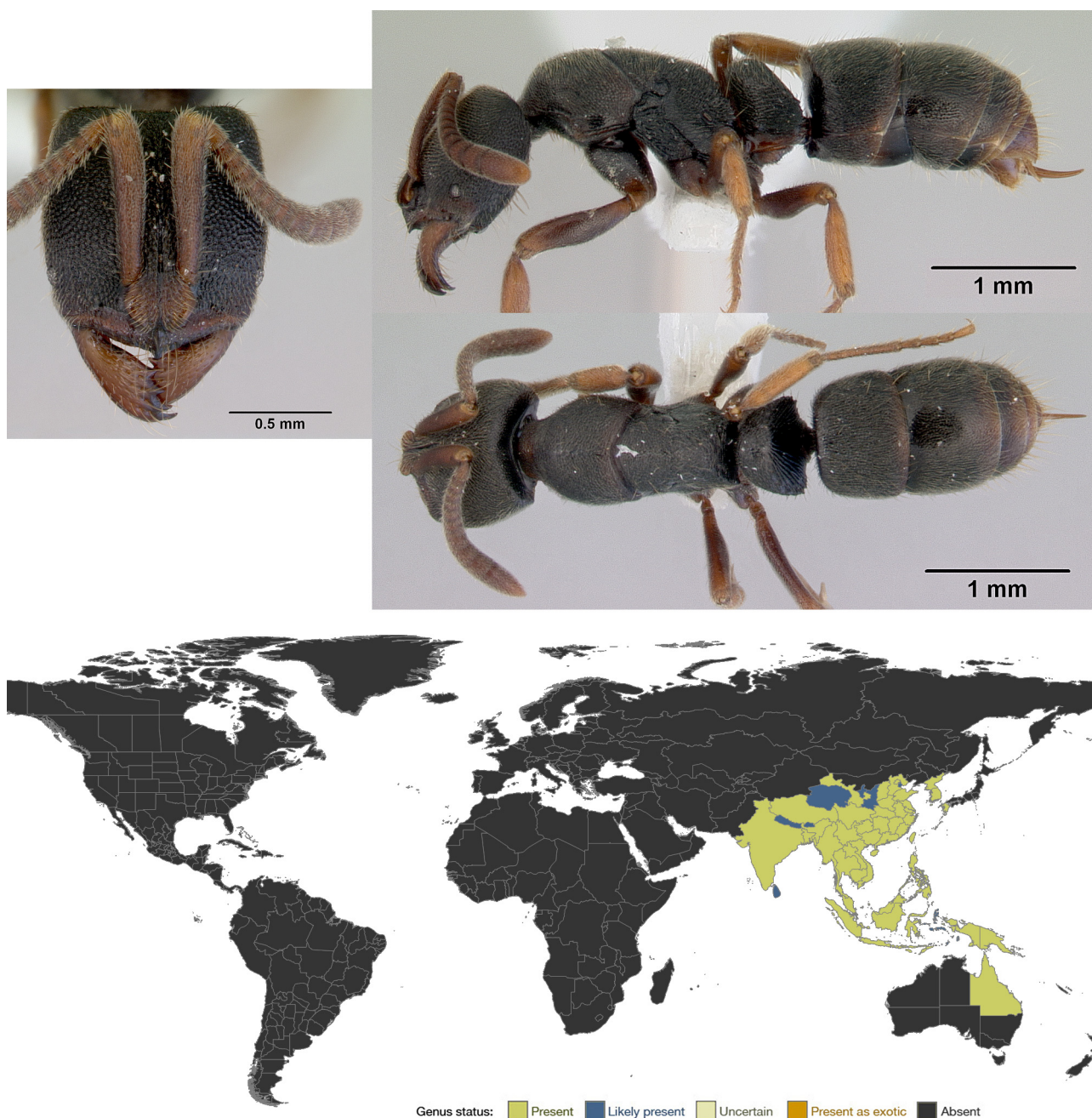
*Ectomomyrmex* Mayr, 1867: 83 (as genus). Type-species: *Ectomomyrmex javanus* Mayr, 1867: 84; by subsequent designation of Bingham, 1903: 85. **Gen. rev.**

*Ectomyrmex* Donisthorpe, 1943b: 641 (incorrect subsequent spelling of *Ectomomyrmex*).

*Ectomomyrmex* is a medium-sized genus (27 described species) restricted to Asia and Australia. They are apparently epigeic generalist predators.

**Diagnosis.** *Ectomomyrmex* workers can be identified by the following combination of characters: head, mesosoma and petiole strongly sculptured, head usually prismatic posteriorly, mesopleuron divided by a transverse groove, and petiole with a sweeping posterior face. *Ectomomyrmex* workers are similar to those of some *Ponera* species (e.g., *P. alpha*), but *Ectomomyrmex* workers lack an anterior fenestra in the subpetiolar process and have two metatibial spurs and a divided mesopleuron. *Ectomomyrmex* is also superficially similar to *Pachycondyla*, but *Ectomomyrmex* lacks the complex metapleural gland orifice and hypopygial spines of *Pachycondyla*, and *Pachycondyla* lacks the prismatic head shape of *Ectomomyrmex*. *Ectomomyrmex* is also somewhat similar to *Cryptopone* and *Pseudoponera*, but differs from them in having strong sculpturing, larger eyes, no basal mandibular pit, a prismatic head, divided mesopleuron, slit-shaped propodeal spiracles, a sweeping posterior petiolar face, and no traction setae on the mesotibiae. *Ectomomyrmex* may be confused with *Pseudoneoponera* or *Bothroponera*, but *Ectomomyrmex* lacks the shaggy pilosity and longitudinally striate tergite A3 of *Pseudoneoponera*, and the large eyes, undivided mesopleuron, and block-like petiole of *Bothroponera*.





**FIGURE 44.** Worker caste of *Ectomomyrmex ruficornis*: lateral and dorsal view of body and full-face view of head (CASENT0172434, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Ectomomyrmex*.

**Synoptic description.** *Worker*. Medium to large (TL 5–12.8 mm) ants with the standard characters of Ponerini. Mandibles triangular, with up to 10 teeth on the masticatory margin and often a faint basal groove. Anterior clypeal margin convex, sometimes medially emarginate. Frontal lobes small to moderate in size. Eyes very small to small, located anterior of head midline. Head usually prismatic posteriorly, with distinct angular ridges between dorsal and lateral surfaces. Mesopleuron divided by a transverse groove. Metanotal groove obsolete or reduced to a simple suture. Propodeum broad to narrowed dorsally, with sharp posterior margins. Propodeal spiracles slit-shaped. Metapleural gland orifice sometimes with a posterior flange. Metatibial spur formula (1s, 1p). Petiole squamiform to nodiform, the scale usually much wider than long, in dorsal view with a convex anterior face and in lateral view a forward-sweeping posterior face. Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Head, mesosoma and petiole deeply striate, rugoreticulate or punctate, the gaster usually finely punctate but sometimes striate (*e.g.* in *E. acutus*). Head and body with abundant short pilosity and light to dense pubescence. Color black.

*Queen*. Similar to worker but slightly larger, winged, with ocelli, larger compound eyes, and the usual modifications of the thoracic sclerites (Ogata, 1987).

*Male*. See description by Ogata (1987).

*Larva*. Not described.

**Geographic distribution.** *Ectomomyrmex* ranges across most of the Indo-Australian and Australasian regions, from India east to Japan and from northwestern China south to northern Australia (Brown, 1963).

**Ecology and behavior.** Very little is known about the habits of *Ectomomyrmex*. Anecdotal observations, and the moderately small eyes of *Ectomomyrmex* workers, suggest that their foraging habits are somewhat intermediate between epigeic and hypogeic. They are apparently generalist arthropod predators (Wilson, 1958c, 1959a), and Ke *et al.* (2008) observed that workers of *E. astutus* were particularly fierce predators of termites in an artificial arena. Wilson (1958c) observed *E. aciculatus* foraging diurnally on the forest floor among and under leaf litter, observed *E. exaratus* foraging on the forest floor, and reported that *E. striatulus* forms small colonies (fewer than 100 workers) and nests in rotting logs. Like its close relatives *Ponera* and *Cryptopone*, workers of *Ectomomyrmex* apparently feign death when disturbed (Wilson, 1958c).

**Phylogenetic and taxonomic considerations.** *Ectomomyrmex* was described by Mayr (1867) to hold the species *E. javanus* and *E. sundaicus* (now a junior synonym of *E. javanus*). Mayr did not designate a type species, but Bingham later (1903) designated *E. javanus* the type species. Subsequent to its original description, *Ectomomyrmex* was variously treated as a distinct genus (*e.g.*, Dalla Torre, 1893; Brown, 1963; Ogata, 1987), as a subgenus of *Pachycondyla* (*e.g.*, Emery, 1901; Wheeler, 1910; Forel, 1917), and eventually as a junior synonym of *Pachycondyla* (Brown, 1973, and most subsequent authors; but see Ogata, 1987).

Molecular evidence gives strong support for a sister relationship between *Ectomomyrmex* and *Ponera*, and not between *Ectomomyrmex* and *Pachycondyla* (Schmidt, 2013). A close relationship between *Ectomomyrmex* and *Ponera* is also supported by morphology (Taylor, 1967). *P. alpha* in particular is quite similar to *Ectomomyrmex*, and it is possible that these genera are not reciprocally monophyletic.

### Species of *Ectomomyrmex*

Wilson (1958c) provided a key to the Melanesian *Ectomomyrmex* fauna.

- E. aciculatus* (Emery, 1901): New Guinea (**comb. rev.**)
- E. acutus* (Emery, 1900): New Guinea (**comb. rev.**)
- E. aequalis* Mann, 1919: Solomon Islands (**comb. rev.**)
- E. annamitus* (André, 1892): Vietnam (**comb. rev.**)
- E. annamitus arcuatus* Forel, 1900: India (**comb. rev.**)
- E. apicalis* (Smith, F. 1857): Borneo (**comb. nov.**)
- E. astutus* (Smith, F., 1858): Australia (**comb. rev.**)
- E. astutus obscurus* (Karavaiev, 1935): Vietnam (**comb. nov.**)
- E. claudatus* Menozzi, 1926: Philippines (**comb. rev.**)
- E. exaratus* (Emery, 1901): New Guinea (**comb. rev.**)
- E. insulanus* (Mayr, 1876): Samoa Island (**comb. rev.**)
- E. javanus* Mayr, 1867: Java (**comb. rev.**)
- E. leeuwenhoekii* (Forel, 1886): India (**comb. rev.**)
- E. leeuwenhoekii jacobsoni* (Forel, 1915): Indonesia (Simalur I.) (**comb. nov.**)
- E. leeuwenhoekii sumatrensis* (Forel, 1901): Indonesia (Sumatra) (**comb. nov.**)
- E. lobocarenum* (Xu, 1996): China (**comb. nov.**)
- E. melancholicus* (Smith, 1865): Indonesia (**comb. nov.**)
- E. modiglianii* (Emery, 1900): Indonesia (Sumatra) (**comb. nov.**)
- E. obtusus* (Emery, 1900): Borneo (**comb. rev.**)
- E. overbeckii* (Viehmeyer, 1916): Singapore (**comb. nov.**)
- E. punctatus* (Karavaiev, 1935): Vietnam (**comb. nov.**)
- E. ruficornis* Clark, 1934: Australia (**comb. rev.**)
- E. sauteri* (Forel, 1912): Taiwan (**comb. nov.**)

*E. scobinus* Wilson, 1958: New Guinea (**comb. rev.**)  
*E. simillimus* (Donisthorpe, 1949): New Guinea (**comb. rev.**)  
*E. striatulus* (Karavaiev, 1935): Indonesia (**comb. rev.**)  
*E. striolatus* (Donisthorpe, 1933): India (**comb. nov.**)  
*E. sumatranus* (Özdikmen, 2010): Indonesia (Sumatra) (**comb. nov.**)  
*E. tonkinus* (Santschi, 1920): Vietnam (**comb. rev.**)  
*E. vermiculatus* (Emery, 1897): Indonesia (**comb. rev.**)  
*E. zhengi* (Xu, 1995): China (**comb. nov.**)

## ***Emeryopone* Forel**

Fig. 45

*Emeryopone* Forel, 1912: 761 (as genus). Type-species: *Emeryopone buttelreepeni* Forel, 1912: 762; by monotypy.

*Emeryopone* is a small genus (five described species) which ranges from Israel to Indonesia. Almost nothing is known about its habits, but its unusual mandibles suggest a specialized diet.

**Diagnosis.** *Emeryopone* workers are easily separated from most other ponerines by their long curved mandibles, which have five long teeth, the apical tooth greatly attenuated. The only genus with similar mandibles is *Belonopelta*, and to a much lesser extent *Thaumatomyrmex*. *Emeryopone* and *Belonopelta* can be separated by their frontal lobes (which are medium sized and separated anteriorly by a posterior extension of the clypeus in *Emeryopone*, and very small and closely approximated in *Belonopelta*) and body sculpturing and pilosity (foveolate with abundant short pilosity and variable pubescence in *Emeryopone*, and pruinose without upright pilosity in *Belonopelta*). *Thaumatomyrmex* has much longer mandibular teeth than *Emeryopone*, much more widely spaced frontal lobes, and larger eyes, among other differences.

**Synoptic description.** *Worker.* Small (TL 3.2–4.9 mm) ants with the standard characters of Ponerini. Mandibles long, narrow, with five teeth, the apical tooth greatly attenuated. Mandibles without a basal groove. Anterior clypeal margin convexly triangular. Frontal lobes small to moderate in size. Eyes small to very small, located far anterior of head midline. Metanotal groove absent or a vestigial suture. Propodeum broad dorsally. Propodeal spiracles round. Metatibial spur formula (1p). Petiole nodiform, the node rounded and wider than long. Subpetiolar process usually with a small lateral fovea near the anterior end. Gaster with a moderate girdling constriction between pre- and postsclerites of A4. Tergite of A4 moderately arched, the gaster mildly recurved. Head and body foveolate, with very light striations on the sides of the mesosoma and with abundant short pilosity and abundant to absent pubescence. Color ferruginous to black.

*Queen.* Described only for *E. melaina*: Similar to worker but slightly larger and alate, with three ocelli, larger eyes, and the modifications of the thoracic sclerites typical for winged ponerine queens (Xu, 1998).

*Male.* Not described.

*Larva.* Not described.

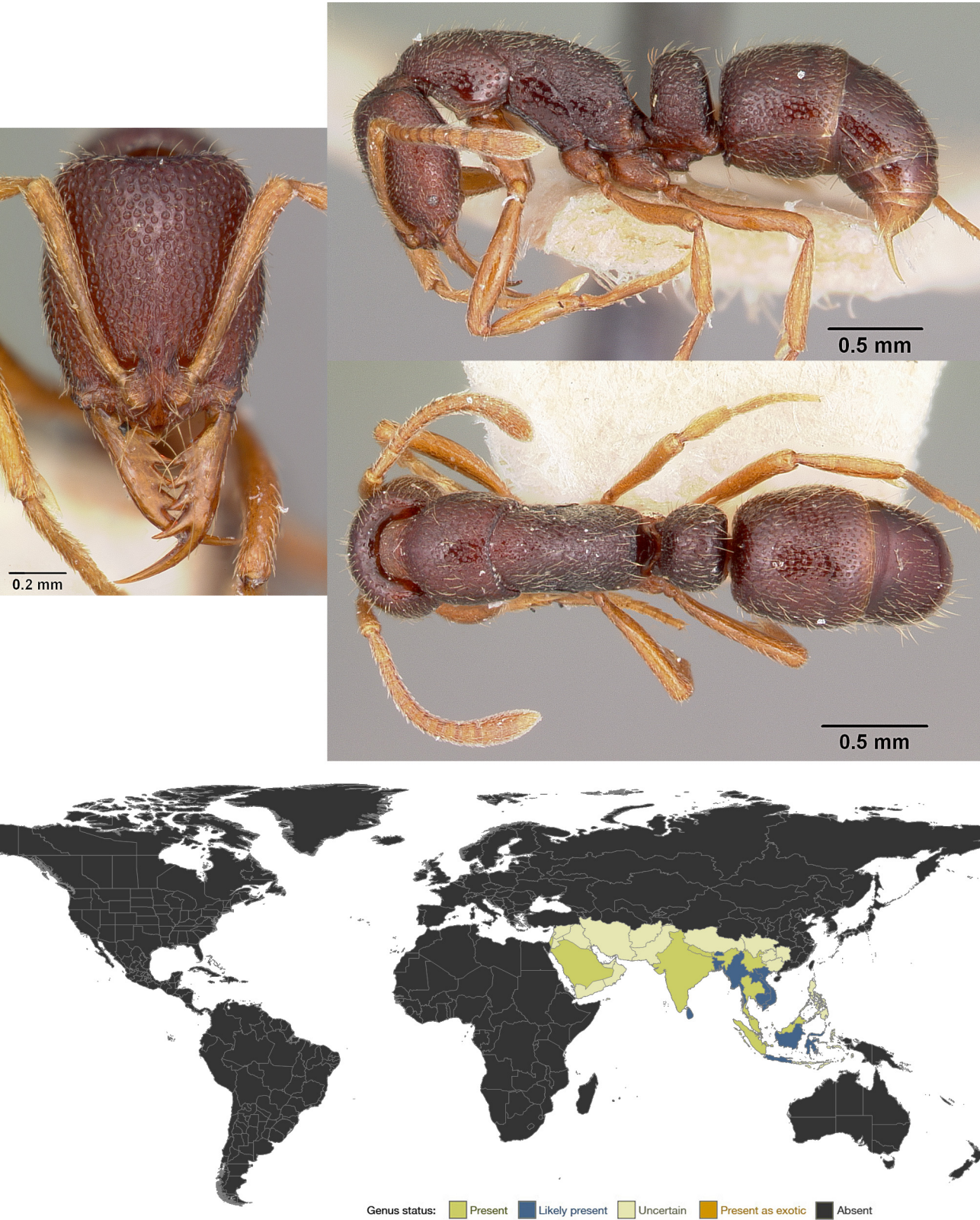
**Geographic distribution.** *Emeryopone* has an unusual distribution, with collections known from Israel, India, Nepal, southern China, Indonesia, and Malaysia (Baroni Urbani, 1975; Xu, 1998; Varghese, 2006; pers. obs.). Collections are rare and probably underestimate the true range of *Emeryopone* (Baroni Urbani, 1975).

**Ecology and behavior.** Basically nothing definite is known about the habits of *Emeryopone*. Based on their morphological characteristics and on collection data they are almost certainly cryptobiotic, and the rarity with which they are collected (Baroni Urbani, 1975; Xu, 1998; Varghese, 2006) suggests a low population density, though this may be an artifact of inadequate collection methods, as apparently has been the case with *Thaumatomyrmex* (see under that genus). The extremely similar mandibular structure of *Emeryopone* and *Belonopelta* suggests a similar diet preference, and though the feeding habits of *Emeryopone* have not been reported, some *Belonopelta* feed to a large degree on diplurans. *Emeryopone* may have a similar diet specialization. The downcurved gaster of *Emeryopone* implies that it hunts in tight spaces.

**Phylogenetic and taxonomic considerations.** The proper taxonomic status of *Emeryopone* is somewhat uncertain. Forel (1912) described *Emeryopone* for the single species *E. buttelreepeni* but noted its similarity with *Belonopelta*, apparently separating it from that genus only by its lack of a medial tooth on the anterior clypeal



margin (which is present in *B. attenuata* but not in *B. delectrix*, described later) and implicitly by its obsolete metanotal groove. Baroni Urbani (1975) later synonymized *Emeryopone* under *Belonopelta*, noting that those two characters are present in varying degrees in the other species he included in *Belonopelta*.



**FIGURE 45.** Worker caste of *Emeryopone buttelreepeni*: lateral and dorsal view of body and full-face view of head (CASENT0104586, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Emeryopone*.

Baroni Urbani's (1975) synonymizing of *Emeryopone* under *Belonopelta* is undermined by his taxonomic treatment of *Belonopelta*: he included both *Simopelta* and *Emeryopone* as junior synonyms of *Belonopelta*, while removing *B. deletrix* to the separate genus *Leiopelta*. Molecular evidence indicates that *Emeryopone* is not even sister to *Simopelta* and there is no morphological evidence to suggest otherwise. Further, P.S. Ward (pers. comm.) has found that *Belonopelta* belongs to the *Pachycondyla* group while Schmidt (2013) placed *Emeryopone* in the *Ponera* group. Thus it seems clear that the morphological similarities between *Belonopelta* and *Emeryopone* are the result of convergence rather than close relationship.

Schmidt's (2013) molecular phylogeny of the Ponerinae places *Emeryopone* within the *Ponera* genus group as sister to the clade composed of *Ponera*, *Ectomomyrmex*, *Cryptopone*, *Austroponera*, *Parvaponera* and *Pseudoponera*. Morphological evidence suggests that *Emeryopone* may actually be sister to *Ponera*, as both genera share an overall similar gestalt and both have a fenestra in the subpetiolar process (absent in one *Emeryopone* species). They differ most obviously in their mandibles and in the vaulting of A4. A sister relationship between *Emeryopone* and *Ponera* cannot be statistically rejected (Schmidt, 2013).

### Species of *Emeryopone*

Varghese (2006) provides a key to *Emeryopone* species.

*E. buttelreepeni* Forel, 1912: Indonesia (Sumatra)

*E. franzi* (Baroni Urbani, 1975): Nepal

*E. loebli* (Baroni Urbani, 1975): Israel

*E. melaina* Xu, 1998: China

*E. narendrani* Varghese, 2006: India

### *Iroponera* gen. nov.

Fig. 46

Type-species: *Iroponera odax* (described below); by present designation.

*Iroponera* is a monotypic genus restricted to south-eastern Australia. It occurs in wet forested habitats and is infrequently encountered.

**Etymology.** The name *Iroponera* is based on the Latin *ironia*, “assumed ignorance”, combined with the suffix “-ponera”, derived from the subfamily name Ponerinae. The name expresses our surprise at finding such a novel genus in a well-collected country like Australia.

**Diagnosis.** *Iroponera* workers are recognizable by the presence of a single metabial spur, absence of eye (although small dimples or slight discolorations are sometimes present where the eyes would be expected) and elongate and narrow mandibles with three or four small, widely spaced teeth. In overall body shape and size *Iroponera* closely resembles *Hypoconera* or *Ponera*, and all of these genera share the single metatibial spur. However, the unique mandibular shape and lack of eyes will separate this genus from others in the subfamily.

**Synoptic description.** *Worker.* Small-sized (TL 2.6 mm) ants with the standard characters of Ponerini. Mandibles elongate and narrow, with three or four small, widely spaced teeth on the masticatory margin, the basal margin essentially absent, and lacking a basal groove or pit. Anterior clypeal margin broadly rounded and convex. Frontal lobes moderately large. Antennae often with a four segmented apical club. Eyes essentially absent, at most with small dimples or slight discolorations present where the eyes would be expected. Metanotal groove reduced to a suture. Propodeum broad dorsally. Propodeal spiracles round to oval. Metatibial spur formula (1p). Petiole nodiform. Helcium projecting from near midheight of anterior face of A3. Prora reduced and apparently absent. Girdling constriction between pre- and postsclerites of A4 apparent. Head, mesosoma and petiole weakly sculptured and with a matte surface, gaster weakly punctate. Head and body with scattered pilosity and a moderately dense pubescence. Color orange.

*Queen.* Not described.

*Male.* Not described.





**FIGURE 46.** Worker caste of *Iroponera odax*: lateral and dorsal view of body and full-face view of head (holotype, MCZC); world distribution of *Iroponera*.

*Larva.* Not described.

**Geographic distribution.** *Iroponera* is restricted to south-eastern Australia (southern New South Wales, Victoria and Tasmania).

**Ecology and behavior.** This genus has been encountered only a handful of times and very little is known regarding its biology. All collections have been made at wetter sites consisting of wet sclerophyll woodlands. Nests occur in soil under rocks or under bark and contain only a few workers. The lack of eyes, small body size and pale color suggest a hypogeic lifestyle, and this may explain their infrequent collection.

**Phylogenetic and taxonomic considerations.** The placement of this genus within the Ponerinae has not been



examined in detail as the taxon was not included in Schmidt's (2013) phylogeny. While superficially similar to *Dolioponera*, another tiny, eyeless, depigmented, slender ponerine with clubbed antennae and generally cryptobiotic habitus, this similarity is undoubtedly convergent. W. L. Brown (pers. comm.) speculated that *Iroponera* might be close to *Cryptopone*, but the lack of basal mandibular pits and mesotibial pusher setae, together with contrasting mesosomal shape and mandibular structure strongly suggest otherwise. In some ways, the *Iroponera* mandibles remind one of *Myopias*, but they are not as long and close differently, nearer to the clypeal margin. Determining the exact placement of this genus within the subfamily will require further data.

### Species of *Iroponera*

*Iroponera* is known from a single species which is described here.

#### *Iroponera odax* sp. nov.

**Type material:** Holotype worker and five paratype workers from Pioneer State Forest, Tasmania, Australia, approx. 41°05'S 147°56'E, 14 January 1992, B.B. Lowery & L. Gregson, sassafras gully, in soil bank (ANIC, holotype ANIC32-066627, paratypes ANIC32-002572).

Worker description (see also genus description above): Head oblong, with nearly straight, parallel sides; posterior corners rather abruptly rounded; vertexal margin very shallowly concave. Frontal lobes broad, together occupying a space greater than 1/3 HW, roofing antennal insertions and nearly all of antennal radicles. Scapes gradually incrassate apicad; funiculus with massive 4-segmented apical club, significantly wider than scape, and at least twice as wide as basal funicular segments. Labrum shallowly bilobed, the lobes broadly rounded. Palpal segment count not determined, but apparently 2,2 or less.

Mesosoma slender, tapering only moderately caudad, with only a weak and brief constriction at the mesonotal groove. Petiole with steeply sloping anterior face; dorsal face distinct, but rounding into posterior face; in dorsal view slightly broader than long, even including the brief anterior cornuae. Subpetiolar process a broad blade with convex margin. Gaster cylindrical, straight, with a distinct constriction after A3; A4 broader than A3, and the same length, not vaulted. A5 as wide as A4, but slightly longer; terminal segments conical and retractile; sting strong.

Sculpture exceedingly fine, densely micropunctulate; opaque, with only A5, gastric apex, propodeal declivity, posterior face of petiolar node and limited parts of the appendages showing a weak shine. Pilosity scattered and with moderately dense pubescence. Color dull, light yellow throughout.

Measurements (holotype): total length 2.5mm, head length 0.62mm, head width 0.44mm (cephalic index 71), mandible length 0.27mm, scape length 0.30mm (scape index 68), Weber's length 0.80mm, petiole length 0.27mm, hind femur length 0.35mm, hind tibia length 0.31mm.

**Material examined:** **Australia.** *New South Wales:* Royal National Park (Ward,P.S.); Mt. Tomah (Ward,P.S.); 25km E Fitzroy Falls (Lowery,B.B.); *Tasmania:* Pioneer State Forest (Lowery, B.B. & Gregson,L.); *Victoria:* Warburton (Mercovich,C.T.).

#### *Parvaponera* gen. nov.

Fig. 47

Type-species: *Belonopelta darwinii* Forel, 1893d: 460; by present designation.

*Parvaponera* is a small, rarely encountered genus known from 7 species and subspecies. It is widely distributed, being found in tropical Africa and Madagascar, Southeast Asia and the Australian region. Its biology is essentially unknown.

**Etymology.** This genus name is derived from the Latin *parva*, alluding to the generally small size of these ants, combined with “pone”, derived from the subfamily name Ponerinae.

**Diagnosis.** Workers of *Parvaponera* can be separated from other Ponerinae by the following combination of characters: eyes small (2-4 facets) or absent, mandibles short, without a basal pit or groove, propodeal spiracle generally elongate or slit-like (oval or nearly circular in a few species), ventral apex of the metatibia with one pectinate and one simple spur and subpetiolar process triangular and with an anterior fenestra and/or a pair of teeth.



**FIGURE 47.** Worker caste of *Parvaponera darwinii*: lateral and dorsal view of body and full-face view of head (CASENT0172437, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Parvaponera*.

They are most likely to be confused with *Centromyrmex*, *Hypoponera* or *Ponera*. While both *Centromyrmex* and *Parvaponera* have reduced eyes, *Parvaponera* lacks pusher-setae on the tibiae as found in *Centromyrmex* (although they are present on the mesobasitarsus in some species of *Parvaponera*) and has a much more complex

subpetiolar process which possesses either an anterior fenestra or posteroventral teeth, both of which are lacking in *Centromyrmex*. While superficially similar to *Hypoponera* and *Ponera*, *Parvaponera* has a pair of spurs present on the metatibia while only a single spur is present in these genera.

**Synoptic description.** *Worker*. Small, slender ants with the standard characters of Ponerini. Mandibles triangular and lacking a basal groove or pit. Clypeus generally with a central tooth or short projection, absent in a few African species. Frontal lobes moderately small. Eyes small in size or absent, located fairly anterior on head. Mesopleuron lacking a transverse groove. Metanotal groove present or absent. Propodeum not narrowed dorsally. Propodeal spiracle generally elongate or slit-like (oval or nearly round in a few African species). A row of short traction setae present on mesobasitarsus in African species (apparently absent in Asian species). Metatibial spur formula (1s, 1p). Petiole squamiform. Prora conspicuous. Girdling constriction between pre- and postsclerites of A4 apparent. Pretergite of A4 without a stridulitrum. Head and body finely punctate and with a matte surface, with sparse pilosity and abundant pubescence. Color variable, testaceous to dark brown.

*Queen*. Similar to worker but slightly larger, alate and with the other caste differences typical for ponerines.

*Male*. Not described.

*Larva*. Not described.

**Geographic distribution.** This small genus shows a broad distribution range, with species occurring in tropical Africa, Madagascar, Southeast Asia, Australia and the Solomon Islands.

**Ecology and behavior.** *P. darwinii* is widespread throughout the Old World tropics and until recently was known only from the queen caste (Terayama, 1990), which along with worker structure suggests a hypogeic lifestyle. Morgan *et al.* (2003) analyzed the Dufour's gland secretions of *P. darwinii* (as "*P. indica*").

**Phylogenetic and taxonomic considerations.** Unfortunately none of the species placed here were included in Schmidt's (2013) molecular phylogeny of the Ponerinae and the current treatment is based on morphology. Because of this the sister relationships of *Parvaponera* within the Ponerinae are uncertain. It shares the presence of stout traction setae on the mesobasitarsi with *Buniapone*, *Centromyrmex*, *Feroponera* and *Promyopias*. The absence of compound eyes in workers is shared with *Boloponera*, *Centromyrmex*, *Dolioponera*, *Feroponera*, *Iroponera* and *Promyopias*. However, it is unlikely that these characters share a common origin and they are more likely the result of adaptation to a cryptic lifestyle. Perhaps most interestingly, the subpetiolar process shares characteristics with *Ponera* in that species of *Parvaponera* have either an anterior fenestra and/or a pair of posteroventral teeth. It will be interesting to learn if this similarity is the result of close relationship or as a result of convergent evolution, as appears to be the case with the mesobasitarsus and reduction in eye size.

### Species of *Parvaponera*

*P. cavimaculata* Wang & Zhao, 2009: China (**comb. nov.**)

*P. darwinii* (Forel, 1893): Australia (**comb. nov.**)

*P. darwinii africana* (Forel, 1909): DRC (**comb. nov.**)

*P. darwinii indica* (Emery, 1899): Myanmar (**comb. nov.**)

*P. darwinii madecassa* (Emery, 1899): Madagascar (**comb. nov.**)

*P. myropola* (Menozzi, 1925): Philippines (**comb. nov.**)

*P. sheldoni* (Mann, 1919): Solomon Isl. (**comb. nov.**)

### *Ponera* Latreille

Fig. 48

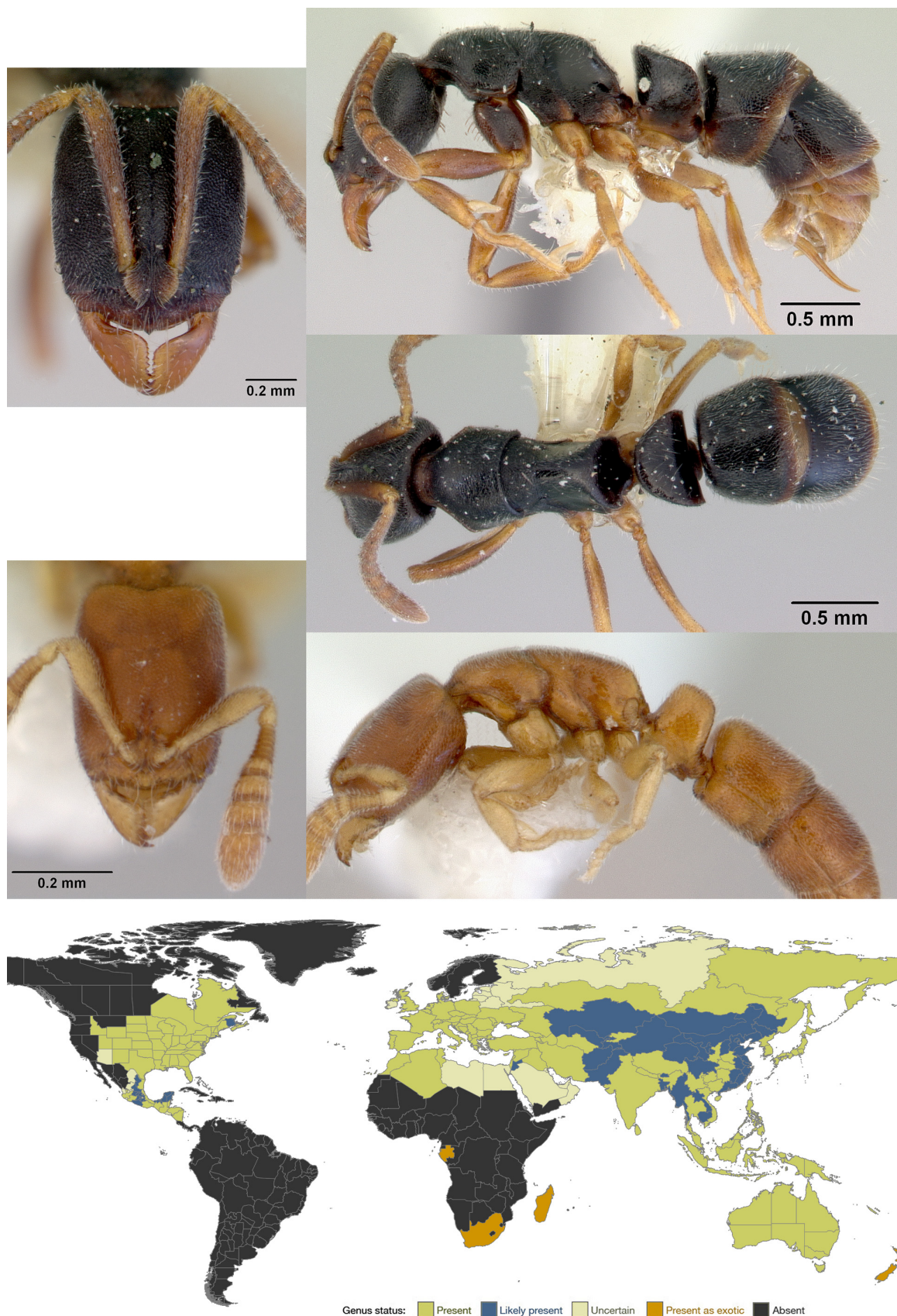
*Ponera* Latreille, 1804: 179 (as genus). Type-species: *Formica coarctata* Latreille, 1802c: 65; by subsequent designation of Westwood, 1840: 83.

*Pseudocryptopone* Wheeler, W.M., 1933a: 12 (as genus). Type-species: *Cryptopone tenuis* Emery, 1900a: 321; by original designation. Wilson, 1957: 356 (*Pseudocryptopone* as junior synonym of *Ponera*).

*Pteroponera* Bernard, 1950: 3 (as genus). Type-species: *Pteroponera sysphinctoides* Bernard, 1950: 4; by monotypy. Brown, 1973: 184 (*Pteroponera* as junior synonym of *Ponera*).

*Selenopone* Wheeler, W.M., 1933a: 19 (as genus). Type-species: *Ponera selenophora* Emery, 1900a: 317; by original designation. Wilson, 1957: 356 (*Selenopone* as junior synonym of *Ponera*).





**FIGURE 48.** Worker caste of *Ponera*. Upper specimen: *Ponera alpha*: lateral and dorsal view of body and full-face view of head (CASENT0172423, April Nobile and [www.antweb.org](http://www.antweb.org)). Lower specimen: *Ponera tenuis*: lateral view of body and full-face view of head (ANIC32-001503 and CASENT0172429, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Ponera*.

*Ponera* is a large genus (53 described species) of small cryptobiotic ponerines. Though Asia is the center of *Ponera* species diversity, a small number of species occur in Europe, Madagascar, and North America.

**Diagnosis.** Workers of *Ponera* are superficially similar to those of several other ponerine genera, including *Hypoponera*, *Cryptopone*, *Euponera* and *Pseudoponera*, but *Ponera* differs from these genera in having an anterior fenestra in the subpetiolar process. A few species of *Hypoponera* apparently also have a fenestra, but they lack the paired posterior teeth on the subpetiolar process that are typical of *Ponera*, and *Hypoponera* has only a single maxillary palp segment while *Ponera* has two. Some *Belonopelta* and *Emeryopone* also have an anterior fenestra in the subpetiolar process, but these genera have narrow mandibles with long attenuated teeth, while *Ponera* has typical triangular mandibles with only short teeth.

**Synoptic description.** *Worker.* Very small to small (TL 1–4 mm) ants with the standard characters of Ponerini. Mandibles triangular, with numerous small teeth or denticles on the masticatory margin and without a basal groove or pit. Anterior clypeal margin mildly convex, sometimes with a median tooth. Frontal lobes small and closely approximated for nearly their entire length. Antennae often with a four or five segmented apical club. Eyes very small and located very far anterior on the sides of the head. Metanotal groove reduced to a suture. Propodeum broad to mildly narrowed dorsally, with sharp posterior margins. Propodeal spiracles round. Metatibial spur formula (1p). Petiole squamiform, in dorsal view with a convex anterior face and a straight posterior face. Subpetiolar process rectangular or rounded, sometimes with a pair of teeth at the posterior margin and always with a thin spot (fenestra) near the anterior end. Gaster with a strong girdling constriction between pre- and postsclerites of A4. Stridulitrum present on pretergite of A4. Hypopygium rarely with a row of stout spines on each side. Head and body lightly punctate, sometimes with light striations on the sides of the mesosoma and sometimes with smooth and shiny regions of the mesosoma. Head and body with sparse pilosity but a dense pubescence. Color variable, testaceous to black. See the more detailed description in Taylor (1967).

*Queen.* Similar to worker but winged, with ocelli, larger compound eyes, and the usual modifications of the thoracic sclerites (Taylor, 1967).

*Male.* See description by Taylor (1967).

*Larva.* Described by Wheeler (1900b), Wheeler & Wheeler (1952, 1971a), Taylor (1967), and Escoubas *et al.* (1987). *Ponera* larvae have three or four pairs of sticky tubercles with which they are attached to nest walls by workers (Taylor, 1967).

**Geographic distribution.** The species diversity of *Ponera* is highest in eastern and southeastern Asia and Melanesia, with only a few species reaching Australia and points east. Like the distantly related but convergent genus *Hypoponera*, *Ponera* seems better adapted to inhabiting temperate regions of the world than most ponerines, as an endemic cluster of *Ponera* species occurs in Europe and North America. A few species are readily spread by human activity (Taylor, 1967; Bolton & Fisher, 2011). Two undescribed *Ponera* species are known from the Malagasy region (Antweb, 2008; but see Bolton & Fisher, 2011), and an undescribed species which may be a *Ponera* is known from Costa Rica (Longino, 2013). See Taylor (1967) for a detailed discussion of *Ponera* biogeography.

**Ecology and behavior.** The ecology and behavior of *Ponera* were reviewed by Taylor (1967). We will only briefly summarize his key points and then note additional research. *Ponera* are among the smallest of all ponerines and are thus well adapted to a cryptobiotic lifestyle. Nests are constructed in rotting wood or under rocks, and colonies are small, usually with around 30 workers, but colonies with up to 60 workers have been reported in *P. pennsylvanica* (Wheeler, 1900a) and an average colony size of 60 workers and a maximum observed colony size of 135 workers was reported for *P. coarctata* (Liebig *et al.*, 1985). Like *Hypoponera*, *Ponera* larvae have specialized sticky tubercles with which workers attach them to nest surfaces, moving them higher to avoid flooding. *Ponera* are probably generalist arthropod predators, though few direct observations of their food preferences have been observed. In cafeteria-style feeding experiments, various *Ponera* species in New Guinea accepted diplurans, collembolans, and spiders, but rejected various other prey. Workers are rarely seen foraging on the ground surface, but are collected from leaf litter, moss, rotting wood, and other confined microhabitats. Workers are sluggish and feign death when disturbed (Wilson, 1957; Pratt *et al.*, 1994). Colony foundation is semi-claustral (Taylor, 1967).

Pratt *et al.* (1994) studied the division of labor in colonies of *P. pennsylvanica*. Most colonies exhibited typical age-related polyethism, with younger workers focusing on brood care and older workers on foraging. Most colonies were monogynous, but some had multiple queens (though the reproductive division of labor among them was unknown). Both winged and ergatoid queens occur in this species (ergatoids have also been reported in *P.*

*coarctata*: Wheeler, 1900a). *P. pennsylvanica* is unusual among ponerines in that it mates in large swarms of reproductives away from the nest (Haskins, 1970; Peeters, 1991a). Pratt *et al.* (1994) observed that foraging in this species is generally performed by solitary workers, but groups of workers will sometimes cooperate to retrieve large prey. Tandem running was used during nest emigrations (this has also been reported for *P. coarctata*: N Carlin, pers. comm. in Hölldobler & Wilson, 1990). See Wheeler (1900a), Kanno (1959), and Mackay & Anderson (1991) for additional details of the habits of *P. pennsylvanica*. Johnson (1987) reported on the distribution and ecology of *P. exotica*.

Liebig *et al.* (1995) observed queen size polymorphism in *P. coarctata*, a close relative of *P. pennsylvanica*, and Liebig *et al.* (1997) found that workers in orphaned colonies of *P. coarctata* form dominance hierarchies through aggressive interactions, and that they exchange liquids via trophallaxis as a form of social appeasement (among ponerines, trophallaxis is otherwise only known from some *Hypoponera*).

**Phylogenetic and taxonomic considerations.** *Ponera* Latreille (1804) is one of the two oldest genus names in the Ponerinae (the other being *Odontomachus*), and is the designated type genus of both Ponerinae and Ponerini. For much of the early taxonomic history of the Ponerinae, *Ponera* served as a sort of default genus into which most new species were placed. This fact is demonstrated by Bolton *et al.* (2006), who list 312 species and subspecies names which have been transferred out of *Ponera* and into other ponerine genera (this is nearly as many as are listed for *Formica*, the oldest ant genus name). Only as the subfamily became gradually more finely divided along generic lines did the current boundaries of *Ponera* start to take shape.

The identity of the type species of *Ponera* is somewhat controversial. Latreille (1804) did not designate a type species when first describing the genus, but later (Latreille, 1810) designated *Ponera crassinoda* (now *Pachycondyla crassinoda*) the type species. Westwood (1840) was either unaware of this designation or chose to ignore it, as he named *P. coarctata* the type species of *Ponera*. Emery (1901) later designated *P. crassinoda* as the type species of *Pachycondyla*. Subsequent authors have universally used the generic names *Ponera* and *Pachycondyla* in the sense of Westwood and Emery. See Taylor (1967) for a more detailed discussion of this issue. We follow recent authors and treat *Ponera coarctata* as the type species of *Ponera*.

*Ponera* has three junior synonyms: *Pseudocryptopone* Wheeler (1933a), *Selenopone* Wheeler (1933a), and *Pteroponera* Bernard (1950), the latter described only from a male specimen and synonymized unceremoniously under *Ponera* by Brown (1973). In removing several species from *Ponera* to create his new genera *Pseudocryptopone* and *Selenopone*, Wheeler (1933a) admitted the flimsy merits of his new generic distinctions, and Wilson (1957) later agreed, synonymizing *Pseudocryptopone* and *Selenopone* back under *Ponera*. The final major change in the taxonomy of *Ponera* came with the thorough revision by Taylor (1967). Taylor recognized that “*Ponera*” actually consisted of two unrelated lineages: true *Ponera*, represented by most of the species formerly placed in *Pseudocryptopone* and *Selenopone*, as well as *Ponera coarctata* and its relatives; and the much larger genus *Hypoponera*. See Taylor (1967) for a more detailed discussion of the taxonomic history of *Ponera*.

Schmidt's (2013) molecular phylogeny of the Ponerinae confirms Taylor's distinction between *Ponera* and *Hypoponera* and places *Ponera* as sister to *Ectomomyrmex*. This relationship is also supported by morphology (Taylor, 1967). While there are no obvious synapomorphies linking *Ponera* and *Ectomomyrmex*, some species of *Ponera* (e.g., *P. alpha*) are quite similar to *Ectomomyrmex* (Taylor, 1967). It is possible that *Ectomomyrmex* will prove to be non-monophyletic with respect to *Ponera*, with the latter genus representing a morphologically reduced clade within *Ectomomyrmex*. The reverse scenario, with *P. alpha* as sister to *Ectomomyrmex* (and *Ponera* hence non-monophyletic) is also possible but less plausible given the morphological reductions in *Ponera* (Taylor, 1967). Many species of *Emeryopone* have an anterior fenestra in their subpetiolar process as in *Ponera*, and this character could represent a synapomorphy of these two genera, though molecular phylogenetic evidence (Schmidt, 2013) suggests that they are not sisters.

### Species of *Ponera*

Taylor (1967) revised the species level taxonomy of *Ponera* and provided a key to species. Since his revision, numerous additional species have been described, especially from China (Xu, 2001a, 2001b; Zhou, 2001) and Japan (e.g., Terayama, 1996). Xu (2001a) provided a key to the Chinese *Ponera* fauna.



*P. affinis* Jerdon, 1851: India  
*P. alisana* Terayama, 1986: Taiwan  
*P. alpha* Taylor, 1967: New Guinea  
*P. augusta* Taylor, 1967: New Guinea  
*P. bableti* Perrault, 1993: Mururoa (Fangataufa Atoll)  
*P. baka* Xu, 2001: China  
*P. bawana* Xu, 2001: China  
*P. bishamon* Terayama, 1996: Japan  
*P. borneensis* Taylor, 1967: Borneo  
*P. chapmani* Taylor, 1967: Philippines  
*P. chiponensis* Terayama, 1986: Taiwan  
*P. clavicornis* Emery, 1900: New Guinea  
*P. coarctata* (Latreille, 1802): Luxembourg  
*P. colaensis* Mann, 1921: Fiji Islands  
*P. diodonta* Xu, 2001: China  
*P. elegantula* Wilson, 1957: New Guinea  
*P. exotica* Smith, M.R., 1962: United States  
*P. guangxiensis* Zhou, 2001: China  
*P. incerta* (Wheeler, W.M., 1933): Java  
*P. japonica* Wheeler, W.M., 1906: Japan  
*P. kohmoku* Terayama, 1996: Japan  
*P. leae* Forel, 1913: Tasmania  
*P. loi* Taylor, 1967: Samoa  
*P. longlina* Xu, 2001: China  
*P. manni* Taylor, 1967: Fiji Islands  
*P. menglana* Xu, 2001: China  
*P. nangongshana* Xu, 2001: China  
*P. oreas* (Wheeler, W.M., 1933): Philippines  
*P. paedericera* Zhou, 2001: China  
*P. pennsylvanica* Buckley, 1866: United States  
*P. pentodontos* Xu, 2001: China  
*P. petila* Wilson, 1957: New Guinea  
*P. pianmana* Xu, 2001: China  
*P. pumila* Jerdon, 1851: India  
*P. rishen* Terayama, 2009: Taiwan  
*P. ruficornis* Spinola, 1851: Brazil  
*P. scabra* Wheeler, W.M., 1928: Japan  
*P. selenophora* Emery, 1900: New Guinea  
*P. shennong* Terayama, 2009: Taiwan  
*P. sinensis* Wheeler, W.M., 1928: Hong Kong  
*P. swezeyi* (Wheeler, W.M., 1933): Hawaii  
*P. syscena* Wilson, 1957: New Guinea  
*P. sysphinctoides* Bernard, 1950: France  
*P. szaboi* Wilson, 1957: New Guinea  
*P. szentivanyi* Wilson, 1957: New Guinea  
*P. taipingensis* Forel, 1913: West Malaysia  
*P. takaminei* Terayama, 1996: Japan  
*P. tamon* Terayama, 1996: Japan  
*P. taiyangshen* Terayama, 2009: Taiwan  
*P. tenuis* (Emery, 1900): New Guinea  
*P. testacea* Emery, 1895: France  
*P. woodwardi* Taylor, 1967: Samoa

*P. xantha* Xu, 2001: China  
*P. xenagos* Wilson, 1957: New Guinea  
*P. yuhuang* Terayama, 2009: Taiwan

Fossil species (*incertae sedis*)

† *P. elegantissima* Meunier, 1923: Germany (Oligocene)  
† *P. lobulifera* Dlussky, 2009: Baltic Amber  
† *P. mayri* Dlussky, 2009: Baltic Amber  
† *P. leptcephala* Emery, 1891: Sicilian Amber  
† *P. minuta* Donisthorpe, 1920: Great Britain (Oligocene)  
† *P. wheeleri* Dlussky, 2009: Bitterfeld Amber

### ***Pseudoponera* Emery**

Fig. 49

*Pseudoponera* Emery, 1900a: 314 (as subgenus of *Pachycondyla*). Type-species: *Ponera quadridentata* Smith, F., 1859: 143 (junior synonym of *Formica stigma* Fabricius, 1804: 400); by monotypy.

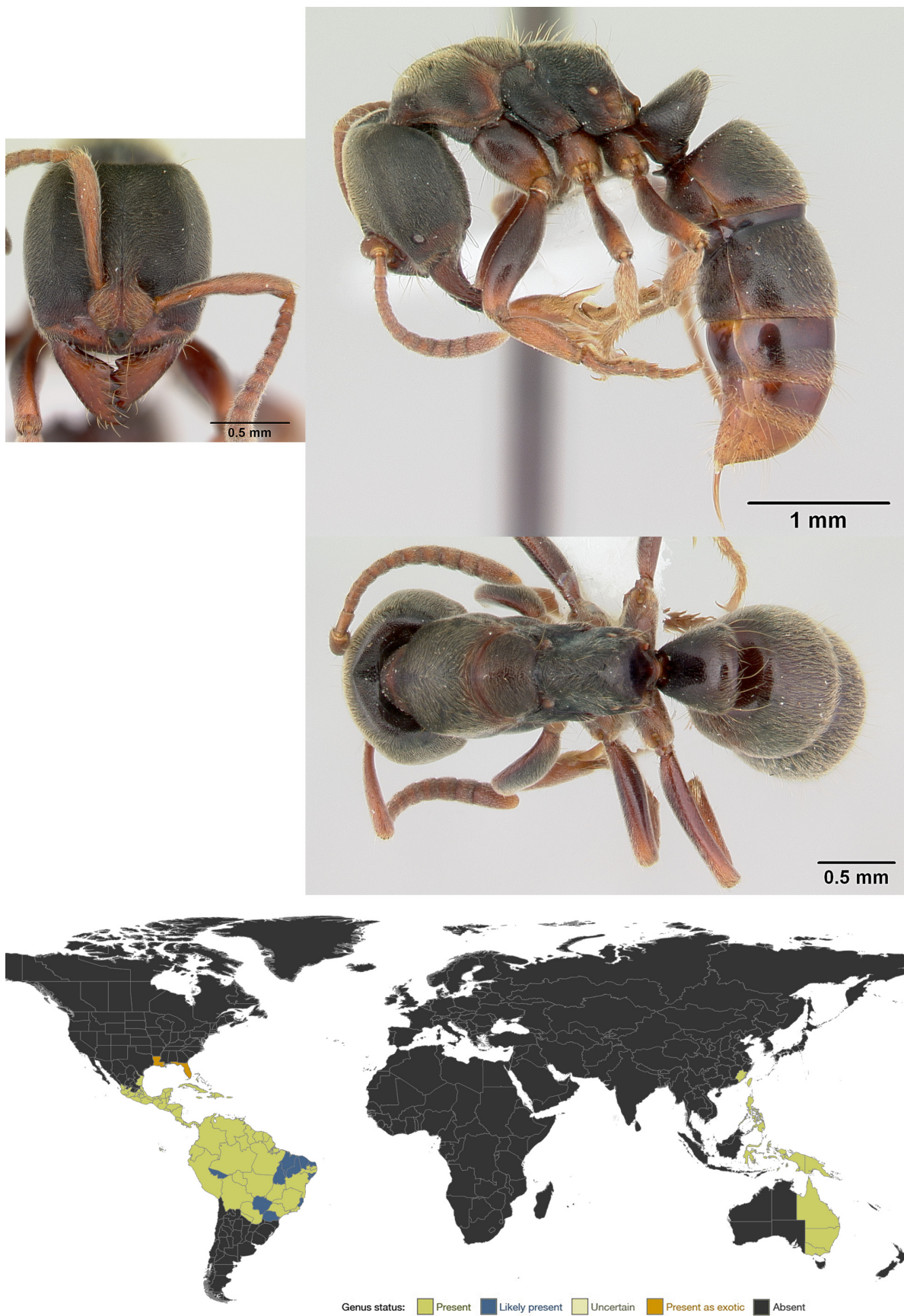
*Trachymesopus* Emery, 1911: 84 (as subgenus of *Euponera*; in Ponerinae, Ponerini). Type-species: *Formica stigma* Fabricius, 1804: 400; by original designation. Bolton, 1995: 48 (*Trachymesopus* as junior synonym of *Pseudoponera*, due to synonymous type species).

*Trachyponera* Santschi, 1928: 43 (incorrect subsequent spelling of *Trachymesopus* Emery).

*Pseudoponera* species are small to medium-sized and found in tropical regions of the Americas and from China south to Australia. The genus currently contains 6 species.

**Diagnosis.** Workers of *Pseudoponera* lack any obvious autapomorphies and superficially resemble those of a number of other genera, including *Austroponera*, *Cryptopone*, *Euponera*, *Hypoponera*, *Mesoponera* and *Rasopone*. Separation from these and other genera of the Ponerinae is based on the following set of characters: compound eyes present, mandible with a basal groove (occasionally weakly developed) but no pit, ventral apex of the metatibia with one pectinate and one simple spur, mesosomal profile nearly continuous but interrupted by a shallowly impressed metanotal groove, propodeal spiracle slit-shaped, subpetiolar process without an anterior fenestra and prora present on the anterior margin of the first gastral sternite. *Pseudoponera* is morphologically most similar to *Austroponera* and some species of *Euponera*. It can be separated from *Austroponera* by the presence of slit-shaped propodeal spiracles (they are round in *Austroponera*) and from *Euponera* by the lack of a basal mandibular pit. *Pseudoponera* is also similar to *Cryptopone*, but differs from it in having eyes, lacking a basal pit on the mandibles, and lacking mesotibial traction setae. *Pseudoponera* workers also strongly resemble those of *Hypoponera*, but have two metatibial spurs instead of one, generally have wider heads, and tend to be slightly larger. *Pseudoponera* is similar to *Mesoponera* but is generally smaller, with denser pilosity, smaller eyes, larger frontal lobes, a wider head, and a broader propodeal dorsum. Workers of *Pseudoponera* could also conceivably be confused with those of *Brachyponera*, but these genera differ in their metanotal groove structure (reduced to a suture in *Pseudoponera* but deeply impressed in *Brachyponera*), and *Pseudoponera* lacks the basal mandibular pits of *Brachyponera*. Finally, *Pseudoponera* can be separated from *Rasopone* by the presence of a basal mandibular groove (occasionally weakly developed) and a slit-shaped rather than round or oval propodeal spiracle.

**Synoptic description.** *Worker.* Medium-sized (TL 3.25–5.5 mm) ants with the standard characters of Ponerini. Mandibles triangular, with roughly five to ten teeth and a basal groove (pit absent or obsolete). Anterior margin of clypeus broadly convex. Frontal lobes moderately large and closely approximated. Scapes flattened basally. Eyes very small to small (2–4 facets in diameter), located far anterior on sides of head. Mesopleuron entire. Metanotal groove present as a shallow impression. Metapleural gland orifice without a posterior U-shaped cuticular lip. Propodeum generally narrowing dorsally (more strongly narrowed anteriorly) and with a distinct dorsal face. Propodeal spiracles elongate and slit-like. Metatibial spur formula (1s, 1p). Petiole generally scale-like, rounded dorsally. Gaster with a strong girdling constriction between pre- and postsclerites of A4, stridulatory organ absent. Head and body finely punctate, sometimes with light striations on the sides of the mesosoma, and with abundant pilosity and dense pubescence. Color variable, generally dark brown to ferruginous.



**FIGURE 49.** Worker caste of *Pseudoponera stigma*: lateral and dorsal view of body and full-face view of head (CASENT0178180, April Nobile and [www.antweb.org](http://www.antweb.org)); world distribution of *Pseudoponera*.



**Queen.** Similar to worker but slightly larger, alate, with ocelli and larger compound eyes, and with the modifications of the thoracic sclerites that are typical of alate ponerine queens.

**Male.** Emery (1911) provided a diagnosis for *Pseudoponera* males, but he circumscribed the genus differently than it is here and some aspects of his diagnosis may no longer apply. Ogata (1987) provided a description for males of *Trachymesopus*, which is synonymous with our definition of *Pseudoponera* (s.s.), but he included *Parvaponera darwinii*, which we place in a separate genus.

**Larva.** Described for various species by Wheeler & Wheeler (1952, 1971a, 1976).

**Geographic distribution.** The majority of species included here in *Pseudoponera* are Neotropical with a single species occurring in eastern Australia. One species, *P. stigma*, is widespread in both the Neotropics and the Asia Pacific (Wetterer, 2012a). It is generally accepted that this is a New World species which has become established in Asia through dispersal by humans. However, Wetterer (2012) points out that there is little direct evidence to support this and the biology of this species is not typical of invasive ants.

**Ecology and behavior.** Very little is known about the ecology and behavior of *Pseudoponera*, and the heterogeneous nature of the genus as defined here casts more doubt than usual on any attempt to extrapolate from observations of single species or species groups to the genus as a whole. On the other hand, the taxa placed here in *Pseudoponera* all share a small body size and apparently cryptobiotic habits, and most of them are probably generalist predators and scavengers. Below are a few brief notes on observations of individual species.

The type species of the genus, *P. stigma*, is a versatile and adaptable species which can apparently utilize a wide range of habitats and nesting sites (Longino, 2013; Wetterer, 2012a). Wilson (1958c) reported that in New Guinea this species is forest-dwelling, nests under the bark of rotting logs, forages singly, has a diffuse nest structure, and has independent colony foundation. Wild (2002) reported that *P. stigma* in Paraguay nests in rotting wood and forages in leaf litter, while in Costa Rica the small colonies of this species have been found from the ground layer up to the canopy (Longino, 2013). Oliveira *et al.* (1998) reported on a colony of *P. stigma* in Brazil which contained 80 workers and was nesting in a rotting log. This colony had multiple dealate queens, but only one of them was mated and succeeded in egg laying. Workers appeared to police egg laying by the other queens. While it is generally accepted that *P. stigma* is a tramp species distributed by human action, especially in eastern Asia and the Pacific, there seems little biological data to support this position and Wetterer (2012a) questioned where this was truly the case. Longino (2013) provided observations of other *Pseudoponera* species in Costa Rica, noting that *P. cauta* is typically found in leaf litter and under wood on the ground, while *P. cognata* apparently nests in dead wood at ground level or even arboreally.

**Phylogenetic and taxonomic considerations.** The taxonomic history of *Pseudoponera* is complex. The genus was erected by Emery (1900a) as a subgenus of *Pachycondyla*, with *Ponera quadridentata* (now *P. stigma*) as the type species by monotypy. Emery described *Pseudoponera* as new again the following year (Emery, 1901), but with *Ponera amblyops* now designated as the type species. Unfortunately the latter type species was recognized throughout most of the subsequent taxonomic literature (e.g., Emery, 1911), despite *P. quadridentata* (= *P. stigma*) being the true type species by the rules of priority. Bolton (2003) identified and remedied this error.

Emery (1900a, 1901) initially considered *Pseudoponera* to be a subgenus of *Pachycondyla*, but subsequent authors alternated between treating it as a separate genus (e.g., Bingham, 1903; Wheeler, 1922b; Donisthorpe, 1943c; also Emery, 1911) or as a subgenus of *Euponera* (e.g., Forel, 1901a; Emery, 1909; Wheeler, 1910). *Pseudoponera* was eventually synonymized under *Pachycondyla* by Brown (1973). We consider *Pseudoponera* to have a single junior synonym. *Trachymesopus* Emery (1911) (and its misspelled form *Trachyponera* Santschi (1928)) is an objective synonym of *Pseudoponera* as they share the same type species (Bolton, 1995).

As defined here, *Pseudoponera* is a collection of small to medium sized cryptobiotic species with no strong synapomorphies linking them to one another. Schmidt's (2013) molecular phylogeny of the Ponerinae includes two species now placed in *Pseudoponera*: *P. stigma* (the type species) and an undescribed species from Costa Rica. The *P. stigma* group is inferred to be sister to the *castanea* group in this phylogeny, and while similar they are morphologically divergent and the *castanea* group is here placed in a separate genus, *Austroponera*. Additionally, while not included in Schmidt's (2013) phylogeny, our morphological analysis has led us to transfer the *Pa. darwinii* group from *Pseudoponera* to a new genus, *Parvaponera*. This treatment is supported by unpublished data provided by P. S. Ward (pers. comm.), who found *Pa. darwinii* and two related but unidentified species to be the sister group of *P. stigma*. Unfortunately these three groups (*Austroponera*, *Parvaponera* and *Pseudoponera*) have not been included in a single analysis and therefore the relationships among them are unresolved. However, the available data suggests that they are closely related.

## Species of *Pseudoponera*

*P. cognata* (Emery, 1896): Costa Rica (**comb. nov.**)

*P. gilberti* (Kempf, 1960): Brazil (**comb. nov.**)

*P. gilloglyi* (Mackay & Mackay, 2010): Mexico (**comb. nov.**)

*P. pachynoda* (Clark, 1930): Australia (**comb. nov.**)

*P. stigma* (Fabricius, 1804): S. America (**comb. nov.**)

*P. succedanea* (Roger, 1863): Cuba (**comb. nov.**)

## *Rasopone* gen. nov.

Fig. 50

Type-species: *Ponera ferruginea* Smith, F. 1858b: 100; by present designation.

*Rasopone* is small genus of Central and South America ants known from 11 species. They are found in a wide range of habitats but are most common in rainforests where they forage in leaf litter and rotten wood.

**Etymology.** *Rasopone* is based on the geographic region of the New World where these ants occur (from the Ancient Egyptian “rsw”, “south wind”) combined with the suffix “-pone”, derived from the subfamily name Ponerinae.

**Diagnosis.** Workers of *Rasopone* lack obvious autapomorphies and are superficially similar to those of a number of other genera, including *Austroponera*, *Hypoconera*, *Neoponera* and *Pseudoponera*. Separation from these and other genera of the Ponerinae is based on the following set of characters: eyes present, mandibles relatively long, mandibular pit or groove absent, mesosomal profile nearly continuous, the metanotal groove shallow or absent, metapleural gland orifice without a posterior U-shaped cuticular lip, propodeal spiracle round or ovoid, mesotibiae dorsally without abundant stout traction setae, ventral apex of the metatibia with both a large pectinate spur and a smaller simple spur, fenestra absent from the petiolar process, prora present on anterior margin of first gastral sternite, and stridulatory organ absent from A4 pretergite. While similar overall, *Rasopone* and *Neoponera* belong to different genus groups and can be separated by the configuration of the metapleural gland opening. *Hypoconera*, while also somewhat similar, has only a single metatibial spur while two are present in *Rasopone*. Separation from *Pseudoponera* is based on the lack of a basal mandibular pit or groove and the presence of a round or ovoid propodeal spiracle. And the Australian and New Zealand genus *Austroponera* differs in possessing a stridulatory organ on A4 and in having a differently configured clypeus.

**Synoptic description.** *Worker.* Medium- to large-sized (TL 4–12 mm) ants with the standard characters of Ponerini.

Mandibles triangular, with roughly seven to twelve teeth, often variable size, and without a basal pit or groove. Anterior margin of clypeus variable, broadly convex or centrally concave, sometimes with a medially tooth. Frontal lobes moderately large and closely approximated. Eyes small to moderately large, located far anterior on sides of head. Mesopleuron generally entire but sometimes divided by a weak transverse impression. Metanotal groove reduced to a suture or shallow angle. Propodeum not narrowing dorsally. Metapleural gland orifice without a posterior U-shaped cuticular lip. Propodeal spiracles round or ovoid. Metatibial spur formula (1s, 1p). Petiole squamiform. Gaster with a girdling constriction between pre- and postsclerites of A4. Head and body finely punctate, sometimes with light striations on the sides of the mesosoma, and with sparse to abundant pilosity and often dense pubescence. Color variable, ferrugineous to dark brown-black.

*Queen.* Similar to worker but slightly larger, alate, with ocelli and larger compound eyes, and with the modifications of the thoracic sclerites that are typical of alate ponerine queens.

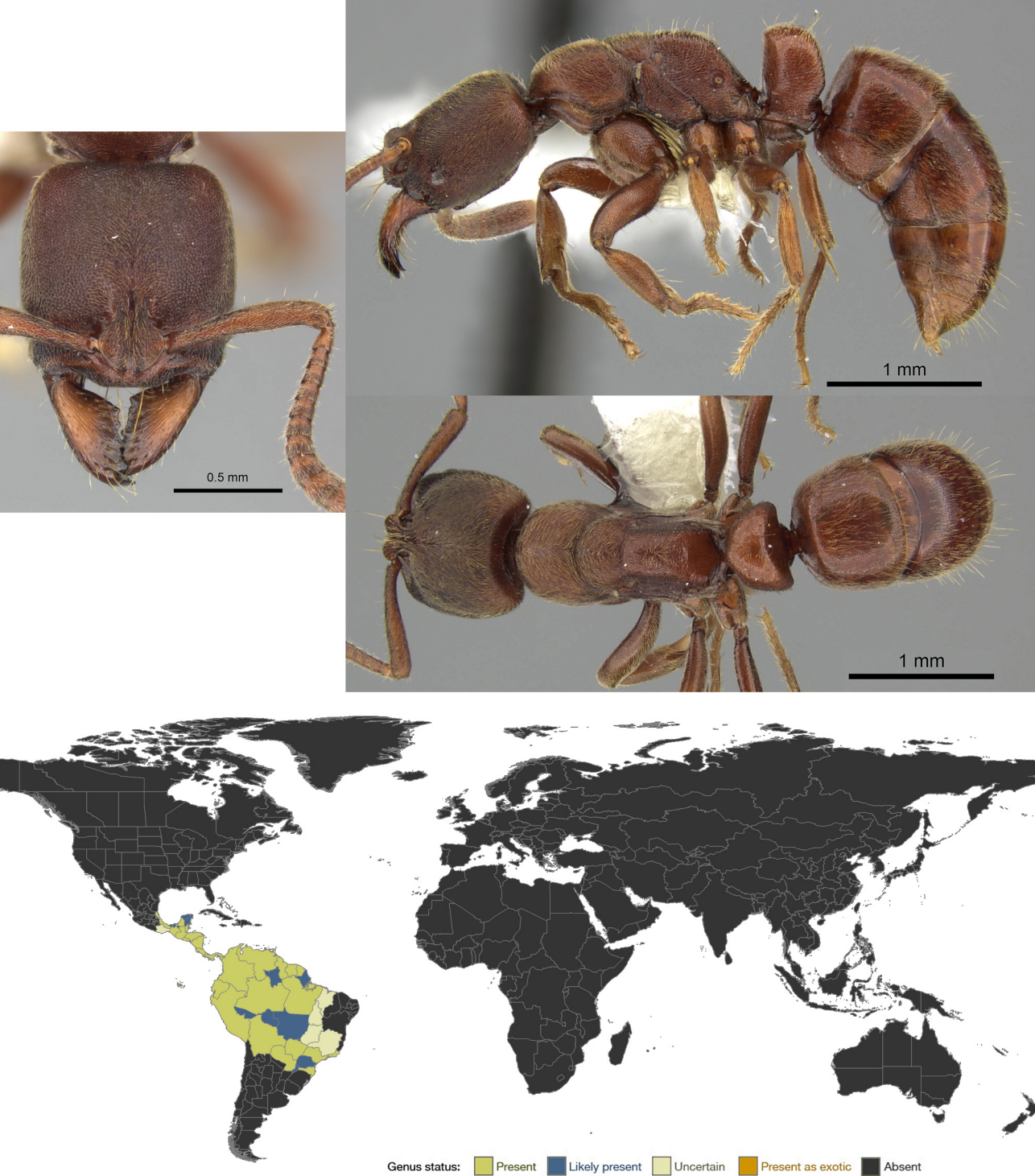
*Male.* See descriptions by Mackay & Mackay (2010) for several of the species placed here.

*Larva.* Described for *R. ferruginea* (Wheeler & Wheeler, 1976) and *R. pergandei* (Wheeler & Wheeler, 1974).

**Geographic distribution.** *Rasopone* is restricted to Central and South America.

**Ecology and behavior.** While these ants are most abundant in forested habitats, they occur in a wide range of habitats, including open disturbed grassy areas, cacao and coffee plantations, mixed dry oak forest, upper montane oak forest, rocky tropical canyons, second growth rainforest, tropical montane evergreen forest, wet montane

forest, primary rainforest, and cloud forest (Mackay & Mackay, 2010). *R. ferruginea* has been collected in caves near the entrances (Reddell & Cokendolpher, 2001). Workers forage in leaf litter and rotten wood and have been collected in subterranean traps baited with Vienna sausage; they are known to be attracted to carrion (Mackay & Mackay, 2010). Most species nest in soil with some also nesting in rotten wood. Baena (1993) reported a specimen of *R. conicula* (listed as *P. pergandei*) collected in a rotten log, and the type series of *R. cernua* was found in a log, suggesting that logs may be the normal nesting site for these species. Most flights of *R. arhuaca* occur in the middle of the summer (Kaspari *et al.*, 2001).



**FIGURE 50.** Worker caste of *Rasopone ferruginea*: lateral and dorsal view of body and full-face view of head (CASENT0249143, Ryan Perry and [www.antweb.org](http://www.antweb.org)); world distribution of *Rasopone*.



**Phylogenetic and taxonomic considerations.** None of the species treated here as belonging to *Rasopone* were included in Schmidt's (2013) phylogeny and our analysis is based on morphology alone. They were examined in detail by Mackay & Mackay (2010) who placed them in two species complexes, the *arhuaca* species complex (*R. arhuaca*, *R. becculata*, *R. cernua*, *R. conicula*, *R. longidentata* and *R. pergandei*) and the *ferruginea* species complex (*R. breviscapa*, *R. ferruginea*, *R. lunaris*, *R. minuta* and *R. rupinicola*). Because all were considered by Mackay & Mackay (2010) to belong to *Pachycondyla* and the focus of their work was species-level identification, the relationships among these species and others in the subfamily were not discussed in detail but rather only in general terms. Further detailed study specifically aimed at elucidating the relationship of this group of species to the remainder of the Ponerinae will be required to fully understand the evolution of this genus.

*Rasopone* is morphologically very similar to species here placed in *Austroponera* and they share many characters. They differ in that *Rasopone* workers lack a stridulatory organ on A4 and in having a differently configured clypeus. These differences are subtle and it may be more appropriate to combine these two genera in the future when their true relationships are better understood. We are, however, proposing both as separate for the time being based on morphological (as outline above) and biogeographic considerations (*Rasopone* is only known from Central and South America while *Austroponera* occurs in the Australian region).

### Species of *Rasopone*

- R. arhuaca* (Forel, 1901): Colombia (**comb. nov.**)
- R. becculata* (Mackay & Mackay, 2010): Ecuador (**comb. nov.**)
- R. breviscapa* (Mackay & Mackay, 2010): Bolivia (**comb. nov.**)
- R. cernua* (Mackay & Mackay, 2010): Ecuador (**comb. nov.**)
- R. conicula* (Mackay & Mackay, 2010): Venezuela (**comb. nov.**)
- R. ferruginea* (Smith, F., 1858): Mexico (**comb. nov.**)
- R. longidentata* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)
- R. lunaris* (Emery, 1896): Paraguay (**comb. nov.**)
- R. minuta* (Mackay & Mackay, 2010): Mexico (**comb. nov.**)
- R. pergandei* (Forel, 1909): Guatemala (**comb. nov.**)
- R. rupinicola* (Mackay & Mackay, 2010): Colombia (**comb. nov.**)

### Acknowledgements

This revision is, in many ways, a continuation of the work Bill Brown began many years ago as part of his "Contributions to the Reclassification of the Formicidae". At the time of his passing in 1997 he was deep into "Part VIIA, Ponerinae, tribe Ponerini, subtribe Poneriti" and had made much progress towards its completion. "Part VII" was to consist of 3 parts (A, Poneriti, B, *Leptogenys* and C, *Hypoconera*) and would complete Bill's reclassification of the Ponerinae. Before his death Steve Shattuck offered to assist with the completion of this series but was reassured by Bill that as the revisions were nearly complete additional help wasn't required. Unfortunately events prevented their completion as planned.

A few years later Steve visited Doris, Bill's wife, to discuss the continuation of Bill's work. Doris generously agreed and passed along Bill's manuscripts and notes relating to the ponerines. Steve then spent the next 10 years working on and off on ponerines, first pulling together Bill's rather scattered notes and then reworking Bill's ideas, transferring them from an earlier "Mayrian" way of thinking to a more modern phylogenetic mindset. During this process it became apparent that the concept of "*Pachycondyla*" that Bill had developed was untenable as it was clearly polyphyletic. This led to questioning the subtribe Poneriti and then the tribe Ponerini, both of which were found to be ill-defined. What started as simply editing a few nearly complete manuscripts had developed into a complete revision of the entire subfamily! Unfortunately other commitments prevented the allocation of time and resources to undertake a project of this scale and Steve's work on the group subsided.

In 2003 Chris Schmidt began a Ph.D. project on the ponerines, which involved developing a molecular phylogeny for the subfamily and the taxonomic revision and ecological/behavioral review that formed the beginning of the current manuscript. This work provided, for the first time, a solid, modern framework for

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.

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