



<http://dx.doi.org/10.11646/zootaxa.3609.2.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:A8B7BD9C-7959-4036-8D76-9BE72D0F07AA>

Revision of the *Pachycondyla wasmannii*-group (Hymenoptera: Formicidae) from the Malagasy region

JEAN CLAUDE RAKOTONIRINA¹ & BRIAN L. FISHER²

¹Madagascar Biodiversity Center, BP 6257, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar.
Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, U.S.A.
Email: jcrakoto25@yahoo.com

²Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, U.S.A.
Email: bfisher@calacademy.org

Abstract

Defining species limits and describing species of ants are important to identify taxa and habitats with elevated diversity in areas of high conservation priority such as the Malagasy region. The *Pachycondyla wasmannii*-group is revised in the Malagasy region where eight species are recognized, four of which are new: *P. masoala* sp. n., *P. planicornis* sp. n., *P. tavaratra* sp. n., and *P. vazimba* sp. n. Four species have been previously described: *P. cambouei* Forel, *P. comorensis* (André), *P. perroti* Forel, and *P. wasmannii* Forel. *Pachycondyla perroti admista* Forel is newly synonymized under *P. perroti*. *Pachycondyla cambouei* is widespread in eastern Madagascar, morphologically variable, and divided into seven morphotypes. An identification key to species and distribution maps are provided for the genus in the Malagasy region. All species are known only from Madagascar except *P. wasmannii*, which occurs also on Anjouan of the Comoros Islands.

Key words: Taxonomy, Ponerinae, *Pachycondyla*, *Bothroponera*, *wasmannii*-group, morphological variation, Malagasy region, Madagascar

Introduction

Islands in the southwestern Indian Ocean, especially Madagascar, are composed of extremely fragmented natural habitats and are renowned for having high levels of endemism and threatened biodiversity (Lourenço & Goodman 2000; Myers *et al.* 2000). In this region, ants are diverse and almost all species are found nowhere else (Fisher 2003). Although efforts to understand and map the diversity of Malagasy ants can be of major importance for preserving the unique biota of the region (Fisher 2005), ants are not among the focal taxonomic groups used in conservation decision making (see Kremen *et al.* 2008).

Several ant lineages have shown significant diversification, whereas other groups are missing or very sparsely represented (Fisher 1997) in the Malagasy region. Documentation of this group of insects is far from comprehensive despite the existence of various earlier taxonomic works (e.g., André 1887; Forel 1891; Emery 1895, 1911; Santschi 1912) as well as more recent efforts (e.g., Brown 1975; Bolton 1975, 1979; Alpert 1992; Ward 1994). Several named species have been insufficiently described, and most species were described in isolation from closely related taxa due to sparse sampling across the region.

More recently, however, efficient collecting methods (Longino & Colwell 1997; Fisher 1999) and remarkable advances in processing protocols (Fisher 2005) have led to the initiation of more in-depth taxonomic works (e.g., Fisher 2000; Heterick 2006; Bolton 2007; Yoshimura & Fisher 2007, 2009; Fisher & Smith, 2008; Fisher 2009; Blaimer 2010; LaPolla *et al.* 2011; Hita Garcia & Fisher 2011). Species are critical units of study in many fields of ecology and evolutionary biology. Knowledge of biological diversity depends primarily on species diversity. Diversity information in turn is highly valuable in assisting conservation efforts and in designing and managing nature reserves (Vane-Wright *et al.* 1991; Vane-Wright 1996; Kremen *et al.* 2008) in areas of high conservation priority like the Malagasy region.

Taxonomic studies can be accelerated and species boundaries accurately hypothesized with the use of modern tools, providing rapid access to current data. The quality of species boundaries inferences determines the accuracy and strength of biodiversity data, making the understanding of species boundaries a critical starting point. In the Malagasy region, there is an urgent need to complete ongoing taxonomic revisions of ants in a timeframe relevant to conservation planning. An improved understanding of ant diversity will demonstrate the importance of ants in the environment and their potential role in land management and the conservation of biotic diversity.

In this paper, the Malagasy *wasmannii*-group of the genus *Pachycondyla* F. Smith (1858) is revised at the species level. This species-group corresponds to the Malagasy species of the genus *Bothroponera* Mayr (1862) sensu Wheeler 1922, which is currently synonymized under *Pachycondyla* (Bolton 1995, 2003; see Schmidt 2009). Members of the species-group occur in a variety of environments in the Malagasy region, including forests, savanna woodlands, and thicket habitats, while their microhabitats include leaf litter ground layers, inside or under rotten wood, or under stones..

Earlier species-level taxonomic works in Madagascar (André 1887; Forel 1887, 1891; Emery 1895, 1911) describe four species and one subspecies of the genus, including *P. cambouei*, *P. comorensis*, *P. perroti*, *P. perroti admista*, and *P. wasmannii*. Recent surveys of the arthropods of Madagascar have augmented these collections with many new specimens. The present contribution seeks to provide a comprehensive taxonomic study of the Malagasy *Pachycondyla wasmannii*-group and to document the morphological variation of the eight recognized species within the region.

Materials and methods

Collections

The collection abbreviations follow Bolton (1975) and Evenhuis (2009). The material upon which this study is based is located and/or was examined at the following institutions:

BMNH:	British Museum of Natural History, London, UK
CASC:	California Academy of Sciences, San Francisco, CA, USA
MCZC:	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
MHNG:	Musée d'Histoire Naturelle, Geneva, Switzerland
MNHN:	Musée National d'Histoire Naturelle, Paris, France
MSNG:	Museo de Storia Naturele, Genoa, Italy
NHMB:	Naturhistorisches Museum, Basel, Switzerland
PBZT:	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar
PSWC:	P.S. Ward Collection, University of California, Davis, CA, USA

Inferring species boundaries

In the present investigation, the species boundaries for the *Pachycondyla wasmannii*-group are defined based on the biological species concept (Mayr, 1963), where species are reproductively isolated entities. Here we use patterns of morphological discontinuities shown by individual workers to detect reproductive boundaries between populations and infer species limits indirectly. Cases where specimens show a continuum of character gradation between populations and a lack of clear phenotypic gaps are interpreted as morphologically variable species (see discussion of morphological forms of *P. cambouei*).

Morphological analysis

Morphological examinations were conducted using a Leica MZ12.5 binocular microscope. A series of measurements was taken from pinned workers representing each species. Size and shape of the queen caste were also evaluated using a similar series of measurements, plus one additional morphometric and index value. All measurements were done with an orthogonal pair of micrometers accurate to the nearest 0.001 mm, but rounded to the second decimal place. All indices are multiplied by 100 and rounded to the nearest whole number. Because more than one specimen was measured, ranges are presented as minimum and maximum values.

Head length (HL): the length of the head in full-face view, taken along a straight line from the mid-point of the anterior margin of clypeus to the mid-point of the posterior margin or to the mid-point of the transverse line that relates to the level of the posterior margins of the occipital lobes if the posterior cephalic margin is concave.

Head width (HW): the maximum width of the head in frontal view, excluding the eyes.

Cephalic index (CI): head width divided by head length.

Scape length (SL): the length of the antennal scape excluding the basal condylar articulation.

Scape index (SI): scape length divided by head width.

Pronotum width (PW): the maximum width of the pronotum in dorsal view.

Weber's length (WL): the maximum length of the mesosoma measured diagonally from the meeting point of the pronotum and the neck to the furthest posterior extension of the metapleuron.

Petiole width (NW): the maximum width of the node in dorsal view.

Petiole height (NH): the height of the node in profile, measured vertically from the level of the ventral margin of the node at which the junction with the subpetiolar process occurs to the highest point of the dorsal margin of the node.

Petiole length (NL): the maximum length of the node in dorsal view, taken from the base of the anterior process to the base of the posterior portion that links to the gastral articulation.

Petiole indices:

Lateral petiole index (LNI): petiole height divided by petiole length.

Dorsal petiole index (DNI): petiole width divided by petiole length.

Additional measurements for the queen caste are as follows:

Eye length (EL): Maximum length of the left eye with head in full-face view.

Ocular index (OI): eye length divided by head width.

Bolton (1994) has described a number of hair types on the ant body. In this study, two terms are used to describe hairs on the body dorsum of *P. wasmannii*-group species from the Malagasy region. Erect or suberect hair is defined as either stout or slender hairs that stand vertically or at an angle equal to or more than 45 degrees. Pubescence describes thin and shorter hairs, which generally lie on the body surface of the ant or at an angle less than 45 degrees for most of their length.

Full descriptions of the queen caste are not presented as the general diagnosis of the workers is applicable to queens as well.

Of the collections of *P. wasmannii*-group species from the Malagasy region, very few have male specimens associated with workers from the same colony, thus males are not included in this revision.

Images

Digital color images of full-face view of the head, lateral view of the entire body, and other miscellaneous images included in the present study were created using a JVC KY-75 digital camera with a Leica MZ16 APO microscope and Synchroscope Auto-Montage (v5.0) software. Along with the images of the dorsal view of the ant, they can be accessed on AntWeb (www.AntWeb.org) using the unique identifying specimen code (e.g., CASENT0104547 or BLF00886(47)-1) attached to the pin of each imaged specimen.

Distribution maps

Distribution maps for each species were drawn using specimen records gathered into a program for specimen data management (Biota, Colwell 1996) and imported into Diva GIS (Hijmans *et al.* 2011). Patterns of phenotypic variation among populations of the same species and morphological similarity between closely related species were assessed with this geographic framework. The geographic coordinates of some older specimens and type materials are insufficiently precise and were excluded from the map.

ICZN Code

In accordance with provisions stated in the International Code of Zoological Nomenclature (ICZN), the designation of a lectotype from syntype specimens is necessary to create a stable nomenclature based on article 74 of the ICZN code. Consequently, the words "present designation" are used when a lectotype that directly corresponds to the original description of a named species is designated. The new species names in the present study are invariant genitive nouns or nominative singular nouns in apposition.

Other abbreviations

The following abbreviations related to locality information are also made for the different status of protected areas and forest habitats in the Malagasy region:

PN:	Parc National
RS:	Réserve Spéciale
F:	Forêt
RF:	Réserve Forestière
RP:	Réserve Privée
FC:	Forêt classée
SF:	Station forestière
RNI:	Réserve Nationale Intégrale

Results

Diagnosis of workers and queens of *P. wasmannii*-group species

It should be noted that all diagnostic characters listed below are not unique to Malagasy *P. wasmannii*-group species but are shared with some *Bothroponera* (sensu Wheeler 1922) species from the Afrotropics.

1. Mandible subtriangular and robust, with masticatory margins bearing 7–9 teeth and denticles; groove running along the lateral portion from the base to the apex, but without a basilateral pit.
2. Palp formula 4,4.
3. Frontal lobes noticeably widely rounded anteriorly, the outer margins posteriorly narrow and compressed laterally at about the level of the eyes.
4. Clypeus usually with a truncate anteromedian margin, the shape of which is straight or slightly excised medially, but in *P. tavaratra* projects into a triangular lobe. The median portion posteriorly pinched into a slight triangle between the frontal lobes and extending backwards as a line at about the midlength of the head.
5. Antenna with 12 segments, the funiculus gradually increasing in width towards the apex and without a distinct club.
6. Compound eyes present and generally quite large but their maximum diameter less than the maximum width of the scape; posterior margin of the eye placed in the front of the midline of the head when viewed in profile.
7. Tibia of the hind legs with a pair of apical spurs, the posterior pectinate and the anterior smaller and simple.
8. Pretarsal claws generally simple, preapical tooth may be present at the base in larger species (*P. comorensis*, *P. tavaratra*).
9. Metanotal groove obsolete or lacking in the worker caste.
10. Mesopleural sulcus either clearly visible in *P. masoala*, *P. wasmannii*, and in some *P. cambouei* or indistinct in *P. perroti*, *P. vazimba*, and in some *P. planicornis*.
11. Propodeum generally broad in dorsal view, the rear margin rounded, not bidentate or bispinose.
12. Propodeal spiracle slit-like.
13. Metapleural gland opening just above the posteroventral angle of mesosoma.
14. Basal fourth of all femora strongly laterally flattened (Fig. 52).
15. Petiole nodiform, usually thick, tapered towards the apex in *P. masoala*.
16. Subpetiolar process hook-like anteriorly and with nearly flattened or very slightly convex surface; sometimes with transverse ridges in the posterior portion in *P. comorensis*, *P. tavaratra*, and in some *P. cambouei*.
17. Helcium almost on the anteroventral angle of the first gastral segment (abdominal segment IV).
18. Strong constriction between the first and second gastral segments.
19. Stridulitrum present.
20. Sting well developed.
21. Queen caste-specific characteristics: broader head, presence of ocelli, eyes larger than the greatest width of antennal scape; mesopleuron divided into an episternum and katepisternum by a transverse sulcus, the mesosomal flight sclerites fully developed; petiole node more flattened anteroposteriorly relative to that of worker; somewhat larger body size with usually larger gaster and denser and more elongate pubescence.

In the Malagasy *P. wasmannii*-group species, the worker caste can generally be identified by the following character combination: mandibles without basi-lateral pit; obsolete metanotal groove; propodeal spiracle opening slit-shaped; hind leg with two tibial spurs, of which one is large and pectinate and the other smaller and simple; roughly basal fourth of all femora strongly laterally flattened; propodeal rear margin simple; petiolar node thick without spines on rear margin; and first and second gastral segments separated by a strong constriction. In addition, the mesosoma and petiole node usually strongly sculptured, frontal lobes broadly rounded, and propodeal dorsum wide.

Synopsis of the taxonomic history of the *P. wasmannii* species-group

The four previously described species in the *P. wasmannii*-group were all described between 1887 and 1892 in the genus *Bothroponera*. We summarize the taxonomic history of *Bothroponera* below.

Bothroponera Mayr, 1862:713, 717 [as subgenus of *Ponera* by Emery, 1895b: 767 and Forel, 1900: 322; as subgenus of *Pachycondyla* by Emery, 1901: 42; Wheeler, 1910: 135, 1911: 160, 1917: 489; Emery, 1911: 74, 75, 76; Arnold, 1915: 55; Forel, 1917: 237; Donisthorpe, 1943: 628. As genus by Forel, 1891: 127; Dalla Torre 1893: 35; Bingham, 1903: 95; Ashmead, 1905: 382; Wheeler 1918: 299, 1922: 1008; Taylor and Brown, 1985: 21; Tiwari, 1999: 11, 27, 28; Schmidt, 2009: 119 (PhD thesis). As junior synonym of *Pachycondyla* by Brown, 1973: 179 [provisional]; Snelling 1981: 389; Hölldobler and Wilson, 1990: 11; Bolton, 1994: 164; Bolton, 2003: 166]. Type species: *Ponera pumicosa* Roger, 1860: 290; by subsequent designation of Emery, 1901: 42.

Synoptic checklist of Malagasy *P. wasmannii*-group species

cambouei Forel 1891

comorensis André 1887

masoala Rakotonirina and Fisher, sp. n.

perroti Forel 1891

= *perroti admista* Forel 1892 syn. n.

planicornis Rakotonirina and Fisher, sp. n.

tavaratra Rakotonirina and Fisher, sp. n.

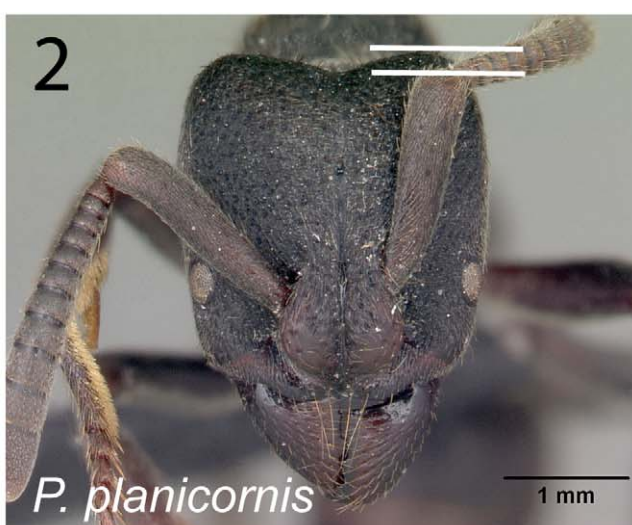
vazimba Rakotonirina and Fisher, sp. n.

wasmannii Forel 1887

Key to species of the Malagasy *P. wasmannii*-group worker:

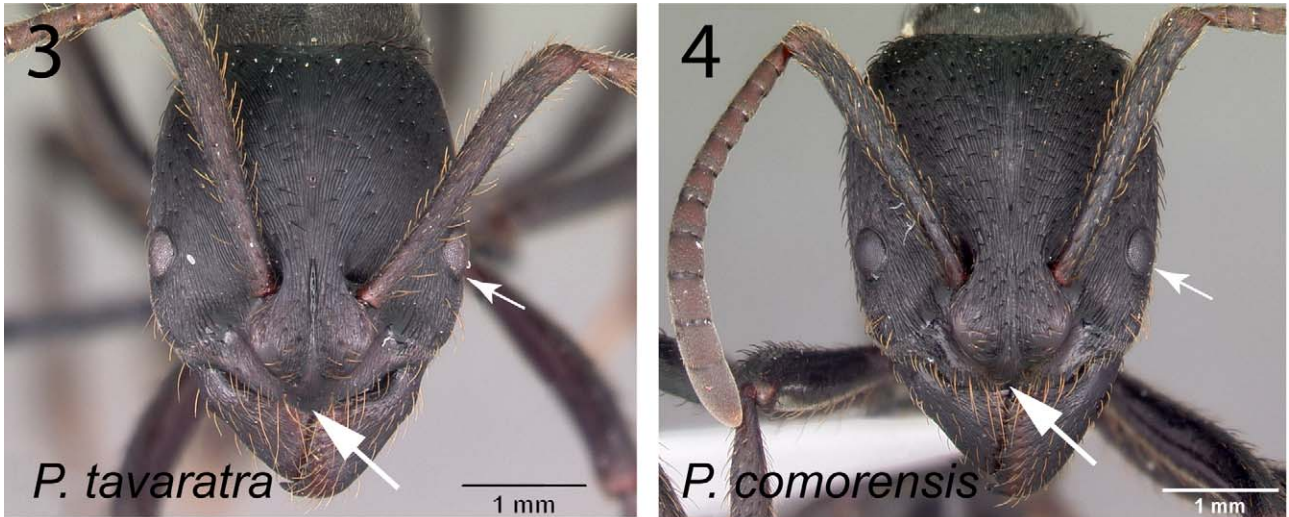
The following key also identifies ergatoid and winged queens to species as long as the form of the mesosoma and the presence of the mesopleural sulcus are not applied.

1. Larger species (HW: 2.49–3.13 mm); with head in full-face view, antennal scape surpassing the posterior margin of the head (SI: 94–104) (Figs 1, 3); dorsum of head and mesosoma finely striate and interspersed with scattered punctures; dorsum of the body covered with erect stout hairs (Figs 30, 38) 2
- Smaller species (HW: 1.19–2.58 mm); with head in full-face view, antennal scape not surpassing the posterior margin of the head (SI: 70–87) (Fig. 2); dorsum of head and mesosoma variably sculptured but not finely striate, dorsum of the body with erect slender hairs and pubescence (e.g., Figs 35, 43, 45) 3



FIGURES 1–2. Full-face view of the head showing the length of the antennal scape; Fig. 1: scape surpassing the posterior cephalic margin; Fig. 2: scape not surpassing the posterior cephalic margin.

2. With head in full-face view, anterior margin of clypeus broadly rounded or medially triangular; eye breaking the outline of the side of the head (Fig. 3); hairs on the dorsum of the mesosoma and petiole node distinctly erect relative to the body surface (Fig. 47). *tavaratra*
- With head in full-face view, anterior margin of clypeus truncate; eye not breaking the outline of the side of the head (Fig. 4); hairs on the dorsum of the body decumbent and much more inclined to the body surface (Fig. 39). *comorensis*



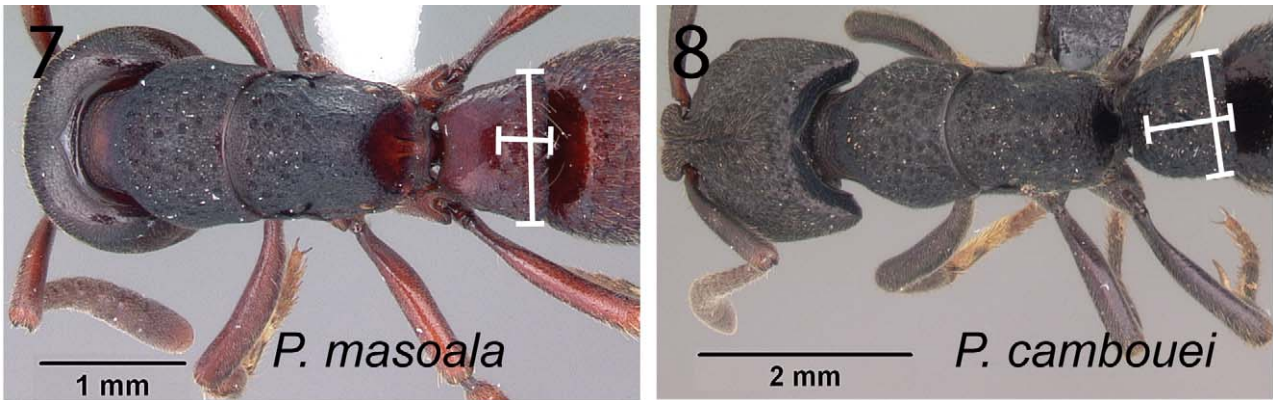
FIGURES 3–4. Shape of the clypeus and location of the eyes when head in full-face view; Fig. 3: *P. tavaratra*, anterior clypeal margin broadly triangular; eyes breaking the lateral margin of head; Fig. 4: *P. comorensis*, anterior clypeal margin truncate; eyes not breaking the lateral margin of head.

3. Basal half of the antennal scape dorsoventrally flattened, the leading edge very thin (Fig. 5); basitarsus of the hind leg laterally compressed, basal half of its inner surface concave *planicornis*
- Basal half of the antennal scape subcylindrical, not dorsoventrally flattened; the leading edge rounded (Fig. 6); basitarsus of the hind leg generally rounded, without concavity 4



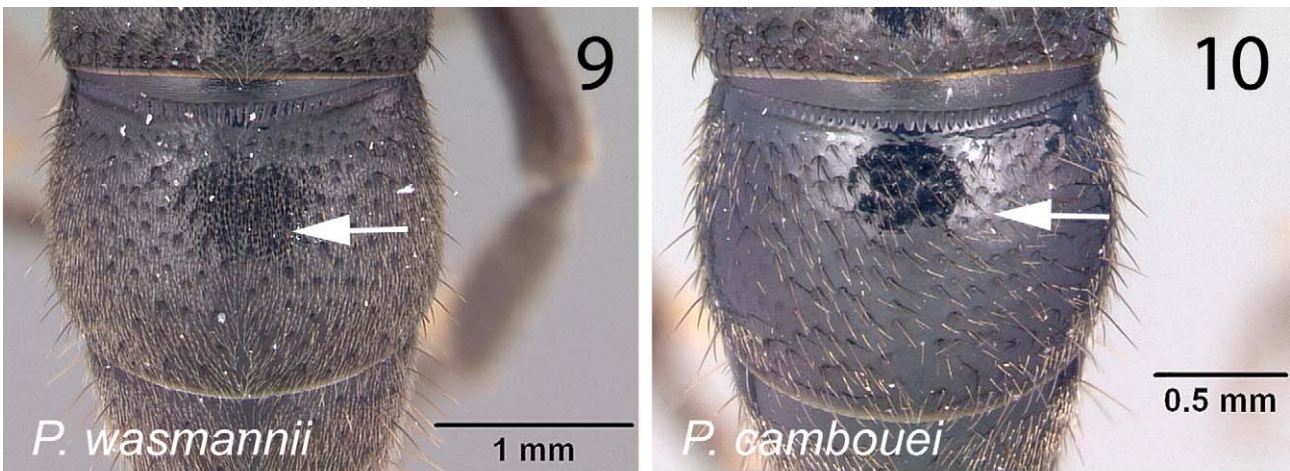
FIGURES 5–6. Antennal scape and leading edge viewed from the back; Fig. 5: basally dorsoventrally flattened and thin in *P. planicornis*; Fig. 6: subcylindrical and rounded (e.g., *P. cambouei*).

4. With petiole in dorsal view, the node flattened, about twice as broad as long (Fig.7); higher than long in profile; erect hairs on dorsum of propodeum most frequently absent (Fig. 41), if present then reduced in number. *masoala*
- With petiole in dorsal view, the node thick, approximately as long as broad (Fig. 8), about as high as long in profile; erect hairs on dorsum of propodeum numerous (e.g., Figs 18, 43, 51) or rarely absent (Fig. 31) 5



FIGURES 7–8. Petiole in dorsal view; Fig. 7: petiole node anteroposteriorly flattened in *P. masoala*, about twice as broad as long; Fig. 8: petiole nodiform, about as long as broad (e.g., *P. cambouei*).

- 5. Anterior half of the fourth abdominal tergite (gastral tergite 2) covered with numerous and very dense small punctures between larger ones (Fig. 9) which become moderate on mesosoma and petiole node; integument usually matte; mostly found in dry forest habitats 6
- Anterior half of the fourth abdominal tergite (gastral tergite 2) mostly smooth and shiny between large punctures, sometimes with randomly scattered small punctures (Fig. 10); mesosoma and petiole node sparsely punctulate between coarse punctae; integument mostly shiny; humid forest species 7



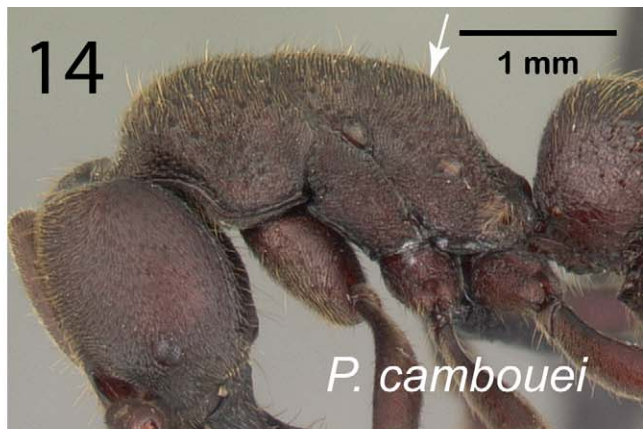
FIGURES 9–10. Fourth abdominal tergite in dorsal view; Fig. 9: Anterior half of the fourth abdominal tergite with dense small punctures between larger ones; Fig. 10: Anterior half of the fourth abdominal tergite smooth and shining.

- 6. Larger species (HW: 1.72–2.21 mm); mesopleural sulcus usually distinct and complete (Fig. 11); dorsum of mesosoma and petiole node covered with more robust and longer standing hairs (Fig. 51); antennal segments 6, 7, and 8 nearly as wide as long; with petiole in dorsal view, the posterior margin straight or with weak median notch; outer surface of the hind tibia with erect hairs *wasmannii*
- Smaller species (HW: 1.38–1.5 mm); mesopleural sulcus indistinct or incomplete (Fig. 12); dorsum of mesosoma and petiole node with short and thin erect hairs (Fig. 49); antennal segments 6, 7, and 8 nearly twice as wide as long (Fig. 48); with petiole in dorsal view, the posterior margin broadly concave; outer surface of the hind tibia usually without erect hairs *vazimba*



FIGURES 11–12. Mesosoma in lateral view; Fig. 11: mesopleural sulcus of *P. wasmannii* complete; Fig. 12: mesopleural sulcus of *P. vazimba* indistinct.

7. With mesosoma in profile, the dorsal outline forming a continuous convexity with a nearly rounded junction between the propodeal dorsum and the declivitous margin (Fig. 13), which is short and strongly inclined posteriorly; in full-face view, head heart-shaped, with the posterior margin strongly concave, and anterior clypeal margin strongly excised medially (Fig. 42); larger species (HW: 2.34–2.58 mm) *perroti*
- With mesosoma in profile, the dorsal outline not forming a continuous convexity, propodeal dorsum meeting the declivity at a distinct angle (Fig. 14); propodeal declivity nearly vertical, but not distinctly inclined posteriorly; in full-face view head not heart-shaped, the posterior margin usually straight (Figs 30, 34, 36) or slightly concave (Figs 26, 28, 32); smaller species (HW < 2.3 mm) *cambouei*



FIGURES 13–14. Mesosoma in profile; Fig. 13: the dorsal outline of mesosoma forming a continuous convexity in *P. perroti*; Fig. 14: the dorsal outline of mesosoma showing a distinct blunt angle between the propodeal dorsum and the declivity in *P. cambouei*.

Species accounts

Pachycondyla cambouei (Forel)

(Figures 6, 8, 10, 14–28, 44–57)

Bothroponera cambouei Forel, 1891: 133, pl. 4, fig. 7 Lectotype worker, present designation, Madagascar, Imerina, Antananarivo (Camboué) AntWeb CASENT0101770 (MHNG) [examined]. Paralectotype worker and queens with same data as lectotype but with specimen codes: CASENT0101028, CASENT0101029 (MHNG) and CASENT0101404, CASENT0101402 (MNHN) [examined]. [Combination in *Pachycondyla* (*Bothroponera*): Emery, 1901: 45, 1911: 78; Combination in *Bothroponera*: Wheeler, 1922: 1007; in *Pachycondyla* by Bolton, 1995: 303].

Worker diagnosis:

With head in full-face view, antennal scape not surpassing posterior cephalic margin; dorsum of head and mesosoma not finely striate; dorsum of the body with erect slender hairs and pubescence; basal half of antennal scape rounded; dorsal outline of mesosoma not forming a continuous convexity; distinct angle discernable between propodeal dorsum and declivitous surface; petiole nodiform, not anteroposteriorly flattened; anterior half of fourth abdominal tergite (gastral tergite 2) mostly smooth and shiny between large punctures.

Worker measurements (n=116): HL: 1.38–2.29, HW: 1.19–2.01, CI: 85–95, SL: 0.92–1.69, SI: 72–87, PW: 0.95–1.71, WL: 1.64–2.89, NL: 0.65–1.05, NW: 0.79–1.26, NH: 0.95–1.54, DNI: 110–137, LNI: 130–169.

Description:

Worker. In full-face view head widest at or slightly behind level of eyes; sides somewhat convex, but weakly converging in front of eyes; shape of posterior margin variable, ranging from straight to strongly medially excised. Compound eyes either large and moderately protruding, or small with diameter less than half of maximum diameter of scape; with head in full-face view, eyes breaking lateral margins of the head. Antennal scape subcylindrical, with rounded leading edge, and not surpassing posterior margin of head. Anterior clypeal margin truncate and either straight or slightly concave. Mandibles triangular, apical margins armed with seven to nine teeth and denticles. With mesosoma in profile, the dorsal outline not forming a continuous convexity, propodeal dorsum meeting declivity at a distinct angle; mesopleural sulcus usually indistinct and incomplete. Petiole nodiform; in lateral view, anterior face, dorsum, and posterior face meet in a rounded angle. With petiole node in dorsal view, posterior margin straight or medially excised. Hind basitarsus nearly rounded and not flattened dorsoventrally, basal half of inside surface not concave.

Mandibles longitudinally striate and covered with sparse piligerous punctures. Dorsum of head finely reticulate-punctate or reticulate rugulose, superimposed by punctures or setae-bearing foveolae; sides with less defined sculpture, but finely reticulate-punctate or reticulate-rugulose, interspersed with small piligerous pits. Mesosoma and petiole node with variable sculpture, dorsally ranging from coarsely densely punctate to reticulate-rugose or irregularly punctate, interspersed with quite closely spaced smaller punctures; generally fine striations running to bottom of large punctures. For lateral portions, sculpturing varies from finely rugulose to transversely striate with scattered punctures. Propodeal declivity smooth and shiny or with granular surface. Third and fourth abdominal tergites covered with large, shallow punctures, interspaces either smooth and shiny or covered with fine, small punctures; in some specimens the large punctures are irregularly spaced and much more accentuated. Dorsum of body covered with erect slender or suberect thick hairs, which are reduced in number or absent on the antennal scape and legs. Pubescence on the third and fourth abdominal tergites either dense, sparse, or lacking. Body colors range from ferruginous red to reddish brown through dark brown to black with lighter appendages.

Queen. Measurements (n=14): HL: 1.53–2.18, HW: 1.41–2.09, CI: 89–98, EL: 0.28–0.42, OI: 17–21, SL: 1.02–1.66, SI: 72–82, PW: 1.21–1.87, WL: 2.36–3.45, NL: 0.63–1.02, NW: 0.94–1.34, NH: 0.92–1.35, DNI: 130–153, LNI: 129–146. Winged queens and ergatoids are present in *cambouei* and its variants. Ergatoid queens and workers look very similar, but the former have ocelli and incomplete thoracic sclerites while the body of alate queens is noticeably larger in general.

Variation:

Pachycondyla cambouei shows a remarkable range of phenotypic diversity. To facilitate discussion of this diversity, the morphological characters of the worker caste are divided into seven forms on the basis of the shape of the occipital corner, the posterior margin of the head, the size of the eyes, the form of the mesosoma, and the abundance of pubescence on the fourth abdominal tergites. However, there is no simple pattern to the degree of variation of these forms. Specifically, a few forms have very restricted geographic boundaries while others show a wide distribution along the humid forests of Madagascar. Each form of *P. cambouei* is described below:

Form 1 (Figs 10, 15, 18, 22, 24–25, 53). Worker measurements (n=35 workers): HL: 1.75–2.17, HW: 1.59–1.99, CI: 88–95, SL: 1.24–1.57, SI: 75–85, PW: 1.23–1.67, WL: 2.15–2.89, NL: 0.82–1.02, NW: 0.96–1.24, NH: 1.16–1.54, DNI: 110–130, LNI: 130–157.

This form corresponds to the typical *P. cambouei*, which is distinguished by much larger eyes, medially excised posterior cephalic margin and normal shape of head and mesosoma, medially excised posterior margin of petiole, and

smooth or sparsely punctate fourth abdominal tergites. Some characters are variable, such as the smooth or shagreenate propodeal declivity, and slender erect hairs with reduced pubescence or shorter and much more robust erect hairs with more pubescence. A few larger worker specimens (HW: 1.86–1.99 mm) from the Masoala area in northeastern Madagascar are included in this form. These larger workers have less defined sculpture and are covered with elongate and slender erect hairs and less pubescence. At first glance, these differences are suggestive of a distinct species, but other specimens from various localities also show patterns of less enhanced sculpture, slender and long erect hairs, and a larger-sized body than a more typical *P. cambouei* specimen.

Form 2 (Figs 8, 16, 26–27, 54). Worker measurements (n= 8): HL: 1.83–2.19, HW: 1.66–1.96, CI: 88–91, SL: 1.33–1.51, SI: 77–81, PW: 1.26–1.48, WL: 2.35–2.69, NL: 0.82–0.97, NW: 0.98–1.18, NH: 1.19–1.44, DNI: 114–121, LNI: 138–148.

Known only from workers collected in the isolated rainforest of the RS Ambohijanahary. This variant is characterized by a backward extension into a lobe of each angle of the posterior margin of the head (Fig. 16). However, workers with more typical characters of *P. cambouei* are also found within a few colonies of this variant, and workers that show intermediate levels of protrusion between this form and form 3 (see below) also occur in FC Didy, FC Andriantantely and PN Mantadia. Workers with intermediate levels of protrusion are included in the latter form.

Form 3 (Figs 6, 17, 28–29, 55). Worker measurements (n=25): HL: 1.92–2.22, HW: 1.72–2.03, CI: 86–93, SL: 1.40–1.58, SI: 77–82, PW: 1.29–1.55, AL: 2.37–3.00, NL: 0.91–0.99, NW: 1.04–1.17, NH: 1.3–1.43, DNI: 112–125, LNI: 140–152.

This variant is distinguished by the fact that the posterolateral margin of the head at each occipital corner protrudes posteriorly into a hornlike tooth. Individual workers with intermediate degrees of expansion of the occipital lobes are known from Ivohibe and PN Mantadia, and this trait varies gradually along its geographical distribution to match the general diagnosis of typical *P. cambouei* (form 1). Interestingly, worker specimens in some colonies from the PN Ranomafana also present this gradual form of hornlike tooth, which for this form may be indicative of some biological meaning in terms of colony behavior.

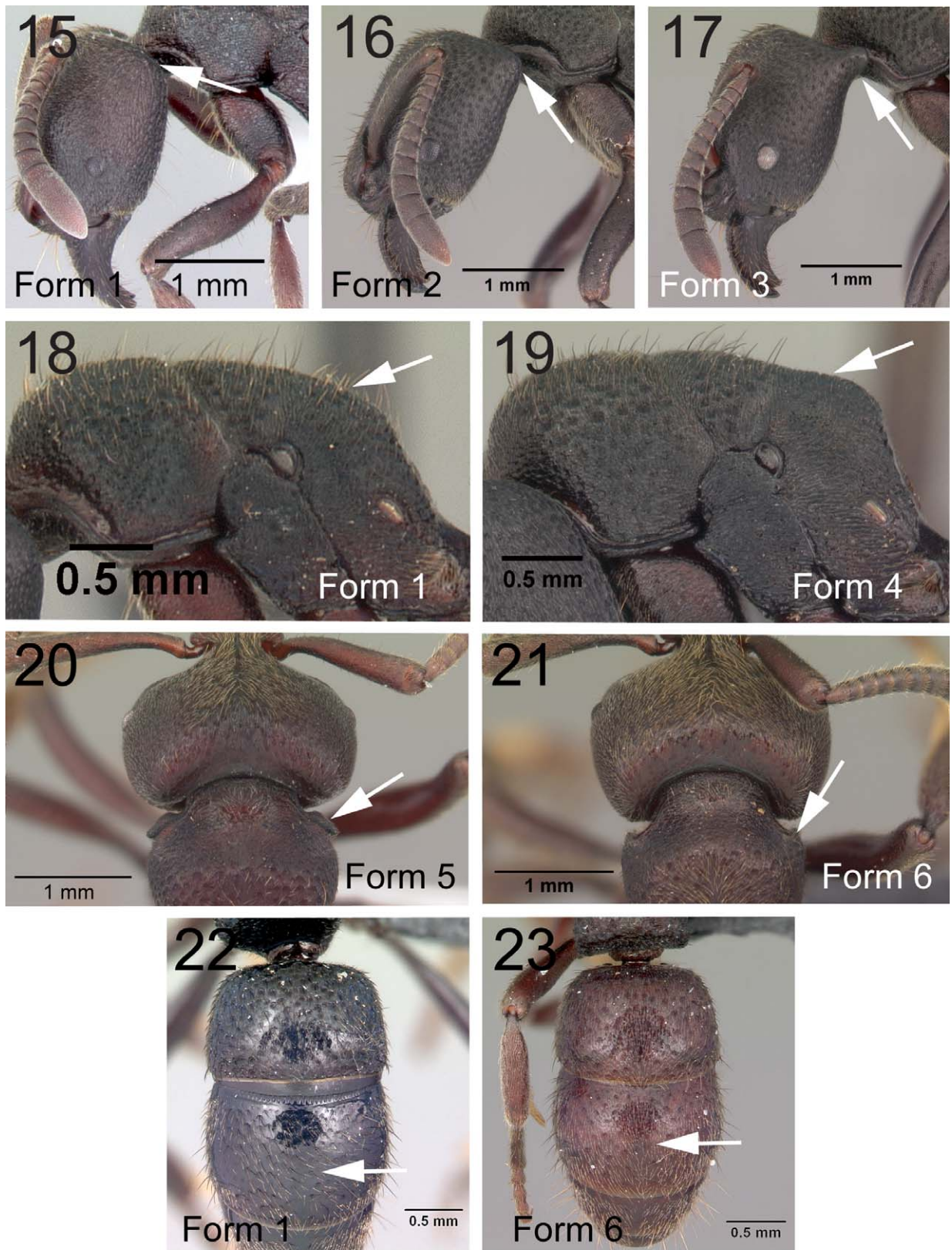
Form 4 (Figs 19, 30–31, 54). Worker measurements (n=10): HL: 1.74–1.97, HW: 1.55–1.82, CI: 89–92, SL: 1.25–1.48, SI: 79–86, PW: 1.21–1.38, WL: 2.14–2.55, NL: 0.84–0.99, NW: 0.97–1.14, NH: 1.22–1.34, DNI: 111–126, LNI: 135–151.

Workers of this form are differentiated by the absence of erect hairs and the absence or great reduction in abundance of pubescence on the dorsum of the propodeum. Numerous specimens that show an intermediate abundance of erect hairs and pubescence on the propodeal dorsum also are known across the range of *P. cambouei*. Specimens of this form could probably be misidentified as *P. masoala* due to the absence of erect hairs on propodeal dorsum and less defined propodeal sculpture. However, the thickness of the petiolar node, which is about as broad as long when viewed laterally, combined with the gradient of characters, are those of a true *P. cambouei*.

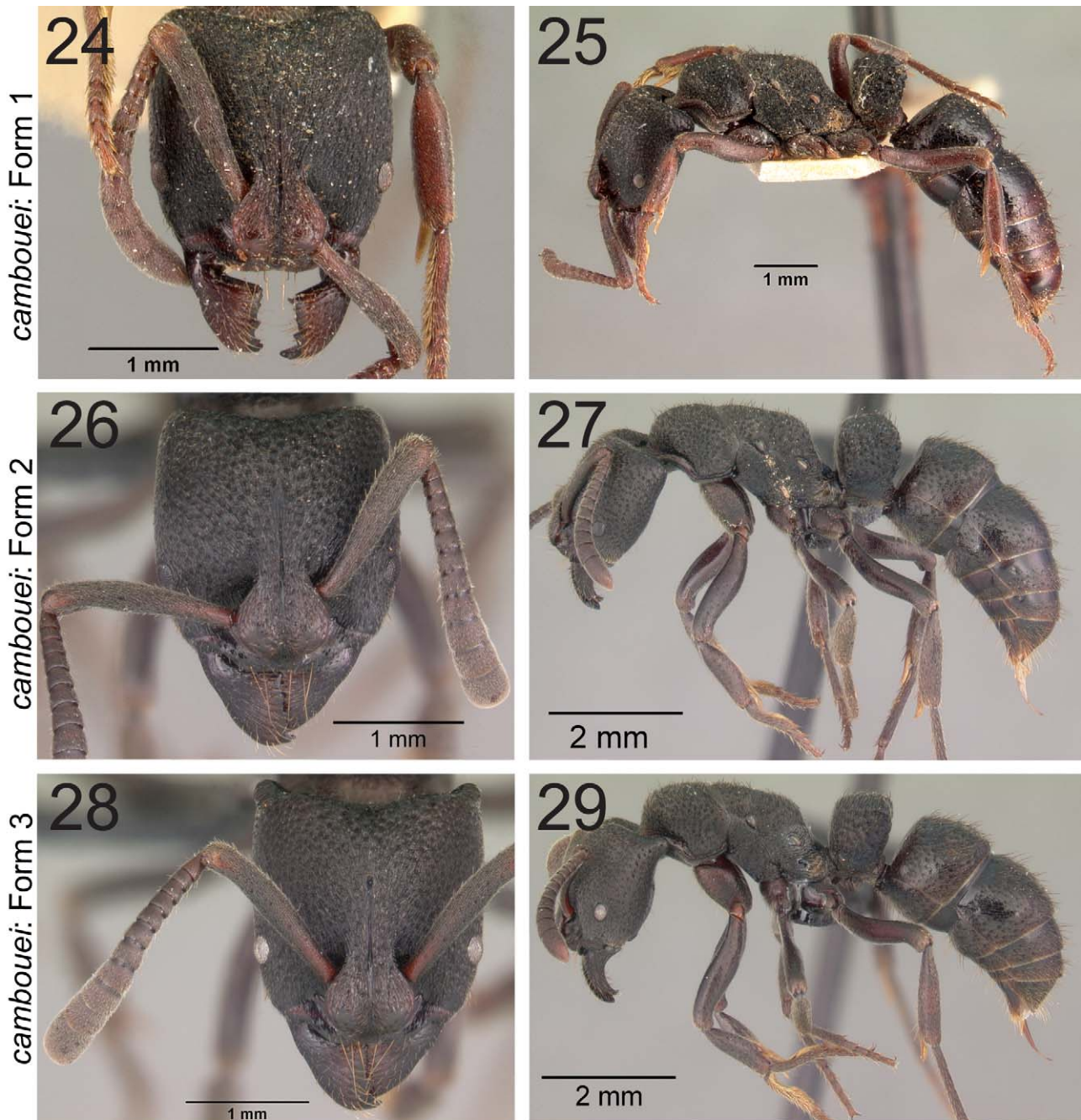
Form 5 (Figs 20, 32–33, 54). Worker measurements (n=5): HL: 2.10–2.29, HW: 1.82–2.01, CI: 87–88, SL: 1.54–1.69, SI: 83–85, PW: 1.49–1.71, WL: 2.71–2.88, NL: 0.92–1.05, NW: 1.15–1.26, NH: 1.48–1.52, DNI: 118–126, LNI: 141–163.

Two different altitudes in PN Masoala in northeast Madagascar yielded a few workers (4) in which both anterodorsal angles of the pronotum are bidentate or tuberculate where they meet the cervical shield, and the ventral surface of the head near the occipital angles is distinctly compressed; the integument of the entire body is ferruginous red. At first glance this form appears to be a morphologically distinct species, but among the four workers, there is one specimen with a pronotum almost angulate in dorsal view, with less developed teeth, the head apparently not strongly flattened ventrally near the occipital corners. An additional worker collected from the same national park presents a rounded anterodorsal angle of the pronotum when viewed dorsally and rounded occipital angles with the head in profile. The presence of these intermediate characters seems to link this variant to the other forms of *P. cambouei*. Colonies with all castes of this form should be collected in order to investigate how this character variation relates to the biology of the population and to clarify relationships with the other forms.

Form 6 (Figs 14, 21, 23, 34–35, 56). Worker measurements (n=30 workers): HL: 1.60–2.07, HW: 1.46–1.87, CI: 86–93, SL: 1.11–1.57, SI: 74–87, PW: 1.12–1.47, WL: 2.02–2.74, NL: 0.76–1.02, NW: 0.93–1.18, NH: 1.08–1.41, DNI: 112–135, LNI: 132–169.



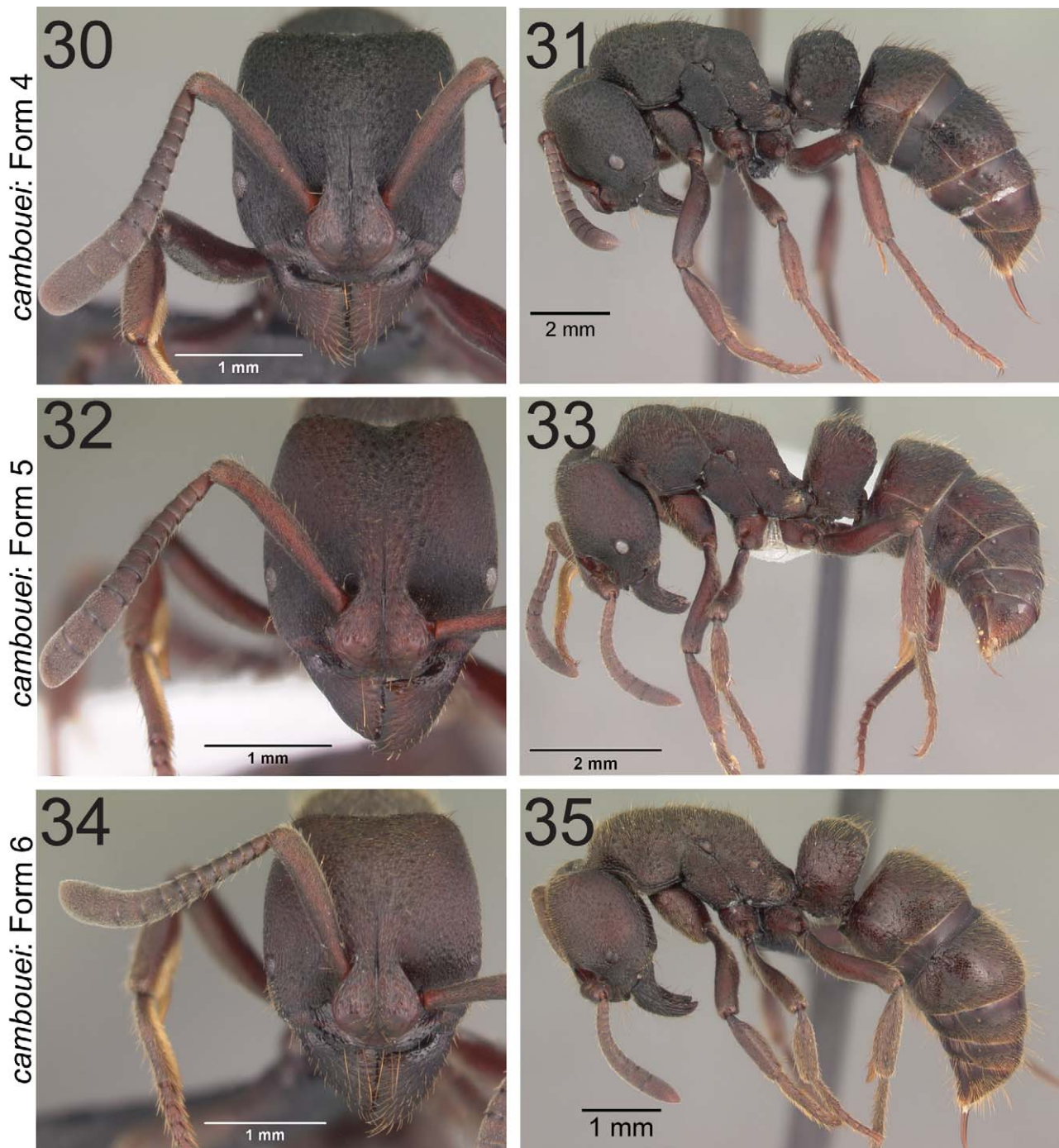
FIGURES 15–23. Morphological character variation within *P. cambouei*. Figs 15–17: Head in profile showing the shape of the occipital corner. Fig. 15: Normally rounded in form 1; Fig. 16: Protruding as a lobe in form 2; Fig. 17: Hornlike extension in form 3. Figs 18–19: Mesosoma in lateral view showing hairs on propodeal dorsum. Fig. 18: Hairs present in form 1; Fig. 19: Hairs absent in form 4. Figs 20–21: Anterodorsal angles of pronotum. Fig. 20: Bidentate in form 5; Fig. 21: Smoothly rounded in form 6. Figs 22–23: Sculpture and pubescence on fourth abdominal tergite. Fig. 22: Smooth and shiny between large punctures and pubescence absent (form 1); Fig. 23: With closely-spaced small punctures between large punctures and abundant pubescence (form 6).



FIGURES 24–29. Full-face view of the head and lateral view of the body of the worker caste of *Pachycondyla cambouei* and its various forms; Figs 24–25: Form 1, CASENT0101404; Figs 26–27: Form 2, CASENT0029098; Figs 28–29: Form 3, CASENT0034270.

This is one of the forms most similar to typical *P. cambouei*. Workers can be recognized by the combination of the following characters: smaller eyes, straight posterior cephalic margin, slightly concave anterior clypeal margin, flagellar segments as long as broad, shagreened propodeal declivity, and less accentuated sculpture. Abdominal tergite 4 densely covered with appressed hairs when viewed dorsally; petiole node with lateral margins strongly converging anteriorly to form a bluntly rounded tip; posterior margin slightly concave with a weak median excision; body color reddish brown. This form is dominant in the humid, high altitude forests of southern Madagascar.

Form 7 (Figs 36–37, 57). Worker measurements (n=20): HL: 1.38–1.65, HW: 1.19–1.44, CI: 85–92, SL: 0.92–1.13, SI: 72–80, PW: 0.95–1.18, WL: 1.64–2.07, NL: 0.65–0.81, NW: 0.79–1.05, NH: 0.95–1.17, DNI: 119–137, LNI: 139–152.



FIGURES 30–39. Full-face view of the head and lateral view of the body of the worker caste of *Pachycondyla cambouei* and its various forms; Figs 30–31: Form 4, CASENT0034474; Figs 32–33: Form 5, BLF0976(40)-2; Figs 34–35: Form 6, CASENT0027983.

As in form 6 but workers tend to have smaller body size, broader than long basal flagellar segments, straight anterior clypeal margin, short and robust mesotibiae, and less pubescence on abdominal tergite 4. In dorsal view, petiole node nearly subquadrate, with straight or slightly concave posterior margin and broadly rounded anterior margin; reddish brown to dark brown in color with lighter gaster and appendages. In the north of Madagascar, workers of this form are slightly sculptured and noticeably shiny, with much longer erect hairs, whereas those from the south possess finer, stronger sculpture and shorter hairs. In this variant, morphological diversity occurs and continuously intergrades into that of form 6. Form 7 dominates the rainforests in northern Madagascar but is absent from the PN Montagne d’Ambre.

Discussion:

A better understanding of species boundaries in Malagasy ants is made possible by recent improvements in collecting methods as well as intensive sampling across the entire region. Although morphological differences can distinguish several forms within *P. cambouei*, enough gradual variation in character states exists across their geographical range to prevent us from hypothesizing separate species for each form. For example, differences in the shape of the posterior margin and the posterior corner of the head, density and size of punctures, and other body sculpture characteristics are not consistent across the region.

Madagascar is characterized by complex topography and habitat heterogeneity. A mountain plateau on the island creates habitats ranging from montane forest at high altitudes and dry forest on its western slopes to lowland rainforest and littoral forests on its eastern side. Continuous environmental gradients exist between each type of habitat. Across these ecological gradients and ecotones, a widespread species like *P. cambouei* would be expected to show some variation, especially if the suitable habitats are isolated (Raxworthy & Nussbaum 1995; Ricklefs 2004; Wiens & Donoghue 2004; Wilmé *et al.* 2006; Boumans *et al.* 2007; Smith *et al.* 2007; Vences *et al.* 2009). An example of isolated populations is the form 2 located in the relict montane rainforests of RS Ambohijanahary, which is nested in extensive dry habitats in the western slope of Madagascar. The area may have served as a habitat refugia during periods of climatic fluctuations (Wilmé *et al.* 2006; Yoder and Heckman 2006; Wollenberg *et al.* 2008; Pearson and Raxworthy 2009; Vences *et al.*, 2009).

To better understand the morphological diversity of *P. cambouei*, especially in a historical context, we hope future studies will include molecular sequence data and other morphological data such as male characters which have proven useful in distinguishing cryptic species of ants (LaPolla *et al.* 2011). The use of molecular sequence data of *P. cambouei* will also help evaluate the biogeographical mechanisms that underlie the evolutionary diversification of taxa in Madagascar (as reviewed by Vences *et al.* 2009).

Distribution and biology:

Pachycondyla cambouei is an endemic, widespread species found from the north throughout the center and the south of Madagascar. It occupies mainly mesic forests at higher and lower altitudes, and also occurs in littoral and transitional forest habitats. This species dominates the representatives of the genus *Pachycondyla* across its distribution range. Two or more different forms within the species occur sympatrically in several localities; these sympatric groupings include forms 2 and 6; forms 3 and 6; forms 3 and 7; forms 6 and 7; forms 1, 4, and 7; and forms 1, 5, and 7. Although this species is generally terrestrial, a few specimens have been found foraging on low vegetation. Forms 2–7 occur generally on the mountaintops, while forms 1 and 4 also can be found in lowland forests. Most forage through leaf litter and rarely on the forest floor. Nest series were discovered for most forms, collected frequently from rotten logs, under stones, in the ground, in rotten tree stumps, and between root mat layers, but seldom in dead twigs or branches above the ground. Workers of *P. cambouei* often play dead when their nests are disturbed. Colonies of forms 5 and 6 have not yet been found, which suggests they may be soil dwellers. The smaller eyes, longer erect hairs, and abundant pubescence in form 6 are also suggestive of an underground life style.

Other material examined:

Form 1. MADAGASCAR: Antananarivo: Antananarivo (Camboué) (MNHN); Tam Perinet; B.M. 1983-201, 27 Apr-3 May 1983 (J.S. Noyes, M.C. Day) (BMNH); Amparihibe (SB); 18; BMNH (E)2003-61, -15.0353, 49.5839 (K.A. Jackson, D. Carpenter) (BMNH); Andrangoloaka (Sikora) (MHNG); Antananarivo; Museum Paris, Grandidier 1893 (Camboué) (MNHN); Imérina; Museum Paris, Grandidier (Camboué) (MNHN); Imerina (Camboué) (MHNG); (W.M. Wheeler) (MCZC); 25 km NNE Ankazobe, -18.1, 47.18333, 1500 m, montane rainforest (P.S. Ward) (MCZC); 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, -18.47333, 47.96, 1300 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Ankazobe, -18.31617, 47.11583, 1241 m, urban/garden (B.L. Fisher *et al.*) (CASC); Kaloy, -18.58998, 47.65102, 1423 m, disturbed montane rainforest (B.L. Fisher *et al.*) (CASC); RNI Sohisika, Sohisika 24.6 km NNE Ankazobe, -18.10322, 47.18692, 1464 m, gallery montane forest (B.L. Fisher *et al.*) (CASC); RS Ambohitantely, F d'Ambohitantely, 20.9 km 72° NE Ankazobe, -18.22528, 47.28683, 1410 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Ambohitantely, F d'Ambohitantely, Jardin Botanique, 24.1 km 59° NE Ankazobe, -18.17139, 47.28182, 1620 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Tsinjoarivo, E Ambatolampy (W.L. Brown) (MCZC); Angavokely, -18.93333, 47.75 (B. Pettersson) (PSWC); Vanjamanitra, Antananarivo, 1380 m (J.M. Betsch) (MCZC); Bongolava, Pref.

Tsiroanomandidy (A. Peyrieras) (MCZC); Antsiranana: 9.2 km WSW Befingotra, RS Anjanaharibe-Sud, -14.75, 49.46667, 1200 m, montane rainforest (B.L. Fisher) (CASC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, -13.79861, 48.16167, 600 m, rainforest (Fisher, Griswold et al.) (CASC); Ankobahoba, 32.3 km N Ambanja, -13.39166, 48.48249, 41 m, disturbed littoral rainforest (B.L. Fisher et al.) (CASC); Betaolana Forest, along Bekona River, -14.52996, 49.44039, 880 m, rainforest (B.L. Fisher et al.) (CASC); F Ambanitaza, 26.1 km 347° Antalaha, -14.67933, 50.18367, 240 m, rainforest (B.L. Fisher) (CASC); F d'Anabohazo, 21.6 km 247° WSW Maromandia, -14.30889, 47.91433, 120 m, tropical dry forest (Fisher, Griswold et al.) (CASC); F de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, rainforest (B.L. Fisher et al.) (CASC); F de Binara, 9.4 km 235° SW Daraina, -13.26333, 49.6, 1100 m, montane rainforest (B.L. Fisher et al.) (CASC); F d'Orangea, 3.6 km 128° SE Remena, -12.25889, 49.37467, 90 m, littoral rainforest (Fisher, Griswold et al.) (CASC); Marojejy R.N.I. #12, -14.44533, 49.78564, 375 m, rainforest (G.D. Alpert) (MCZC); Marojejy, tributary Manantenina R., -14.43333, 49.75, 750 m (Quinter & Nguyen) (CASC); Nosy Be, RNI Lokobe, 6.3 km 112° ESE Hellville, -13.41933, 48.33117, 30 m, rainforest (Fisher, Griswold et al.) (CASC); PN Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, -14.44333, 49.74333, 1325 m, montane rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, -14.435, 49.76, 775 m, rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, -14.43667, 49.775, 450 m, rainforest (B.L. Fisher et al.) (CASC); PN Montagne d'Ambre, 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, montane rainforest (Fisher, Griswold et al.) (CASC); PN Montagne d'Ambre, Antomboka, -12.51269, 49.17807, 970 m, montane rainforest (B.L. Fisher et al.) (CASC); PN Montagne d'Ambre, Crête, -12.58132, 49.13368, 1110 m, montane rainforest (B.L. Fisher et al.) (CASC); RS Manongarivo, 12.8 km 228° SW Antanambao, -13.97667, 48.42333, 780 m, rainforest (B.L. Fisher) (CASC); Makirovana Forest: -14.1667, 49.95, 715 m; -14.1604, 49.9522, 550 m; -14.1707, 49.9541, 415 m, rainforest (B.L. Fisher et al.) (CASC); Fianarantsoa: 29.5 km WNW Tolanaro, Vasiha Mt., -24.93694, 46.75361, 200 m, rainforest (K.C. Emberton et al) (CASC); 45 km S Ambalavao, -22.21667, 47.01667, 720–785 m, rainforest (B.L. Fisher) (CASC); 8.0 km NE Ivohibe, -22.42167, 46.89833, 1200 m, montane rainforest (Sylvain) (CASC); 9.0 km NE Ivohibe, -22.42667, 46.93833, 900 m, rainforest (Sylvain) (CASC); F d'Ambalagoavy Nord, Ikongo, Ambatombe, -21.8275, 47.33889, 625 m (R. Harin'Hala & M.E. Irwin) (CASC); F d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, montane rainforest (Fisher, Griswold et al.) (CASC); F de Vevembe, 66.6 km 293° Farafangana, -22.791, 47.18183, 600 m, rainforest, transition to montane forest (B.L. Fisher et al.) (CASC); PN Ranomafana, Ambatolahy Forest, montane rainforest (Alpert et al.) (MCZC); PN Andringitra, F Ravaro 12.5 km SW Antanifotsy, -22.21167, 46.845, 1500–1800 m (S. Razafimandimby) (CASC); PN Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, -23.84083, 46.9575, 1250 m, montane rainforest (B.L. Fisher et al.) (CASC); PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, -21.29, 47.43333, 1100 m, montane rainforest (Fisher, Griswold et al.) (CASC); RS Ivohibe: 8.0 km E Ivohibe, -22.48333, 46.96833, 1200 m, montane rainforest (Sylvain) (CASC); RS Ivohibe, 7.5 km ENE Ivohibe, -22.47, 46.96, 900 m, rainforest (Sylvain) (CASC); Ranomafana Nat. Park, Maharira Forest, -21, 47, 1190 m, montane forest (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Miranony Forest, -21.25, 47.41667, 700 m, montane forest (Emile Rajeriarison) (MCZC); RF d'Agnalazaha, Mahabo, 42.9 km 215° Farafangana, -23.19383, 47.723, 20 m, littoral rainforest (B.L. Fisher et al.) (CASC); RS Manombo 24.5 km 228° Farafangana, -23.01583, 47.719, 30 m, rainforest (B.L. Fisher et al.) (CASC); Mahajanga: 10 km N Mahatsinjo, -17.84028, 47.02472, 1355 m, tropical dry forest (Alpert et al.) (MCZC); RS Marotandrano, Marotandrano 48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transition humid forest (B.L. Fisher et al.) (CASC); Toamasina: 33 km south of Moramanga, Rte. d'Anosibe, -19.25, 48.21667, forest humus and litter (A. Peyrieras) (MCZC); 5.3 km SSE Ambanizana, Andranobe, -15.66667, 49.96667, 425 m, rainforest (B.L. Fisher) (CASC); 6.3 km S Ambanizana, Andranobe, -15.68131, 49.958, 25 m, rainforest (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, -15.56667, 50, 825 m, rainforest (B.L. Fisher) (CASC); Ambanizana, PN Masoala, -15.57167, 50.00611, 800–897 m, montane rainforest (D. Andriamalala, D. Silva et al.) (CASC); Ambanizana, PN Masoala, -15.57222, 50.00694, 930–1110 m, montane rainforest (D. Andriamalala, D. Silva et al.) (CASC); Amparihibe (SB), 18 and 31, BMNH (E) 2003-61, [-15.0353, 49.5839] (K.A. Jackson, D. Carpenter) (BMNH); Ambatovy, 12.4 km NE Moramanga, -18.84963, 48.2947, 1010 m, montane rainforest (B.L. Fisher et al.) (CASC); Ambatovy, 12.4 km NE Moramanga, -18.84773, 48.29568, 1000 m, grassland (B.L. Fisher et al.) (CASC); Ambatovy, 12.4 km NE Moramanga, -18.85813, 48.28488, 1040 m, grassland (B.L. Fisher et al.) (CASC); Ambatovy, 12.4 km NE Moramanga, -18.84963, 48.2947, 1010 m, montane

rainforest (B.L.Fisher et al.) (CASC); F Ambatovy, 14.3 km 57° Moramanga, -18.85083, 48.32, 1075 m, montane rainforest (B.L. Fisher) (CASC) Analalava, 7.0 km 255° Mahavelona, -17.7095, 49.454, 50 m, littoral rainforest (B.L. Fisher et al.) (CASC); Analamay, -18.80623, 48.33707, 1068 m, montane rainforest (Malagasy ant team) (CASC); Beforona, 29 km east of Perinet, -18.96667, 48.58333, 500 m, forest (A. Peyrieras) (MCZC); Bevolota 17.1 km N Andasibe, -18.77071, 48.43164, 995 m, montane rainforest (B.L. Fisher et al.) (CASC); Didyforét (A. Pauly) (CASC); FC Andriantantely, -18.695, 48.81333, 530 m, rainforest (H.J. Ratsirarson) (CASC); FC Sandranantitra, -18.04833, 49.09167, 450 m, rainforest (H.J. Ratsirarson) (CASC); Ile Sainte Marie, F Kalalao, 9.9 km 34° Ambodifotatra, -16.9225, 49.88733, 100 m, rainforest (B.L. Fisher et al.) (CASC); La Mandraka, 1280 m, montane forest (W.L. & D.E. Brown) (MCZC); Mahavelona (Foulpointe), -17.66667, 49.5, forest (A. Pauly) (CASC); Manakambahiny, near Vavatenina Forest, -17.46667, 49.35 (A. Pauly) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold et al.) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -15.18833, 49.615, 470 m, rainforest (Fisher, Griswold et al.) (CASC); Morarano-Chrome, 25 km W, forêt (A. Pauly) (CASC); PN Mantadia, -18.79167, 48.42667, 895 m, rainforest (H.J. Ratsirarson) (CASC); PN Andasibe-Mantadia, F de Mantadia, 25.7 km 248° Moramanga, -18.81402, 48.43028, 1040 m, rainforest (F.N. Raharimalala, B. Blaimer) (CASC); PN Zahamena, -17.73359, 48.72625, 950 m, rainforest (B.L. Fisher et al.) (CASC); PN Zahamena, Besaky River, -17.75244, 48.85321, 760 m, rainforest (B.L. Fisher et al.) (CASC); PN Zahamena, Onibe River, -17.75908, 48.85468, 780 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Zahamena, Sahavorondrano River, -17.75257, 48.85725, 765 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Zahamena, Tetezambatana Forest, near junction of Nosivola and Manakambahiny Rivers, -17.74298, 48.72936, 860 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Mananara-Nord, 7.1 km 261° Antanambe, -16.455, 49.7875, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Parcelle K7 Tampolo, -17.28333, 49.41667, 10 m, littoral forest (Malagasy ant team) (CASC); Parcelle K9 Tampolo, -17.175, 49.268, 10 m, littoral forest (Malagasy ant team) (CASC); Perinet (E.S. Ross) (MCZC); Perinet and vic., -18.93333, 48.41667, rainforest (W.L. Brown) (MCZC); Perinet; B.M. 1983-201 (J.S. Noyes, M.C. Day) (BMNH); Res. Ambodiriana, 4.8 km 306° Manompana, along Manompana River, -16.67233, 49.70117, 125 m, rainforest (B.L. Fisher *et al.*) (CASC); Res. Perinet, rainforest (L.Bartolozzi, S.Tiati & C.Raharimina) (MCZC); RNI Betampona, Camp Rendriendry 34.1 km 332° Toamasina, -17.924, 49.19967, 390–550 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, -17.88667, 49.2025, 520 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Betampona 35.1 km NW Toamasina, -17.91801, 49.20074, 500 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, 34.08 km 332° Toamasina, -17.91977, 49.20039, 525 m, rainforest (B.L. Fisher) (CASC); RS Ambatovaky, Sandrangato River, -16.81753, 49.29498, 360 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.77274, 49.26551, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.7755, 49.26427, 430 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.7633, 49.26692, 520 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.76912, 49.26704, 475 m, rainforest (B.L. Fisher *et al.*) (CASC); SF Tampolo, 10 km NNE Fenoarivo Atn., -17.2825, 49.43, 10 m, littoral rainforest (B.L. Fisher) (CASC); Sahafina forest 11.4 km W Brickaville, -18.81445, 48.96205, 140 m, rainforest (B.L. Fisher *et al.*) (CASC); SF Analamazaotra, Analamazaotra 1.3 km S Andasibe, -18.38466, 48.41271, 980 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Torotorofotsy, -18.87082, 48.34737, 1070 m, montane rainforest, marsh edge (Malagasy ant team) (CASC); Torotorofotsy, -18.87467, 48.3725, 960 m, rainforest (Woodhead & Vences) (CASC); 1 km W Andampibe, Cap Masoala, -15.69361, 50.18139, 125 m, lowland forest (G.D. Alpert) (MCZC); Rés. Ambodiriana 45 km NW Toamasina (P. Rabeson) (MCZC); vic Andasibe (=Perinet), 950 m, forest (W.L. & D.E. Brown) (MCZC); Toliara: 29.5 km WNW Tolanaro, Vasiha Mt., -24.92306, 46.74083, 700 m, rainforest (K.C. Emberton *et al.*) (CASC); 10 km NW Enakara, Rés Andohahela, -24.56667, 46.81667, 420 m, rainforest (B.L. Fisher) (CASC); 11 km NW Enakara, Rés. Andohahela, -24.56667, 46.83333, 800 m, rainforest (B.L. Fisher) (CASC); 13 km NW Enakara, Rés. Andohahela, -24.55, 46.8, 1250 m, montane rainforest (B.L. Fisher) (CASC); 13 km NW Enakara, Rés Andohahela, -24.55, 46.8, 1280 m, montane rainforest (B.L. Fisher) (CASC); 2.7 km WNW 302° Ste. Luce, -24.77167, 47.17167, 20 m, littoral rainforest (J.-Baptiste) (CASC); 6 km SSW Eminiminy, Res. Andohahela, -24.73333, 46.8, 330 m, rainforest (E. Rajeriarison) (MCZC); Andohahela, -24.77639, 46.70528, 320 m, tropical dry forest (P. Rabeson) (MCZC); Andohahela, Parcel #1 versante E., 300 m, rainforest (L. Bartolozzi, S. Tiati & C. Raharimina) (MCZC); Res. Andohahela, 6 km ESE Imonty, -24.84444, 46.75361, 1000 m, rainforest (P. Rabeson) (MCZC); Res.Andohahela, 9 km SSW Eminiminy, -24.75, 46.78333, 500 m, rainforest (E. Rajeriarison) (MCZC);

FC Analavelona, 29.2 km 343° NNW Mahaboboka, -22.675, 44.19, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); FC Analavelona, 33.2 km 344° NNW Mahaboboka, -22.64333, 44.17167, 1300 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); F Ivohibe 55.0 km N Tolagnaro, -24.569, 47.204, 200 m, rainforest (B.L. Fisher *et al.*) (CASC); Manatantely, 8.9 km NW Tolagnaro, -24.9815, 46.92567, 100 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, -24.7585, 46.85367, 275 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, -24.76389, 46.75167, 900 m, montane rainforest (Fisher, Griswold Arthropod Team) (CASC); PN d'Andohahela, Manampanihy River, 5.4 km 113° ESE Mahamavo, 36.7 km 343° NNW Tolagnaro, -24.76389, 46.76683, 650 m, rainforest (Fisher, Griswold Arthropod Team) (CASC); Res. Andohahela, 5 km SSW Eminiminy, -24.73333, 46.8, 200 m (E. Rajeriarison) (MCZC); RS Ambohijanahary, F d'Ankazotsihitafototra, 34.6 km 314° NW Ambaravarana, -18.26, 45.41833, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Ambohijanahary, F d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravarana, -18.26667, 45.40667, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Kalambatritra, Ambinanitelo, -23.4502, 46.45658, 1325 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.4635, 46.4631, 1270 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.463, 46.47057, 1269 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.4635, 46.4631, 1270 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.463, 46.47057, 1269 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Befarara, -23.4178, 46.4478, 1390 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Betanana, -23.4144, 46.459, 1360 m, montane rainforest (B.L. Fisher *et al.*) (CASC).

Form 2. Toliara: RS Ambohijanahary, F d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravarana, -18.26667, 45.40667, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC).

Form 3. Antsiranana: PN Montagne d'Ambre [1st campsite], -12.51444, 49.18139, 960 m, rainforest (M.E. Irwin, E.I. Schlinger, R. Harin'Hala) (CASC); PN Montagne d'Ambre [Petit Lac road], -12.52028, 49.17917, 1125 m, rainforest (R. Harin'Hala) (CASC); Fianarantsoa: 14 km W of park headquarters, Ranomafana National Park, -21.22707, 47.36874, 1100 m, cloud forest (M.E. Irwin & E.I. Schlinger) (CASC); 2 km W Andrambovato, along river Tatamaly, -21.51167, 47.41, 1075 m, montane rainforest (B.L. Fisher *et al.*) (CASC); 3 km W Ranomafana, nr. Ifandiana, -21.25, 47.41667, 950 m, forest (P.S. Ward) (PSWC); 3 km WNW Ranomafana, nr. Ifanadiana, -21.25, 47.43333, 840 m, roadside (P.S. Ward) (PSWC); 45 km S. Ambalavao, -22.21667, 47.01667, 785 m, rainforest (B.L. Fisher) (CASC); 7.6 km 122° Kianjavato, FC Vatovavy, -21.4, 47.94, 175 m, rainforest (B.L. Fisher *et al.*) (CASC); 7 km W Ranomafana, 1100 m (C. Kremen, R. Van Epps & L. Rasabo) (MCZC); 7 km W Ranomafana, -21.26667, 47.41667, 1000 m, rainforest (M. Stebbins, W.E. Steiner *et al.*) (MCZC); 9.0 km NE Ivohibe, -22.42667, 46.93833, 900 m, rainforest (Sylvain) (CASC); Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., -21.2665, 47.42017, 1020 m, mixed tropical forest (R. Harin'Hala) (CASC); Isalo Nat. Park, Ranohira, Canyon de Sinze, -22.48333, 45.55, 800 m, gallery forest (E. Rajeriarison) (MCZC); Nat. Park Ranomafana, Ambatolahy Forest (E. Rajeriarison) (MCZC); PN Ranomafana (L. Bartolozzi, S. Tiati, & C. Raharimina) (MCZC); PN Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, -23.83517, 46.96367, 940 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, -23.84083, 46.9575, 1250 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Ranomafana, Sahamalaotra River, 6.6 km 310° NW Ranomafana, -21.23667, 47.39667, 1150 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, -21.29, 47.43333, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Ranomafana Talatakely, -21.24833, 47.425, 900 m, between main bridge and park entrance (J.S. Schweikert) (CASC); PN Ranomafana: Talatakely, -21.24833, 47.42667, in guava forest (C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raheirilalao, J.S. Ranorianarisoa, J.S. Schweikert) (CASC); P.N. Ranomafana: Talatakely, -21.24833, 47.42667, in bamboo forest (C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raheirilalao, J.S. Ranorianarisoa, J.S. Schweikert) (CASC); RS Ivohibe 8.0 km E Ivohibe, -22.48333, 46.96833, 1200 m, montane rainforest (Sylvain) (CASC); RS Ivohibe, 6.5 km ESE Ivohibe, -22.49667, 46.955, 1575 m, montane rainforest (Sylvain) (CASC); RS Ivohibe, 7.5 km ENE Ivohibe, -22.47, 46.96, 900 m, rainforest (Sylvain) (CASC); radio tower, Ranomafana National Park, Fianarantsoa Prov., -21.25083, 47.40717, 1130 m, forest edge, mixed tropical forest, open area (M. Irwin, R. Harin'Hala) (CASC); Ranomafana, -21.25, 47.36667 (A. Pauly) (CASC); Ranomafana (A. Kingman) (MCZC); Ranomafana Nat. Park, 700 m, rainforest (W.E. Steiner) (MCZC); Ranomafana Nat. Park, 7 km W, 900 m, montane rainforest (W.E. Steiner) (MCZC); Ranomafana Nat. Park, Fivondronana Ifanadiana Talatakely, 1100 m (J.E. Cadle) (MCZC); Ranomafana

Nat. Park, near Andranoroa, low tree forest (I. Constable) (MCZC); Ranomafana Nat. Park, near research cabin, -21.25, 47.41667 (V.P. Lee, K.J. Rivardo, leg.) (CASC); Ranomafana Nat. Park, SE research cabin, montane rainforest (P. Rabeson) (MCZC); Ranomafana Nat. Park, Talataky Forest, montane rainforest (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Valoloaka Forest, 1200 m, montane forest (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Vohiparara, 1160 m, montane rainforest (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Vohiparara Sahamalaotra, -21.24444, 47.39694, rainforest (P. Rabeson) (MCZC); Ranomafana Nat. Park, Mahirira Forest, -21, 47, 1350 m (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Miaranony Forest, -21.25, 47.41667, 800 m, montane forest (E. Rajeriarison) (MCZC); Ranomafana, Miaranony village (A. Kingman) (MCZC); research cabin at Talataky, Ranomafana National Park, -21.25041, 47.41945, 900 m, mixed tropical forest (M.E. Irwin & E.I. Schlinger) (CASC); Vohiparara broken bridge, Fianarantsoa Prov., -21.22617, 47.36983, 1110 m, high altitude rainforest (R. Harin'Hala) (CASC); Vohiparara, 13 km W Ranomafana, foresta secundaria (L. Bartolozzi, S. Tiati, & C. Raharimina) (MCZC); Toamasina: 19 km ESE Maroantsetra, -15.48333, 49.9, 350 m, rainforest (P.S. Ward) (PSWC); 1 km SSW Andasibe, -18.93333, 48.41667, 420 m, forest (P.S. Ward) (MCZC); 1 km SSW Andasibe, -18.93333, 48.41667, 420 m, forest (P.S. Ward) (PSWC); 1 km SSW Andasibe (=Perinet) -18.93333, 48.41667, 920 m, rainforest (P. S. Ward) (MCZC); 6 km ESE Andasibe (=Perinet), -18.95, 48.46667, 900 m, rainforest (P.S. Ward) (MCZC); 6 km ESE Andasibe(-Périnet), -18.95, 48.46666667, 900 m, rainforest (P.S. Ward) (PSWC); Andranoaria, 15 km S Anosibe An 'alam. (C. Raharimina) (MCZC); FC Andriantantely, -18.695, 48.81333, 530 m, rainforest (H.J. Ratsirarson) (CASC); FC Didy, -18.19833, 48.57833, 960 m, rainforest (H.J. Ratsirarson) (CASC); FC Sandranantitra, -18.04833, 49.09167, 450 m, rainforest (H.J. Ratsirarson) (CASC); PN Mantadia, -18.79167, 48.42667, 895 m, rainforest (H.J. Ratsirarson) (CASC); Perinet and vic., -18.93333, 48.41667, rainforest (W.L. Brown) (MCZC); Perinet and vic., -18.93333, 48.41667, rainforest (W.L. Brown) (MCZC); Res. Perinet, Andasibe, 870 m (Alpert *et al.*) (MCZC); vic Andasibe (=Perinet), 950 m (W.L. Brown) (MCZC); Toliara: F Ivohibe 55.6 km N Tolagnaro, -24.56167, 47.20017, 650 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, -24.7585, 46.85367, 275 m, rainforest (B.L. Fisher *et al.*) (CASC).

Form 4. Antsiranana: 6.5 km SSW Befingotra, RS Anjanaharibe-Sud, -14.75, 49.5, 875 m, rainforest (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, RS Anjanaharibe-Sud, -14.75, 49.46667, 1280 m, montane rainforest (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, RS Anjanaharibe-Sud, -14.75, 49.46667, 1200 m, montane rainforest (B.L. Fisher) (CASC); Makirovana Forest: -14.1651, 49.9477, 900 m, montane rainforest; -14.1604, 49.9522, 550 m, rainforest (B.L. Fisher *et al.*) (CASC); Toamasina: Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -15.18833, 49.615, 470 m, rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, -15.17833, 49.635, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC).

Form 5. Toamasina: 6.9 km NE Ambanizana, Ambohitsitondroina, -15.56667, 50, 825 m, rainforest (B.L. Fisher) (CASC); 5.3 km SSE Ambanizana, Andranobe, -15.66667, 49.96667, 425 m, rainforest (B.L. Fisher) (CASC).

Form 6. Antananarivo: 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, -18.47333, 47.96, 1300 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); 2 km W Ivato (G.D. Alpert) (MCZC); Ambohidratrimo, -18.821, 47.44183, 1362 m, urban garden (B.L. Fisher *et al.*) (CASC); F de galerie, Andranorovitra, 24.0 km NNE Ankazobe, -18.11243, 47.19757, 1491 m, disturbed gallery montane forest (B.L. Fisher *et al.*) (CASC); F de galerie, Telomirahavavy, 23.4 km NNE Ankazobe, -18.12167, 47.20627, 1520 m, disturbed gallery montane forest (B.L. Fisher *et al.*) (CASC); Ilafy, -18.85415, 47.56575, 1385 m, urban garden (B.L. Fisher *et al.*) (CASC); RNI Sohisika, Sohisika 24.6 km NNE Ankazobe, -18.10322, 47.18692, 1464 m, gallery montane forest (B.L. Fisher *et al.*) (CASC); RS Ambohitantely, F d'Ambohitantely, 20.9 km 72° NE Ankazobe, -18.22528, 47.28683, 1410 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Ambohitantely, F d'Ambohitantely, Jardin Botanique, 24.1 km 59° NE d Ankazobe, -18.17139, 47.28182, 1620 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Antsiranana: Bemanevika, 10 km N de Sambava souspref. de Bealanana, -14.13333, 50.11667 (A. Peyrieras) (MCZC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, -14.43667, 49.775, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); PN montagne d'Ambre, 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Fianarantsoa: 2 km W Andrambovato, along River Tatamaly, -21.51167, 47.41, 1075 m, montane rainforest (B.L. Fisher *et al.*) (CASC); 43 km S Ambalavao, Rés. Andringitra, -22.23333, 47, 825 m, rainforest (B.L. Fisher) (CASC); 7.6 km 122°

Kianjavato, FC Vatovavy, -21.4, 47.94, 175 m, rainforest (B.L. Fisher *et al.*) (CASC); 7 km W Ranomafana, 1000 m, rainforest (W.E. Steiner) (MCZC); 8 km E Kianjavato, Vatovavy Forest, -21.39306, 47.94194, 170 m, lowland forest (Alpert *et al.*) (MCZC); 9.0 km NE Ivohibe, -22.42667, 46.93833, 900 m, rainforest (Sylvain) (CASC); Belle Vue trail, Ranomafana National Park, -21.2665, 47.42017, 1020 m, mixed tropical forest (R. Harin'Hala) (CASC); F d'Ambalagoavy Nord, Ikongo, Ambatombe, -21.8275, 47.33889, 625 m (R. Harin'Hala & M.E. Irwin) (CASC); F d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); F de Vevembe, 66.6 km 293° Farafangana, -22.791, 47.18183, 600 m, rainforest, transition to montane forest (B.L. Fisher *et al.*) (CASC); Isalo Nat. Park, Ranohira, Canyon de Sinze, -22.48333, 45.55, 800 m, gallery forest (E. Rajeriarison) (MCZC); PN Andringitra, F Ravaro 12.5 km SW Antanifotsy, -22.21167, 46.845, 1500–1800 m (S. Razafimandimby) (CASC); PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, -21.29, 47.43333, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Parc naturel communautaire, 28.1 km SW Ambositra, -20.78493, 47.17328, 1727 m, disturbed montane rainforest along roadside (B.L. Fisher *et al.*) (CASC); RS Ivohibe 8.0 km E Ivohibe, -22.48333, 46.96833, 1200 m, montane rainforest (Sylvain) (CASC); RS Ivohibe, 7.5 km ENE Ivohibe, -22.47, 46.96, 900 m, rainforest (Sylvain) (CASC); Ranomafana Nat. Park, Talatakely Forest, montane rainforest (E. Rajeriarison) (MCZC); Ranomafana Nat. Park, Miaranony Forest, -21.25, 47.41667, 800 m, montane forest (E. Rajeriarison) (MCZC); RS Manombo 24.5 km 228° Farafangana, -23.01583, 47.719, 30 m, rainforest (B.L. Fisher *et al.*) (CASC); Mahajanga: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transition humid forest (B.L. Fisher *et al.*) (CASC); Toamasina: 16 km S Moramanga, -19.08333, 48.23333, 950 m, rainforest (P.S. Ward) (PSWC); 6.9 km NE Ambanizana, Ambohitsitondroina, -15.56667, 50.0095, 825 m, rainforest (B.L. Fisher) (CASC); Ambanizana, PN Masoala, -15.57167, 50.00611, 900–950 m, montane rainforest (D. Andriamalala, D. Silva *et al.*) (CASC); FC Andriantantely, -18.695, 48.81333, 530 m, rainforest (H.J. Ratsirarson) (CASC); FC Didy, -18.19833, 48.57833, 960 m, rainforest (H.J. Ratsirarson) (CASC); F Ambatovy, 14.3 km 57° Moramanga, -18.85083, 48.32, 1075 m, montane rainforest (Malagasy ant team) (CASC); F d'Analava Mandrisy, 5.9 km 195 Antanambe, -16.48567, 49.847, 10 m, littoral rainforest (B.L. Fisher *et al.*) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -15.18833, 49.615, 470 m, rainforest (Fisher, Griswold *et al.*) (CASC); PN Mantadia, -18.79167, 48.42667, 895 m, rainforest (H.J. Ratsirarson) (CASC); PN Marojejy, -14.43817, 49.774, 488 m, rainforest (Rin'Ha, Irwin) (CASC); RNI Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, -17.924, 49.19967, 390 m, rainforest (B.L. Fisher *et al.*) (CASC); SF Analamazaotra, Analamazaotra 1.3 km S Andasibe, -18.38466, 48.41271, 980 m, montane rainforest (B.L. Fisher *et al.*) (CASC); Torotorofotsy, -18.87082, 48.34737, 1070 m, montane rainforest, marsh edge (Malagasy ant team) (CASC); Toliara: 11 km NW Enakara, Rés. Andohahela, -24.56667, 46.83333, 800 m, rainforest (B.L. Fisher) (CASC); 13 km NW Enakara, Rés. Andohahela, -24.55, 46.8, 1250 m, montane rainforest (B.L. Fisher) (CASC); FC Analavelona, 29.2 km 343° NNW Mahaboboka, -22.675, 44.19, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); FC Analavelona, 29.4 km 343° NNW Mahaboboka, -22.675, 44.18667, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); F de Petriky, 12.5 km W 272° Tolagnaro, -25.06167, 46.87, 10 m, littoral rainforest (B.L. Fisher) (CASC); Mandena, 8.4 km NNE 30° Tolagnaro, -24.95167, 47.00167, 20 m, littoral rainforest (B.L. Fisher) (CASC); PN Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, -24.7585, 46.85367, 275 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, -24.76389, 46.75167, 900 m, montane rainforest (Fisher-Griswold Arthropod Team) (CASC); RS Ambohijanahary, F d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravarana, -18.26667, 45.40667, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); RS Kalambatritra, Ambinanitelo, -23.4502, 46.45658, 1325 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.4635, 46.4631, 1270 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Ampanihy, -23.463, 46.47057, 1269 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Kalambatritra, Befarara, -23.4178, 46.4478, 1390 m, montane rainforest (B.L. Fisher *et al.*) (CASC).

Form 7. Antsiranana: 6.5 km SSW Befingotra, RS. Anjanaharibe-Sud, -14.75, 49.5, 875 m, rainforest (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, RS. Anjanaharibe-Sud, -14.75, 49.46667, 1200 m, montane rainforest (B.L. Fisher) (CASC); Ambondrobe, 41.1 km 175° Vohemar, -13.71533, 50.10167, 10 m, littoral rainforest (B.L. Fisher) (CASC); Bemanevika, 10 km N de Sambava souspref. de Bealanana, -14.13333, 50.11667 (A. Peyrieras) (MCZC); F de Binara, 9.4 km 235° SW Daraina, -13.26333, 49.6, 1100 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, -14.43667, 49.775, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Manongarivo, 12.8 km 228° SW Antanambao, -

13.97667, 48.42333, 780 m, rainforest (B.L. Fisher) (CASC); RS Manongarivo, 14.5 km 220° SW Antanambao, -13.99833, 48.42833, 1175 m, montane rainforest (B.L. Fisher) (CASC); Ambondrobe, 41.1 km 175° Vohemar, -13.71533, 50.10167, 10 m, littoral rainforest (B.L. Fisher) (CASC); Makirovana Forest, -14.1707, 49.9541, 415 m, rainforest (B.L. Fisher *et al.*) (CASC); Fianarantsoa: 9.0 km NE Ivohibe, -22.42667, 46.93833, 900 m, rainforest (Sylvain) (CASC); RS Ivohibe 8.0 km E Ivohibe, -22.48333, 46.96833, 1200 m, montane rainforest (Sylvain) (CASC); PN Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, -21.29, 47.43333, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Belle Vue trail, Ranomafana National Park, -21.2665, 47.42017, 1020 m, mixed tropical forest (R. Harin'Hala) (CASC); Mahajanga: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transitional humid forest (B.L. Fisher *et al.*) (CASC); Toamasina: 6.9 km NE Ambanizana, Ambohitsitondroina, -15.56667, 50.000, 825 m, rainforest (B.L. Fisher) (CASC); Ambanizana, PN Masoala, -15.57167, 50.00611, 900–950 m, montane rainforest (D. Andriamalala, D. Silva *et al.*) (CASC); FC Andriantantely, -18.695, 48.81333, 530 m, rainforest (H.J. Ratsirarson) (CASC); FC Didy, -18.19833, 48.57833, 960 m, rainforest (H.J. Ratsirarson) (CASC); FC Sandranantitra, -18.04833, 49.09167, 450 m, rainforest (H.J. Ratsirarson) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -15.18833, 49.615, 470 m, rainforest (Fisher, Griswold *et al.*) (CASC); PN Mantadia, -18.79167, 48.42667, 895 m, rainforest (H.J. Ratsirarson) (CASC); PN Zahamena, Onibe River, -17.75908, 48.85468, 780 m, rainforest (B.L. Fisher *et al.*) (CASC); Toliara: 11 km NW Enakara, Rés. Andohahela, -24.56667, 46.83333, 800 m, rainforest (B.L. Fisher) (CASC); 13 km NW Enakara, Res. Andohahela, -24.55, 46.8, 1250 m, montane rainforest (B.L. Fisher) (CASC); PN Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, -24.76389, 46.75167, 900 m, montane rainforest (Fisher-Griswold Arthropod Team) (CASC); 0.7 km WNW 302° Ste. Luce, -24.77167, 47.17167, 20 m, littoral rainforest (J.-Baptiste) (CASC); F de Petriky, 12.5 km W 272° Tolagnaro, -25.06167, 46.87, 10 m, littoral rainforest (B.L. Fisher) (CASC); Mandena, 8.4 km NNE 30° Tolagnaro, -24.95167, 47.00167, 20 m, littoral rainforest (B.L. Fisher) (CASC).

***Pachycondyla comorensis* (André)**

(Figures 1, 4, 38–39, 59)

Ponera comorensis André, 1887: 292. Lectotype worker, present designation, Antsiranana, Nosy Be (Ernest André 1914) AntWeb specimen code: CASENT0101406 (MNHN) [examined]. Paralectotype workers with the same data but pins coded as CASENT0101407 (MNHN) and CASENT0102011 (MSNG) [examined]. [Combination in *Bothroponera*: Forel, 1891: 129, pl. 4, fig. 5; Dalla Torre 1893: 36; Combination in *Pachycondyla* (*Bothroponera*): Emery, 1901: 45, Forel, 1907: 14, Emery 1911: 78; Combination in *Bothroponera*: Wheeler, 1922: 1007; Combination in *Pachycondyla* by Bolton, 1995: 304].

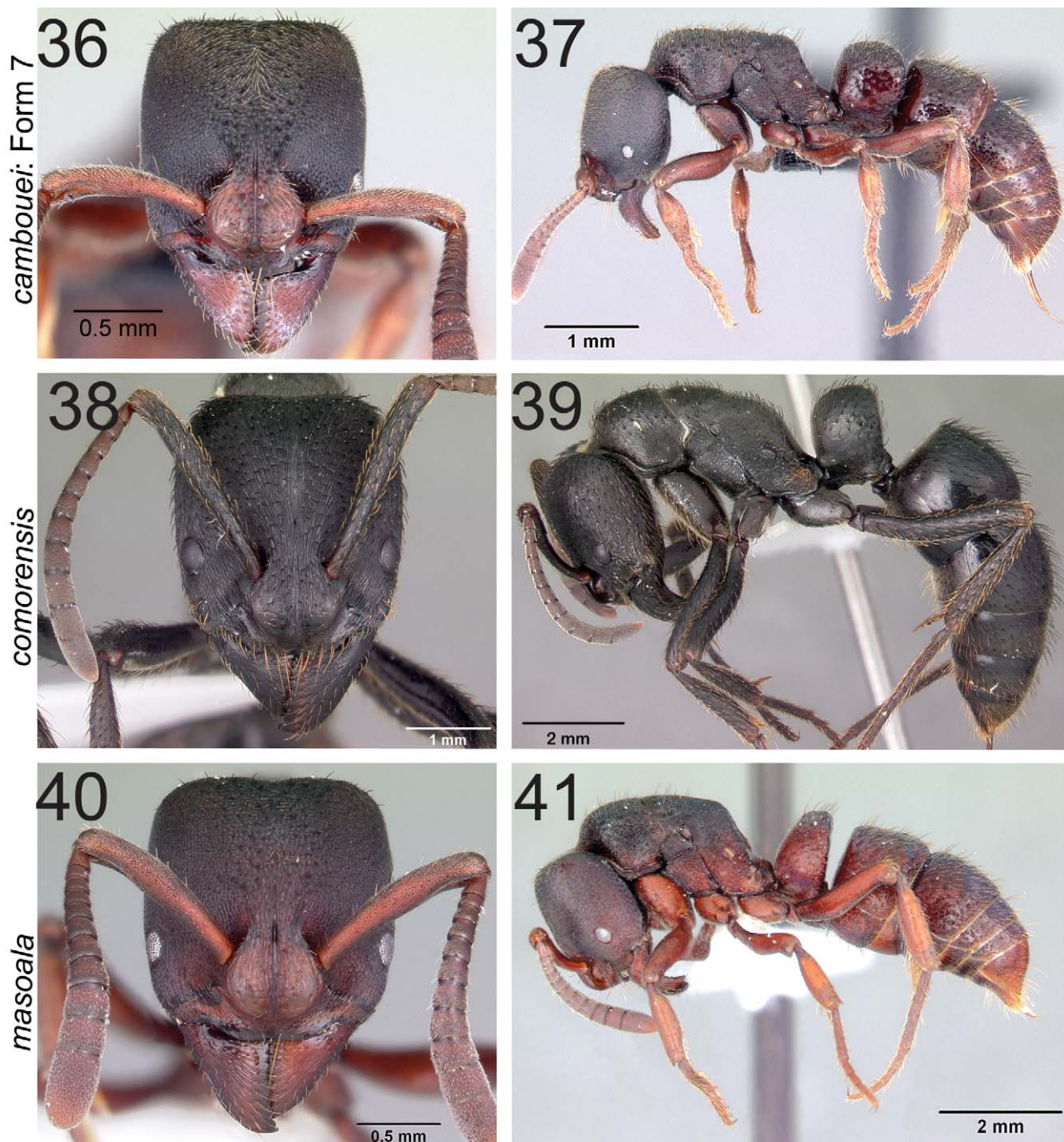
Worker diagnosis:

Larger species (HW: 2.49–3.13 mm), antennal scape extending beyond the rear cephalic border; anterior margin of clypeus truncate; eyes not breaking the outline of the sides of head; dorsum of head and mesosoma finely striate, with sparse punctures; stout erect hairs on dorsum of head and the rest of body much more inclined to the body surface.

Worker measurements (n=10): HL: 2.94–3.49, HW: 2.49–3.13, CI: 85–92, SL: 2.47–2.95, SI: 94–99, PW: 1.95–2.30, WL: 4.13–4.98, NL: 1.34–1.62, NW: 1.45–1.67, NH: 1.64–1.94, DNI: 99–115, LNI: 110–126.

Description:

Worker. Head roughly as long as broad, broadest behind eyes on posterior third; sides very slightly convex but converging near base of mandibles; posterior margin weakly emarginate medially. Eyes moderately large, located more to the front and not breaking outline of sides of head. Antennal scape relatively long and extending beyond posterior cephalic margin. Anterior margin of clypeus truncate, not projecting into lobe, but rather straight or feebly notched medially; with head in profile, median portion perpendicular to mandibular surface. Mandibles triangular, apical margins bearing eight to nine teeth and denticles. With mesosoma in profile, outline of dorsum almost continuously convex, without distinct angle between propodeal dorsum and declivity, lateral margins of the latter also generally indiscernable. Mesopleural sulcus visible but incomplete. With petiole in dorsal view, anterior margin rounded and posterior margin straight. In profile, petiole nodiform, with rounded anterodorsal portion and distinct angle in the posterodorsal margin.



FIGURES 36–41. Full-face view of the head and lateral view of the body of the worker caste. Figs 36–37: Form 7 of *Pachycondyla cambouei*, AntWeb CASENT0034493; Figs 38–39: *Pachycondyla comorensis*, CASENT0410164; Figs 40–41: *Pachycondyla masoala*, CASENT0317384.

Mandibles costate or sometimes smooth with effaced fine striation, and with scattered punctures from which hairs arise. Dorsum of head densely striate and superimposed with piliferous punctures from level of eyes and frontal lobes; striation radiating towards occipital corners on each side of midline of head. Dorsal sculpture of pronotum variable, either densely finely costulate or smooth and shiny with trace of striation between sparse punctures, mesonotal and propodeal dorsum with transverse, dense, and fine striation or microreticulation which becomes fairly effaced on some specimens. Lateral portion of mesosoma characterized by a mixture of fine and dense striation and reticulate–rugulation. Declivitous surface transversely finely striate or almost smooth. Lateral portion of petiole node and first two gastral segments microreticulate to densely finely striate, with scattered large punctures which turn into a smooth and shiny surface on dorsum. Upper surface of body with suberect or appressed

black, stout hairs, which are shorter on the dorsum of the head and become yellowish brown to brown on appendages; with mesosoma in frontal view, these hairs inclined towards the midline of the mesosoma dorsum, suberect along the dorsolateral margin and much more appressed near the midline. Slender brownish hairs present on ventral surface of head, gaster, and coxae. Body covered with abundant pubescence except head, dorsum of propodeum, petiole node, and third and anterior half of fourth abdominal segments. Coloration is black with reddish articulations and apices of appendages.

The queen caste is unknown for *P. comorensis*.

Discussion:

Pachycondyla comorensis can be easily confused with *P. tavaratra* at first glance. Yet the shape of the anterior clypeal margin, the location of the eyes, and the standing degrees of pilosity on the dorsum of the body allow the separation of these two species. *Pachycondyla comorensis* has a truncated anterior clypeal margin, eyes that do not break the outline of the sides of the head, and subdecumbent to decumbent stout hairs on the dorsum of the body. The morphological similarity of these two species could be attributed to their adaptation to different ecological habitats in northern Madagascar. *Pachycondyla comorensis* generally inhabits dry forest and lowland rainforest habitats, whereas *P. tavaratra* occupies montane rainforests. Data from different collecting events over several years suggest that these large species may not have a morphologically typical queen caste as do other species within the genus, but reproduce through one or more ergatoid or gamergates in the same colony. The absence of alate queens reduces the spatial connection between geographically distant populations because dispersal must occur by budding.

Distribution and biology:

Pachycondyla comorensis is known only from Madagascar, where it generally occupies dry and lowland humid forests and the coastal region in the north of the island (Fig. 59). Despite its name, *P. comorensis* is not known from the Comoros. This is one of two species with longer antennal scapes which are probably used to forage on the soil surface and in leaf litter. Colonies have been found frequently in the ground, in rotten logs, under stones, rarely in dead twigs and rotten sticks on the ground, and under layers of roots and litter on rock.

Other material examined:

MADAGASCAR: Antsiranana: [Nd. Madagascar, Amber Gebirge Nd. Madagascar H. Rolle, Berlin, S.W.11.] (MHNG); [Nossi-bé; Museum Paris Collection, Ernest André 1914] (MNHN); [Nossi-bé] (MSNG); F Lokobe, Nossi-Be Island (E.S. Ross) (MCZC); Nossi-Be (G.B. King) (MCZC); Nosy Be, 4 km ESE Andoany (=Hellville), -13.41667, 48.3, 200 m, rainforest (P.S. Ward) (MCZC); Nosy Be, Lokobe Forest, -13.41639, 48.30722, 20 m, lowland forest (G.D. Alpert) (MCZC); Nosy Be: RNI Lokobe, 6.3 km 112° ESE Hellville, -13.41933, 48.33117, 30 m, rainforest (Fisher, Griswold *et al.*) (CASC); Nosy Be: 4 km ESE Andoany (=Hellville), -13.41667, 48.3, 200 m, rainforest (P.S. Ward) (PSWC); NE, 80 km N Ambilobe; no. 2103 (J.M. Wilson) (BMNH); 5 km S Sambava, -14.65, 50.16667, coastal forest and vanilla (W.L. & D.E. Brown) (MCZC); ridge behind Sambava, second growth forest (W.L. & D.E. Brown) (MCZC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, -13.79861, 48.16167, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); F Ambato, 26.6 km 33° Ambanja, -13.4645, 48.55167, 150 m, rainforest (B.L. Fisher) (CASC); F d'Antsahabe, 11.4 km 275° W Daraina, -13.21167, 49.55667, 550 m, tropical dry forest (B.L. Fisher) (CASC); F d'Ampombofofo, -12.09949, 49.33874, 25 m, littoral forest (B.L. Fisher *et al.*) (CASC); F d'Ampondrabe, 26.3 km 10° NNE Daraina, -12.97, 49.7, 175 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); F d'Analabe, 30.0 km 72° ENE Daraina, -13.08333, 49.90833, 30 m, littoral rainforest (B.L. Fisher *et al.*) (CASC); F de Bekaraoka, 6.8 km 60° ENE Daraina, -13.16667, 49.71, 150 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); F de Binara, 7.5 km 230° SW Daraina, -13.255, 49.61667, 375 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); RS Manongarivo, 10.8 km 229° SW Antanambao, -13.96167, 48.43333, 400 m, rainforest (B.L. Fisher) (CASC); RS Manongarivo, 12.8 km 228° SW Antanambao, -13.97667, 48.42333, 780 m, rainforest (B.L. Fisher) (CASC); RS Ankarana, 7 km SE Matsaborimanga, -12.9, 49.11667, 150 m, rainforest (P.S. Ward) (PSWC); RS Ankarana, -12.90056, 49.14722, 150 m (G.D. Alpert) (MCZC); RS Ankarana, 13.6 km 192° SSW Anivorano Nord, -12.86361, 49.22583, 210 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano Nord, -12.90889, 49.10983, 80 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Ambre, 3.5 km 235° SW Sakaramy, -12.46889, 49.24217, 325 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); Makirovana Forest, -14.103, 50.0198, 390 m; -14.1707, 49.9541, 415 m; -14.1604, 49.9522, 550 m, rainforest (Fisher *et al.*) (CASC).



FIGURES 42–47. Full-face view of the head and lateral view of the body of the worker caste. Figs 42–43: *Pachycondyla perroti*, CASENT0048930; Figs 44–45: *Pachycondyla planicornis*, CASENT0096369; Figs 46–47: *Pachycondyla tavaratra*, CASENT0410152.

***Pachycondyla masoala* Rakotonirina and Fisher, sp. n.**

(Figures 7, 40–41, 52, 58)

Holotype worker: Toamasina, 6.3 km S Ambanizana, Andranobe, -15.6813, 49.958, 25 m, sifted litter, rainforest, 14 Nov 1993 (B.L. Fisher), collection code: BLF00886, specimen code: CASENT0317384 (CASC).

Paratypes: 8 workers with the same data as holotype but specimen coded: BLF0886(13)-2, BLF0886(48)-2; 13

Nov 1993 (B.L. Fisher), collection code: BLF0882, specimen codes: BLF0882(23)-2, BLF0882(2)-2, BLF0882(5)-1, BLF0882(32)-1, BLF0882(34)-1, BLF0882(42)-1 (BMNH, MHNG, MCZC, CASC, PBZT).

Worker diagnosis:

With head in full-face view, antennal scape not surpassing the posterior cephalic margin; dorsum of head and mesosoma not finely striate; dorsum of the body with erect slender hairs and pubescence; erect hairs and pubescence on dorsum of propodeum absent or reduced in number; petiole node anteroposteriorly flattened and tapered towards its apex, about twice as broad as long in dorsal view.

Worker measurements (n=10): HL: 1.69–1.83, HW: 1.54–1.67, CI: 91–93, SL: 1.22–1.31, SI: 76–82, PW: 1.16–1.31, WL: 2.04–2.26, NL: 0.69–0.81, NW: 1.02–1.14, NH: 1.18–1.29, HTL: 1.19–1.29, DNI: 135–159, LNI: 156–178.

Description:

Worker. Head somewhat elongate, sides almost straight behind level of eyes and narrowest in front, posterior margin noticeably medially excised. Compound eyes moderately large, but diameter smaller than maximum width of antennal scape. Scape relatively short, not surpassing posterior margin of head, leading edge rounded. Clypeus anteriorly truncate, and slightly notched medially. Mandibles triangular, the apical margins armed with seven to eight teeth and denticles. With mesosoma in lateral view, dorsal margin not forming a continuous convexity; propodeal dorsum and declivity separated by distinct angle; mesopleural suture visible. Propodeum slightly compressed laterally. In lateral view, node of petiole squeezed anteroposteriorly, anterior margin inclined posteriorly and posterior margin truncate, making dorsal margin shorter relative to ventral border. With petiole in dorsal view, node broader than long, posterior margin excavated medially. Head sculpture densely and finely reticulate–rugulose, superimposed with punctures which are larger in the dorsum behind level of eyes and become larger towards posterior margin.

Mandibles striate, interspersed with shallow piligerious punctures. Dorsum of pronotum and mesonotum densely reticulate–rugulose and covered with dense, coarse punctures; propodeum generally with fine reticulate punctures or rugulose. Sides of mesosoma densely and finely reticulate–rugulose. Petiole node laterally almost smooth and shining; small dorsal surface covered with closely spaced large and shallow punctures; adjacent punctures separated by sharp ridge. Third and fourth abdominal tergites with dense and large shallow punctures, which become sparse and irregularly scattered on the posterior half of the latter segment. Pilosity present on dorsum of body except on propodeum; pubescence reduced. Integument shiny, reddish brown or dark brown to black in color with lighter gaster and appendages.

Queen. Measurements (n=1): HL: 1.94, HW: 1.88, CI: 97, SL: 1.42, SI: 75, EL: 0.344, OI: 18, PW: 1.45, WL: 2.83, NL: 0.74, NW: 1.33, NH: 1.26, DNI: 180, LNI: 170.

Morphologically similar to worker except modifications of the queen caste, with head slightly broader, body size notably much larger.

Discussion:

Pachycondyla masoala can be confused with form 4 of *P. cambouei* because of the absence of erect hairs on the propodeal dorsum. However, a flattened petiole node, which shows a shorter dorsal margin in profile, separates it from *P. cambouei*, which has a thick petiole node.

Distribution and biology:

Pachycondyla masoala is only known from the lower elevations of humid forests in northeastern Madagascar (Fig. 58) around the PN Masoala, and in the Makirovana forest near Sambava. One nest was found under a dense layer of roots and litter on a rock, but the species generally forages on the forest floor and through leaf litter.

Other material examined:

Antsiranana: 14 km W Cap Est, Ambato, -15.29128, 50.33803, 150 m, secondary rainforest (Alpert *et al.*) (MCZC); Makirovana Forest, -14.17066, 49.95409, 415 m, rainforest (B.L. Fisher *et al.*) (CASC); Makirovana Forest: -14.1604, 49.9522, 550 m, -14.1707, 49.9541, 415 m, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Toamasina: 5.3 km SSE Ambanizana, Andranobe, -15.66667, 49.96667, 425 m, rainforest (B.L. Fisher) (CASC);

6.3 km S Ambanizana, Andranobe, -15.6813, 49.958, 25 m, rainforest (B.L. Fisher) (CASC); Nosy Mangabe, -15.5, 49.76667, 150–300 m, rainforest (P.S. Ward) (PSWC).

***Pachycondyla perroti* (Forel)**

(Figures 13, 42–43, 60)

Bothroponera perroti Forel, 1891: 131 pl. 4, fig. 6. Holotype worker, Madagascar, Toamasina, Fenerive (E. Perrot), AntWeb specimen code: CASENT0101401 (MNHN) [examined]. [Further description by Dalla Torre 1893: 36. Combination in *Ponera* (*Bothroponera*): Emery, 1899: 267; in *Pachycondyla* (*Bothroponera*): Emery, 1901: 45; Combination in *Bothroponera*: Wheeler, 1922: 1007; in *Pachycondyla*: Bolton, 1995: 308].

Bothroponera perroti admista Forel, 1892: 251. Lectotype worker, present designation Madagascar, Anosibe Bezanozano Province Moramanga (Sikora), AntWeb specimen code: CASENT0101035 (MHNG) [examined]. Syn. n. Paralectotype worker with the same data but specimen coded as CASENT0101034 (MHNG) [examined]. [Raised to species: Dalla Torre, 1893: 35; returned to subspecies: Wasmann, 1897: 250, Forel, 1897: 188, Emery, 1901: 45. Combination in *Ponera* (*Bothroponera*): Emery, 1899: 267; in *Pachycondyla* (*Bothroponera*): Emery, 1901: 45, 1911: 78; Combination in *Bothroponera*: Wheeler, 1922: 1008; in *Pachycondyla*: Bolton, 1995: 302].

Worker diagnosis:

With head in full-face view, antennal scape not surpassing posterior cephalic margin; dorsum of head and mesosoma not finely striate, dorsum of the body with erect slender hairs and pubescence; basal half of antennal scape rounded; dorsal outline of mesosoma forming a continuous convexity with a nearly rounded junction between propodeal dorsum and declivitous surface; anterior half of fourth abdominal tergite (gastral tergite 2) mostly smooth and shiny between large punctures.

Worker measurements (n=26): HL: 2.42–2.71, HW: 2.27–2.58, CI: 91–98, SL: 1.69–2.01, SI: 69–81, PW: 1.58–1.81, WL: 3.10–3.55, NL: 0.87–1.04, NW: 1.02–1.23, NH: 1.18–1.45, DNI: 108–130, LNI: 125–144.

Description

Worker. Head as long as broad, but narrower in front than behind, with slightly convex sides; posterior margin markedly medially excised, and strongly concave. With head in full-face view, eyes large but less than maximum width of antennal scape, located more to the front and not splitting the sidelines of head. Scape subcylindrical, with rounded leading edge, not reaching the posterior margin of head. Median lobe of clypeus not projecting anteriorly, anterior margin truncate and strongly notched medially. Mandible triangular, the masticatory margin bearing eight short, robust, and distinct teeth. With mesosoma in profile, the outline of dorsum a continuous convexity, with rounded junction of propodeal dorsum and declivitous surface. Mesopleural sulcus not clearly visible or absent. Hind legs with rounded basitarsus, the inside surface of which is not concave. In dorsal view, petiole node anteriorly rounded and posteriorly truncate. Sculpture of head dorsum finely ruguloreticulate and usually superimposed with punctures which become larger on the front toward the posterior margin; the lateral surface reticulate-punctulate.

Mandibles faintly rugulose basally, with scattered piligerous punctures, and increasingly smooth and shining approaching the apical margin; in some specimens mandibles striate or smooth and shiny apart from the piligerous pits. Dorsum of mesosoma and petiole, and first two gastral tergites, with sparse and coarse shallow punctures, the spaces between which are smooth or with closely spaced, small punctures. Lateral portion of mesosoma and petiole node densely and finely reticulate to reticulate rugulose, superimposed with small punctures; occasionally the petiole is coarsely punctate or with effaced large punctures. Brown-yellowish, slender and erect hairs covering the entire body except the lateral portion of mesosoma; pubescence quite abundant. Integument matte or shiny, coloration dark red to black, with lighter tip of gaster and appendages.

Queen. Measurements (n=7): HL: 2.52–2.81, HW: 2.44–2.81, CI: 96–101, SL: 1.86–2.07, SI: 69–76, EL: 0.48–0.51, OI: 17–20, PW: 2.00–2.31, WL: 3.82–4.16, NL: 1–1.11, NW: 1.34–1.50, NH: 1.41–1.51, DNI: 131–142, LNI: 136–143. The queen of *P. perroti* is relatively similar to workers, but with the typical differences of the queen caste: Head relatively broader, body size much larger, and mesopleural sulcus distinct.

Discussion:

Pachycondyla perroti is recognized by the following combination of characters: continuous convexity of the dorsal outline of its mesosoma, nearly rounded junction of the propodeal dorsum and declivity, strong median excision of the posterior cephalic margin, and strongly concave anterior margin of clypeus.

Along its geographical range, *P. perroti* shows a large range of phenotypic variation. Based on these morphological variations, and the scarcity of specimens collected earlier in Madagascar, this species likely misled taxonomists, who erected a separate subspecies, *P. perroti admista* Forel, for a different populations. Forel (1892) had to decide on the species-level status of *admista* without being able to compare it with the type of *P. perroti* or with additional samples of *P. perroti* throughout its range. However, the large number of samples of *P. perroti* collected during recent ant inventories in Madagascar, covering most of this ant's distributional range, present evidence to synonymize the subspecies *perroti admista* under *P. perroti*.

Distribution and biology:

Pachycondyla perroti is endemic to Madagascar, generally occurs in the humid habitats in the east of the island, ranging from the littoral region to the mountaintops, as well as the transitional forests of the Ampasindava peninsula (Ambilanivy Forest) and Daraina in the western slope of the northern part of the island (Fig. 60). This species is also known to occupy secondary and disturbed habitats. Although the large size of the species offers an opportunity for behavioral studies, very little is known about its biology. Field work over the past 15 years has found this species foraging most frequently on the ground and in leaf litter, and very rarely on lower vegetation. It usually nests in rotten logs, soil layers, or rarely tree stumps.

Other material examined:

MADAGASCAR: Antsiranana: Ambohitsara, 10 km SW Antalaha (MCZC); Chutes de la Mort (E.S. Ross) (MCZC); 10 km Cap Est, 5 km W, -15.36667, 50.43333, 20 m, lowland secondary forest (B.L. Fisher) (MCZC); 14 km W Cap Est, Ambato, -15.29128, 50.33803, 100 m, secondary rainforest (G.D. Alpert) (MCZC); 2.0 km S Andrakata, -14.65, 49.71667, 520 m, disturbed rainforest (B.L. Fisher) (CASC); 30 km N Antalaha, 3 km W of a hill (G.D. Alpert) (MCZC); 5 km SW Antalaha, -14.93806, 50.26167, 50 m, secondary forest (G.D. Alpert) (MCZC); 5 km SW Antalaha, secondary forest (G.D. Alpert) (MCZC); RS Anjanaharibe-Sud, 6.5 km SSW Befingotra, -14.75, 49.5, 875 m, rainforest (B.L. Fisher) (CASC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, -13.79861, 48.16167, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Betaolana Forest, Ambodihazovolabe village along Ambolokopatrika River, -14.54484, 49.45163, 740 m, disturbed forest patch next to tavy (B.L. Fisher *et al.*) (CASC); F Ambanitaza, 26.1 km 347° Antalaha, -14.67933, 50.18367, 240 m, rainforest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, -13.21167, 49.55667, 550 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); Fotodriana, Cap Masoala, -15.69694, 50.27028, 25 m, rainforest (G.D. Alpert) (MCZC); Marojejy RNI. #12, -14.44533, 49.78564, 375 m, rainforest (G.D. Alpert) (MCZC); PN Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, -14.435, 49.76, 775 m, rainforest (B.L. Fisher) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, -14.43667, 49.775, 450 m, rainforest (B.L. Fisher) (CASC); PN Marojejy, -14.43817, 49.774, 488 m, rainforest (Rin'Ha, Irwin) (CASC); PN Montagne d'Ambre, 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, montane rainforest (Fisher, Griswold *et al.*) (CASC), PN Montagne d'Ambre, Antomboka, -12.51269, 9.17807, 970 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Manongarivo, 10.8 km 229° SW Antanambao, -13.96167, 48.43333, 400 m, rainforest (B.L. Fisher) (CASC); RS Manongarivo, 12.8 km 228° SW Antanambao, -13.97667, 48.42333, 780 m, rainforest (B.L. Fisher) (CASC); Fianarantsoa: F d'Ambalagoavy Nord, Ikongo, Ambatombe, -21.8275, 47.33889, 625 m (R. Harin'Hala & M.E. Irwin) (CASC); PN Ranomafana, Miaranony Forest, 700 m, montane forest (E. Rajeriarison) (MCZC); Mahajanga: RS Marotandrano, Marotandrano 48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transition humid forest (B.L. Fisher *et al.*) (CASC); Toamasina: 19 km ESE Maroantsetra, -15.48333, 49.9, 350 m, rainforest (P.S. Ward) (MCZC); 5.3 km SSE Ambanizana, Andranobe, -15.66667, 49.96667, 600 m, rainforest (B.L. Fisher) (CASC); 6.3 km S Ambanizana, Andranobe, -15.6813, 49.958, 100 m, rainforest (B.L. Fisher) (CASC); Ile Sainte Marie, F Kalalao, 9.9 km 34° Ambodifotatra, -16.9225, 49.88733, 100 m, rainforest (B.L. Fisher *et al.*) (CASC); Mahavelona (Foulpointe); -17.66667, 49.5, sandy forest (A. Pauly) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, -15.28833, 49.54833, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, -

15.18833, 49.615, 470 m, rainforest (Fisher, Griswold *et al.*) (CASC); Nosy Mangabe, 7.43 km S Maroantsetra, -15.4973, 49.76223, 5 m, littoral rainforest edge (B.L. Fisher *et al.*) (CASC); PN Mananara-Nord, 7.1 km 261° Antanambe, -16.455, 49.7875, 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Parcelle K7 Tampolo, -17.28333, 49.41667, 10 m, littoral forest (Malagasy ant team) (CASC); Réserve. Ambodiriana, 4.8 km 306° Manompana, along Manompana River, -16.67233, 49.70117, 125 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, -17.924, 49.19967, 390 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, -17.88667, 49.2025, 520 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, 35.1 km NW Toamasina, -17.91801, 49.20074, 500 m, rainforest (B.L. Fisher *et al.*) (CASC); RNI Betampona, 34.08 km 332° Toamasina, -17.91977, 49.20039, 525 m, rainforest (B.L. Fisher) (CASC); RNI Betampona, 34.1 km 332° Toamasina, -17.916135, 49.20185, 550 m, rainforest (B.L. Fisher) (CASC); RS Ambatovaky, Sandrangato River, -16.81753, 49.29498, 360 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.81745, 49.2925, 400 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.77274, 49.26551, 450 m, rainforest (B.L. Fisher *et al.*) (CASC); RS Ambatovaky, Sandrangato River, -16.76912, 49.26704, 475 m, rainforest (B.L. Fisher *et al.*) (CASC); SF Tampolo, 10 km NNE Fenoarivo Atn, -17.2825, 49.43, 10 m, littoral rainforest (B.L. Fisher) (CASC); Sahafina Forest 11.4 km W Brickaville, -18.81445, 48.96205, 140 m, rainforest (B.L. Fisher *et al.*) (CASC); 1 km W Andampibe, Cap Masoala, -15.69361, 50.18139, 125 m, rainforest (G.D. Alpert) (MCZC); 4 km W Rantovato, Cap Masoala, rainforest (G.D. Alpert) (MCZC); F Ivohibe 55.6 km N Tolagnaro, -24.56167, 47.20017, 650 m, rainforest (B.L. Fisher *et al.*) (CASC).

***Pachycondyla planicornis* Rakotonirina and Fisher, sp. n.**

(Figures 2, 5, 44–45, 61)

Holotype worker: Antsiranana, Betaolana Forest, along Bekona River, -14.52996, 49.44039, 880 m, ex rotten log, rainforest, 5 March 2009 (B.L. Fisher *et al.*), collection code: BLF22566, specimen code: CASENT0151943 (CASC).

Paratypes: 2 workers, same data as holotype but with following specimen codes: CASENT0247232 and CASENT0247233 (CASC, BMNH).

Worker diagnosis:

With head in full-face view, antennal scape not surpassing posterior cephalic margin; dorsum of head and mesosoma not finely striate, dorsum of body with erect slender hairs and pubescence; basal half of antennal scape dorsoventrally flattened, with thin leading edge; lateral portion of hind basitarsus flattened, the basal half of the inner surface concave; dorsal outline of mesosoma not forming a continuous convexity; junction of propodeal dorsum and declivitous surface angulate; petiolar node thick; anterior half of fourth abdominal tergite (gastral tergite 2) mostly smooth and shiny between large punctures.

Worker measurements (n=7): HL: 2.09–2.25, HW: 1.93–2.07, CI: 90–92, SL: 1.42–1.49, SI: 70–75, PW: 1.38–1.50, WL: 2.86–3.02, NL: 0.84–0.98, NW: 1.05–1.23, NH: 1.10–1.22, DNI: 118–127, LNI: 118–149.

Description:

Worker. In frontal view, head longer than broad, broadest on posterior third, posterior margin strongly concave and medially excised, sides converging in front of eyes. Compound eyes large; with head in full-face view, located slightly to the front but still breaking outline of sides of head. Antenna with basally, dorsoventrally flattened scape, and thin leading edge; with head in full-face view, scape broad from base to apex, fairly short and not extending beyond posterior margin. Median lobe of clypeus not projecting anteriorly, anterior margin distinctly truncate and medially notched. Mandibles triangular, armed with eight distinct teeth and denticles. In lateral view, although propodeal declivity on a lower level relative to dorsum of mesosoma, dorsal outline not forming a continuous convexity, with propodeal dorsum joining declivity in distinct angle; mesopleural sulcus either visible or indistinct. Basitarsus of hind legs flattened laterally, basal half of the inner surface noticeably concave. In profile, petiole nodiform, rounded anterodorsally and at distinct angle posterodorsally.

Mandibles coarsely striate with piligerous punctulae. Dorsum of head densely and finely reticulate-rugulose, interspersed with scattered punctures. Dorsal surface of mesosoma coarsely punctate or densely and finely reticulate-rugulose, superimposed with variable-sized punctures; lateral portion with compact and fine reticulate-rugulation and scattered punctures; propodeal declivity generally smooth. Dorsal surface of node covered with sparse, large and shallow punctures; sides coarsely, shallowly punctate with effaced rugulation. Gastral tergite smooth and shiny between widely spaced, shallow punctures or with dense, small punctures. Brown, slender, erect hairs and pubescence present on dorsum of head and body. Integument dark brown to black, with lighter shade on appendages.

Queen and male castes are unknown for this species.

Discussion:

Pachycondyla planicornis is very similar to *P. cambouei* and *P. perroti*, but it can be distinguished by the fact that the basal half of its antennal scape is dorsoventrally flattened and its hind tibia is laterally compressed. It is a locally rare species even though its geographical range on Madagascar is quite large.

Distribution and biology:

Pachycondyla planicornis is a rare species, restricted geographically to the mesic forests of eastern Madagascar (Fig. 61). It is only known from lowland forest of the PN Marojejy and Betaolana (along Bekona River) in the northeast of the island, through the sandy forest of Mahavelona (Foulpointe) in the east, to the montane rainforest of the PN Ranomafana in the southeast. Collection data indicate that foraging is carried out on the ground surface, and nests are located mainly in rotten logs.

Other material examined:

Antsiranana: Marojejy, dense forest (J.M. Betsch) (MCZC); PN Marojejy, -14.4382, 49.774, 487 m, rainforest (Rin'Ha, Irwin) (CASC); Makirovana Forest, -14.1707, 49.9541, 415 m, rainforest (B.L. Fisher *et al.*) (CASC); Fianarantsoa: Belle Vue trail, Ranomafana National Park, -21.2665, 47.42017, 1020 m, mixed tropical forest (R. Harin'Hala) (CASC); Toamasina: Mahavelona (Foulpointe); -17.66667, 49.5, in sandy forest (A. Pauly) (CASC).

***Pachycondyla tavaratra* Rakotonirina and Fisher, sp. n.**

(Figures 3, 38–39, 62)

Holotype worker: Antsiranana, Forêt de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, under stone, rainforest, 4 Oct 2003 (B.L. Fisher *et al.*), collection code: BLF09750, specimen code: CASENT0077442 (CASC).

Paratypes: 4 workers with the same data as holotype but specimen coded: CASENT0077438, CASENT0077440, CASENT0247228, CASENT0247229 (BMNH, MHNG, CASC).

Worker diagnosis:

Larger species (HW: 2.49–3.13 mm), antennal scape reaching the posterior margin of head; anterior margin of clypeus broadly triangular; eyes extending beyond the lateral border of head; dorsum of head and mesosoma finely striate, with sparse punctures; stout erect hairs on dorsum of mesosoma and petiole node erected relative to the body surface.

Worker measurements (n=7): HL: 3.05–3.13, HW: 2.55–2.73, CI: 84–88, SL: 1.91–2.09, SI: 99–104, PW: 1.91–2.09, WL: 4.11–4.46, NL: 1.35–1.50, NW: 1.35–1.62, NH: 1.67–1.85, DNI: 100–114, LNI: 116–130.

Description

Worker. Head approximately longer than broad, sides convex and broadest around level of eyes, posterior cephalic margin almost straight. Eyes generally large, breaking outline of sides of the head. Scape elongate, reaching posterior margin of head. Anterior margin of clypeus projecting into triangular median lobe, which makes a blunt angle with mandibular surface when head is viewed in profile. Mandibular masticatory margins armed with eight to

nine teeth and denticles. In profile, outline of dorsum of mesosoma forming an uninterrupted convexity, with rounded angle at junction of propodeal dorsum and declivitous surface; declivitous surface is very inclined anteriorly and has imperceptibly visible lateral margins. Mesopleural sulcus indistinct or absent. With petiole in lateral view, node thick, and junction of anterior face and dorsum rounded, whereas dorsum and posterior face meet at distinct angle. In dorsal view, anterior face rounded and posterior face truncate. Sculpture resembles that of *P. comorensis*, head covered with dense striation superimposed with scattered punctures; striation converging from posterolateral portion of head towards midline and level of eyes through frontal lobes.

Mandibles coarsely costate interspersed with piligerous pits. Pronotum with dense and fine costulae, while mesonotum and propodeum are covered with transverse, dense and fine striation or microreticulation. Lateral portion of mesosoma densely, finely reticulate-rugulose or with striation in different directions, interspersed with sparse large punctures. Declivitous surface microreticulate or transversely finely striate. Lateral surface of petiole node and gastral segments microreticulate, their dorsum densely finely costulate to finely microreticulate. Dorsum of body covered with black, stout hairs which tend to be brown on the appendages; with mesosoma viewed from front, these hairs incline towards its midline and are more erect at dorsolateral margin. Slender, brownish hairs present on ventral surface of head, gaster, and coxae. Pubescence abundant on lateral portion of mesosoma, petiole node, and gastral segments, but almost absent from dorsum of propodeum, petiole node, and dorsum of first and anterior half of second gastral segments. Integument black, head and mesosoma with silky brilliance; articulations and apex of appendages reddish.

As for *P. comorensis*, queen caste is not known for *P. tavaratra*, but some individual workers collected from several colonies possess single ocelli, which suggests that these workers might have assumed the reproductive role of the queen. Males are not examined in this revision. Research should be undertaken in the future to understand the colony structure and reproductive organization of the species.

Discussion:

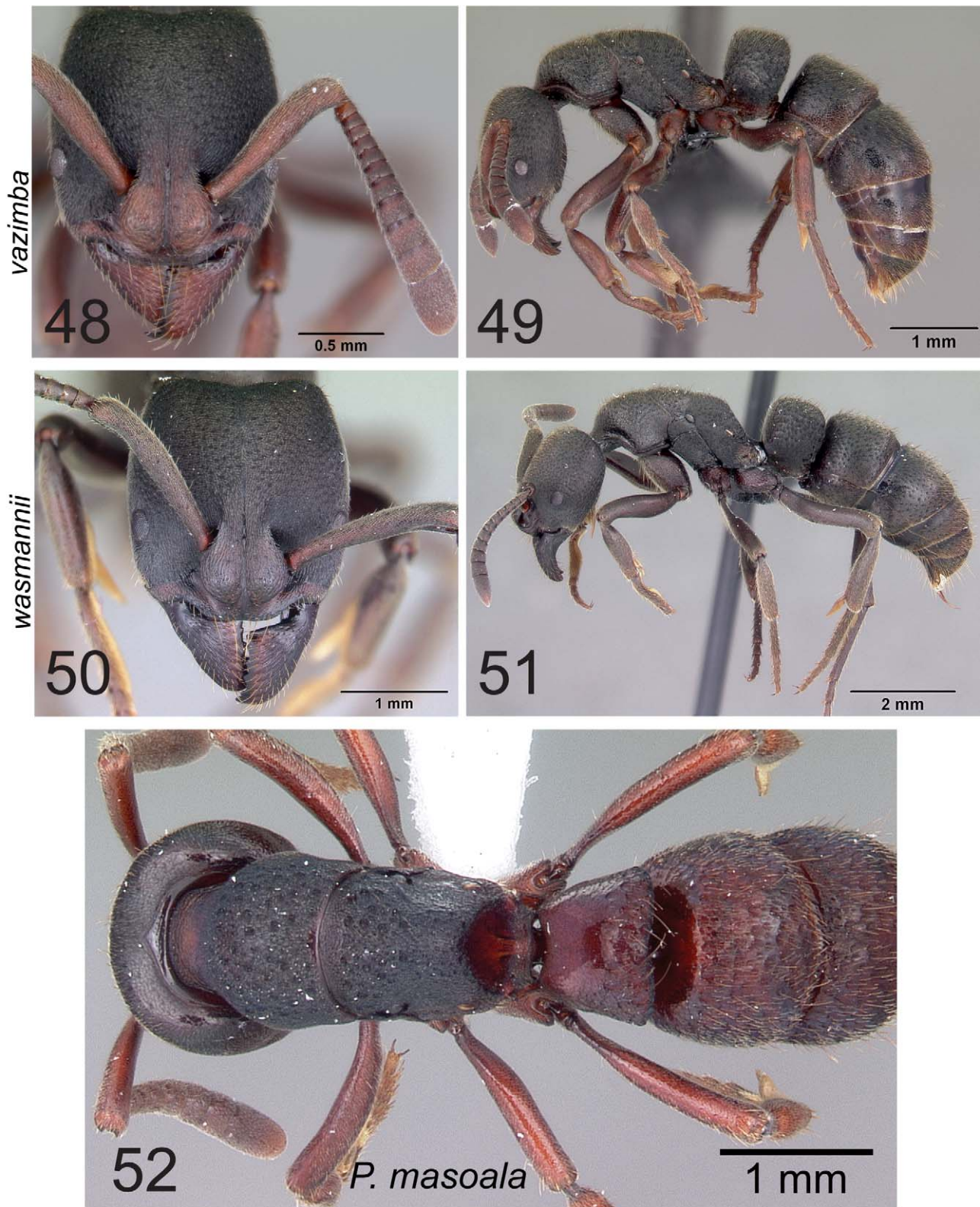
Pachycondyla tavaratra is very similar to *P. comorensis*, but can be distinguished easily by the triangular projection of the anteromedian clypeal margin, the elongate standing erect hairs on the upper surface of the body, and the location of the eyes, which break the outline of the sides of the head.

Distribution and biology:

Pachycondyla tavaratra occurs in northern Madagascar, and was collected mostly from the high altitude rainforests of the PN Montagne d'Ambre and Forêt de Binara (Fig. 62). Rarely has it been recorded from lower altitudes at Andavakoera and Binara forests. This species forages mostly on the ground and generally nests in rotten logs and soil layers or rarely under rocks. Its longer antennal scapes are suggestive of foraging conducted on the forest floor and through leaf litter.

Other material examined:

Antsiranana, PN Montagne d'Ambre, 975 m (G. D. Alpert) (MCZC); PN Montagne d'Ambre, 1000–1100 m (W.L. & D.E. Brown) (MCZC); PN Montagne d'Ambre: 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Montagne d'Ambre, Antomboka, -12.50035, 49.175, 885 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Antomboka, -12.51269, 49.17807, 970 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Crête, -12.58132, 49.13368, 1110 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Petit lac, -12.53664, 49.17412, 1130 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Pic Bades, -12.5186, 49.18625, 900 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Roussettes, -12.52574, 49.17238, 1025 m, montane rainforest (B.L. Fisher *et al.*) (CASC); F d'Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, -13.11833, 49.23, 425 m, rainforest (B.L. Fisher *et al.*) (CASC); F de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, rainforest (B.L. Fisher *et al.*) (CASC); F de Binara, 9.4 km 235° SW Daraina, -13.26333, 49.6, 1100 m, montane rainforest (B.L. Fisher *et al.*) (CASC).



FIGURES 48–52. Full-face view of the head and lateral view of the body of the worker caste, and form of the femora of the Malagasy *Pachycondyla* in dorsal view. Figs 48–51: Full-face and lateral views of worker: Figs 48–49: *Pachycondyla vazimba*, CASENT0034562; Figs 50–51: *Pachycondyla wasmannii*, CASENT0031384; Fig. 52: Dorsal view of *P. masoala* showing the flattened basal portion of the femora.

***Pachycondyla vazimba* Rakotonirina and Fisher, sp. n**

(Figures 12, 48–49, 63)

Holotype worker: MADAGASCAR: Mahajanga, Parc National Namoroka, 16.9 km 317° NW Vilanandro, -16.4067, 45.31, 100 m, ex rotten log, tropical dry forest, 12–16 Nov 2002 (Fisher, Griswold *et al.*), collection code: BLF06686, specimen code: CASENT0486413 (CASC).

Paratypes: series of 5 workers with the same data as holotype but with specimen codes CASENT0486411, CASENT0247224, CASENT0247225, CASENT0247226, CASENT0247227 (BMNH, MHNG, CASC, PBZT).

Worker diagnosis:

With head in full-face view, antennal scape not surpassing the posterior cephalic margin; dorsum of head and mesosoma not finely striate; basal half of antennal scape rounded; dorsum of mesosoma and petiole node with short and thin erect hairs; junction of propodeal dorsum and declivitous surface at a distinct angle; mesopleural suture absent or incomplete; antennal segments 6, 7, and 8 nearly twice as wide as long; with petiole in dorsal view, the posterior margin broadly concave; anterior half of fourth abdominal tergite (gastral tergite 2) covered with numerous and very dense small punctures between larger ones, mesosoma and petiole node with moderate such sculpture; outer surface of hind tibia usually without erect hairs; integument matte.

Worker measurements (n=10): HL: 1.59–1.75, HW: 1.38–1.50, CI: 85–90, SL: 1.08–1.22, SI: 76–82, PW: 1.06–1.21, WL: 2.04–2.33, NL: 0.75–0.84, NW: 0.91–1.05, NH: 1.05–1.18, DNI: 119–132, LNI: 133–149.

Description:

Worker. Head longer than broad, widest immediately behind level of eyes; sides feebly convex along their length and converging in front of level of eyes; posterior margin weakly medially excised. Compound eyes small, diameter approximately less than half maximum width of scape. Antennal scape with rounded leading edge, not attaining posterior margin of head; antennal segments 6, 7, and 8 nearly twice as wide as long. Anterior margin of clypeus truncated and straight. Mandibles triangular, the apical margins armed with seven to nine teeth or denticles. In lateral view, dorsal outline of mesosoma not continuously convex, but rather roughly straight and interrupted by nearly angulate junction of propodeal dorsum to declivitous surface. Mesopleural sulcus indistinct or absent. Propodeal declivity triangularly shaped and narrower towards the dorsal surface. Basitarsus of hind legs generally rounded, without concavity on basal half of inside surface. With petiole in dorsal view, node anteriorly convex and posteriorly broadly concave. Dorsum of head densely and finely reticulate-punctate to reticulate-rugulose, and interspersed with larger punctures.

Mandibles striate with scattered piliferous pits. Dorsum of mesosoma and petiole node through the fourth abdominal segment densely finely reticulate-punctate, with sparse, shallow, and larger punctures. Sides of mesosoma and node of petiole densely and finely reticulate-rugulose. Lateral portion of abdominal segments 3 and 4 finely reticulate-punctate or with dense, small punctures. Dorsum of mesosoma, petiole node, and gaster covered with slender and short hairs which are usually absent on outer surface of hind tibiae. Body color dark brown to black, with reddish orange appendages and articulations. Integument relatively matte between the large punctures.

Queen. Measurements (n=5): HL: 1.63–1.91, HW: 1.52–1.79, CI: 92–94, SL: 1.13–1.48, SI: 75–86, EL: 0.30–0.35, OI: 19–22, PW: 1.32–1.51, WL: 2.45–2.90, NL: 0.70–0.89, NW: 1.05–1.18, NH: 1.02–1.23, DNI: 123–156, LNI: 131–146. Worker characters are generally duplicated in the queen caste, except the latter is only slightly larger, and the body is covered by denser and more elongate pubescence.

Discussion:

Worker specimens of *Pachycondyla vazimba* are very similar to those of *P. wasmannii*, but their smaller size, the indistinct mesopleural suture, the absence of erect hairs on the outer surface of the hind tibia, and the broader than long shape of antennal segments 6, 7, and 8 render *P. vazimba* separable from *P. wasmannii*.

Distribution and biology:

The distribution of *P. vazimba* is generally limited to western Madagascar (Fig. 63). This species occurs mostly in the dry forest habitats of the PN Ankarafantsika in the north through Beza-Mahafaly Forest in the south.

Interestingly, along its north-south range it also can be found in the gallery forests of the PN Isalo, Forêt de Mite, and Fiherenana, and in the disjunct montane rainforest of Analavelona. When nesting in rotten logs, dead branches on the ground and in the soil layer, *P. vazimba* forages most often in leaf litter and infrequently on the forest floor, habits related to its smaller eyes, shorter antennal scape, and shorter legs.

Other material examined:

Antsiranana: Nosy Be, RNI Lokobe, 6.3 km 112° ESE Hellville, -13.41933, 48.33117, 30 m, rainforest (Fisher, Griswold *et al.*) (CASC); Fianarantsoa: PN Isalo, Sahanafa River, 29.2 km 351° N Ranohira, -22.31333, 45.29167, 500 m, gallery forest (Fisher, Griswold *et al.*) (CASC); dry wash, 1 km E of Isalo National Park Interpretive Center, -22.62667, 45.35817, 885 m (R. Harin'Hala) (CASC); Mahajanga: Manerinerina, 76.6 km N Antsohihy, -14.10744, 48.11046, 247 m, disturbed forest (B.L. Fisher *et al.*) (CASC); PN Ankarafantsika, F de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, -16.22806, 47.14361, 135 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, -16.26722, 47.04861, 210 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 9.8 km 300° WNW Vilanandro, -16.46667, 45.35, 140 m (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 17.8 km 329° WNW Vilanandro, -16.37667, 45.32667, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 16.9 km 317° NW Vilanandro, -16.40667, 45.31, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, -16.925, 44.36833, 30 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Baie de Baly, 12.4 km 337° NNW Soalala, -16.01, 45.265, 10 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); Mahavavy River, 6.2 km 145° SE Mitsinjo, -16.05167, 45.90833, 20 m, gallery forest (Fisher, Griswold *et al.*) (CASC); PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, -18.70944, 44.71817, 150 m, tropical dry forest on Tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodroa River, -19.13222, 44.81467, 100 m, tropical dry forest on Tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, -19.14194, 44.828, 50 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Toliara: Beza Mahafaly, 27 km E Betioky, -23.65, 44.63333, 135 m, tropical dry forest (B.L. Fisher) (CASC); Beza-Mahafaly, 27 km E Betioky, -23.65, 44.63333, 135 m, tropical dry forest (B.L. Fisher) (CASC); Fiherenana, -23.17694, 43.96083, 100 m, gallery forest (Frontier Project) (CASC); F de Kirindy, 15.5 km 64° ENE Marofandilia, -20.045, 44.66222, 100 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); F de Mite, 20.7 km 29° WNW Tongobory, -23.52417, 44.12133, 75 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); Makay Mts., -21.21836, 45.3106, 510 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.22336, 45.32628, 480 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.30997, 45.12946, 590 m, dry forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.23343, 45.32913, 460 m, gallery forest with bamboo (B.L. Fisher *et al.*) (CASC); PN Kirindy Mite, 16.3 km 127° SE Belo sur Mer, -20.79528, 44.147, 80 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Réserve Beza Mahafaly, Parcel 1, -23.65833, 44.62889, 175 m, dry forest (Alpert *et al.*) (MCZC); Réserve Beza Mahafaly, Parcel 1, -23.65, 44.63333, 130 m, tropical dry forest (P.S. Ward) (MCZC); Sept Lacs, -23.52833, 44.15556, 80 m, gallery forest (Frontier Project) (CASC).

***Pachycondyla wasmannii* (Forel)**

(Figures 9, 11, 50–51, 64)

Bothroponera wasmannii Forel 1887: 383. Lectotype worker, present designation, Madagascar, Antsiranana, Nosy Be (C. Keller) AntWeb specimen code CASENT0101039 (MHNG) [examined]. Paralectotype workers, with the same data but coded as CASENT0101040, CASENT0101041 (MHNG) [examined]. [Redescription:Forel, 1891: 128, pl. 4, fig. 4; Dalla Torre, 1893: 37. Misspelled as *wasmanni*: Emery, 1895: 336, Forel, 1897: 188, 196 with description of queen and male castes. Combination in *Ponera* (*Bothroponera*) and additional note on queen by Emery, 1899: 267; in *Pachycondyla* (*Bothroponera*):Emery, 1901: 45, 1911: 78; Combination in *Bothroponera*: Wheeler, 1922: 1008; in *Pachycondyla*:Bolton, 1995: 311].



cambouei: Form 1
(typical *cambouei*)



cambouei: Form 2 (full square)
Form 4 (full triangle)
Form 5 (full circle)



cambouei: Form 3



cambouei: Form 6



cambouei: Form 7



masoala

FIGURES 53–58. Distributional maps of *Pachycondyla wasmannii*-group from the Malagasy region. Figs 53–57: *P. cambouei*: Fig. 53: Form 1, Fig. 54: Form 2 (full square), Form 4 (full triangle), Form 5 (full circle); Fig. 55: Form 3, Fig. 56: Form 6, Fig. 57: Form 7; Fig. 58: *P. masoala*.

59

*comorensis*

60

*perroti*

61

*planicornis**tavaratra*

62

*vazimba*

63

*wasmannii*

64

FIGURES 59–64. Distributional maps of *Pachycondyla wasmannii*-group from the Malagasy region. Fig. 59: *P. comorensis*; Fig. 60: *P. perroti*; Fig. 61: *P. planicornis*; Fig. 62: *P. tavaratra*; Fig. 63: *P. vazimba*; Fig. 64: *P. wasmannii*.

Worker diagnosis:

With head in full-face view, antennal scape not surpassing the posterior cephalic margin; dorsum of head and mesosoma not finely striate; basal half of antennal scape rounded; dorsum of mesosoma and petiole node with short and thin erect hairs; junction of propodeal dorsum and declivitous surface at a distinct angle; mesopleural suture distinct; antennal segments 6, 7, and 8 nearly as wide as long; with petiole in dorsal view, the posterior margin straight or with weak median notch; anterior half of fourth abdominal tergite (gastral tergite 2) covered with numerous and very dense small punctures between larger ones, mesosoma and petiole node with moderate such sculpture; outer surface of hind tibia usually with erect hairs; integument matte.

Worker measurements (n=12): HL: 1.96–2.37, HW: 1.72–2.21, CI: 87–94, SL: 1.32–1.78, SI: 76–83, PW: 1.28–1.79, WL: 2.50–3.36, NL: 0.94–1.20, NW: 1.07–1.48, NH: 1.27–1.64, DNI: 105–132, LNI: 124–159.

Description:

Worker. In full-face view, head broadest behind level of eyes, the sides slightly convex throughout their length; the posterior margin feebly concave; eyes quite large, maximum diameter nearly equal to greatest width of antennal scape. Scape subcylindrical, relatively short, not surpassing posterior cephalic margin; segments 6, 7, and 8 almost as long as broad. Anteromedian margin of clypeus truncate and either straight or very weakly emarginated medially. Mandibles triangular, masticatory margins armed with seven to eight teeth and denticles. In profile, dorsal outline of mesosoma without uninterrupted convexity; propodeal dorsum meeting declivitous surface in a distinct angle; mesopleural sulcus distinct and complete. Hind legs with rounded basitarsus. Petiole nodiform and thick, with anterior and posterior margins that in dorsal view are respectively broadly convex and straight with weak median notch. Head finely reticulate-punctate to finely ruguloreticulate, interspersed with large punctures behind level of eyes.

Mandibles striate, with sparse punctures from which hairs arise. Dorsum of mesosoma, petiole node, and first gastral tergite covered with large punctures, the spaces between which are reticulate-punctate. Lateral portion of pronotum, mesopleuron, and lower half of propodeum generally finely reticulate-rugulose or with dense, fine rugulation. Second gastral tergite particularly with very dense, piligerous, small pits between large punctures. Standing erect hairs present on dorsum of the body, with very abundant pubescence; outer surface of hind tibiae covered with erect hairs. Dark brown to black in color with usually lighter appendages. Most specimens fairly matte except those collected from rainforest habitats.

Queen. Measurements (n=7): HL: 2.20–2.39, HW: 2.08–2.24, CI: 92–95, SL: 1.62–1.82, SI: 77–84, EL: 0.39–0.41, OI: 17–19, PW: 1.63–1.87, WL: 3.31–3.71, NL: 0.99–1.16, NW: 1.34–1.48, NH: 1.31–1.51, DNI: 127–148, LNI: 125–136. Winged queens are very similar to workers, but have a body modified with the general characteristics of the queen caste. Winged queen has a much broader head. Ergatoid queens also present in *P. wasmannii*, which look comparable to worker caste but have one ocellus and reduced thoracic sclerites.

Discussion:

Although *P. wasmannii* is very similar to *P. vazimba*, it can be distinguished readily by its larger size, with a distinct and complete mesopleural suture, antennal segments 6, 7, and 8 nearly as wide as long, and more erect hairs on the dorsum of mesosoma and petiole node.

Apparently there are two forms found within this species. These are geographically isolated due to the presence of high mountain chains in northwestern Madagascar. The first form, in which gastral tergite 2 is densely, finely punctate between larger punctures and has a matte integument, occupies the west and southwest regions of Madagascar. In contrast, the second form is characterized by worker specimens that have a shining integument, and gastral tergite 2 is covered with nearly effaced, closely spaced, small punctures between larger, shallow punctures. This form has been collected in the northwest and northeast of the island. However, workers with intermediate degrees of these phenotypic variations also occur.

Distribution and biology:

Pachycondyla wasmannii is an endemic, widespread species of the Malagasy region. It occurs generally in western Madagascar and in Anjouan of the Comoros Islands (Fig. 64). Most frequently this species has been collected from the dry forests and woodland habitats in the west of Madagascar. However, it is known also from subhumid gallery forests in the western slopes, littoral, transitional, and humid forests in the north and southeast of the island, and

from disjunct montane rainforests on the high plateau. This species is also capable of colonizing human-modified habitats. There are two morphological forms; the first occurs in the dry and gallery forest habitats in the west of Madagascar, whereas the second is generally known from the transitional mesic forests and some of the rainforest sites in the north and northeast of the island. Across its distribution range, *P. wasmannii* dominates the *Pachycondyla* in dry forest habitats where it is sympatric only with *P. vazimba*. In its remaining distribution range, other species within the genus co-occur with *P. wasmannii*, and *P. cambouei*, which is widely distributed throughout the humid forests, becomes the dominant species. *Pachycondyla wasmannii* nests mainly in rotten logs; however, it can also be found on rotten sticks and branches on the ground, in soil layers, under rocks, beneath litter moss on rocks, and under rotten logs. It typically forages on the forest floor and through leaf litter, and very rarely on low-growing vegetation. Workers of this species usually fake death (thanatosis) after a nest disturbance.

One interesting geographic point about *P. wasmannii* is its presence on Anjouan Island in the Comoros but not Mayotte Island, although the latter is geographically closer to Madagascar. How it arrived on Comoros could shed light on our understanding of the historical biogeography and the origins of the Malagasy species of *Pachycondyla*.

Other material examined:

THE COMOROS: Anjouan, Mount Ntringui, -12.19865, 44.41866, 740 m, montane forest (B.L. Fisher *et al.*) (CASC); Mount Ntringui, -12.19641, 44.41791, 550 m, rainforest (B.L. Fisher *et al.*) (CASC). MADAGASCAR: Antananarivo: RS Ambohitantely, F d Ambohitantely, 20.9 km 72° NE d Ankazobe, -18.22528, 47.28683, 1410 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Tsinjoarivo, E. Ambatolampy, dry forest (W.L. Brown) (MCZC), Antsiranana: [Nosibé] (Völtzkow) (MHNG); [Nossi bé p. Madagascar] (C. Keller) (MHNG); 14 km W Cap Est, Ambato, -15.29139, 50.33806, 200 m, secondary raiforest (Alpert *et al.*) (MCZC); 15 km S Sambava, 10 m, coastal forest (J.M. Betsch) (MCZC); 48 km ENE Morondava, -20.06667, 44.65, tropical dry forest (D.M. Olson) (MCZC); 5 km S Antalaha, Ambodikoko Hill (G.D. Alpert) (MCZC); 5 km SW Antalaha, -14.93806, 50.26167, 50 m, secondary forest (G.D. Alpert) (MCZC); 84 km SW Sambava to Andapa, 70–160 m, degraded forest (W.L. and D.E. Brown) (MCZC); Ambanja, -13.68268, 48.45245, 30 m, urban/garden (B.L. Fisher *et al.*) (CASC); Ambondrobe, 41.1 km 175° Vohemar, -13.71533, 50.10167, 10 m, littoral rainforest (B.L. Fisher) (CASC); Ampasindava, F d'Ambilanivy, 3.9 km 181° S Ambaliha, -13.79861, 48.16167, 600 m, rainforest (Fisher, Griswold *et al.*) (CASC); Ankarana, -12.9, 49.1, 100 m (G.D. Alpert) (MCZC); F Ambanitaza, 26.1 km 347° Antalaha, -14.67933, 50.18367, 240 m, rainforest (B.L. Fisher) (CASC); F Ambato, 26.6 km 33° Ambanja, -13.4645, 48.55167, 150 m, rainforest (B.L. Fisher) (CASC); F d' Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, -13.11833, 49.23, 425 m, rainforest (B.L. Fisher) (CASC); F d' Antsahabe, 11.4 km 275° W Daraina, -13.21167, 49.55667, 550 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); F d'Ampombofofo, -12.09949, 49.33874, 25 m, littoral forest (B.L. Fisher *et al.*) (CASC); F d'Ampondrabe, 26.3 km 10° NNE Daraina, -12.97, 49.7, 175 m, tropical dry forest (B.L. Fisher) (CASC); PN Sahamalaza, F d'Anabohazo, 21.6 km 247° WSW Maromandia, -14.30889, 47.91433, 120 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); F d'Analabe, 30.0 km 72° ENE Daraina, -13.08333, 49.90833, 30 m, littoral rainforest (B.L. Fisher) (CASC); F de Bekaraoka, 6.8 km 60° ENE Daraina, -13.16667, 49.71, 150 m, tropical dry forest (B.L. Fisher *et al.*) (CASC); F de Binara, 7.5 km 230° SW Daraina, -13.255, 49.61667, 375 m, tropical dry forest (B.L. Fisher) (CASC); F de Binara, 9.1 km 233° SW Daraina, -13.26333, 49.60333, 650–800 m, rainforest (B.L. Fisher *et al.*) (CASC); F d'Orangea, 3.6 km 128° SE Remena, -12.25889, 49.37467, 90 m, littoral rainforest (Fisher, Griswold *et al.*) (CASC); Marojejy RNI #12, -14.44533, 49.78564, 375 m, rainforest (G.D. Alpert) (MCZC); Montagne des Français, 7.2 km 142° SE Antsiranana (=Diego Suarez), -12.32278, 49.33817, 180 m, tropical dry forest (Alpert *et al.*) (CASC); Nosy Be, 4 km ESE Andoany (=Hellville), -13.41667, 48.3, 200 m, rainforest (P.S. Ward) (PSWC); Nosy Be, Lokobe Forest, -13.41639, 48.30722, 20 m (G.D. Alpert) (MCZC); Nosy Be, RNI Lokobe, 6.3 km 112° ESE Hellville, -13.41933, 48.33117, 30 m, rainforest (Fisher, Griswold *et al.*) (CASC); PN Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, -14.43667, 49.775, 450 m, rainforest (B.L. Fisher) (CASC); PN Montagne d'Ambre, 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Montagne d'Ambre, Antomboka, -12.50035, 49.175, 885 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Antomboka, -12.51269, 49.17807, 970 m, montane rainforest (B.L. Fisher *et al.*) (CASC); PN Montagne d'Ambre, Pic Bades, -12.5186, 49.18625, 900 m, montane rainforest (B.L. Fisher *et al.*) (CASC); RS Manongarivo, 10.8 km 229° SW Antanambao, -13.96167, 48.43333, 400 m, rainforest (B.L. Fisher) (CASC); RS Manongarivo, 12.8 km 228° SW Antanambao, -13.97667, 48.42333, 780 m, rainforest (B.L. Fisher)

(CASC); RS Manongarivo, 14.5 km 220° SW Antanambao, -13.99833, 48.42833, 1175 m, montane rainforest (B.L. Fisher) (CASC); RS Ankarana, 7 km SE Matsaborimanga, -12.9, 49.11667, 150 m, rainforest (P.S. Ward) (MCZC); RS Analamerana, 16.7 km 123° Anivorano-Nord, -12.80467, 49.37383, 225 m, tropical dry forest (B.L. Fisher) (CASC); RS Analamerana, 28.4 km 99° Anivorano-Nord, -12.74667, 49.49483, 60 m, tropical dry forest (B.L. Fisher) (CASC); RS Ankarana, -12.90056, 49.14722, 150 m, dry forest (Alpert *et al.*) (MCZC); RS d'Ambre, 3.5 km 235° SW Sakaramy, -12.46889, 49.24217, 325 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Ankarana, 13.6 km 192° SSW Anivorano Nord, -12.86361, 49.22583, 210 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Ankarana, 22.9 km 224° SW Anivorano Nord, -12.90889, 49.10983, 80 m, tropical dry forest (Alpert *et al.*) (CASC); PN Marojejy, 8 km NW Manantenina, -14.43333, 49.78333, 450 m, montane rainforest (E.L. Quinter) (CASC); Vohemar, -13.37723, 50.0205, 25 m, cultivated land (B.L. Fisher *et al.*) (CASC); Makirovana Forest: -14.1604, 49.9522, 550 m, rainforest (B.L. Fisher *et al.*) (CASC); Makirovana Forest, -14.17066, 49.95409, 415 m and 225 m, rainforest (B.L. Fisher *et al.*) (CASC); Makirovana Forest, -14.10295, 50.01984, 390 m, rainforest (B.L. Fisher *et al.*) (CASC); Fianarantsoa: 15 km E Sakaraha, -22.9, 44.68333, 760 m, tropical dry forest (P.S. Ward) (MCZC); 30 km NNW Ranohira, Isalo Nat. Park, -22.31722, 45.29333, 455 m, canopy forest (G.D. Alpert) (MCZC); F d'Analalava, 29.6 km 280° W Ranohira, -22.59167, 45.12833, 700 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); F d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); PN Isalo, Ranohira, Canyon de Sinze, -22.48333, 45.55, 800 m, rainforest (E. Rajeriarison) (MCZC); PN Ranomafana, -21.01667, 47.01667, 700 m, montane forest (E. Rajeriarison) (MCZC); PN Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, -23.83517, 46.96367, 940 m, rainforest (B.L. Fisher *et al.*) (CASC); PN Isalo, 9.1 km 354° N Ranohira, -22.48167, 45.46167, 725 m, gallery forest (Fisher, Griswold *et al.*) (CASC); PN Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, -22.29833, 45.35167, 990 m, Uapaca woodland (Fisher, Griswold *et al.*) (CASC); PN Isalo, Sahanafa River, 29.2 km 351° N Ranohira, -22.31333, 45.29167, 500 m, gallery forest (Fisher, Griswold *et al.*) (CASC); 9 km NNW Ranohira, PN Isalo, -22.48333, 45.38333, 800 m, rainforest (P.S. Ward) (MCZC); Tsaranoro, 32.8 km 229° Ambalavao, -22.08483, 46.77633, 950 m, rainforest (B.L. Fisher *et al.*) (CASC); Mahajanga: 124 km SE Mahajanga (G.D. Alpert) (MCZC); Ampamakiambato, 45 km SW Ambanja, -13.97545, 48.15929, 145 m, disturbed forest in tsingy (B.L. Fisher *et al.*) (CASC); F Ambohimanga, 26.1 km 314° Mampikony, -15.96267, 47.43817, 250 m, tropical dry forest (B.L. Fisher) (CASC); F de Tsimembo, 11.0 km 346° NNW Soatana, -18.99528, 44.4435, 50 m, tropical dry forest (Fisher, Griswold Arthropod Team) (CASC); F de Tsimembo, 8.7 km 336° NNW Soatana, -19.02139, 44.44067, 20 m, tropical dry forest (Fisher, Griswold Arthropod Team) (CASC); Mahavavy River, 6.2 km 145° SE Mitsinjo, -16.05167, 45.90833, 20 m, gallery forest (Fisher, Griswold *et al.*) (CASC); Manerinerina, 76.6 km N Antsohihy, -14.10744, 48.11046, 247 m, disturbed forest (B.L. Fisher *et al.*) (CASC); PN Ankarafantsika, SF Ampijoroa, 5.4 km 331° NW Andranofasika, -16.29889, 46.813, 70 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Ankarafantsika, Ampijoroa SF, 40 km 306° NW Andranofasika, -16.32083, 46.81067, 130 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Ankarafantsika, F de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, -16.22806, 47.14361, 135 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Baie de Baly, 12.4 km 337° NNW Soalala, -16.01, 45.265, 10 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 16.9 km 317° NW Vilanandro, -16.40667, 45.31, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 17.8 km 329° WNW Vilanandro, -16.37667, 45.32667, 100 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Namoroka, 9.8 km 300° WNW Vilanandro, -16.46667, 45.35, 140 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); PN Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, -18.70944, 44.71817, 150 m, tropical dry forest on tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Tsingy de Bemaraha, 2.5 km 62° ENE Bekopaka, Ankidrodra River, -19.13222, 44.81467, 100 m, tropical dry forest on tsingy (Fisher-Griswold Arthropod Team) (CASC); PN Tsingy de Bemaraha, 3.4 km 93° E Bekopaka, Tombeau Vazimba, -19.14194, 44.828, 50 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, -16.26722, 47.04861, 210 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RF Beanka, 50.2 km E Maintirano, -18.02649, 44.05051, 250 m, tropical dry forest on tsingy (B.L. Fisher *et al.*) (CASC); RF Beanka, 52.7 km E Maintirano, -18.0622, 44.52587, 300 m, tropical dry forest on tsingy (B.L. Fisher *et al.*) (CASC); RF Beanka, 53.6 km E Maintirano, -18.04014, 44.53394, 272 m, tropical dry forest on tsingy (B.L. Fisher *et al.*) (CASC); RF Beanka, 54.3 km E Maintirano, -18.06009, 44.54086, 262 m, tropical dry forest on tsingy (B.L. Fisher *et al.*) (CASC); RS Bemarivo, 23.8 km 223° SW Besalampy, -16.925, 44.36833, 30 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); RS Marotandrano, Marotandrano

48.3 km S Mandritsara, -16.28322, 48.81443, 865 m, transitional humid forest (B.L. Fisher *et al.*) (CASC); Toamasina: 1 km W Andampibe, Cap Masoala, -15.69361, 50.18139, 125 m, rainforest (G.D. Alpert) (MCZC); 8 km SW Cap Est, -15.30694, 50.45417, 15 m, littoral forest (G.D. Alpert) (MCZC); Toliara: 29 km NNW Ranohira, PN Isalo, -22.31614, 45.29625, 490 m, canopy forest (G.D. Alpert) (MCZC); 48 km ENE Morondava, Kirindy, -20.06667, 44.65, 30 m, tropical dry forest (D.M. Olson) (CASC); 48 km ENE Morondava, Kirindy Forest, -20.07444, 44.67611, 100 m, tropical dry forest (P. Rabeson) (MCZC); 50 kms N Morondava, -20.06667, 44.58333, primary dry forest (A. Pauly) (CASC); 9 km NNW Ranohira, P.N. Isalo, -22.48333, 45.38333, 800 m, rainforest (P.S. Ward) (BMNH); Andohahela, Parcel #1 versante E, 300 m, rainforest (L. Bartolozzi, S. Tiati & C. Raharimina) (MCZC); Bekonazy = 0.5 km S (n. of Morondava), forest with baobab (W.L. Brown) (MCZC); Beza Mahafaly, 27 km E Betioky, -23.65, 44.63333, 135 m, tropical dry forest (B.L. Fisher) (CASC); Fiherenana, -23.17694, 43.96083, 100 m, gallery forest (Frontier Project) (CASC); FC Analavelona, 29.2 km 343° NNW Mahaboboka, -22.675, 44.19, 1100 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); FC Analavelona, 33.2 km 344° NNW Mahaboboka, -22.64333, 44.17167, 1300 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); F de Beroboka, 5.9 km 131° SE Ankidranoka, -22.23306, 43.36633, 80 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); F de Kirindy, 15.5 km 64° ENE Marofandilia, -20.06855, 44.65956667, 30 m, tropical dry forest (B.L. Fisher) (CASC); F de Mite, 20.7 km 29° WNW Tongobory, -23.52417, 44.12133, 75 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); F de Petriky, 12.5 km W 272° Tolagnaro, -25.06167, 46.87, 10 m, littoral rainforest (B.L. Fisher) (CASC); F de Zombitse near Sakaraha, 650 m (E.S. Ross) (MCZC); F Ivohibe 55.0 km N Tolagnaro, -24.569, 47.204, 200 m, rainforest (B.L. Fisher *et al.*) (CASC); F Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.227, 45.33222, 475 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.22336, 45.32628, 480 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.22344, 45.3135, 550 m, gallery forest with bamboo (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.31664, 45.1296, 620 m, dry forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.21836, 45.3106, 510 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.20978, 45.34184, 525 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.30997, 45.12946, 590 m, dry forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.21761, 45.33917, 500 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.23343, 45.32913, 460 m, gallery forest with bamboo (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.21985, 45.32396, 500 m, gallery forest on sandy soil (B.L. Fisher *et al.*) (CASC); Manatantely, 8.5 km NW Tolagnaro, -24.9875, 46.92617, 85 m, rainforest (B.L. Fisher *et al.*) (CASC); Manatantely, 8.9 km NW Tolagnaro, -24.9815, 46.92567, 100 m, rainforest (B.L. Fisher *et al.*) (CASC); Manombo, -22.8123, 43.73932, 165 m, gallery forest, TS3 (Frontier Wilderness Project) (CASC); Manombo, -22.80257, 43.76505, 227 m, dry forest, SC2 (Frontier Wilderness Project) (CASC); Manombo, -22.8123, 43.73932, 165 m, gallery forest, TS3 (Frontier Wilderness Project) (CASC); PN Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, -24.76389, 46.75167, 900 m, montane rainforest (Fisher-Griswold Arthropod Team) (CASC); PN Kirindy Mite, 16.3 km 127° SE Belo sur Mer, -20.79528, 44.147, 80 m, tropical dry forest (Fisher-Griswold Arthropod Team) (CASC); PN Zombitse, 19.8 km 84° E Sakaraha, -22.84333, 44.71, 770 m, tropical dry forest (Fisher, Griswold *et al.*) (CASC); Réserve Beza Mahafaly, Parcel 1, -23.65833, 44.62889, 185 m (P. Rabeson) (MCZC); RP Berenty, -25.01667, 46.3, 25 m, tropical dry forest (B.L. Fisher) (CASC); RP Berenty, F de Bealoka, Mandraré River, 14.6 km 329° NNW Amboasary, -24.95694, 46.2715, 35 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); RP Berenty, F de Malaza, Mandraré River, 8.6 km 314° NW Amboasary, -25.00778, 46.306, 40 m, gallery forest (Fisher-Griswold Arthropod Team) (CASC); RP Berenty, -25.00667, 46.30333, 85 m, gallery forest (Rin'Ha, Irwin) (CASC); RS Ambohijanahary, F d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, -18.26667, 45.40667, 1050 m, montane rainforest (Fisher, Griswold *et al.*) (CASC); Sept Lacs, -23.52833, 44.15556, 80 m, gallery forest (Frontier Project) (CASC); Southern Isoky-Vohimena Forest, 59 km NE Sakaraha, -22.46667, 44.85, 730 m, tropical dry forest (B.L. Fisher) (CASC); Vohibasias Forest, 59 km NE Sakaraha, -22.46667, 44.85, 780 m, tropical dry forest (B.L. Fisher) (CASC); Zombitsy Forest, 15 km NE Sakaraha, -22.8925, 44.67833, 750 m, secondary forest (E. Rajeriarison) (MCZC).

Acknowledgments

We greatly appreciate the help of N. D-S. Papilloud, S. Cover, B. Merz, R. Poggi, and P.S. Ward for providing type material and specimens from their collections. Special thanks to the arthropod team at the Madagascar Biodiversity Center for field collections, laboratory processing, and specimen sorting. For comments on an earlier version of this paper, we are thankful to Georg Fischer, Paco Hita Garcia, and Phil Ward; their input greatly improved the manuscript. This study was part of the MSc research of JCR supported by the Lakeside Foundation Funds of the California Academy of Sciences. Funding support also came from National Science Foundation grants DEB-0072713, DEB-0344731, and DEB-0842395.

References

- Alpert, G.D. (1992) Observations on the genus *Terataner* in Madagascar (Hymenoptera: Formicidae). *Psyche*, 99, 117–127.
- André, E. (1887) Description de quelques fourmis nouvelles ou imparfaitement connues. *Revue d'Entomologie*, 6, 280–298.
- Arnold, G. (1915) A monograph of the Formicidae of South Africa Part I. Ponerinae, Dorylinae. *Annals of the South African Museum*, 14, 1–159.
- Ashmead, W.H. (1905) A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. *The Canadian Entomologist*, 37, 381–384. <http://dx.doi.org/10.4039/Ent37381-11>
- Bermingham, E. & Moritz, C. (1998) Comparative phylogeography: concepts and applications. *Molecular Ecology*, 7, 367–369. <http://dx.doi.org/10.1046/j.1365-294x.1998.00424.x>
- Bingham, C.T. (1903) *The Fauna of British India, Including Ceylon and Burma. Hymenoptera Vol. II. Ants and Cuckoo-wasps*. Taylor and Francis, London, 506 pp.
- Blaimer, B.B. (2010) Taxonomy and natural history of the *Crematogaster* (*Decacrema*)-group (Hymenoptera: Formicidae) in Madagascar. *Zootaxa*, 2714, 1–39.
- Bolton, B. (1975) A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian region, with a review of the Malagasy species. *Bulletin of the British Museum (Natural History) (Entomology)* 31, 235–305.
- Bolton, B. (1979) The ant tribe Tetramoriini (Hymenoptera: Formicidae). The genus *Tetramorium* Mayr in the Malagasy region and in the New World. *Bulletin of the British Museum (Natural History) (Entomology)*, 38, 129–181.
- Bolton, B. (1994) *Identification Guide to the Ant Genera of the World*. Harvard University Press, Cambridge, Massachusetts, 222 pp. <http://dx.doi.org/10.1017/S0007485300034453>
- Bolton, B. (1995) *A New General Catalogue of the Ants of the World*. Harvard University Press, Cambridge, Massachusetts, 504 pp.
- Bolton, B. (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B. (2007) Taxonomy of the dolichoderine ant genus *Technomyrmex* Mayr (Hymenoptera: Formicidae) based on the worker caste. *Contributions of the American Entomological Institute*, 35, 1–150.
- Boumans, L., Vieites, D.R., Glaw, F. & Vences, M. (2007) Geographical patterns of deep mitochondrial differentiation in widespread Malagasy reptiles. *Molecular Phylogenetics and Evolution*, 45, 822–839. <http://dx.doi.org/10.1016/j.ympev.2007.05.028>
- Brown, W.L., Jr. (1973) A comparison of the Hylean and Congo-West African rain forest ant faunas. pp. 161–185 In: Meggers, B.J., Ayensu, E.S. & Duckworth, W.D. (Eds.), *Tropical Forest Ecosystems in Africa and South America: a Comparative Review*. Smithsonian Institution Press, Washington, District of Columbia, viii + 350 pp.
- Brown, W.L., Jr. (1975) Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cyldromyrmecini, Acanthostichini, and Aenictogitini. *Search Agriculture (Entomology)*, 5, 1–115.
- Colwell, R.K. (1996) Biota. The biodiversity database manager. Sinauer Associates, Sunderland, Massachusetts, , 860 pp. plus application software. <http://dx.doi.org/10.1093/sysbio/46.3.574>
- Dalla Torre, K.W. (1893). *Catalogus Hymenopterorum Hucusque Descriptorum Systematicus et Synonymicus. Vol. 7. Formicidae (Heterogyna)*. W. Engelmann, Leipzig, 289 pp.
- Donisthorpe, H. (1943) A list of the type-species of the genera and subgenera of the Formicidae. *Annals and Magazine of Natural History*, 10, 617–688. <http://dx.doi.org/10.1080/03745481.1943.9728055>
- Emery, C. (1895) Mission scientifique de M. Ch. Alluaud dans le territoire de Diego-Suarez (Madagascar-Nord). (Avril-août 1893). *Annales de la Société Entomologique de Belgique*, 39, 336–345.
- Emery, C. (1899) Formiche di Madagascar raccolte dal Sig. A. Mocquereys nei pressi della Baia di Antongil (1897–1898). *Bullettino della Società Entomologica Italiana*, 31, 263–290.
- Emery, C. (1901) Notes sur les sous-familles des Dorylines et Ponérines (Famille des Formicides). *Annales de la Société Entomologique de Belgique*, 45, 32–54.
- Emery, C. (1911) Hymenoptera. Fam. Formicidae. Subfam. Ponerinae. *Genera Insectorum*, 118, 1–125.
- Evenhuis, N.L. (2009) The insect and spider collections of the world website. Available from <http://hbs.bishopmuseum.org/codens> (accessed 20 February 2012)

- Fisher, B.L. (1997) Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). *Journal of Natural History*, 31, 269–302. <http://dx.doi.org/10.1080/00222939700770141>
- Fisher, B.L. (1999) Improving inventory efficiency: a case study of leaf litter ant diversity in Madagascar. *Ecological Applications*, 9, 714–731. [http://dx.doi.org/10.1890/1051-0761\(1999\)009\[0714:IEACS\]2.0.CO;2](http://dx.doi.org/10.1890/1051-0761(1999)009[0714:IEACS]2.0.CO;2)
- Fisher, B.L. (2000) The Malagasy fauna of *Strumigenys*. In: Bolton, B. (Ed.) *The ant tribe Dacetini*. Memoirs of the American Entomological Institute, pp. 612–696.
- Fisher, B.L. (2003) Formicidae, ants. In: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 811–819.
- Fisher, B.L. (2005) A model for a global inventory of ants: a case study in Madagascar. *Proceedings of the California Academy of Sciences*, 56, 86–97.
- Fisher, B.L. & Smith, M.A. (2008) A revision of Malagasy species of *Anochetus* Mayr and *Odontomachus* Latreille (Hymenoptera: Formicidae). *PLoS ONE* 3(5), e1787. <http://dx.doi.org/10.1371/journal.pone.0001787>
- Fisher, B.L. (2009) Two new dolichoderine ant genera from Madagascar: *Aptinoma* gen. n. and *Ravavy* gen. n. (Hymenoptera: Formicidae). *Zootaxa*, 2118, 37–52.
- Forel, A. (1887) Fourmis récoltées à Madagascar, par le Dr. Conrad Keller. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 7, 381–389.
- Forel, A. (1891) Les Formicides. [part]. In: Grandidier, A. 1891. *Histoire physique, naturelle, et politique de Madagascar*. Volume XX. Histoire naturelle des Hyménoptères. Deuxième partie (28e fascicule). Hachette et Cie, Paris, v + 237 pp.
- Forel, A. (1892) Les Formicides. [concl.]. In: Grandidier, A. 1892. *Histoire Physique, Naturelle, et Politique de Madagascar*. Volume XX. Histoire naturelle des Hyménoptères. Deuxième partie. Supplément au 28e fascicule. Hachette et Cie, Paris, pp. 229–280.
- Forel, A. (1897) Ameisen aus Nossi-Bé, Majunga, Juan de Nova (Madagaskar), den Aldabra-Inseln und Sansibar, gesammelt von Herrn Dr. A. Voeltzkow aus Berlin. *Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft*, 21, 185–208.
- Forel, A. (1900) Les Formicides de l'Empire des Indes et de Ceylan. Part VII. *Journal of the Bombay Natural History Society*, 13, 303–332.
- Forel, A. (1907) Formiciden aus dem Naturhistorischen Museum in Hamburg. II. Teil. Neueingänge seit 1900. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg*, 24, 1–20.
- Forel, A. (1917) Cadre synoptique actuel de la faune universelle des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 51, 229–253.
- Goodman, S.M. & Ganzhorn, J.U. (2004) Biogeography of lemurs in the humid forests of Madagascar: the role of elevational distribution and rivers. *Journal of Biogeography*, 31, 47–55. <http://dx.doi.org/10.1111/j.1365-2699.2004.00953.x>
- Heterick, B.E. (2006) A revision of the Malagasy ants belonging to the genus *Monomorium* Mayr, 1855 (Hymenoptera: Formicidae). *Proceedings of the California Academy of Sciences*, 69–202.
- Hijmans, R.J., Guarino, L. & Mathur, P. (2011) *DIVA-GIS, version 7.5*. A geographic information system for the analysis of species distribution data. Available from: <http://www.diva-gis.org> [accessed 23 February 2012].
- Hita Garcia, F. & Fisher, B.L. (2011) The ant genus *Tetramorium* Mayr (Hymenoptera: Formicidae) in the Malagasy region—introduction, definition of species groups, and revision of the *T. bicarinatum*, *T. obesum*, *T. sericeiventre* and *T. tosii* species groups. *Zootaxa*, 3039, 1–72.
- Hölldobler, B. & Wilson E.O. (1990) *The Ants*. Harvard University Press. Cambridge, Massachusetts, xii + 732 pp. <http://dx.doi.org/10.1126/science.248.4957.897>
- Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis, E. Jr., Nussbaum, R.A., Raxworthy, C.J., Razafimpahanana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C. & Zjhra, M.L. (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, 320, 222–225. <http://dx.doi.org/10.1126/science.1155193>
- LaPolla, J.S., Hawkes, P.G. & Fisher, B.L. (2011) Monograph of *Nylanderia* (Hymenoptera: Formicidae) of the World, Part I: *Nylanderia* in the Afrotropics. *Zootaxa*, 3110, 10–36.
- Longino, J.T. & Colwell, R.K. (1997) Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecological Applications*, 7, 1263–1277. <http://dx.doi.org/10.2307/2641213>
- Lourenço, W.R. & Goodman, S.M. (Eds). (2000) *Diversité et Endémisme à Madagascar*. Actes du II colloque international biogéographie de Madagascar, Société de Biogéographie, Paris, vi + 379 pp.
- Mayr, G. (1862) Myrmecologische Studien. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien*, 12, 649–776.
- Mayr, E. (1963) *Animal Species and Evolution*. Harvard University Press, Cambridge, Massachusetts, 797 pp. <http://dx.doi.org/10.1002/ajpa.1330210315>
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <http://dx.doi.org/10.1038/35002501>
- Pastorini, J., Thalmann, U. & Martin, R.D. (2003) A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 5879–5884. <http://dx.doi.org/10.1073/pnas.1031673100>
- Pearson, R.G. & Raxworthy, C.J. (2009) The evolution of local endemism in Madagascar: watershed versus climatic gradient hypotheses evaluated by null biogeographic models. *Evolution*, 63, 959–967. [140 · *Zootaxa* 3609 \(2\) © 2013 Magnolia Press](http://dx.doi.org/10.1111/j.1558-</p>
</div>
<div data-bbox=)

5646.2008.00596.x

- Raxworthy, C.J. & Nussbaum, R.A. (1995) Systematics, speciation and biogeography of the dwarf chameleons (*Brookesia*; Reptilia, Squamata, Chamaeleontidae) of northern Madagascar. *Journal of Zoology*, 235, 525–558. <http://dx.doi.org/10.1111/j.1469-7998.1995.tb01767.x>
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecological Letters*, 7, 1–15. <http://dx.doi.org/10.1046/j.1461-0248.2003.00554.x>
- Roger, J. (1860) Die *Ponera*-artigen Ameisen. *Berliner Entomologische Zeitschrift*, 4, 278–312.
- Santschi, F. (1912) Fourmis d'Afrique et de Madagascar. *Annales de la Société Entomologique de Belgique*, 56, 150–167.
- Schmidt, C.A. (2009) *Molecular Phylogenetics and Taxonomic Revision of Ponerine Ants (Hymenoptera: Formicidae: Ponerinae)*. PhD thesis, University of Arizona, Tucson, Arizona, 263 pp.
- Smith, F. (1858). *Catalogue of the Hymenopterous Insects in the Collection of the British Museum. Part VI. Formicidae*. British Museum, London, 216 pp.
- Smith, S.A., Nieto Montes deOca, A., Reeder, T.W. & Wiens, J.J. (2007) A phylogenetic perspective on elevational species richness patterns in middle American treefrogs: why so few species in lowland tropical forests? *Evolution*, 61, 1188–1207. <http://dx.doi.org/10.1111/j.1558-5646.2007.00085.x>
- Snelling, R.R. (1981) Systematics of social Hymenoptera. In: Hermann, H.R. (Ed.), *Social Insects, Volume 2*. Academic Press, New York, pp. 369–453.
- Tiwari, R.N. (1999) Taxonomic studies on ants of southern India (Insecta: Hymenoptera: Formicidae). *Memoirs of the Zoological Survey of India*, 18, 1–96.
- Taylor, R.W. & Brown, D.R. (1985) Formicoidea. In D.W. Walton (Ed.), *Zoological Catalogue of Australia. Vol. 2. Hymenoptera, Vespoidea and Sphecoidea*. Australian Government Publishing Service, Canberra, pp. 1–149.
- Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect? Systematics and the agony of choice. *Biological Conservation*, 55, 235–254. [http://dx.doi.org/10.1016/0006-3207\(91\)90030-D](http://dx.doi.org/10.1016/0006-3207(91)90030-D)
- Vane-Wright, R.I. (1996) Systematics and the conservation of biological diversity. *Annals of the Missouri Botanical Garden*, 83, 47–57. <http://dx.doi.org/10.2307/2399967>
- Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. (2009) Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, 24, 456–465. <http://dx.doi.org/10.1016/j.tree.2009.03.011>
- Ward, P.S. (1994) *Adetomyrma*, an enigmatic new ant genus from Madagascar (Hymenoptera: Formicidae), and its implications for ant phylogeny. *Systematic Entomology*, 19, 159–175. <http://dx.doi.org/10.1111/j.1365-3113.1994.tb00585.x>
- Wasmann, E. (1897) Bemerkungen über einige Ameisen von Madagascar. *Zoologischer Anzeiger*, 20, 249–250.
- Wheeler, W.M. (1910) *Ants: Their Structure, Development and Behavior*. Columbia University Press, New York, xxv + 663 pp.
- Wheeler, W.M. (1911) A list of the type species of the genera and subgenera of Formicidae. *Annals of the New York of Academy of Sciences*, 21, 157–175. <http://dx.doi.org/10.1111/j.1749-6632.1911.tb56932.x>
- Wheeler, W.M. (1917) The mountain ants of western North America. *Proceedings of the American Academy of Arts and Sciences*, 52, 457–569. <http://dx.doi.org/10.2307/20025695>
- Wheeler, W.M. (1918) A study of some ant larvae, with a consideration of the origin and meaning of the social habit among insects. *Proceedings of the American Philosophical Society*, 57, 293–343.
- Wheeler, W.M. (1922) Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. *Bulletin of the American Museum of Natural History*, 45, 1005–1055.
- Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology, and species richness. *Trends in Ecology and Evolution*, 19, 639–644. <http://dx.doi.org/10.1016/j.tree.2004.09.011>
- Wilmé, L., Goodman, S.M. & Ganzhorn, J.U. (2006) Biogeographic evolution of Madagascar's microendemic biota. *Science*, 312, 1063–1065. <http://dx.doi.org/10.1126/science.1122806>
- Wollenberg, K.C., Vieites, D.R., van der Meijden, A., Glaw, F., Cannatella, D.C. & Vences, M. (2008) Patterns of endemism and species richness in Malagasy cophyline frogs support a key role of mountainous areas for speciation. *Evolution*, 62, 1890–1907. <http://dx.doi.org/10.1111/j.1558-5646.2008.00420.x>
- Yoder, A.D. & Heckman, K. (2006) Mouse lemur phylogeography revises a model of ecogeographic constraint in Madagascar. In Fleagle, J. & Lehman, S.M (Eds.), *Primate Biogeography: Progress and Prospects*. Kluwer, New York, New York, pp. 255–268.
- Yoshimura, M. & Fisher, B.L. (2007) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): key to subfamilies and treatment of the genera of Ponerinae. *Zootaxa*, 1654, 21–40.
- Yoshimura, M. & Fisher, B.L. (2009) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Proceratiinae. *Zootaxa*, 2216, 1–21.