



Taxonomic revision of the Malagasy *Camponotus grandidieri* and *niveosetosus* species groups (Hymenoptera, Formicidae) using qualitative and quantitative morphology

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Abstract

The *Camponotus grandidieri* species group and *Camponotus niveosetosus* species group of the Malagasy region are revised. Species delimitation was inferred from the evidence of both qualitative morphological analysis and multivariate morphometry. The multivariate method combined the Nest Centroid (NC)-clustering method and Partitioning Algorithm based on Recursive Thresholding (PART) function to generate hypotheses about species boundaries (clusters) based on 19 continuous morphological traits of minor workers. The proposed species hypotheses were tested by cumulative cross-validated Linear Discriminant Analysis (LOOCV-LDA) and Principal Component Analysis in a shape space (shape PCA). Morphometric ratios for the subsets of minor and major workers were used in species descriptions and redefinitions. Here,

eight species are recognized, of which three are newly described and five are redescribed. Four species belong to the *Camponotus grandidieri* species group: *auropubens* Forel, *efitra* n. sp., *grandidieri* Forel, and *maintikibo* n. sp.; and four species belong to the *Camponotus niveosetosus* species group: *descarpentriensi* Santschi, *madagascarensis* Forel stat. rev., *mita* n. sp., and *voeltzkowii* Forel. *Camponotus auropubens aldabrensis* Forel and *C. olivieri freyeri* Santschi are synonymized under *C. auropubens*. *Camponotus grandidieri atrabilis* Santschi and *C. grandidieri comorensis* Santschi are synonymized under *C. grandidieri*. Illustrated species identification keys for both minor and major castes, taxonomic discussions, images, and distribution maps for each species superimposed on the ecoregions of Madagascar are also provided.

Key words: Species delimitation, *grandidieri* species group, *niveosetosus* species group, morphometric analysis, NC-Clustering, partitioning, Malagasy region, Madagascar

Introduction

Camponotus, the genus of carpenter ants, is one of the most highly diverse ant genera in the Malagasy region (Fisher 1997), and the species occupy a wide variety of microhabitats across different terrestrial ecosystems in Madagascar and neighboring islands. This high diversity, local abundance, and the probable ecological importance of *Camponotus* make the genus an important model organism for ecological monitoring and assessment in the region. Although 78 species and subspecies of *Camponotus* have been described from the Malagasy region by earlier ant taxonomists (e.g.: Roger 1863; André 1887; Forel 1892, 1897, 1914; Emery 1896, 1925; Santschi 1921; Wheeler 1922; Donisthorpe 1949), the majority of species have yet to be described. Combined with the many new collections generated by modern intensive research surveys of ants in Madagascar and neighboring islands (Fisher 2005), this state of affairs puts the genus *Camponotus* in great need of comprehensive taxonomic revision. The recent taxonomic revision of the *edmondi* group (Rakotonirina, Csösz & Fisher 2016) added 10 new species. The present contribution revises the taxonomy of the Malagasy members of the *grandidieri* and *niveosetosus* species groups.

Earlier taxonomic studies of Malagasy *Camponotus* placed species in subgenera (e.g.: Forel 1913; Santschi 1914; Wheeler 1922b; Emery 1925). The *grandidieri* species group is currently equivalent to the subgenus *Myrmotrema* and the *niveosetosus* species group to the subgenus *Myrmopiromis*. Although we continue the practice of placing these taxa in their respective subgenera, this study does not address the support of these subgenera as monophyletic lineages. Because initial results suggest many of the subgenera are not natural, we employ the species group nomenclature in the present study. The two species groups occur across the Ethiopian and Afrotropical region, but here we focus only on the Malagasy representatives. The Malagasy region contains four species of the *grandidieri* group, of which *C. auropubens* Forel and *C. grandidieri* Forel are widespread and two new species described here are endemic to Madagascar. Members of this species group are known to inhabit the four ecoregions of Madagascar and a wide range of forests across neighboring islands in the Malagasy region. Four species of the *Camponotus niveosetosus* species group occur in the Malagasy region, all of which are endemic to Madagascar. These species occupy the sub-humid forest habitats in the central plateau, the transitional forests in the north, and the western dry forest of the island. Morphologically similar species, including *C. niveosetosus* Mayr and *C. niveosetosus irredux* Forel, are found elsewhere in the Afrotropical region, but are not treated here.

In highly diverse genera like *Camponotus*, independent information other than qualitative morphological characters has proved crucial in species delimitation and specimen identification. This is demonstrated by the recent revision of the *C. edmondi* species group (Rakotonirina, Csösz & Fisher 2016) that, in addition to biological and geographical distribution data, utilized multivariate statistical methods for analyzing morphometric data. We apply similar methods in the present contribution to recognize eight species, four in the *grandidieri* species group and four in the *niveosetosus* species group. The findings of our qualitative morphology-based study are congruent with those of the quantitative morphological analysis.

Materials and methods

Abbreviation of depositories

CASC	California Academy of Sciences, San Francisco, CA, USA
MCZC	Museum of Comparative Zoology, Cambridge, MA, USA
MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar
PSWC	P.S. Ward Collection, University of California at Davis, CA, USA
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany

Materials. The present study is based on all specimens of the *Camponotus grandidieri* and *niveosetosus* species groups collected from the arthropod survey project conducted in Madagascar and the surrounding islands in the Malagasy region by the members of the Madagascar Biodiversity Center and other ant researchers. Most surveys were carried out from 1992 through 2015. Data of all pinned specimens examined in the present contribution are available on the web portal AntWeb (<http://www.antweb.org>) and can be accessed using the unique identifying specimen code (e.g.: CASENT0179458) which is affixed to each pin. Images are linked to their specimens via their unique specimen code.

In total, 225 specimens from 110 collecting events were measured during the course of this study (see Supplementary material). Collection codes with prefix ANTC, BLF, GG, MG, SMG or PSW, indicate distinct collecting events.

Methods. Patterns of morphological discontinuities and phenotypic similarity for all individual pinned specimens were studied under a Leica M125 binocular microscope.

Digital color images of lateral and dorsal views of the entire body and full-face views of the head of each species were created using a JVC KY-75 or Leica DFC450 digital camera with a Leica Z16 APO microscope and Leica Application Suite software (v3.8). These images are available online on AntWeb (www.antweb.org). Distribution maps for all species were generated by importing specimen distribution records into the Diva GIS program (Hijmans *et al.* 2011). The major ecoregions of Madagascar were superimposed on the distribution of each species. Specimens with inadequate geographic coordinates were excluded from these maps.

Article 74 in the ICZN's code states that the designation of a lectotype from syntype specimens, which directly match the original description of a named species is desirable to stabilize the nomenclature. Therefore, the phrase "present designation" is used to indicate a lectotype. New species epithets used in the present work are arbitrary combinations of letters and are thus invariant, as are genitive nouns or nominative singular nouns in apposition.

Measurements. Morphometric measurements were taken using a Leica M 125 stereomicroscope equipped with a cross-scaled ocular micrometer and an orthogonal pair of micrometers. All measurements and indices are presented as arithmetic means and ranges are shown as minimum and maximum values in parentheses. Body size dimensions are expressed in millimeters (mm) and all values are rounded to the second decimal place. The morphological measurements follow Rakotonirina *et al.* (2016). The following 20 characters were evaluated:

- 1) Maximum cephalic length (CL): The maximum midline length of the head in full-face view, measured from the midpoint of the posterior margin to the midpoint of the anterior margin of the clypeus.
- 2) Maximum cephalic width (CW): The maximum distance between the lateral margins of the compound eyes in full-face view.
- 3) Maximum head capsule width (CWb): The maximum width of the head excluding the compound eyes.
- 4) Postocular distance (PoOc): The distance between the posteromedian margin of the head and the level of the posterior margin of the compound eyes measured along the midline of the head in full-face view.
- 5) Preocular distance (PrOc): The distance between the anteromedian margin of the clypeus and the level of the anterior margin of the compound eyes measured along the midline of the head in full-face view.
- 6) Clypeal length (ClyL): the maximum midline length of the clypeus measured from the posterior margin to the anterior margin in anterodorsal view, in which the anterior and posterior clypeal margins are aligned to the same focus, except in the major worker of *C. madagascarensis*, where the head was in full-face view. Median concavity on either or both margins reduces the length of the clypeus.
- 7) Frontal carina distance (FR): The maximum distance between the frontal carinae.

- 8) Torular carina distance (TCD): The minimum distance between the torular arches that surround the antennal insertion.
- 9) Maximum tentorial pit distance (GPD): The longest distance between the centers of the fossae located at or very close to the posterolateral margin of the clypeus.
- 10) Scape length (SL): Straight line length of the first antennal segment excluding the basal condyle.
- 11) Eye length (EL): Maximum diameter of the compound eye.
- 12) Oculo-mandibular distance (OMD): The smallest distance between the anterior margin of the compound eye and the mandibular insertion to the head.
- 13) Mesosoma width (MW): Maximum width of the pronotum in dorsal view, which in the *C. grandidieri* species group and the *C. niveosetosus* species group is also the maximum mesosomal width (hence “mesosoma width”).
- 14) Mesosoma length (ML): The longest median anatomical line that connects the posteriormost point of the propodeal lobe with the anteriormost point of the pronotal collar; preferentially measured in lateral view, but if one of the reference points is not visible, dorsal view may be used.
- 15) Mesothoracico-propodeal distance (MPD): With the promesonotal suture and the anterior petiolar foramen margin in the same plane of focus in dorsal view, the maximum midline length between the promesonotal suture and the posteriormost point of the propodeal process dorsal to the petiolar insertion (See Fig. 1, Rakotonirina *et al.* 2016).
- 16) Mesothoracico-propodeal height (MPH): With the mesosoma in lateral view, the length of the line between the anteroventral corner of the mesopleuron dorsal to the insertion of the mesocoxa, and the dorsalmost point of the propodeum that is crossed by the measured line. The line is perpendicular to the diagonal line of the mesosoma that connects the anteriormost point of the pronotal shield and the posteriormost point of the propodeal process dorsal to the petiolar insertion, in lateral view.
- 17) Maximum hind tibia length (HTL): Straight line length of the hind tibia measured from the constriction immediately before its proximal insertion to its distalmost point, excluding the bristles or spines.
- 18) Petiolar width (PEW): The maximum width of the petiole in dorsal view.
- 19) Petiolar node height (NOH): The maximum distance between the petiolar spiracle and the dorsalmost point of the petiolar node.
- 20) Cephalic size (CS): The arithmetic mean of CL and CWb.

Multivariate statistical methods

The datasets. The datasets assessed in the present study consisted of (1) raw measurements of the 19 morphological characters, and the one calculated character CS (a widely applied size indicator), of each measured specimen (See Supplementary material for basic measurements of the specimens), and (2) the ratios (indices) of measurements of one measured trait (variable) to another to calculate the body proportions (Table 1).

During the course of this revision, multivariate statistical analysis of morphometric data was run to obtain information considered helpful for delimiting species and facilitating specimen identification.

Data preparation. Static trait allometry of variables for worker castes is present in the Malagasy *Camponotus* (e.g. Rakotonirina *et al.* 2016). The presence of different allometric properties splits workers into two different castes, minors and majors, preventing us from analyzing the two castes together. Instead, we selected minor workers for morphometric analyses, because they are more abundant in the material examined and tend to be encountered more often outside their nests. Matrix scatterplots were used to check for error variance in the raw data.

The species hypothesis by NC clustering technique and PART method. The generation of species hypotheses followed the procedures in Csösz & Fisher (2016). In the NC clustering procedure, which was run using the package CLUSTER (Maechler *et al.* 2014) and MASS (Venables & Ripley 2002), consistent morphometric discontinuities are used to indicate the difference between groups, and all samples that are more similar in morphometric data are grouped together within the same cluster in a dendrogram.

Collection codes (ANTC, BLF, GG, MG, SMG, or PSW numbers) were used as grouping factors in the NC-clustering analyses. Initially, the method employs dimensionality reduction of the data through cumulative Linear Discriminant Analysis (LDA). Then, the dissimilarity matrix obtained from pairwise distances of linear discriminant scores between each pair of samples is used to map the grouping on a dendrogram.

TABLE 1. Ratios of morphometric data for minors and majors of the species. Upper line: mean of ratios \pm standard deviation, lower line in square brackets: minimum and maximum values. Note: if only two specimens were available then minimum, maximum values are given.

Species	Castes	CS	CWb/CL	CW/CL	PoOe/CL	PrOe/CL	FR/CS	TCD/CS
<i>europubens</i>	Minor (N=18)	1.36 \pm 0.14 [1.19, 1.70]	0.88 \pm 0.03 [0.84, 0.92]	0.85 \pm 0.02 [0.82, 0.89]	0.19 \pm 0.01 [0.18, 0.21]	0.52 \pm 0.06 [0.49, 0.76]	0.34 \pm 0.03 [0.33, 0.45]	0.25 \pm 0.01 [0.24, 0.26]
	Major (N=7)	1.98 \pm 0.32 [1.54, 2.41]	1.02 \pm 0.07 [0.91, 1.10]	0.90 \pm 0.04 [0.86, 0.97]	0.22 \pm 0.02 [0.19, 0.26]	0.52 \pm 0.02 [0.50, 0.56]	0.34 \pm 0.01 [0.32, 0.36]	0.25 \pm 0.01 [0.24, 0.26]
<i>efitra</i>	Minor (N=23)	0.91 \pm 0.16 [0.76, 1.58]	0.87 \pm 0.02 [0.84, 0.91]	0.88 \pm 0.02 [0.84, 0.94]	0.22 \pm 0.01 [0.20, 0.25]	0.49 \pm 0.01 [0.46, 0.53]	0.39 \pm 0.01 [0.37, 0.41]	0.28 \pm 0.01 [0.27, 0.29]
	Major (N=8)	1.95 \pm 0.43 [1.35, 2.43]	0.88 \pm 0.02 [0.83, 0.90]	0.80 \pm 0.02 [0.78, 0.84]	0.29 \pm 0.03 [0.23, 0.33]	0.51 \pm 0.01 [0.49, 0.52]	0.36 \pm 0.01 [0.35, 0.37]	0.25 \pm 0.05 [0.13, 0.27]
<i>grandidieri</i>	Minor (N=24)	1.23 \pm 0.13 [1.05, 1.64]	0.92 \pm 0.03 [0.88, 0.99]	0.92 \pm 0.02 [0.89, 0.95]	0.16 \pm 0.01 [0.15, 0.19]	0.50 \pm 0.01 [0.47, 0.52]	0.36 \pm 0.03 [0.34, 0.48]	0.27 \pm 0.01 [0.26, 0.29]
	Major (N=10)	1.97 \pm 0.21 [1.56, 2.21]	1.03 \pm 0.04 [0.95, 1.08]	0.92 \pm 0.02 [0.89, 0.95]	0.20 \pm 0.01 [0.18, 0.23]	0.52 \pm 0.01 [0.50, 0.54]	0.34 \pm 0.05 [0.19, 0.38]	0.26 \pm 0.01 [0.25, 0.28]
<i>maintikibo</i>	Minor (N=15)	0.97 \pm 0.06 [0.84, 1.08]	0.84 \pm 0.01 [0.82, 0.86]	0.85 \pm 0.03 [0.79, 0.89]	0.21 \pm 0.01 [0.19, 0.22]	0.55 \pm 0.02 [0.52, 0.59]	0.31 \pm 0.01 [0.29, 0.33]	0.24 \pm 0.01 [0.23, 0.26]
	Major (N=4)	1.71 \pm 0.06 [1.66, 1.78]	0.88 \pm 0.01 [0.86, 0.89]	0.83 \pm 0.02 [0.81, 0.85]	0.22 \pm 0.06 [0.13, 0.26]	0.56 \pm 0.01 [0.55, 0.57]	0.34 \pm 0.01 [0.34, 0.35]	0.26 \pm 0.00 [0.26, 0.27]
<i>descarpentriesi</i>	Minor (N=12)	1.33 \pm 0.09 [1.11, 1.46]	0.88 \pm 0.01 [0.86, 0.90]	0.88 \pm 0.02 [0.85, 0.91]	0.18 \pm 0.01 [0.17, 0.19]	0.56 \pm 0.01 [0.54, 0.57]	0.33 \pm 0.01 [0.31, 0.35]	0.26 \pm 0.01 [0.25, 0.27]
	Major (N=2)	1.94 \pm 0.09 [1.88, 2.01]	0.98 \pm 0.02 [0.97, 1]	0.87 \pm 0.02 [0.85, 0.87]	0.24 \pm 0.02 [0.23, 0.25]	0.52 \pm 0.01 [0.52, 0.53]	0.32 \pm 0.00 [0.31, 0.32]	0.24 \pm 0.00 [0.24, 0.25]
<i>madagascarensis</i>	Minor (N=27)	1.32 \pm 0.20 [0.93, 1.81]	0.83 \pm 0.03 [0.76, 0.89]	0.82 \pm 0.05 [0.78, 1.05]	0.24 \pm 0.02 [0.21, 0.27]	0.52 \pm 0.01 [0.51, 0.54]	0.33 \pm 0.01 [0.31, 0.35]	0.25 \pm 0.01 [0.24, 0.27]
	Major (N=8)	2.44 \pm 0.24 [2.05, 2.76]	0.89 \pm 0.03 [0.86, 0.95]	0.78 \pm 0.02 [0.75, 0.82]	0.30 \pm 0.01 [0.29, 0.32]	0.51 \pm 0.01 [0.50, 0.53]	0.34 \pm 0.01 [0.32, 0.36]	0.24 \pm 0.01 [0.23, 0.25]
<i>mita</i>	Minor (N=11)	1.42 \pm 0.08 [1.33, 1.57]	0.83 \pm 0.01 [0.81, 0.84]	0.80 \pm 0.01 [0.78, 0.82]	0.20 \pm 0.01 [0.18, 0.21]	0.55 \pm 0.01 [0.54, 0.57]	0.36 \pm 0.01 [0.35, 0.37]	0.25 \pm 0.01 [0.24, 0.26]
	Major (N=9)	2.16 \pm 0.09 [2.00, 2.27]	0.97 \pm 0.02 [0.94, 0.99]	0.84 \pm 0.01 [0.81, 0.85]	0.21 \pm 0.02 [0.16, 0.22]	0.56 \pm 0.02 [0.52, 0.57]	0.36 \pm 0.01 [0.35, 0.37]	0.25 \pm 0.00 [0.24, 0.26]
<i>voelzkowii</i>	Minor (N=48)	1.32 \pm 0.12 [1.08, 1.55]	0.91 \pm 0.03 [0.87, 1.07]	0.89 \pm 0.03 [0.86, 1.04]	0.17 \pm 0.01 [0.15, 0.23]	0.57 \pm 0.03 [0.54, 0.70]	0.36 \pm 0.02 [0.34, 0.39]	0.26 \pm 0.01 [0.23, 0.29]
	Major (N=9)	2.16 \pm 0.09 [2.00, 2.27]	0.97 \pm 0.02 [0.94, 0.99]	0.84 \pm 0.01 [0.81, 0.85]	0.21 \pm 0.02 [0.16, 0.22]	0.56 \pm 0.02 [0.52, 0.57]	0.36 \pm 0.01 [0.35, 0.37]	0.25 \pm 0.00 [0.24, 0.26]

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TABLE 1. (Continued)

Species	Castes	ClyL/CL	ClyL/GPD	SL/CS	EL/CS	OMD/CS	MW/ML
<i>europubens</i>	Minor (N=18)	0.30±0.01 [0.29, 0.32]	0.70±0.03 [0.65, 0.79]	1.08±0.06 [0.97, 1.20]	0.32±0.01 [0.29, 0.34]	0.46±0.01 [0.44, 0.47]	0.51±0.01 [0.50, 0.53]
	Major (N=7)	0.37±0.11 [0.32, 0.61]	0.96±0.24 [0.78, 1.51]	0.84±0.10 [0.73, 1.00]	0.27±0.02 [0.24, 0.29]	0.47±0.02 [0.45, 0.49]	0.53±0.01 [0.51, 0.54]
<i>efira</i>	Minor (N=23)	0.27±0.01 [0.24, 0.32]	0.59±0.06 [0.51, 0.83]	0.97±0.07 [0.71, 1.03]	0.31±0.02 [0.23, 0.33]	0.43±0.01 [0.42, 0.45]	0.52±0.02 [0.49, 0.54]
	Major (N=8)	0.31±0.01 [0.30, 0.32]	0.82±0.07 [0.70, 0.89]	0.67±0.11 [0.55, 0.86]	0.22±0.03 [0.20, 0.26]	0.44±0.00 [0.44, 0.45]	0.54±0.03 [0.51, 0.60]
<i>grandidieri</i>	Minor (N=24)	0.30±0.01 [0.28, 0.33]	0.66±0.03 [0.60, 0.71]	1.04±0.04 [0.97, 1.10]	0.33±0.02 [0.30, 0.37]	0.45±0.01 [0.42, 0.47]	0.55±0.01 [0.52, 0.58]
	Major (N=10)	0.33±0.01 [0.32, 0.36]	0.88±0.07 [0.78, 0.97]	0.77±0.07 [0.69, 0.93]	0.27±0.01 [0.25, 0.29]	0.49±0.01 [0.46, 0.50]	0.55±0.02 [0.53, 0.58]
<i>maintikibo</i>	Minor (N=15)	0.29±0.01 [0.27, 0.30]	0.63±0.02 [0.60, 0.66]	1.16±0.03 [1.09, 1.22]	0.27±0.01 [0.26, 0.29]	0.47±0.01 [0.46, 0.49]	0.53±0.02 [0.50, 0.55]
	Major (N=4)	0.36±0.01 [0.35, 0.37]	0.90±0.03 [0.87, 0.93]	0.77±0.02 [0.75, 0.80]	0.21±0.01 [0.20, 0.22]	0.42±0.12 [0.23, 0.49]	0.54±0.02 [0.51, 0.57]
<i>descarpentriési</i>	Minor (N=12)	0.31±0.02 [0.28, 0.33]	0.65±0.04 [0.58, 0.72]	1.14±0.02 [1.11, 1.17]	0.27±0.01 [0.26, 0.29]	0.48±0.01 [0.46, 0.49]	0.49±0.01 [0.47, 0.50]
	Major (N=2)	0.23±0.01 [0.23, 0.23]	0.56±0.06 [0.51, 0.60]	0.85±0.1 [0.78, 0.92]	0.23±0.01 [0.22, 0.24]	0.48±0.01 [0.47, 0.49]	0.56±0.02 [0.54, 0.57]
<i>madagascarensis</i>	Minor (N=27)	0.30±0.01 [0.29, 0.32]	0.69±0.05 [0.63, 0.81]	1.22±0.10 [0.98, 1.34]	0.26±0.02 [0.23, 0.29]	0.47±0.01 [0.44, 0.49]	0.51±0.02 [0.47, 0.58]
	Major (N=8)	0.32±0.00 [0.32, 0.33]	0.89±0.04 [0.81, 0.95]	0.76±0.05 [0.73, 0.87]	0.19±0.01 [0.17, 0.21]	0.44±0.05 [0.31, 0.47]	0.50±0.01 [0.48, 0.52]
<i>mita</i>	Minor (N=11)	0.31±0.01 [0.30, 0.32]	0.69±0.02 [0.65, 0.72]	1.15±0.04 [1.06, 1.18]	0.26±0.01 [0.24, 0.27]	0.51±0.01 [0.49, 0.52]	0.55±0.01 [0.53, 0.57]
	Major (N=9)	0.27±0.02 [0.24, 0.31]	0.59±0.04 [0.47, 0.73]	1.10±0.05 [1.01, 1.19]	0.28±0.01 [0.25, 0.30]	0.46±0.02 [0.42, 0.55]	0.67±0.04 [0.60, 0.86]
<i>voelzkwii</i>	Minor (N=48)	0.31±0.01 [0.28, 0.32]	0.78±0.02 [0.73, 0.81]	0.76±0.01 [0.75, 0.79]	0.22±0.01 [0.21, 0.23]	0.49±0.01 [0.45, 0.50]	0.60±0.01 [0.59, 0.62]

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TABLE 1. (Continued)

Species	Castes	PEW/CS	MPD/ML	HTL/CS	ML/CS	MPH/ML	NOH/CS
<i>auropubens</i>	Minor (N=18)	0.36±0.01 [0.32, 0.38]	0.74±0.02 [0.71, 0.78]	1.20±0.05 [1.12, 1.31]	1.58±0.05 [1.47, 1.69]	0.42±0.01 [0.40, 0.45]	0.27±0.02 [0.23, 0.30]
	Major (N=7)	0.33±0.04 [0.28, 0.38]	0.74±0.01 [0.73, 0.76]	0.93±0.14 [0.63, 1.03]	1.36±0.10 [1.25, 1.53]	0.43±0.01 [0.42, 0.45]	0.24±0.04 [0.19, 0.29]
<i>efitra</i>	Minor (N=23)	0.31±0.02 [0.28, 0.36]	0.75±0.01 [0.73, 0.76]	0.93±0.05 [0.70, 0.98]	1.54±0.07 [1.26, 1.62]	0.42±0.02 [0.39, 0.45]	0.21±0.02 [0.17, 0.23]
	Major (N=8)	0.28±0.03 [0.25, 0.32]	0.74±0.03 [0.71, 0.81]	0.69±0.08 [0.60, 0.83]	1.19±0.13 [1.04, 1.38]	0.44±0.02 [0.41, 0.48]	0.21±0.02 [0.19, 0.22]
<i>grandidieri</i>	Minor (N=24)	0.35±0.02 [0.29, 0.39]	0.74±0.01 [0.71, 0.76]	1.11±0.04 [1.05, 1.21]	1.55±0.05 [1.44, 1.63]	0.44±0.02 [0.40, 0.47]	0.27±0.02 [0.24, 0.31]
	Major (N=10)	0.32±0.02 [0.28, 0.36]	0.74±0.02 [0.70, 0.76]	0.94±0.12 [0.83, 1.22]	1.31±0.07 [1.23, 1.50]	0.46±0.02 [0.41, 0.49]	0.24±0.01 [0.22, 0.26]
<i>maintikibo</i>	Minor (N=15)	0.32±0.02 [0.30, 0.36]	0.74±0.01 [0.73, 0.78]	1.22±0.02 [1.18, 1.26]	1.70±0.03 [1.63, 1.73]	0.43±0.01 [0.41, 0.45]	0.24±0.02 [0.22, 0.27]
	Major (N=4)	0.30±0.07 [0.19, 0.35]	0.77±0.01 [0.76, 0.79]	0.94±0.02 [0.91, 0.96]	1.42±0.02 [1.40, 1.45]	0.44±0.02 [0.42, 0.47]	0.26±0.03 [0.24, 0.30]
<i>descarpentriesti</i>	Minor (N=12)	0.35±0.02 [0.33, 0.40]	0.70±0.02 [0.66, 0.73]	1.25±0.04 [1.21, 1.33]	1.62±0.05 [1.56, 1.74]	0.40±0.01 [0.39, 0.42]	0.31±0.02 [0.28, 0.33]
	Major (N=2)	0.34±0.01 [0.33, 0.35]	0.75±0.00 [0.75, 0.75]	1.07±0.05 [1.03, 1.10]	1.42±0.07 [1.38, 1.47]	0.43±0.01 [0.42, 0.43]	0.29±0.02 [0.27, 0.31]
<i>madagascarensis</i>	Minor (N=27)	0.33±0.02 [0.30, 0.39]	0.75±0.02 [0.72, 0.78]	1.25±0.09 [1.03, 1.40]	1.66±0.09 [1.45, 1.79]	0.41±0.03 [0.35, 0.47]	0.24±0.03 [0.18, 0.30]
	Major (N=8)	0.29±0.02 [0.26, 0.33]	0.75±0.02 [0.71, 0.77]	0.88±0.03 [0.84, 0.94]	1.26±0.04 [1.19, 1.32]	0.43±0.03 [0.38, 0.46]	0.21±0.02 [0.17, 0.23]
<i>mita</i>	Minor (N=11)	0.39±0.02 [0.36, 0.41]	0.80±0.01 [0.78, 0.82]	1.33±0.03 [1.27, 1.38]	1.72±0.03 [1.66, 1.76]	0.49±0.02 [0.46, 0.53]	0.28±0.02 [0.24, 0.32]
	Major (N=9)	0.29±0.01 [0.27, 0.30]	0.73±0.01 [0.74, 0.76]	0.87±0.02 [0.84, 0.90]	1.18±0.02 [1.12, 1.23]	0.47±0.01 [0.45, 0.49]	0.26±0.01 [0.23, 0.28]
<i>voltzkowii</i>	Minor (N=48)	0.35±0.03 [0.24, 0.49]	0.56±0.03 [0.49, 0.67]	1.22±0.05 [1.13, 1.33]	1.41±0.06 [1.29, 1.53]	0.54±0.05 [0.46, 0.71]	0.29±0.03 [0.23, 0.37]
	Major (N=9)	0.29±0.01 [0.27, 0.30]	0.73±0.01 [0.74, 0.76]	0.87±0.02 [0.84, 0.90]	1.18±0.02 [1.12, 1.23]	0.47±0.01 [0.45, 0.49]	0.26±0.01 [0.23, 0.28]

The PART method, which is based on Recursive Thresholding, was used to determine the number of clusters that match the morphometric discontinuities found by the NC clustering technique. In this method, the package “clusterGenomics” (Nilsen & Lingjaerde 2013) and the function PART are run to partition samples. In addition, the two clustering methods “hclust” and “kmeans” are used with 1000 bootstrap iterations to optimize the search for the ideal cluster number. The results are shown on the dendrogram in colored bars via the function “mark.dendrogram” (Beleites & Sergio 2015).

Testing species hypotheses using confirmatory Linear Discriminant Analysis (LDA) and principal component analysis in isometry free shape space (shape PCA). Cumulative LDA with leave-one-out cross-validation (LOOCV-LDA) was performed to validate the species hypothesized by the exploratory process (Seifert *et al.* 2014). To reliably confirm the species recognized in the exploratory process, shape PCA based on body proportion, which relates to the shape of the organisms, was run within the defined shape space (Baur & Leuenberger 2011). This technique gives insights into the presence of the species within the shape space by determining the shape values and using isometric size as a vector.

Each species recognized by qualitative morphological characters and exploratory processes and confirmed by the cumulative LDA and PCA based on body shape was then described using qualitative and quantitative morphological characters of the worker castes (minor and major).

An identification key to species is presented based on diagnostic characters of the workers. Morphological terminology follows Bolton (1994) and integument sculpture terminology follows Harris (1979).

Results and discussion

Definition of the *Camponotus grandidieri* species group

The *Camponotus grandidieri* species group can be globally recognized by the combination of the following characters: straight anteromedian clypeal margin, which is not projecting anteriorly into a triangular lobe; clypeus without median longitudinal carina; with mesosoma in dorsal view, humeral angle rounded and not protruding anteriorly into a tubercle; propodeum tapering dorsally; sculpture of the gena and at least the anterior half of the head capsule for the major workers is superimposed with two to seven smaller areoles embedded in scattered larger punctures.

The *grandidieri* species group is known to occur across the Afrotropical and the Malagasy regions. Its currently described species and subspecies are as follows:

Camponotus auropubens Forel, 1894 (Mozambique)

Camponotus auropubens absalon Santschi, 1915 (South Africa)

Camponotus auropubens aldabrensis Forel, 1897 (Malagasy region)

Camponotus auropubens argentopubens Santschi, 1915 (Angola)

Camponotus auropubens jacob Santschi, 1915 (Mozambique)

Camponotus grandidieri Forel, 1886 (Malagasy region)

Camponotus grandidieri atrabilis Santschi, 1915 (Malagasy region)

Camponotus grandidieri ruspolii Forel, 1892 (Somalia)

Camponotus grandidieri eumendax Özdikmen, 2010. [Replacement name for *Camponotus grandidieri mendax* Emery, 1895 (South Africa).]

Definition of the *Camponotus niveosetosus* species group

The *Camponotus niveosetosus* species group can be globally distinguished by the anteromedian clypeal margin having a projecting, bluntly triangular lobe, with the head in full-face view; the presence of a median longitudinal carina on the clypeus; a rounded humerus, which is not projecting anteriorly into a tuberculate angle when the mesosoma is viewed dorsally; the posterior portion of the head, mesosoma dorsum, and the lateral margin of the propodeal declivity with scattered, whitish, erect hairs. The major worker caste possesses finely and densely

reticulate punctate to finely areolate sculpture, which is superimposed with two to seven smaller areoles embedded in the scattered larger punctures; the puncture wall is not well defined on the gena and the lateral portion of the head; the anterior clypeal margin is roughly straight or broadly convex medially.

The members of the *niveosetosus* species group are distributed in the Afrotropical and Malagasy regions. The following synoptic list presents the currently described species and subspecies included in the group:

- Camponotus berthoudi* Forel, 1879 (South Africa)
- Camponotus descarpentriasi* Santschi, 1926 (Malagasy region)
- Camponotus niveosetosus* Mayr, 1862 (Botswana, Kenya, Namibia, South Africa)
- Camponotus niveosetosus irredux* Forel, 1910 (South Africa)
- Camponotus madagascarensis* Forel, 1886 stat. rev. (Malagasy region)
- Camponotus victoriae* Arnold, 1959 (South Africa)
- Camponotus voeltzkowii* Forel, 1894 (Malagasy region)

Checklist of the species from the Malagasy region treated in the present study

Camponotus grandidieri species group

- auropubens*** Forel, 1894 (Mozambique, Madagascar, Seychelles)
 - = *auropubens aldabrensis* Forel, 1897 **syn. n.**
 - = *foraminosus aldabrensis* var. *fryeri* Forel, 1912 unavailable name
 - = *olivieri fryeri* Santschi, 1915. Replacement name for *Camponotus foraminosus aldabrensis* var. *fryeri* Forel **syn. n.**
- efitra*** Rakotonirina, Csösz & Fisher, **sp. n.** (Madagascar)
- grandidieri*** Forel, 1886 (Comoros, Madagascar, Mauritius, Mayotte, Seychelles)
 - = *grandidieri atrabilis* Santschi, 1915 **syn. n.**
 - = *grandidieri comorensis* Santschi, 1915 **syn. n.**

- maintikibo*** Rakotonirina, Csösz & Fisher, **sp. n.** (Madagascar)

Camponotus niveosetosus species group

- descarpentriasi*** Santschi, 1926 (Madagascar)
- madagascarensis*** Forel, 1886 **stat. rev.** (Madagascar)
- mita*** Rakotonirina, Csösz & Fisher, **sp. n.** (Madagascar)
- voeltzkowii*** Forel, 1894 (Madagascar)

Shared morphological traits of the *Camponotus grandidieri* and *niveosetosus* species groups of the Malagasy region

Members of the *Camponotus grandidieri* group and the *C. niveosetosus* group, as in the case of most *Camponotus*, present two different worker castes, minors and majors. In addition, various worker forms show continuous morphological variation between these castes. To distinguish both species groups from all other Malagasy *Camponotus*, using workers of either caste, the following combination of characters can be used:

- 1) Mandible triangular, basal margin shorter than apical margin, which is armed with six teeth.
- 2) Palp formula: 6,4. Maxillary palp long.
- 3) Head elongate in full-face view, lateral borders slightly diverging posteriorly; posterior border more or less convex. Lateral cephalic margins start rounding at posterior fifth of head, while in *Mayria* this rounding starts at posterior third of head. In the *grandidieri* group, the posterior section of the head appears angulate and in *Mayria* the posterior portion of the head looks more rounded.
- 4) Clypeus transversely trapezoidal. Clypeus with angulate anterolateral portion and straight anterior margin in *grandidieri* group; anteromedian margin slightly projecting into triangular lobe in *niveosetosus* group.
- 5) Antenna with 12 antennomeres; flagellomeres longer than broad and gradually decreasing in length towards the apex.
- 6) Antennal scape long, roughly its apical third to distal portion extending beyond posterior margin of the head.

- 7) Frontal lobe narrow anteriorly, wider at midlength and partially concealing the antennal insertion; frontal carinae becoming narrower posteriorly at level of anterior margin of eyes.
- 8) Compound eye large and protruding, sometimes breaking the outline of lateral cephalic margin, located from roughly posterior fourth to posterior sixth of the head. Compound eyes located from posterior fourth to posterior sixth of the head.
- 9) Mesosoma in lateral view, with broadly convex promesonotum; widest at level of pronotum in dorsal view.
- 10) Promesonotal suture visible.
- 11) Pronotum with rounded humeral angle, which is not projecting anteriorly; no sharp margination between pronotal dorsum and lateral portion. Pronotum anterodorsally marginate with a protruding humeral angle in *Myrmopiromis*, but in the *grandidieri* and *niveosetosus* species groups the humeral angle is rounded.
- 12) Mesopleuron and propodeal surface together distinctly longer than lateral portion of pronotum in lateral view.
- 13) Propodeal lobe lacking.
- 14) Metapleural gland absent.
- 15) Procoxa of normal size, maximum width as large as the width of mesopleuron. Maximum width of procoxa as large as width of mesopleuron; in *Myrmepinotus* (*edmondi* species group) procoxa is larger than width of mesopleuron.
- 16) Tibial spur single on mesotibia and metatibia.
- 17) Petiolar node generally compressed anteroposteriorly. Petiolar node tapering dorsally except in *C. efitra* and *C. maintikibo*, anterior face rounding to posterior face with short dorsal margin.
- 18) Sculpture of body dorsum ranging from finely and densely reticulate punctate to finely and densely imbricate; lateral portion from finely areolate to finely coriarius. Gastral tergites sometimes finely and densely strigulate. Most of the species of the Malagasy *Camponotus* have a smooth and shining integument, except the members of the *edmondi* species group and the subgenus *Myrmopiromis*.
- 19) Whitish, erect hairs on dorsum of head and body. Erect hairs slender and pointed on head, pronotum and anterior portion of mesonotum; thicker, stout and blunt or spatulate on propodeal dorsum, petiolar node, and anterior section of gastral tergites. In the *grandidieri* and *niveosetosus* groups, the erect hairs are thicker and their tips are split into two points; the distance between the two closest hairs is larger than half of the length of the longest hairs; the members of other subgenera have fewer erect hairs (e.g. *Mayria*); in the typical *Myrmopiromis* the distance between two closely spaced hairs is smaller than half of the length of the long hairs.
- 20) Pubescence present, short or long, sparse or abundant. Pubescence is as plentiful or more plentiful than the erect hairs in the groups studied in the present contribution, and less abundant than erect hairs in typical *Myrmopiromis* ants.
- 21) Major worker similar to minor worker, but characterized, in addition to the larger head and mesosoma, by the following distinctive traits: lateral portion of head particularly sculptured as finely and densely reticulate punctate, imbricate or areolate, and superimposed with two to seven smaller areoles embedded in scattered large punctures, from which an appressed hair arises medially; antennal scape shorter, its apex barely surpassing or not extending beyond posterior cephalic margin.

Multivariate statistical analysis of morphometric data

The NC-clustering dendrogram revealed eight clusters. The patterns of these eight clusters are also recognized by the partitioning function PART in combination with the two “hclust” and “kmeans” clustering methods (Fig. 1). These eight clusters are interpreted as eight species in the present contribution.

The presence of the eight clusters was also supported by simple cumulative LDA (without LOOCV) and cumulative LDA with leave-one-out cross-validation (LOOCV) at 100% and 98.25% of identification success respectively. In the LOOCV-LDA, nearly all of the specimens in the present study were correctly identified (Table 2): *C. auropubens* (100%), *C. efitra* (100%), *C. madagascarensis* (100%), *C. maintikibo* (100%), *C. mita* (100%). Three species show lower classification success: *C. descarpentriesi* (92.31%), *C. grandidieri* (95.8%), *C. voeltzkowii* (97.91%).

One specimen of *C. grandidieri* and another one of *C. descarpentriesi* were misidentified by LOOCV-LDA as

C. auropubens and *C. madagascarensis* respectively. These misidentifications may be because *C. auropubens* and *C. grandidieri*, both belonging to the *C. grandidieri* species group, are very similar to each other, and the same is true for *C. descarpentriresi* and *C. madagascarensis*, which both fall into the *C. niveosetosus* species group. Morphologically very similar species often exhibit overlapping ranges of quantitative measurements (Fig. 2) and share qualitative morphological traits. The misidentification of one specimen of *C. voeltzkowii* as *C. auropubens* may also indicate the similarity of these species and may therefore support uniting the two species groups revised in the present study.

TABLE 2. Identification matrix of species showing the identification success (percentage), the observed identification (rows) and the predicted identification (columns) based on Leave One Out Cross Validation LDA. Numbers in the matrix are specimen counts.

Observed species	predicted species							Identification success (%)	
	<i>auropubens</i>	<i>descarpentriresi</i>	<i>efitra</i>	<i>grandidieri</i>	<i>madagascarensis</i>	<i>maintikibo</i>	<i>mita</i>		<i>voeltzkowii</i>
<i>auropubens</i>	17								100
<i>descarpentriresi</i>		12			1				92.31
<i>efitra</i>			23						100
<i>grandidieri</i>	1			23					95.8
<i>madagascarensis</i>					24				100
<i>maintikibo</i>						15			100
<i>mita</i>							11		100
<i>voeltzkowii</i>	1							47	97.91
Total	19	12	23	23	25	15	11	47	98.25

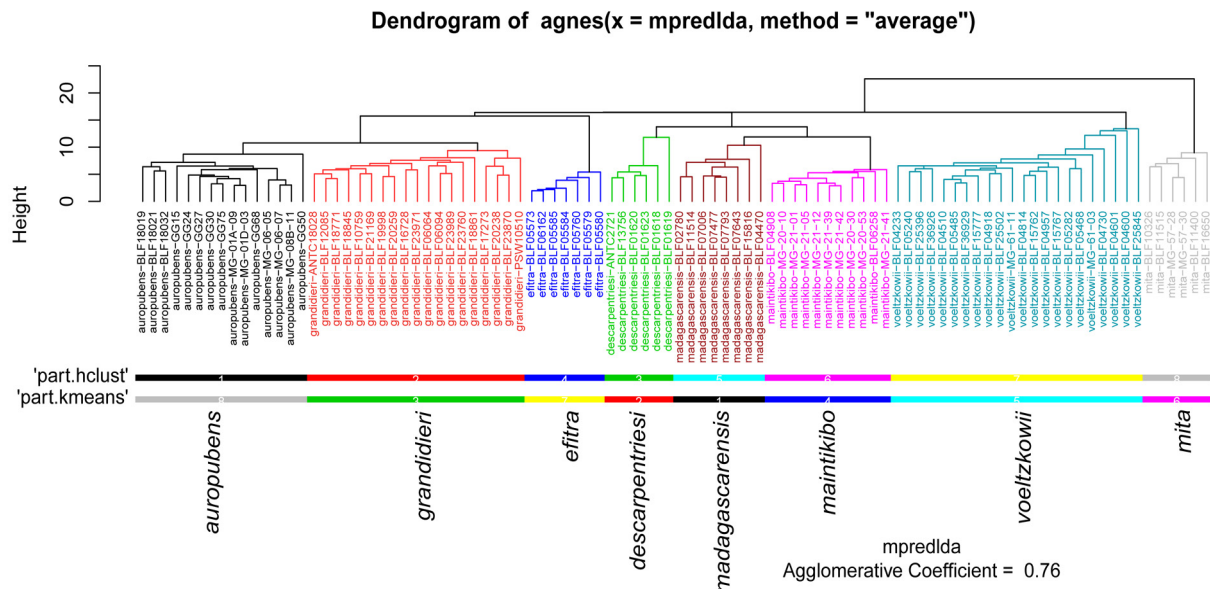


FIGURE 1. Dendrogram of NC-clustering of the eight species recognized in the *grandidieri* and *niveosetosus* species groups. Color bars represent the species hypothesis generated by PART using two “hclust” and “kmeans” clustering methods. The corresponding label on the tip of the branch (the species name followed by the specimen code) are given the same color codes.

The shape PCA analysis (Fig. 2) showed that *C. auropubens* and *C. grandidieri* overlap slightly in their body proportions. This overlap made it difficult to sort specimens using qualitative morphology alone. We had to rely on the length of the erect hairs on the uppermost portion of the petiolar node, on the posterodorsal angle of the propodeum, and on the junction between the lateral propodeal surface and declivity, none of which are considered in the multivariate morphometric analysis, to distinguish between these similar-looking species.

In contrast, the plot for the *niveosetosus* species group (Fig. 3) distinctly separates *C. descarpentriesi* and *C. madagascarensis*, which suggests that although both species look morphologically very similar, they differ in their body proportions. Because *Camponotus auropubens* occurs in Madagascar and the Seychelles islands and *C. grandidieri* is widely distributed across the Malagasy region, these species may have a wide range of morphological variation across their spatial distribution. To overcome confusion resulting from the presence of the overlap in body proportions between *C. auropubens* and *C. grandidieri*, more specimens from both species should be measured.

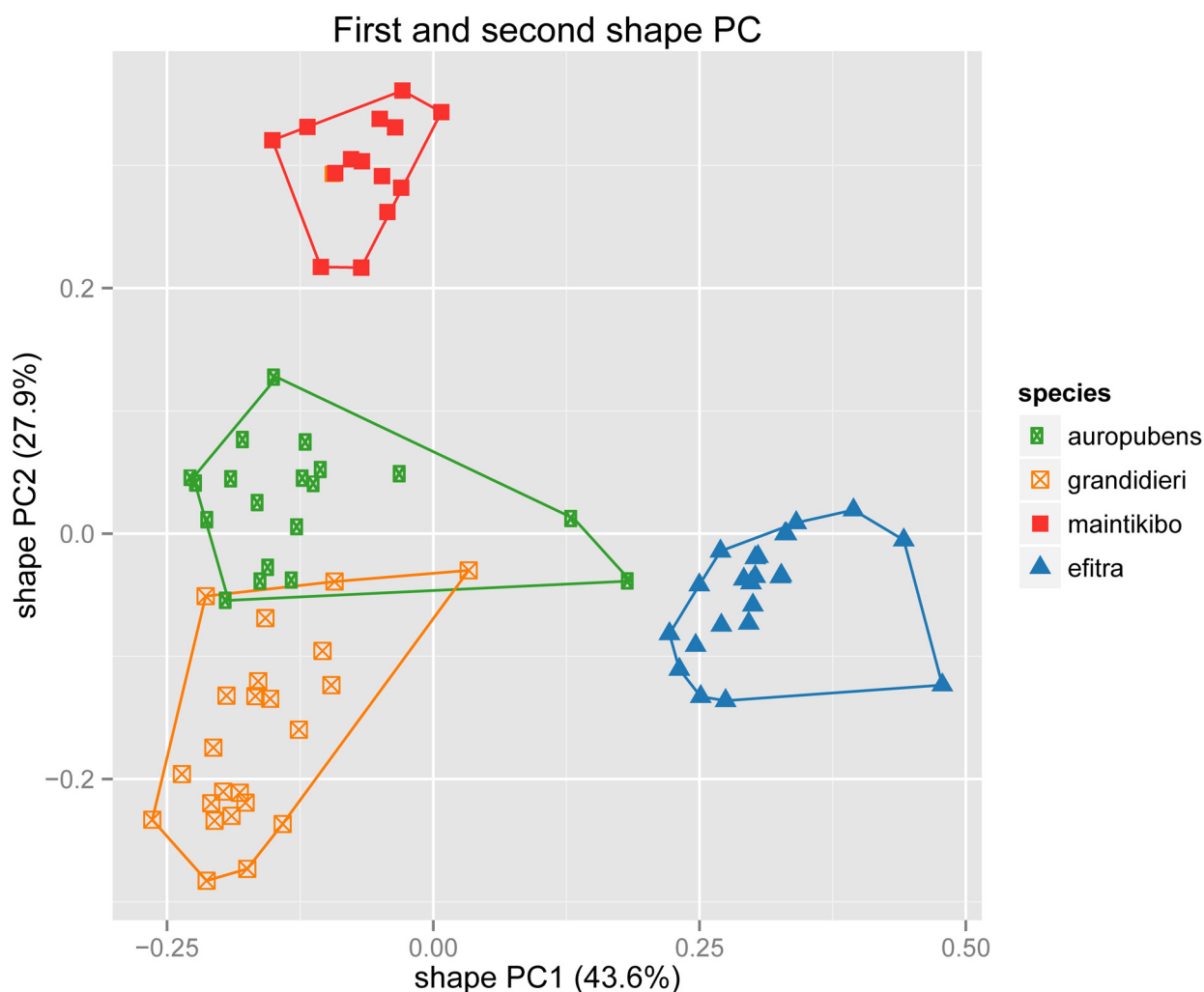


FIGURE 2. Scatterplot of PCA analysis in shape space for the members of the *C. grandidieri* species group.

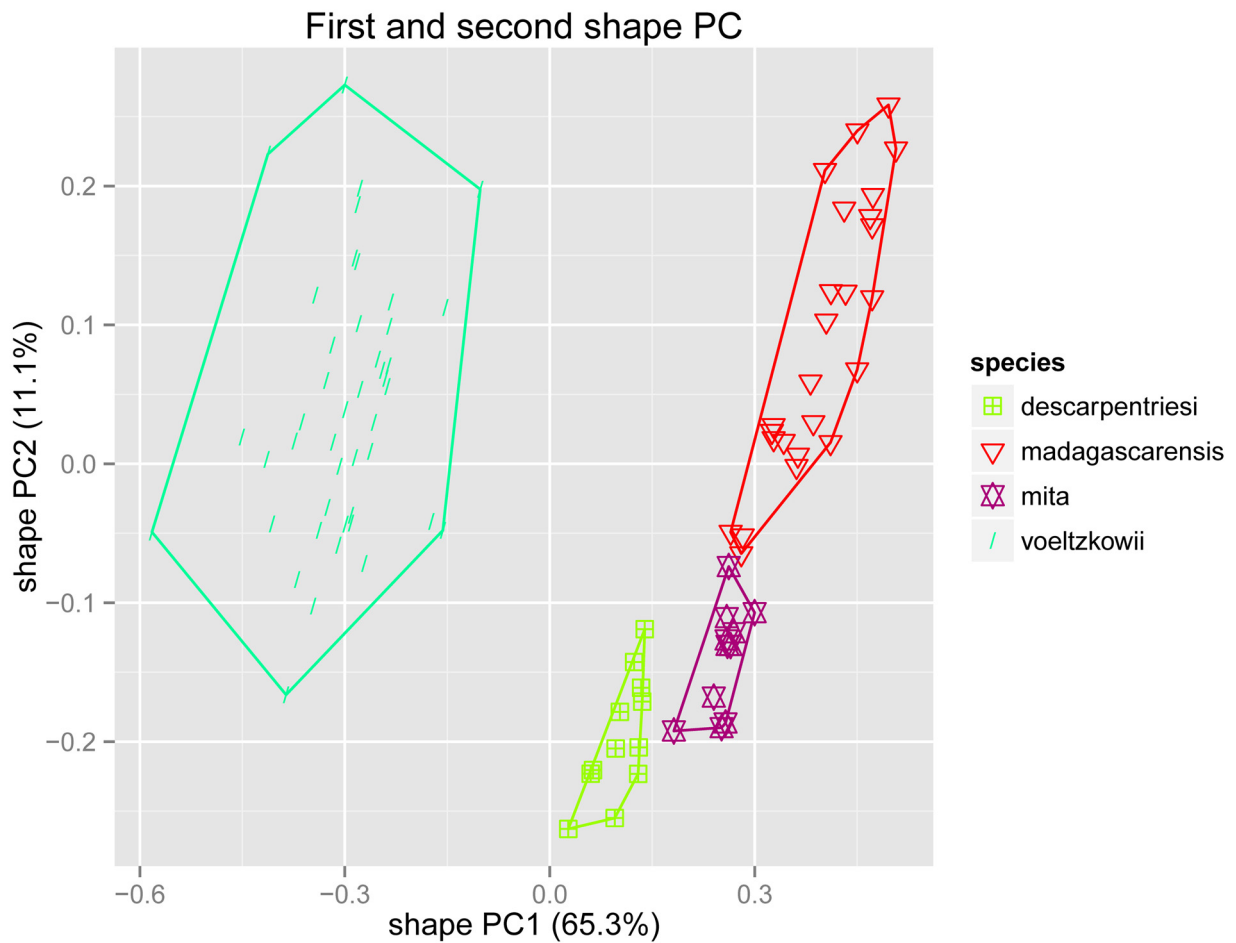


FIGURE 3. Scatterplot of PCA analysis in shape space for the members of the *C. niveosetosus* species group.

Identification key to worker caste of the Malagasy *Camponotus grandidieri* and *niveosetosus* species groups

1. With combination of the following characters: humeral angle rounded; maximum width of procoxa as large as the width of mesopleuron; petiolar node tapering dorsally or its anterior face rounding to posterior face with short dorsal margin; sculpture of body dorsum ranging from finely and densely reticulate punctate to finely and densely imbricate, lateral portion from finely areolate to finely coriarius; sculpture of the gena and at least the anterior half of the head capsule for the major workers is superimposed with two to seven smaller areoles embedded in scattered larger punctures. 2
- Without combination of above characters. other *Camponotus*
2. Numerous scattered whitish erect hairs covering mesosoma and posterior fifth portion of head; distance among hairs on promesonotum smaller than length of hair (Fig. 4A); lateral margin of propodeal declivity with scattered erect hairs, not arranged in a row. 3
- A few pairs of whitish erect hairs confined to posteromedian portion of head; mesosoma dorsum with sparse erect hairs; distance among hairs on promesonotum usually larger than length of hair (Fig. 4B); a row of whitish erect hairs along lateral margin of propodeal declivity 6

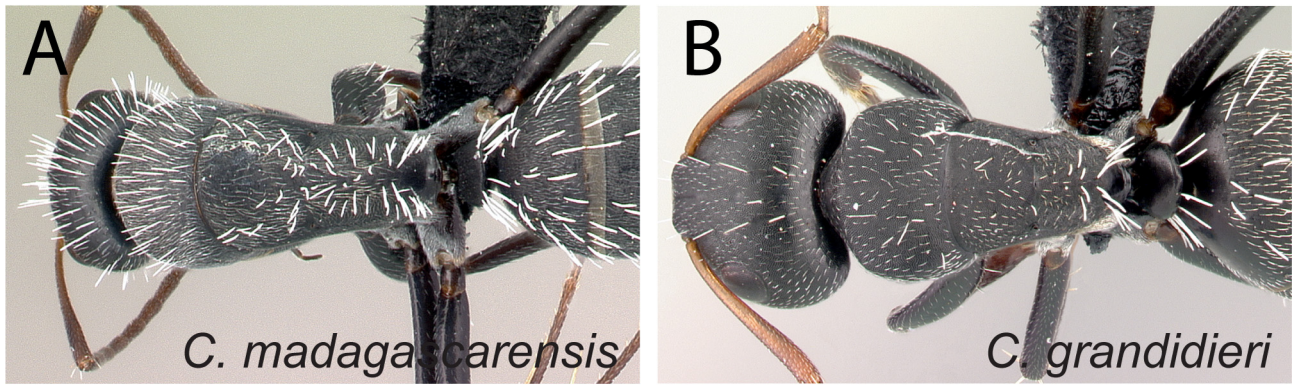


FIGURE 4. Body in dorsal view. A: *C. madagascarens* (CASENT0125551). B: *C. grandidieri* (CASENT0066758).

- 3. In profile, mesosoma long and low (MPH/ML: 0.35–0.47), propodeal dorsum longer than declivitous face (Fig. 5A); erect hairs lacking immediately behind lateral margin of clypeus. 4
- In profile, mesosoma short and high (MPH/ML: 0.45–0.71), propodeal dorsum shorter than declivitous face (Fig. 5B); a few scattered erect hairs present immediately behind lateral margin of clypeus. 5

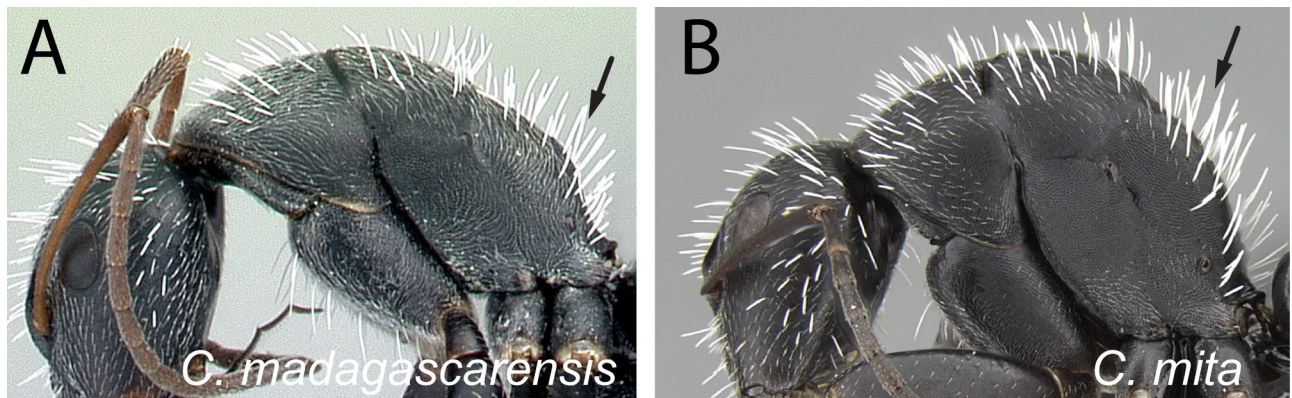


FIGURE 5. Head and mesosoma in lateral view. A: *C. madagascarens* (CASENT0125551). B: *C. mita* (CASENT0498906).

- 4. In full-face view, whitish erect hairs on posterior portion of head scattered laterally to level of anterior margin of eyes (Fig. 6A); eyes located at least in posterior fourth of head; in dorsal view, dorsal margin of petiolar node with two rows of erect hairs extending from upper half to apex; transverse pale strip on posterior margin of abdominal tergites large, width 1/5 the visible width of tergite (Fig. 6B). *madagascarens*
- In full-face view, whitish erect hairs on posterior portion of head spread mostly to posterolateral angle of head, not reaching level of anterior margin of eyes (Fig. 6C); eyes located on posterior fifth of head; in dorsal view, dorsal margin of petiolar node with only one row of erect hairs extending from upper half to apex; transverse pale strip on posterior margin of abdominal tergites narrow, width 1/8 the visible width of tergite (Fig. 6D). *descarpentriesi*

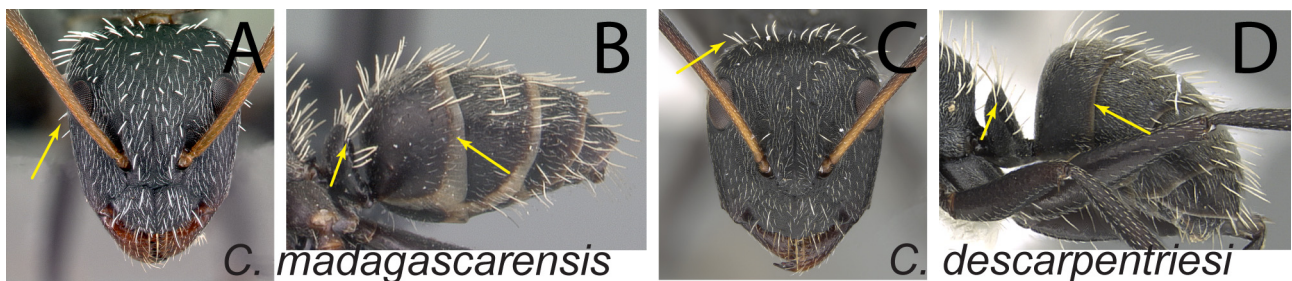


FIGURE 6. Head in full-face view, petiole and gastral segments in lateral view. A–B: *C. madagascarens* (CASENT0125551, CASENT0101383). C–D: *C. descarpentriesi* (CASENT0763876).

5. Basal half of antennal scape noticeably flattened dorsoventrally; with head in full-face view, head elongate (minor CWb/CL: 0.83, 0.81–0.84; CW/CL: 0.80, 0.78–0.82), base of scape near basal condyle forming a lobe-like extension (Fig. 7A); dorsum of body with fewer scattered erect hairs and thin, short, and sparse pubescence; tibiae without suberect hairs *mita*
- Basal half of antennal scape cylindrical, not strongly flattened; with head in full-face view, head subquadrate (minor CWb/CL: 0.91, 0.87–1.07; CW/CL: 0.89, 0.86–1.04), base of scape near basal condyle simple, not forming a lobe-like extension (Fig. 7B); dorsum of body with numerous erect hairs and abundant and coarse pubescence; tibiae with sparse, suberect hairs *voeltzkowii*

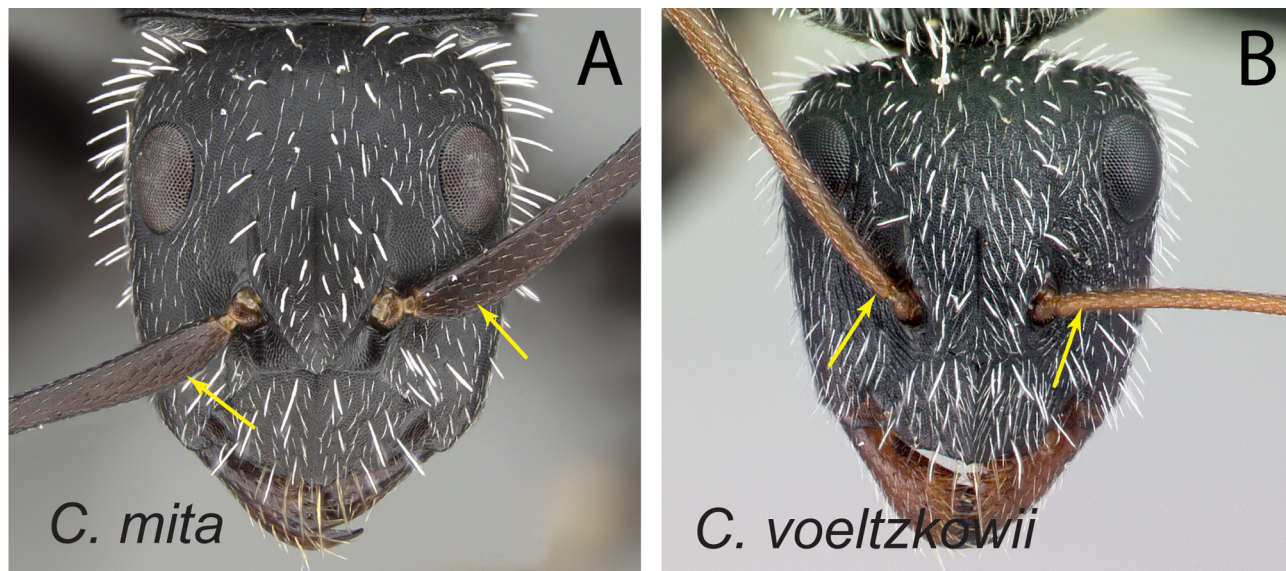


FIGURE 7. Head in full-face view. A: *C. mita* (CASENT0498906). B: *C. voeltzkowii* (CASENT0121619).

6. Body bicolored, with head, mesosoma, petiolar node and legs yellowish orange, light brown to reddish brown and gastral segments dark brown to black (Fig. 8A, 8B); opening of propodeal spiracle roughly circular 7
- Body uniformly black, legs and antennae much lighter in color (Fig. 8C); opening of propodeal spiracle elongate or slitlike 8



FIGURE 8. Body in lateral view. A: *C. maintikibo* (CASENT0763877). B: *C. efitra* (CASENT0453926). C: *C. grandidieri* (CASENT0060136).

7. Head, mesosoma, and petiolar node yellowish-orange, gastral segments anteriorly yellowish and posteriorly black (Fig. 8A); roughly distal half portion of antennal scape surpassing posterior margin of head (SL/CS: 1.16, 1.09–1.22); dorsum of propodeum approximately straight and inclined posteriorly (Fig. 9A) *maintikibo*
- Head, mesosoma, and petiolar node brown to reddish-brown, gastral segments uniformly dark brown to black (Fig. 8B); with head in full-face view, roughly apical third of antennal scape surpassing posterior margin of head (SL/CS: 0.97, 0.71–1.03); dorsum of propodeum convex (Fig. 9B) *efitra*

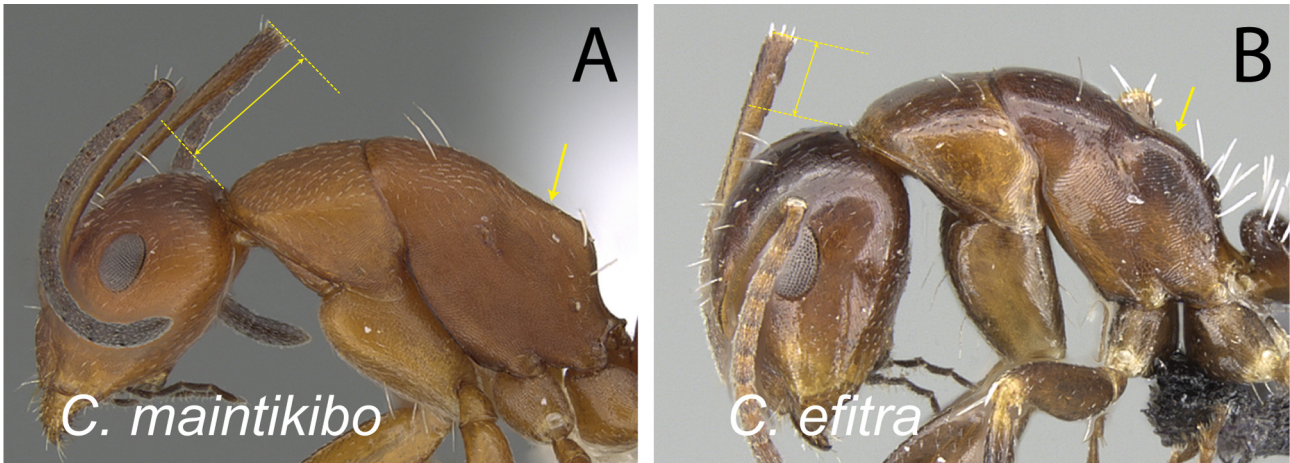


FIGURE 9. Head and mesosoma in lateral view. A: *C. maintikibo* (CASENT0763877). B: *C. efitra* (CASENT0453926).

- 8. Erect hairs on uppermost portion of petiolar node, on posterodorsal angle of propodeum, and on the junction between lateral propodeal surface and declivity shorter than distance between posteroventral angle of mesosoma and propodeal spiracle (Fig. 10A); mesosoma more slender (MW/ML: (minor) 0.51, 0.50–0.53; (major) 0.53, 0.51–0.54) *auropubens*
- Erect hairs on uppermost portion of petiolar node, on posterodorsal angle of propodeum, and on the junction between lateral propodeal surface and declivity at least equal to or longer than distance between posteroventral angle of mesosoma and propodeal spiracle (Fig. 10B); mesosoma more robust (MW/ML: (minor) 0.55, 0.52–0.58; (major) 0.55, 0.53–0.58) *grandidieri*

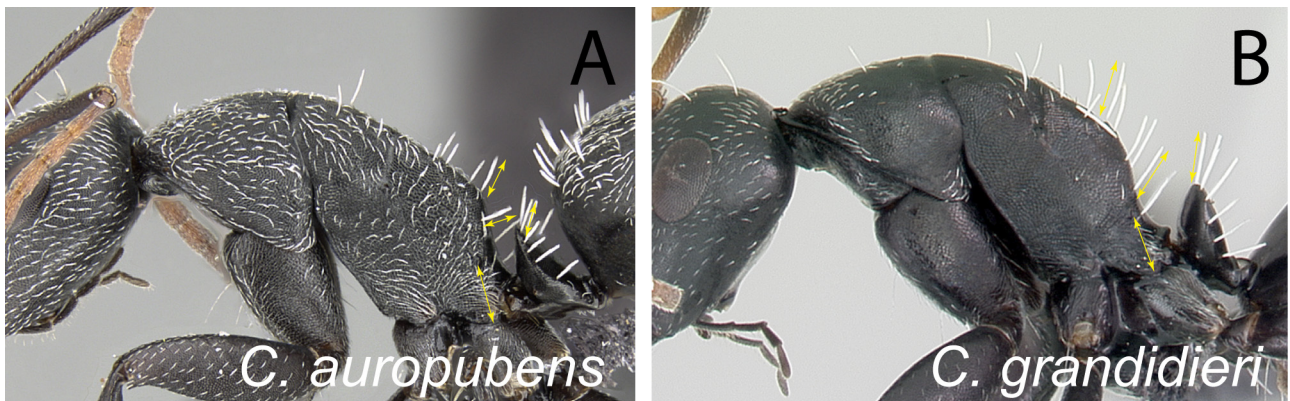


FIGURE 10. Head and mesosoma in lateral view. A: *C. auropubens* (CASENT0133774). B: *C. grandidieri* (CASENT0060136).

Species accounts

The *grandidieri* species group

***Camponotus auropubens* Forel**

(Figures 10A, 11, 19)

Camponotus foraminosus auropubens Forel, 1894: 67. Lectotype major worker, Mozambique, Delagoa Bay [Maputo] (Liengme), AntWeb CASENT0910475 (MHNG) [examined]. Paralectotype worker of same data as lectotype but with specimen code: CASENT0911819 (NHMB) [examined]. [As subspecies of *Camponotus foraminosus*; Emery, 1896: 376; Wheeler, 1922c: 250; of *Camponotus grandidieri*: Mayr, 1895: 150. Raised to species: Santschi, 1915: 267; Arnold, 1924: 728; Emery, 1925: 131. Combination in *Camponotus (Myrmotrema)*: Santschi, 1914: 41; Wheeler, 1922b: 979; Emery, 1925: 131; Bolton, 1995: 131].

Camponotus foraminosus aldabrensis Forel, 1897: 203. Lectotype minor worker, Seychelles, Aldabra (Voeltzkow), AntWeb CASENT0172791 (MCZC) [examined]. [As subspecies of *Camponotus auropubens*: Santschi, 1915: 267; of *Camponotus*

foraminosus: Wheeler, 1922a: 1050. Combination in *Camponotus* (*Myrmotrema*): Santschi, 1915: 267; Wheeler, 1922a: 1050 Emery, 1925: 131.]. **Syn. n.**

Camponotus foraminosus aldabrensis var. *fryeri* Forel, 1912: 166. Workers, Seychelles, Aldabra (Fryer). Unavailable name.

Camponotus olivieri subsp. *freyeri* Santschi, 1915: 270. First available use of *Camponotus foraminosus aldabrensis* var. *fryeri* Forel, 1912: 166. Lectotype minor worker, **present designation**, Seychelles, Aldabra (Fryer) AntWeb CASENT0910490 (MHNG) [examined]. Paralectotype workers, with same data as lectotype, but major CASENT0910489 (MHNG), minor CASENT0104617 (ZMHB) [examined]. **Syn. n.**

Diagnosis. Body color black. A few pairs of whitish erect hairs confined to posteromedian portion of head; gap between two hairs on promesonotum usually larger than length of hair. Erect hairs on uppermost portion of petiolar node, posterodorsal angle of propodeum and junction between lateral propodeal surface and declivity shorter than distance between posteroventral angle of mesosoma and propodeal spiracle.

Description. Minor worker. In full-face view head small (CS: 1.36 ± 0.14 ; 1.19–1.70) and longer than broad (CWb/CL: 0.88 ± 0.03 ; 0.84–0.92), lateral margins roughly straight and slightly converging anteriorly; posterior margin more or less convex. Median portion of clypeus transversely trapezoidal (ClyL/GPD: 0.70 ± 0.03 ; 0.65–0.79). Eyes rarely breaking lateral outlines of head, their posterior level located at posterior fifth portion of head (PoOc/CL: 0.19 ± 0.01 ; 0.18–0.21). Anterior clypeal margin truncate with blunt lateral angle; posterior margin weakly notched medially. Mandible triangular, masticatory margin with six sharp teeth. Antennal scape long, roughly its apical third portion extending beyond posterior cephalic border. In lateral view, promesonotal dorsum generally convex, without anterior and dorsolateral margination; propodeal dorsum straight and inclined posteriorly. In dorsal view, mesosoma widest at level of pronotum and decreasing in width towards propodeal declivity; propodeum tapering dorsally. Opening of propodeal spiracle slitlike. Petiolar node flattened anteroposteriorly and tapering dorsally. Tibial spurs of middle and hind legs pectinate.

Dorsum of head and mesosoma with much finer and denser reticulate punctures than lateral portion. Gastral tergites finely and densely reticulate-punctate. Mandible imbricate-punctate. Whitish erect hairs thinner on dorsum of head and promesonotum, becoming thicker on propodeum, petiolar node, and gastral segments. Composition of hairs: a few pairs on median portion of head from clypeus to near posterior cephalic margin; pronotum with a few pairs, mesonotum with one to three pairs, propodeal dorsum and junction of lateral propodeal surface and declivity with scattered hairs. Posterodorsal angle of propodeum, junction between lateral propodeal surface, and declivity and dorsalmost posterolateral margin of petiolar node with whitish erect hairs shorter than distance between opening of propodeal spiracle and posteroventral angle of mesosoma. Pubescence on dorsum of body longer than distance between hairs; pubescence present on upper half of mesopleuron. Body color black and more or less matte; appendages basally reddish or dark brown, apical portion and antennae brown to light brown.

Major worker. Characteristics of minor worker, except: head much larger and subquadrate (CS: 1.98 ± 0.32 ; 1.54–2.41; CWb/CL: 1.02 ± 0.07 ; 0.91–1.10); lateral margins broadly convex. Mandible more strongly built. Median portion of clypeus elongate and more rectangular (ClyL/GPD: 0.88 ± 0.07 ; 0.78–0.97; ClyL/CL: 0.37 ± 0.11 ; 0.32–0.61). Eyes located medially farther from lateral border of head (CWb/CL: 1.02 ± 0.07 ; 0.91–1.10; CW/CL: 0.90 ± 0.04 ; 0.86–0.97), their posterior margins level at posterior fourth of head capsule (PoOc/CL: 0.22 ± 0.02 ; 0.19–0.26). Roughly one fourth of apical portion of scape extending beyond posterior cephalic margin. In dorsal view, metanotal groove slightly impressed; metanotum not visible. Sculpture of lateral portion of head from near base of mandible, along level of frontal carina to near posterior cephalic margin imbricate, superimposed with larger punctures that are equipped with two to five smaller punctures from which one appressed hair arises. Whitish erect hairs numerous on promesonotum. Basal portion of legs and mandibles reddish to dark brown; apical portion and antenna much lighter in color.

Remarks. Individual workers of *C. auropubens* are difficult to separate from those of *C. grandidieri* by visual inspection of body shape. This is indicated by the overlap of the ratio values between the measured morphological characters (See Table 1). However, careful observation of the patterns of erect hairs on the dorsum of the body indicates that the latter species has longer erect hairs on the uppermost portion of the petiolar node, posterodorsal angle of propodeum, and junction between lateral propodeal surface and declivity. These hairs are longer than the distance between the posteroventral angle of the mesosoma and the propodeal spiracle.

The NC-Clustering technique demonstrates that the morphological distinction between *C. auropubens* and *C. grandidieri* is corroborated by the partitioning method using hclust and kmeans algorithms to find the possible number of clusters. *Camponotus auropubens* is 100% successfully classified by confirmatory LDA.

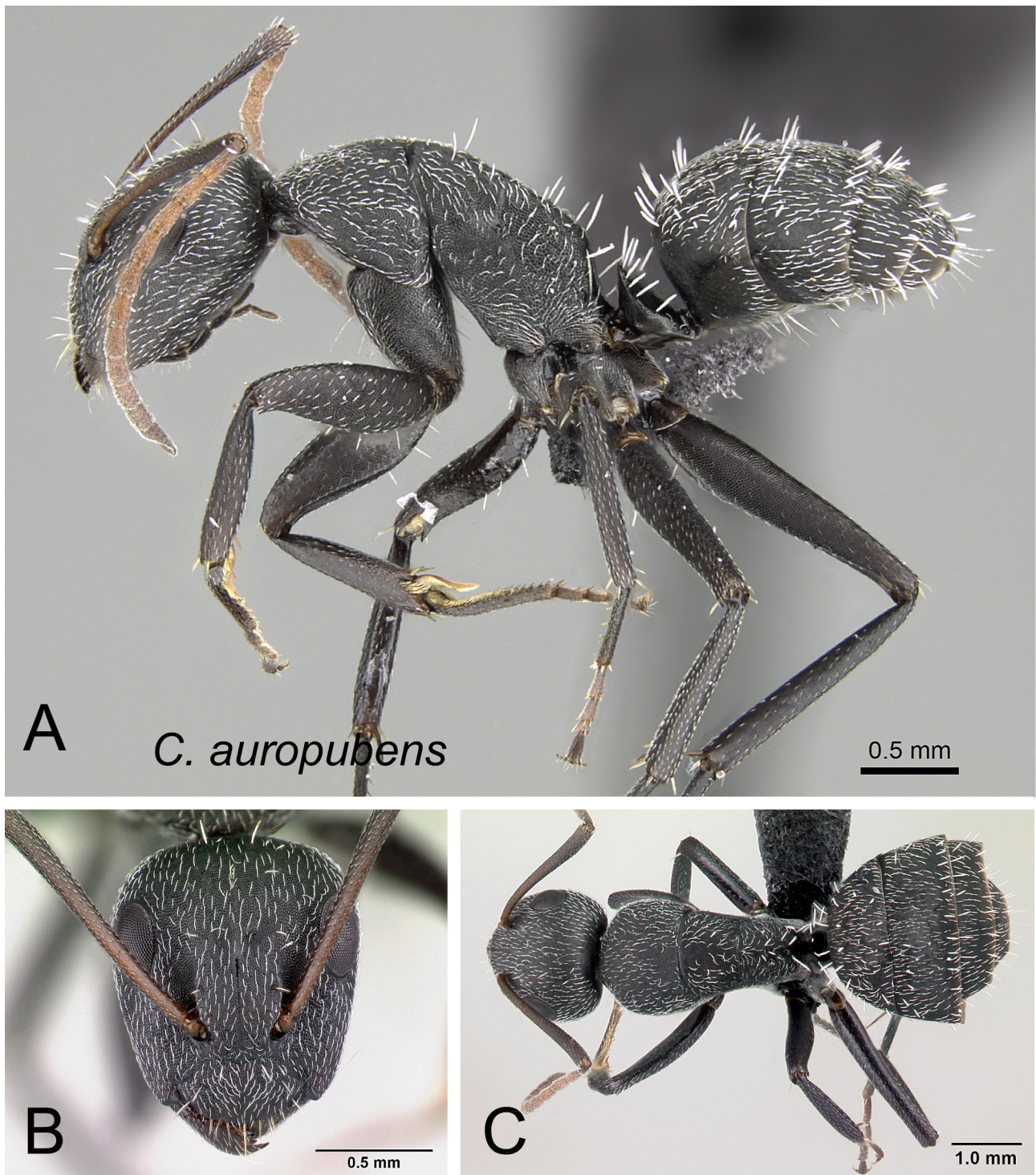


FIGURE 11. *Camponotus auropubens* minor worker CASENT0133774. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Camponotus auropubens* is widespread in the Afrotropics. In the Malagasy region, it is known from Madagascar and Seychelles. In Madagascar, the species has been found only from the north of the island, on the coastal scrub of Sakalava bay, the dry forest of the Montagne Française and Joffre Ville. In Seychelles, the species occurs in casuarina forest, coastal scrub, and along lowland coastal areas of some of the Aldabra and Cosmoledo atolls. The species nests in rotten logs and forages on the ground in these habitats.

Additional material examined. **MADAGASCAR:** Province **Antsiranana:** Baie Sakalava, -12.2733, 49.39064, 10 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Antsiranana, 7 km N Joffre Ville [camp 2 of Fisher], -

12.33333, 49.25, 360 m, in forest, (Irwin, Schlinger, Harin'H) (CASC); Montaigne Francais, -12.325, 49.33333, 150 m, along forested limestone ridge, (R. Harin'Hala) (CASC); **SEYCHELLES**: Mahe, (Grandidier) (ZMHB); Aldabra, (Fryer) (ZMHB); Aldabra Atoll, Malabar Island, -9.37417, 46.43852, 5 m, casuarina forest, (S.M. Goodman) (CASC); Cosmoledo Atoll [Wizard Island], Bary next to the house, Pointe Sicon, -9.73528, 47.64778, <10 m, lowland coastal, coraline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], Bary place next to the camp (50m), -9.7425, 47.65167, <10 m, lowland coastal, coralline island, (G. Galman) (CASC), Cosmoledo Atoll [Wizard Island], Casuarina forest, 200m from the camp, -9.74, 47.65333, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], Mapou (*Pisonia grandis*) forest, -9.75806, 47.63778, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], next to bois matelot, in front of the ocean, sand, -9.76028, 47.64194, <10 m, lowland coastal, coraline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], on the dune, grass, -9.75611, 47.64667, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], on the dune, next to Pemphis, -9.75444, 47.64806, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); Cosmoledo Atoll [Wizard Island], on the dune, next to *Tournefortia argentea*, -9.75306, 47.64889, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); Cosmoledo: Menai (J. Gerlach) (CASC); Grande Ile, Cosmoledo (J. Gerlach) (CASC).

***Camponotus efitra* Rakotonirina, Csósz & Fisher sp. n.**

(Figures 8B, 9B, 12, 20)

Holotype worker. MADAGASCAR: Province **Toliara**: Réserve Spéciale de Cap Sainte Marie, 12.3 km 262° W Marovato, -25.58167, 45.16833, 200 m, spiny forest/thicket, ex dead tree stump, 11–15 Feb 2002 (Fisher, Griswold *et al.*) collection code: BLF05584, specimen code: CASENT0453926 (CASC).

Paratypes. 5 workers with same data as holotype but with specimen codes: CASENT0453927, CASENT0763879, CASENT0763880, CASENT0763881, CASENT0763882 (CASC, BMNH, MHNG).

Diagnosis. Body bicolored, either entirely black and appendages brown or head, mesosoma, and petiolar node and appendages brown to reddish-brown and gastral segments dark brown to black. Roughly apical third of antennal scape surpassing posterior cephalic margin. Dorsum of propodeum convex.

Description. Minor worker. In full-face view, head more or less elongate (CWb/CL: 0.87±0.02, 0.84–0.91), lateral margins roughly straight and posteriorly diverging and rounding to the convex posterior margin. Eyes concealing lateral outlines of head, their posterior level located at posterior fourth to fifth portion of head (PoOc/CL: 0.22±0.01, 0.20–0.25). Clypeus transversely trapezoidal (ClyL/GPD: 0.59±0.06, 0.51–0.83), anteromedian margin convex or broadly triangular, posterior margin weakly notched medially. Mandible subtriangular, apical margin armed with six sharp teeth. Antennal scape long, approximately its apical third portion surpassing posterior cephalic margin. In lateral view, mesosoma without anterior and dorsolateral margination; in lateral view, promesonotal dorsum convex, posterior portion of outline sloping to the impressed metanotal groove; propodeal dorsum forming a separate weak convexity. In dorsal view, mesosoma widest at level of pronotum, and decreasing in width towards propodeal declivity. Opening of propodeal spiracle rounded. In lateral view, petiolar node more or less flattened anteroposteriorly and inclined anteriorly, its dorsum rounding to the anterior and posterior faces. Tibial spurs of middle and hind legs pectinate with very short serrate comb.

Head and mesosoma and petiolar node imbricate, with sparse small punctures from which an appressed hair arises, gastral tergite coriarius. Mandible finely and densely imbricate superimposed with piligerous punctures. Whitish erect hairs thinner on dorsum of head, promesonotum, and gastral tergites; thicker on propodeum and petiolar node. Composition of hairs: a few pairs on median portion of head from clypeus to near posterior cephalic margin; few and scattered on pronotum, one pair on mesonotum, one pair on posterodorsal propodeal angle, a row of hairs on junction of lateral propodeal surface and declivity, a row of hairs from upper half of lateral portion to dorsolateral angle of petiolar node, two rows of hairs at middle and near posterior margin of first four gastral tergites. Pubescence on dorsum of head and mesosoma longer than those on gastral tergites; pubescence more closely spaced on head capsule and farther apart from mesosoma to gaster. Body bicolored and shining: either body entirely black to dark brown with reddish-brown to brown appendages; or head, mesosoma, petiolar node, and appendages reddish-brown to brown and gastral segments black to dark brown.

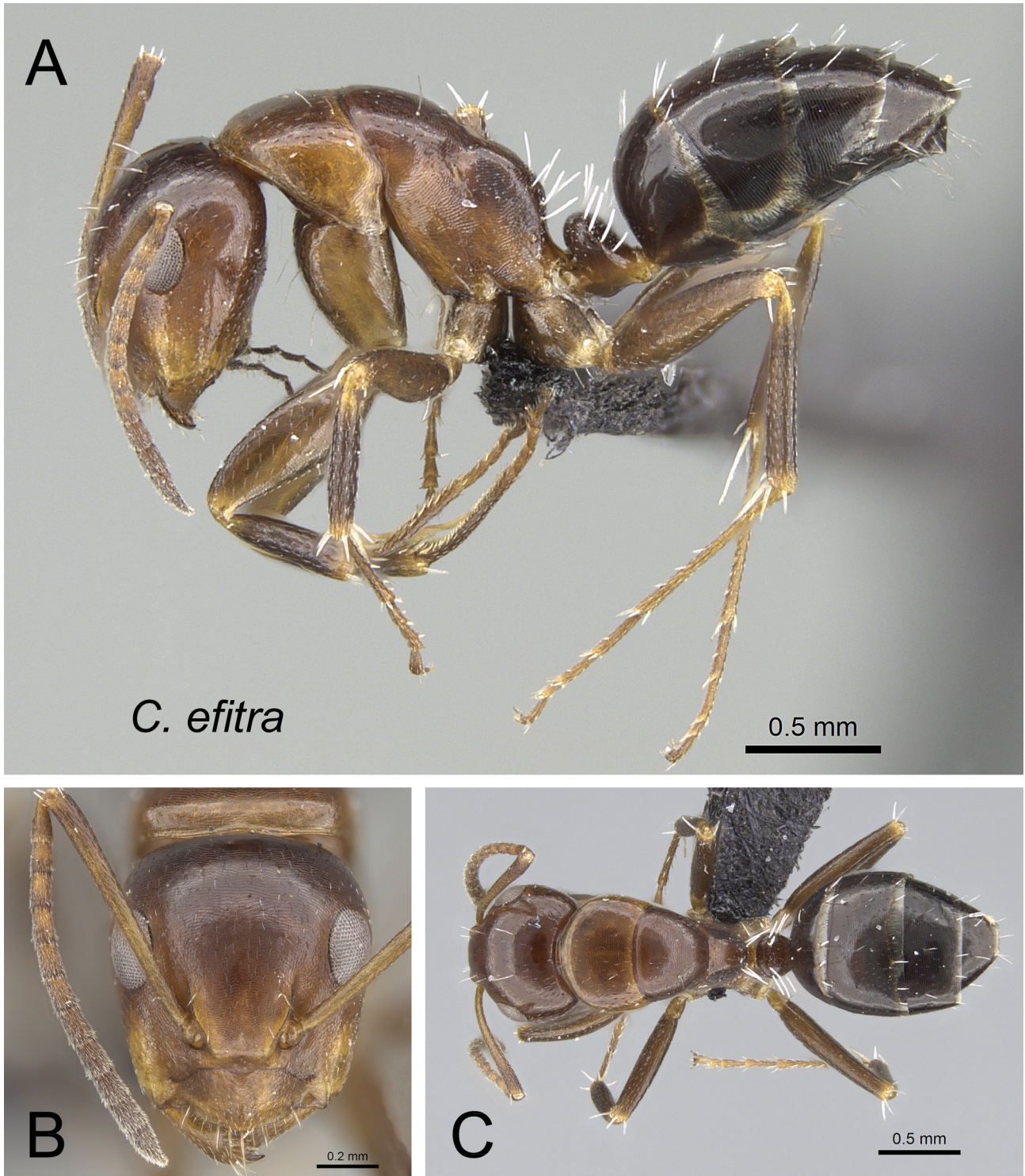


FIGURE 12. *Camponotus efitra* minor worker CASENT0453926. A: lateral view. B: head in full-face view. C: dorsal view.

Major worker. Characteristics of minor worker, except: head much larger (CS: 1.95 ± 0.43 , 1.35–2.43); lateral margins broadly convex, slightly concave at level of eye and abruptly converging to the base of mandible; posterior margin broadly concave medially. Mandible more robust. Clypeus with elongate median portion (ClyL/GPD: 0.82 ± 0.07 , 0.70–0.89), its anteromedian margin broadly convex. With head in full-face view, eyes located farther from lateral cephalic border (CWb/CL: 0.88 ± 0.02 , 0.83–0.90; CW/CL: 0.80 ± 0.02 , 0.78–0.84), their level of rear margins situated at posterior fourth or third of head capsule (PoOc/CL: 0.29 ± 0.03 , 0.23–0.33). Scape short, not extending beyond posterior cephalic margin. Apart from a more impressed metanotal groove, dorsal outline of

mesosoma roughly uniformly convex, sloping from mesonotum to posterodorsal angle of propodeum. Posteromedian portion of head finely and densely reticulate punctate; lateral portion from near base of mandible to near posterior margin covered with coriarius sculpture superimposed with sparse punctures from which an appressed hair arises.

Discussion. *Camponotus efitra* can be confused with *C. maintikibo*, but the former generally has a dark body color ranging from brown to reddish-brown to black; the body color of the latter is yellowish orange. In the *C. maintikibo* minor worker, the propodeal dorsum is approximately straight, inclined posteriorly, and continuously related to the promesonotum, whereas in *C. efitra* the propodeal dorsum forms a separate convexity from a dome-like promesonotum.

The *Camponotus efitra* cluster is located next to the *C. auropubens* and *C. grandidieri* clusters. These results are corroborated by the data obtained from the partitioning technique, and confirmed by shape PCA and LDA with an identification success of 100%.

Distribution and biology. This species is restricted to the spiny forests and thickets between 25 m and 250 m in altitude in the south of Madagascar. Workers of *C. efitra* have mostly been captured by beating low vegetation, pitfall, and Malaise traps. One colony was found in a dead tree stump. *Camponotus efitra* is sympatric with *C. maintikibo*, *C. grandidieri*, and *C. voeltzkowii*.

Additional material examined. MADAGASCAR: Province **Toliara:** 3.5 km 236° SW Marovato, -25.55389, 45.25583, 230 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); 6.1 km 182° S Marovato, -25.58167, 45.295, 20 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); 7.0 km 156° SSE Lavanono, -25.47111, 44.9885, 50 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Androy Region, District of Tsihombe, 74 km S of Tsihombe, Cap Ste Marie Reserve, -25.58767, 45.163, 36 m, spiny bush, (Rin'ha, Mike) (CASC); Mahafaly Plateau, 6.2 km 74° ENE Itampolo, -24.65361, 43.99667, 80 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Parc National de Tsimanampetsotsa, 6.7 km 130° SE Efoetse, 23.0 km 175° S Beheloka, -24.10056, 43.76, 25 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Parc National de Tsimanampetsotsa, Mitoho Cave, 6.4 km 77° ENE Efoetse, 17.4 km 170° S Beheloka, -24.04722, 43.75317, 40 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale de Cap Sainte Marie, 12.3 km 262° W Marovato, -25.58167, 45.16833, 200 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale de Cap Sainte Marie, 14.9 km 261° W Marovato, -25.59444, 45.14683, 160 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); 3 km E Itampolo, Malaise across path of lower bench of Andrimpano Forest, -24.65783, 43.95617, 45 m, dry forest, (ME Irwin, Rin'ha) (CASC); 5 km E Itampolo, Malaise across path of plateau of Andrimpano Forest, -24.65033, 43.96317, 130 m, dry forest, (ME Irwin, Rin'ha) (CASC); Mikea Forest, deciduous dry forest, Tulear Province, -22.90367, 43.4755, 30 m, deciduous dry forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Mikea Forest, spiny forest, Tulear Province, -22.91333, 43.48222, 37 m, spiny forest, (R. Harin'Hala) (CASC); Tsimanampetsotsa National Park, Mitoho Forest, Malaise across trail at escarpment base, -24.0485, 43.75233, 120 m, dense dry forest, (ME Irwin, Rin'ha) (CASC); Tsimanampetsotsa National Park, Mitoho Forest, -24.0485, 43.75233, 150 m, dense dry forest, (ME Irwin, Rin'ha) (CASC).

***Camponotus grandidieri* Forel**

(Figures 4B, 8C, 10B, 13, 22)

Camponotus grandidieri Forel, 1886: 3. Lectotype minor worker, **present designation**, Madagascar (Voeltzkow), AntWeb CASENT0101121 (NHMB) [examined]. Paralectotypes: 4 workers with same data as lectotype but specimen coded: CASENT0101120 (NHMB); CASENT0101368, CASENT0101369, CASENT0101370 (MHNG) and 3 males on same pin with specimen code CASENT0101371 (MHNG) [examined]. [As subspecies of *Camponotus foraminosus*: Mayr, 1893: 195; Forel, 1907: 14. Revived to a species status: Forel, 1914: 270. Combination in *Camponotus (Myrmotrema)*: Forel, 1913: 145; Wheeler, 1922a: 1050; Emery, 1925: 132; Bolton, 1995: 131].

Camponotus grandidieri atrabilis Santschi, 1915: 269, 273. Lectotype minor worker, **present designation**, Madagascar, Toamasina province, Sainte Marie (Voeltzkow), AntWeb CASENT0101122 (NHMB) [examined]. Paralectotypes: 2 workers of same data as lectotype but with specimen code: CASENT0101123 (NHMB), CASENT0102452 (MHNG). [Original combination in *Camponotus (Myrmotrema)*: Wheeler, 1922a: 1051; Emery, 1925: 132; Bolton, 1995: 86]. **Syn. n.**

Camponotus grandidieri comorensis Santschi, 1915: 269, 274. Lectotype major worker, **present designation**, Comoros Islands, Grande Comores (H. Pobéguin), AntWeb CASENT0101125 (NHMB) [examined]. Paralectotype worker of same

data as lectotype but with specimen code: CASENT0101124 (NHMB). [Combination in *Camponotus (Myrmotrema)*: Forel, 1913: 145; Wheeler, 1922a: 1051; Emery, 1925: 132; Bolton, 1995: 93]. **Syn. n.**

Diagnosis. Body color black. A few pairs of whitish erect hairs confined to posteromedian portion of head; gap between two hairs on promesonotum usually larger than length of hair. Erect hairs on uppermost portion of petiolar node, posterodorsal angle of propodeum, and junction between lateral propodeal surface and declivity equal to or longer than distance between posteroventral angle of mesosoma and propodeal spiracle.

Description. Minor worker. In full-face view head small (CS: 1.23 ± 0.13 ; 1.05–1.64) and as long as broad (CWb/CL: 0.92 ± 0.03 ; 0.88–0.99), but slightly converging anteriorly; posterior margin more or less convex. Median portion of clypeus transversely trapezoidal (ClyL/GPD: 0.66 ± 0.03 ; 0.60–0.71). Eyes either breaking lateral outlines of head or not, their posterior level located at posterior sixth portion of head (PoOc/CL: 0.16 ± 0.01 ; 0.15–0.19). Anterior clypeal margin truncate with obtuse lateral angle; posterior margin weakly notched medially. Mandible triangular, apical margin armed with six sharp teeth. Antennal scape long, approximately its distal portion surpassing posterior cephalic margin. In lateral view, outline of promesonotal dorsum broadly convex, without anterior and dorsolateral margination; propodeal dorsum inclined posteriorly. In dorsal view, mesosoma widest at level of pronotum and decreasing in width toward propodeal declivity. Propodeal spiracle opening slitlike. Petiolar node scalelike and tapering dorsally. Mesotibial and metatibial spurs pectinate.

Dorsolateral portion of head and mesosoma finely and densely reticulate punctate, punctures on lateral portion of mesosoma much larger. Gastral tergites with imbricate sculpture or much finer and denser reticulate punctures anteriorly, that become sparser posteriorly. Mandible imbricate superimposed with sparse piligerous punctures. Whitish erect hairs thinner and shorter on head and pronotum, becoming thicker from mesonotum through petiolar node and gastral segments. Hairs arranged as follows: a few pairs on median portion of head from clypeus to near posterior cephalic margin; a few pairs on pronotum, one to three pairs on mesonotum, scattered on propodeal dorsum and junction of lateral propodeal surface and declivity; a row on upper half of posterolateral margin of petiolar node. Some erect hairs on dorsum of petiolar node, posterodorsal angle of propodeum and junction between lateral propodeal surface and declivity equal to or longer than distance between posteroventral angle of mesosoma and opening of propodeal spiracle. On mesosoma, pubescence shorter than distance between hairs; on gastral tergites pubescence longer than distance between hairs; pubescence lacking on upper half of mesopleuron. Body color black and dull; appendages basally reddish or dark brown, apical portion and antennae brown to light brown.

Major worker. With characteristics of minor worker, except: head much larger (CS: 1.97 ± 0.21 ; 1.56–2.21; CWb/CL: 1.03 ± 0.04 ; 0.95–1.08); lateral margins slightly convex and converging to base of more robust mandibles. Apical margin of mandible with up to seven teeth. Median portion of clypeus more rectangular (ClyL/GPD: 0.88 ± 0.07 ; 0.78–0.97). Eyes located more medially (CWb/CL: 1.03 ± 0.04 ; 0.95–1.08; CW/CL: 0.92 ± 0.02 ; 0.89–0.95) and more anteriorly, their posterior level on posterior fifth of head (PoOc/CL: 0.20 ± 0.01 ; 0.18–0.23). One fifth of apical portion of scape extending beyond posterior cephalic margin. In dorsal view, small portion of metanotum visible along midline of mesosoma, between metanotal groove and propodeum. Sculpture of lateral portion of head from near base of mandible, along level of interior ocular margin, to level of postocular margin imbricate, superimposed with sparse, larger punctures, which are equipped with two to four smaller punctures from which one appressed hair arises medially. More pairs of whitish erect hairs on median portion of head; numerous on promesonotum. Body color the same as minor except mandibles, anterior portion of clypeus, and anterolateral portion of head darker in color.

Discussion. See discussion under *C. auropubens*.

The species delimitation for *C. grandidieri* on the basis of qualitative morphology-based analysis is supported by the combination of exploratory analysis of NC-clustering and partitioning methods with the confirmatory analysis of LDA and shape PCA. The species is identified correctly by simple confirmatory LDA at 100% success.

Distribution and biology. *Camponotus grandidieri* is widespread in Africa and the Malagasy region. In the latter it occupies many different types of habitats, but is absent on Reunion Island. It has been collected from coastal scrub and littoral forest to spiny forest and tropical dry forest through montane rainforest and savannah woodland. It is also known from mangrove forest and human-dominated areas such as urban gardens and roadsides. Across these habitats, colony nests have been found most often in dead branches above the ground and in rotten logs, and rarely in dead tree stumps, rot pockets and trunks of live trees, under rocks, and under root mats and litter on rocks. Individual workers forage on the ground and on lower vegetation.

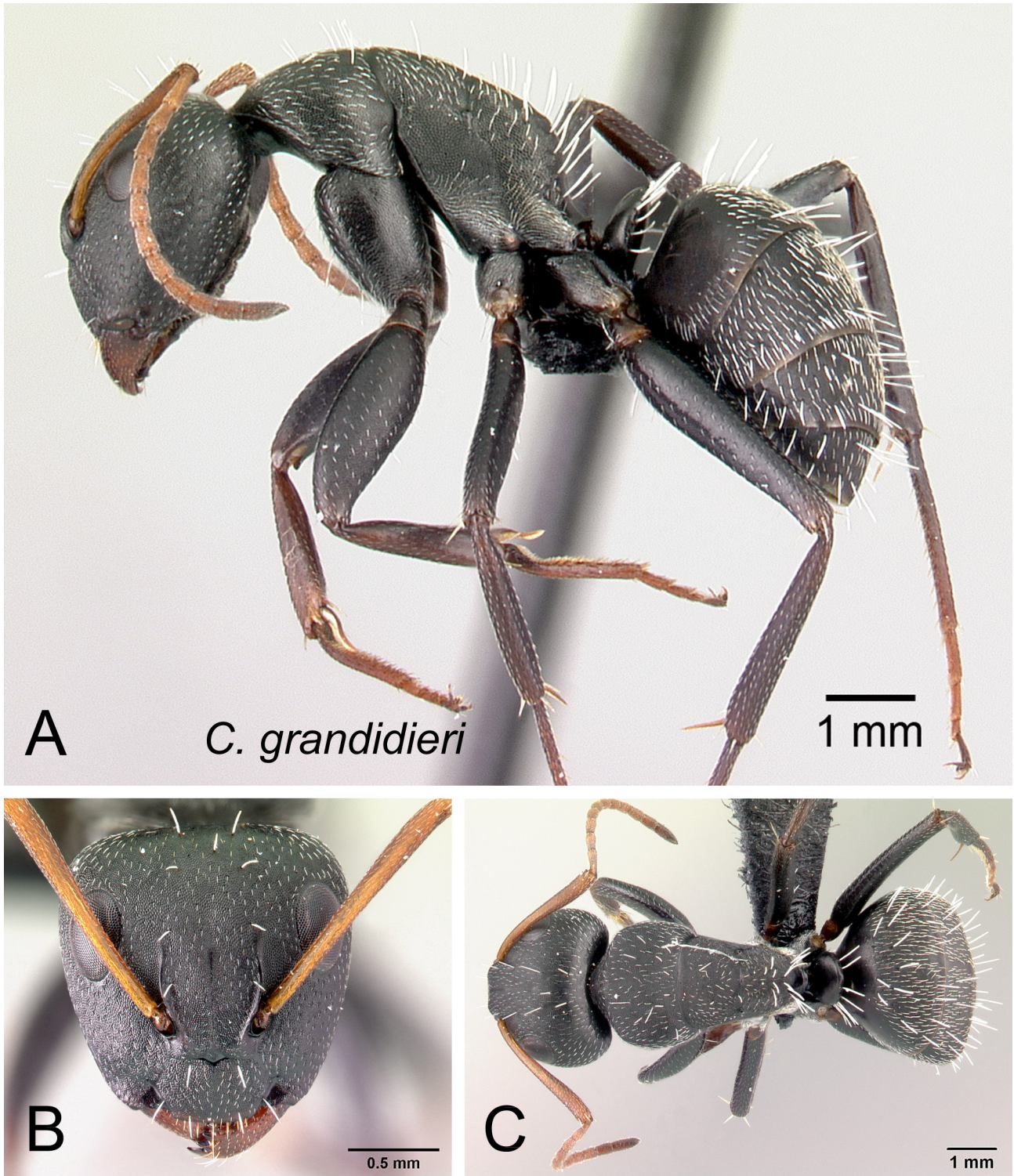


FIGURE 13. *Camponotus grandidieri* minor worker CASENT0066758. A: lateral view. B: head in full-face view. C: dorsal view.

Additional material examined. COMOROS: Anjouan: Bimbini, -12.19635, 44.23752, 5 m, coastal scrub, mangrove, (B.L. Fisher *et al.*) (CASC); -12.18771, 44.35929, 65 m, coastal roadside, (B.L. Fisher *et al.*) (CASC); -12.38051, 44.50217, 20 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); -12.18771, 44.35929, 65 m, coastal roadside, (B.L. Fisher *et al.*) (CASC); -12.25764, 44.38915, 20 m, along roadside, (B.L. Fisher *et al.*) (CASC); -12.22265, 44.2882, 10 m, coastal scrub, along road, (B.L. Fisher *et al.*) (CASC); **Grande Comores:** Domani, -11.51778, 43.28, 25 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Domani, -11.48805, 43.2777, 5 m, mangroves, (B.L. Fisher

et al.) (CASC); Goudjoulachamle, -11.44826, 43.27373, 80 m, coastal scrub on lava, (B.L. Fisher *et al.*) (CASC); Pidjani, -11.75447, 43.45148, 35 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Trou du Prophète, -11.38087, 43.31335, 10 m, coconut plantation on beach, (B.L. Fisher *et al.*) (CASC); **Mohéli**: Lac Boundouni, -12.37915, 43.85165, 25 m, dry forest, (B.L. Fisher *et al.*) (CASC); Madahali, -12.37421, 43.86857, 50 m, coastal dry forest scrub, (B.L. Fisher *et al.*) (CASC); Ouallah, -12.34234, 43.66851, 1 m, mangrove, (B.L. Fisher *et al.*) (CASC); Ouallah, -12.32717, 43.65952, 10 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); (Vöeltzkow) (NHMB); **EUROPA ISLAND**: [Insel Europa Westlich von Madagascar], (Voeltzkow) (MHNG); Europa Island, -22.34775, 40.37041, 10 m, spiny forest on coral, (B.L. Fisher) (CASC); -22.39054, 40.37935, 15 m, coastal dune vegetation, (B.L. Fisher) (CASC); -22.34775, 40.37041, 10 m, spiny forest on coral, (B.L. Fisher) (CASC); -22.33909, 40.38752, 8 m, coastal dune vegetation, (B.L. Fisher) (CASC); **MADAGASCAR**: Province **Antsiranana**: [Madagascar], (NHMB); [Nosibé], (Vöeltzkow) (MHNG); Ambanja, -13.68268, 48.45245, 30 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Ambilobe, -13.19728, 49.04868, 61 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Ambilobe, -13.19728, 49.04868, 61 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Ambondrobe, 41.1km 175° Vohemar, -13.71533, 50.10167, 10 m, littoral rainforest, (B.L. Fisher) (CASC); Andrafiabe, 2.6 km E; Reserve Special d'Ankarana, Antsiranana Province, -12.91667, 49.05, forest edge in savanna, (M.E. Irwin & E.I. Schlinger) (CASC); Antalaha, -14.9013, 50.28095, 23 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Antongombato, 2.2 km SW Antsiranana, -12.37285, 49.22893, 74 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Antsaraingy, -12.89492, 49.65785, 13 m, savannah woodland, (B.L. Fisher *et al.*) (CASC); Antsaraingy, -12.89713, 49.65916, 37 m, littoral forest, (B.L. Fisher *et al.*) (CASC); Antsiranana, -12.27777, 49.29155, 43 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Daraina, -13.255, 49.61667, 100 m, roadside, (B.L. Fisher) (CASC); Orangea dry forest, Baie de dune 900 m E of Camps Minier, -12.23283, 49.3665, 152 m, dry forest, (Mike, Rinha) (CASC); Forêt Ambato, 26.6 km 33° Ambanja, -13.4645, 48.55167, 150 m, rainforest, (B.L. Fisher) (CASC); Galoko chain, Mont Galoko, -13.58745, 48.71419, 380 m, rainforest, (B.L. Fisher *et al.*) (CASC); Nosy Faly, -13.36435, 48.49137, 40 m, open secondary vegetation, (B.L. Fisher *et al.*) (CASC); Nosy faly, Tafiambotry, 35.3 km N Ambanja, -13.3654, 48.48775, 7 m, littoral rainforest, (B.L. Fisher *et al.*) (CASC); Rés. Analamerana, 28.4 km 99° Anivorano-Nord, -12.74667, 49.49483, 60 m, tropical dry forest, (B.L. Fisher) (CASC); Sakaramy 7 km N of Joffre Ville, -12.33333, 49.25, 360 m, low rain forest in open area, (Mike, Frank, Rinha) (CASC); Sambava, -14.26145, 50.16295, 23 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Taizambato, 22.9 km NE Ambanja, -13.5092, 48.56722, 16 m, coconut plantation, (B.L. Fisher *et al.*) (CASC); Vohemar, -13.37723, 50.0205, 25 m, cultivated land, (B.L. Fisher *et al.*) (CASC); Vohemar, -13.35967, 50.0039, 16 m, urban/garden, (B.L. Fisher *et al.*) (CASC); 7 km N Joffre Ville [camp 2 of Fisher], -12.33333, 49.25, 360 m, in dry forest, (R. Harin'Hala) (CASC); Montaigne Francais, -12.325, 49.33333, 150 m, along forested limestone ridge, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [first campsite], -12.51444, 49.18139, 960 m, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [lemur trail], -12.51667, 49.18333, 975 m, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [Petit Lac road], -12.52028, 49.17917, 1125 m, rainforest, (R. Harin'Hala) (CASC); Sakalava Beach [vegetated beach dunes], -12.26278, 49.3975, 10 m, across sandy trail in dwarf littoral forest, (R. Harin'Hala) (CASC); Province **Fianarantsoa**: Ampandravelo II Non Protected Area, 10.78 km NE Ranohira, -22.53917, 45.51548, 873 m, shrubland, (A. Ravelomanana) (CASC); dry wash, 1 km E of Isalo National Park Interpretive Center, Fianarantsoa Prov., -22.62667, 45.35817, 885 m, dry wash, (R. Harin'Hala) (CASC); Forest d' Ambalamanakana, -20.73333, 47.2, (A. Pauly) (CASC); Ampangabe III Non Protected Area, 21.26 km W Itremo, -20.6125, 46.60883, 1412 m, savannah woodland, (A. Ravelomanana) (CASC); Antohatsahomby III Non Protected Area, 22.79 km NW Itremo, -20.54806, 46.58599, 1499 m, Uapaca woodland, (A. Ravelomanana) (CASC); Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, grassland, (Fisher, Griswold *et al.*) (CASC); Horombe Region, District of Ihosy, Betapia (Border of Fianarantsoa and Tulear), 9 km SW of Ilakaka Saphir town, -22.62883, 45.36117, 1036 m, Uapaca forest, (Rin'ha, Mike) (CASC); Manakara, -22.14817, 48.02267, 10 m, urban gardens, coastal Casuarina equisetifolia, (B.L. Fisher *et al.*) (CASC); Province **Mahajanga**: Antsalova, -18.68333, 44.61667, 100 m, (D.C. Lees) (PSWC); Bemeraha, 9 km E Antsalova, -18.65, 44.71667, tsingy, (D.C. Lees) (PSWC); Forêt de Tsimembo, 8.7 km 336° NNW Soatana, -19.02139, 44.44067, 20 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Melaky Region, District of Maintirano, Asondrodava dry forest against dune, 15 km N of Maintirano, -17.96533, 44.0355, 16 m, dry forest, (Irwin, Rinha) (CASC); Melaky Region, District of Besalampy, Marofototra palm forest, 17 km W of Besalampy, -16.72167, 44.42367, 10 m, palm trees on sand, (Irwin, Rinha) (CASC); Parc National de Baie de Baly, 12.4 km 337° NNW Soalala, -16.01, 45.265,

10 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Province **Toamasina**: Ste Marie, (Voeltzkow) (MHNG); (Tamatave), Prison de Tamatave, -18.16667, 49.38333, (A. Pauly) (CASC); 2.1 km 315° Mahavelona, -17.67017, 49.49583, 30 m, eucalyptus plantation, (B.L. Fisher *et al.*) (CASC); Ambalahasina, 62.4 km 19° Toamasina, -17.59452, 49.46785, 15 m, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Ampasimbe, 118 km 17° Toamasina, -17.09283, 49.47783, 25 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Ampasina-Maningory, 104 km 13° Toamasina, -17.21467, 49.4055, 20 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Andasibe National Park, botanic garden near entrance, West of ANGAP office, -18.92639, 48.40783, 1025 m, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); Anosintany, 139 km 21° Toamasina, -16.91117, 49.58867, 10 m, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Antaratasy, 43.5 km 23° Toamasina, -17.76733, 49.47767, 15 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Antetazambaro, 16 km 21° Toamasina, -17.05283, 49.567, 10 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Brickaville, -18.82183, 49.07017, 24 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Moramanga, 29 km E of Moramanga, Andasibe National Park, -18.93767, 48.41167, 822 m, rainforest, (Mike, Rin'ha) (CASC); Fenoarivo, 85.7 km 13° Toamasina, -17.38117, 49.415, 10 m, beach/coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Ile Sainte Marie, Forêt Ambohidenana, 22.8 km 44° Ambodifotatra, -16.82433, 49.96417, 20 m, littoral rainforest, (B.L. Fisher *et al.*) (CASC); Mahanoro, -19.89933, 48.80883, 15 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Mahavelona (Foulpointe), -17.66667, 49.5, clay forest, lagoon forest, between Canal des Pangalanes and beach, Forest Analalava, (A. Pauly) (CASC); Mananara, -16.16798, 49.76768, 19 m, urban garden, (B.L. Fisher *et al.*) (CASC); Maroantsetra, -15.43442, 49.73907, 19 m, urban garden, (B.L. Fisher *et al.*) (CASC); Nosy Mangabe, -15.5, 49.76667, <5 m, littoral vegetation, (P.S. Ward) (PSWC); Parcelle E3 Tampolo, -17.28104, 49.43012, 10 m, littoral forest, (Malagasy ant team) (CASC); Station Forestière Tampolo, 10 km NNE Fenoarivo Atn., -17.2825, 49.43, 10 m, littoral rainforest, (B.L. Fisher) (CASC); Tamatave, -18.15467, 49.41267, 20 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Tampolo, -17.28333, 49.41667, 10 m, littoral forest, (Malagasy ant team) (CASC); Tanambao Nosibe, 29.6 km 23° Toamasina, -17.89117, 49.45617, 15 m, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Toamasina-Port, -18.16033, 49.42717, 5 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Toamasina-Ville, -18.15517, 49.4095, 10 m, urban garden, (B. Blaimer, F.N. Raharimalala) (CASC); Vatondry, -19.33283, 48.9795, 16 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Province **Toliara**: 3.7 km 102° ESE Belo sur Mer, -20.73472, 44.04, 10 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Anosy Region, District of Amboasary, 58 km SW of Fort Dauphin, 8 km NW of Amboasary, Berenty Special Reserve, -25.021, 46.3055, 36 m, spiny forest, (Mike, Rin'ha) (CASC); Atsimo-Andrefana Region, -23.45314, 43.76448, 20 m, coastal spiny bush on sandy soil, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Atsimo-Andrefana Region, Sarodrano, -23.52243, 43.74031, 15 m, Didiereaceae forest on sand dunes, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Forêt de Beroboka, 5.9 km 131° SE Ankidranoka, -22.23306, 43.36633, 80 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Forêt de Tsinjoriaky, 6.2 km 84° E Tsifota, -22.80222, 43.42067, 70 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Makay Mts., -21.34228, 45.18314, 410 m, gallery forest on sandy soil, (B.L. Fisher *et al.*) (CASC); Manderano, -23.5275, 44.08833, 70 m, gallery forest, (Frontier Project) (CASC); Parc National d'Andohahela, Forêt de Manatalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, -24.81694, 46.61, 150 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Parc National de Kirindy Mite, 16.3 km 127° SE Belo sur Mer, -20.79528, 44.147, 80 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Ranobe, -23.04085, 43.61012, 30 m, gallery forest, Frontier Wilderness Project, (CASC); Sakaraha, -22.91233, 44.53283, 470 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Toliara, -23.3575, 43.669, 20 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Ambohimahavelona village 33 km NE of Tulear, Andoharano dry forest, -23.44083, 43.89967, 43-46 m, dry forest/spiny bush, (ME Irwin, Rin'ha) (CASC); Mikea Forest, deciduous dry forest, Tulear Province, -22.90367, 43.4755, 30 m, deciduous dry forest, (R. Harin'Hala) (CASC); near ANGAP office, Zombitse National Park, Tulear Province, -22.8865, 44.69217, 840 m, deciduous spiny forest, (R. Harin'Hala) (CASC); 11km SE Ampasimanolotra (=Brickaville), -18.9, 49.13333, 5 m, littoral vegetation, (P.S. Ward) (PSWC); Andilana, Nosy Bé, -13.25, 48.18333, <5 m, (D.M. Olson) (PSWC); Manankinany, -17.03333, 49.53333, (L.A. Nilsson) (PSWC); Nosy Be: 4km ESE Andoany (=Hellville), -13.41667, 48.3, <5 m, littoral vegetation, (P.S. Ward) (PSWC); Rantabe, N Soanierana Ivongo, -16.88333, 49.65, (L.A. Nilsson) (PSWC); **MAURITIUS: Rodrigues**: Anse Fumier, -19.7149, 63.4163, (Michael Madl) (CASC); Baie Pistache, -19.7149, 63.4163, (Michael Madl) (CASC); Citronelle, -19.7149, 63.4163, (Michael Madl) (CASC); Grand Montagne, -19.70572, 63.46498, 358 m, (L. Lach) (CASC); Balaclava, (Michael Madl) (CASC); Botanical Gardens, -20.10628, 57.58033, 100 m, (A.V. Suarez) (CASC); IAA,

(S. Buckland) (N. Cole) (L. Lach) (CASC); **Ile aux Aigrettes**, -20.41883, 57.7305, 1 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Ile Aux Aigrettes, -20.41902, 57.73018, on island, (A.V. Suarez) (CASC); **Ile Marianne**, -20.36667, 57.78333, 5 m, (L. Lach) (CASC); La Nicolière Reserve, (Michael Madl) (CASC); La Nicolière Reserve, (Michael Madl) (Brice Noonan, University of Mississippi); Le Pouce Mt., 700–800 m, native forest, (W.L. Brown) (MCZC); Le Pouce, (L. Lach) (CASC); Magenta, -20.31667, 57.45, 150 m, dry closed forest, (P.S. Ward) (UCDC); Mahebourg, (N. Room) (CASC); Montagne du lion, -20.36306, 57.72611, 393 m, Wet II vegetation, many traveler's palms, (J. Casquet) (CASC); Perrier Nature Reserve, -20.35207, 57.49417, 564 m, (A.V. Suarez) (CASC); Pieter Both Mt., Moka Range, -20.19217, 57.55533, 770 m, closed vegetation, (B.L. Fisher *et al.*) (CASC); **Port Louis**, (F. Blard) (UCDC); Port Louis Waterfront, -20.15528, 57.5, (A.V. Suarez) (CASC); Scaevola, (L. Lach) (CASC); Side of Le Pouce, -20.19167, 57.50667, 176 m, 100% butterfly liana (*Hiptage benghalensis*, invasive), (J. Casquet) (CASC); **Souillac**, (Michael Madl) (Brice Noonan, University of Mississippi); Souillac, (Michael Madl) (CASC); SSR Botanical Gardens, -20.10757, 57.57923, (L. Lach) (CASC); **MAYOTTE: Coconi**: DAF Campus, -12.83333, 45.13333, (R. Jocqué) (CASC); **Combani**, south coast track between the airport and lagoon, -12.81069, 45.2793, 7 m, native littoral and secondary vegetation, Jacques Rochat/Insectarium de La Réunion, (CASC); **Convalescence**, -12.76667, 45.18333, road verges, (R. Jocque & G. DeSmet) (CASC); **Convalescence**, north coast from airport, -12.80099, 45.28701, 1 m, monospecific mangrove (*Sonneratia alba*) (J. Rochat, S. Gasnier, G. Paulus/Insectarium de La Réunion) (CASC); **Dapani**, -12.97495, 45.16183, 1 m, mangrove, coastal scrub, (B.L. Fisher *et al.*) (CASC); Dapani, Labattoir, western slope of the hill, -12.79216, 45.27709, 71 m, secondary thicket and diverse vegetation, (CASC); **Dziani Karihani**, Ilang-Ilang plantation, -12.78333, 45.11667, (R. Jocque & G. DeSmet) (CASC); **Mont Chongui summit**, -12.99567, 45.13428, 550 m, rainforest, (B.L. Fisher *et al.*) (CASC); **Mt. Benara**, track to reserve gate, -12.86667, 45.18333, 250 m, (R. Jocque & G. DeSmet) (CASC); **Ngouja**, grazed dry forest, (R. Jocqué) (CASC); Petite Terre, -12.79119, 45.29403, 125 m, coastal scrub degraded, (B.L. Fisher *et al.*) (CASC); **Petite Terre**, Dziani Dzaha, -12.78333, 45.11667, (R. Jocque & G. DeSmet) (CASC); **Tanaraki**, -12.75754, 45.0678, 10 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); **Tsingoni**, -12.78333, 45.1, mangrove, (R. Jocque & G. DeSmet) (CASC); **SEYCHELLES: Aldabra Atoll**: Malabar Island, -9.37417, 46.43852, 5 m, casuarina forest, (S.M. Goodman) (Brice Noonan, University of Mississippi); **Picard**, old settlement, -9.39606, 46.20465, 2 m, coastal scrub, (B.L. Fisher) (CASC); **Aride Island**, -4.21407, 55.6682, 10 m, native forest, (B.L. Fisher *et al.*) (CASC); Aride Island, -4.21167, 55.66924, 75 m, mixed forest, (B.L. Fisher *et al.*) (CASC); Aride Island, (J. Gerlach) (CASC); **Conception Island**, -4.66527, 55.37086, 20 m, mixed forest, (B.L. Fisher *et al.*) (CASC); Conception Island, -4.66311, 55.36821, 65 m, mixed forest, (B.L. Fisher *et al.*) (CASC); **Cosmoledo Atoll**: [Wizard Island], on the dune, next to *Tournefortia argentea*, -9.75306, 47.64889, <10 m, lowland coastal, coralline island, (G. Galman) (CASC); **Cousine**, -4.35107, 55.64785, (Robert Andrew Bell) (CASC); Cousine, -4.3507, 55.64777, *P. grandis* forest, (René Gaigher) (CASC); Curieuse Island, -4.28364, 55.72697, 5 m, mangrove, (B.L. Fisher *et al.*) (CASC); **Félicité Island**, -4.31991, 55.86909, 75 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Félicité Island, -4.32012, 55.86683, 20 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); La Digue Island, -4.34419, 55.84187, 200 m, mixed native forest, (B.L. Fisher *et al.*) (CASC); **La Digue Island**, -4.35613, 55.84331, 300 m, forest, (B.L. Fisher *et al.*) (CASC); La Digue Island, -4.34419, 55.84187, 25 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); La Digue Island, Veuve Réserve, -4.35697, 55.82791, 15 m, littoral forest, (B.L. Fisher *et al.*) (CASC); **L'Ilot Island**, (J. Gerlach) (CASC); **Mahé Island**: Baie Lazare, (Vincent Robert) (CASC); Cascade, -4.67494, 55.49819, 150 m, roadside, (B.L. Fisher *et al.*) (CASC); Glacis la Réserve, -4.71023, 55.50435, 300 m, forest and glacis, (B.L. Fisher *et al.*) (CASC); Mont Copolia, -4.65121, 55.45835, 520 m, forest, (B.L. Fisher *et al.*) (CASC); Mont Serbert, -4.67859, 55.50408, 490 m, glacis vegetation, (B.L. Fisher *et al.*) (CASC); Port Launay, -4.65323, 55.40207, 12 m, mangrove, (B.L. Fisher *et al.*) (CASC); Port Launay, -4.65892, 55.41067, 10 m, mangrove, (B.L. Fisher *et al.*) (CASC); Port Launay, -4.65892, 55.41067, 10 m, mangrove, (B.L. Fisher *et al.*) (CASC); Vingt Cinq Sous, -4.62894, 55.40912, 460 m, mixed forest along road, (B.L. Fisher *et al.*) (CASC); Mare Aux Cochon, (J. Gerlach) (CASC); Praslin, -4.34985, 55.7489, dry palm forest/scrub, (Robert Andrew Bell) (CASC); **Praslin Island**: -4.33457, 55.74543, in palm forest, (Robert Andrew Bell) (CASC); Praslin, -4.34977, 55.72881, 20 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); Praslin, -4.33374, 55.72235, 10 m, mangrove, coconut, beach scrub, (B.L. Fisher *et al.*) (CASC); Fond Peper, -4.33341, 55.7408, 200 m, mixed forest, (B.L. Fisher *et al.*) (CASC); Newcome, -4.301, 55.6926, 130 m, palm forest, (B.L. Fisher *et al.*) (CASC); Praslin tower, -4.34093, 55.74514, 370 m, mixed forest, (B.L. Fisher *et al.*) (CASC); **Silhouette Island**: -4.49076, 55.25341, 20 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); La Passe, -4.48484, 55.25074, 35 m, park/garden, (B.L. Fisher *et al.*) (CASC);

on coastal path to Anse Mondon, -4.46951, 55.24159, 10 m, coastal scrub, (B.L. Fisher *et al.*) (CASC); on path to Anse Mondon, -4.46893, 55.22936, 255 m, forest, (B.L. Fisher *et al.*) (CASC); on path to Anse Mondon, -4.46893, 55.22936, 255 m, forest, (B.L. Fisher *et al.*) (CASC); St. Pierre, (J. Gerlach) (CASC); Vaches Marins, (J. Gerlach) (CASC).

***Camponotus maintikibo* Rakotonirina, Csősz & Fisher sp. n.**

(Figures 8A, 9A, 14, 21)

Holotype worker. MADAGASCAR: Province **Toliara:** Parc National d'Andohahela, Forêt de Manatalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, -24.81694, 46.61, 150 m, spiny forest/thicket, ground forager, 12–16 Jan 2002 (Fisher, Griswold *et al.*) collection code: BLF04908, specimen code: CASENT0763877 (CASC).

Paratypes. 2 workers with same data as holotype and specimens coded: CASENT0000633, CASENT0763878 (CASC, MHNG).

Diagnosis. Body bicolored, head, mesosoma, and petiolar node yellowish-orange, gastral segments anteriorly yellowish and posteriorly black. Roughly distal half of antennal scape surpassing posterior cephalic margin. Dorsum of propodeum approximately straight and inclined posteriorly.

Description. Minor worker. In full-face view, head elongate (CWb/CL: 0.84±0.01, 0.82–0.86), lateral margins straight and posteriorly diverging, their junction to the convex posterior margin concealed by eyes. Eyes protruding, their posterior level at posterior fifth portion of head (PoOc/CL: 0.21±0.01, 0.19–0.22). Median portion of clypeus transverse (ClyL/GPD: 0.63±0.02, 0.60–0.66), anterior margin projecting into broadly convex lobe, posterior margin weakly notched medially. Mandible subtriangular, apical margin armed with six sharp teeth. Antennal scape long, around distal portion extending beyond posterior border of head. In lateral view, mesosoma without anterior and dorsolateral margination; dorsal outline of mesosoma uniformly convex, sloping gradually from mesonotum to posterodorsal angle of propodeum; metanotal groove obsolete or indistinct; propodeal dorsum longer than declivity height. In dorsal view, mesosoma widest at level of pronotum, and decreasing in width toward propodeal declivity. Opening of propodeal spiracle rounded. In lateral view, petiolar node more or less scalelike and slightly inclined anteriorly, either tapering dorsally or its dorsum rounding to the anterior and posterior faces. Mesotibia and metabia each with a single simple spur.

Head, mesosoma, and petiolar node imbricate, with sparse small punctures from which an appressed hair arises, gastral tergites transversely strigulate. Mandible coriarius, superimposed with piligerous punctures. Whitish erect hairs thinner on dorsum of head and promesonotum becoming thicker on propodeum, petiolar node, and gastral tergites. Composition of hairs: a few pairs on median portion of head from clypeus to near posterior cephalic margin; a few scattered on pronotum, one to two pairs on mesonotum, a few scattered on propodeal dorsum, a row of hairs on lateral margin of declivity and from upper half of lateral portion to dorsolateral angle of petiolar node, two rows of hairs at about middle and near posterior margin of first four gastral tergites. Pubescence on dorsum of head and mesosoma longer than those on gastral tergites; hairs of pubescence set closer on head capsule but further apart from mesosoma to gaster. Integument dully bicolor: head, mesosoma, and petiolar node yellowish orange, gastral segments anteriorly yellowish and posteriorly black; antennal scape and other appendages yellowish and funiculus dark brown.

Major worker. Characteristics of minor worker, except: head larger and subquadrate (CS: 1.71±0.06, 1.66–1.78; CWb/CL: 0.88±0.01, 0.86–0.89); lateral margins straight, suddenly converging near base of mandible; posterior margin broadly convex. Mandible more robust and armed with seven to eight teeth. Median portion of clypeus elongate (ClyL/GPD: 0.90±0.03, 0.87–0.93), anteromedian margin broadly rounded. Eyes smaller relative to head size (EL/CS: 0.21±0.01, 0.20–0.22); with head in full-face view, located medially farther from lateral cephalic border (CWb/CL: 0.88±0.01, 0.86–0.89; CW/CL: 0.83±0.02, 0.81–0.85), their level of posterior margins placed roughly at posterior fourth of head capsule (PoOc/CL: 0.22±0.06, 0.13–0.26). Scape short, merely extending beyond posterior cephalic margin. Promesonotal dorsum domelike, posterior portion of outline sloping to the impressed metanotal groove, making propodeal dorsum at lower level; propodeal dorsum as long as or shorter than declivity height. Posteromedian portion of head finely and densely reticulate punctate; lateral portion from near base of mandible to near posterior margin finely and densely areolate, superimposed with sparse, and poorly delimited punctures, in which two to seven smaller punctures are embedded and from which one appressed

hair arises medially. Dorsum of mesosoma finely and densely reticulate punctate and lateral portion finely areolate; gastral tergites finely imbricate to finely strigulate.

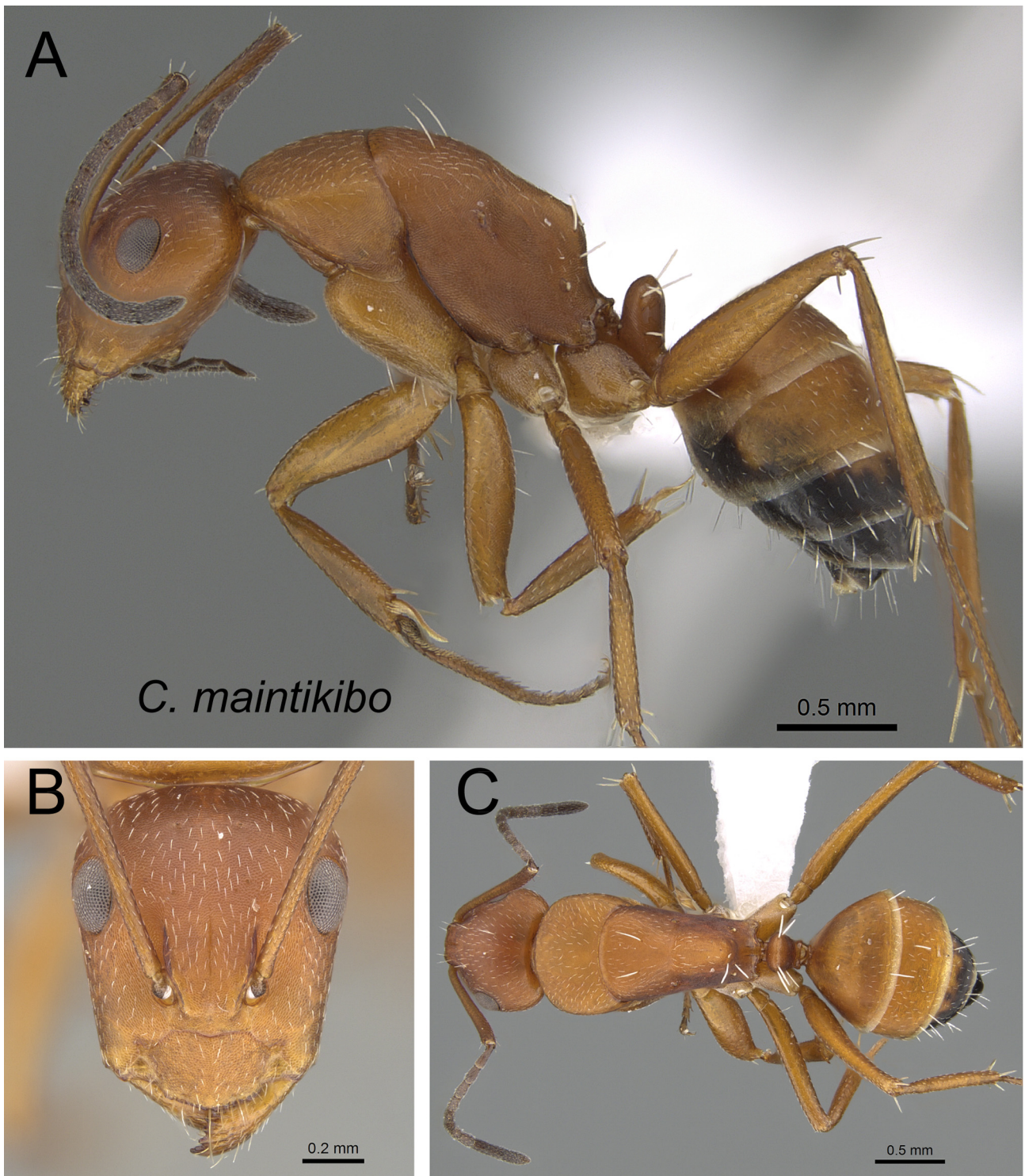


FIGURE 14. *Camponotus maintikibo* minor worker CASENT0763877. A: lateral view; B: head in full-face view; C: dorsal view.

Discussion. See discussion under *C. eftra*.

The grouping of *C. maintikibo* in the same cluster shown by the dendrogram of multivariate morphometric analysis is confirmed by the cumulative LDA at 100% identification success, corroborating the species hypothesized by the taxonomic revision based on qualitative morphology. In the dendrogram, the *C. maintikibo*

cluster is grouped next to the *C. descarpentriasi* and *C. madagascarensis* clusters, which indicates that the three species are more similar to each other than other species. However, the latter two species belong to the *niveosetosus* species group whereas *C. maintikibo* qualitatively belongs to the *grandidieri* species group, whose members look very similar to *C. maintikibo*. This suggests that both species groups could be combined into one.

Distribution and biology. Known only from Madagascar, *C. maintikibo* occurs in the dry forests and transitional areas of Andohahela National Park and in the spiny forest and thicket of Tsimanampetsotsa National Park in the southern portion of Madagascar. In these localities, workers were found foraging on the ground and were collected from Malaise or pitfall traps. The species co-occurs with *C. efitra* and two widespread species *C. grandidier* and *C. voeltzkowii*.

Additional material examined. MADAGASCAR: Province **Toliara:** Anosy Region, District of Amboasary, Andohahela National Park Parcelle III, Ihazofotsy, 32 km NE Amboasary, -24.83083, 46.53617, 58 m, dry forest, spiny forest, (Michael Irwin, Frank Parker, Rin'ha) (CASC); Anosy Region, District of Fort-Dauphin, Andohahela National Park Parcelle II, Tsimela, 42 km W of Fort-Dauphin, -24.93683, 46.62667, 177 m, transition forest, (Michael Irwin, Frank Parker, Rin'ha) (CASC); Parc National d'Andohahela, Forêt de Manatalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, -24.81694, 46.61, 150 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Parc National de Tsimanampetsotsa, Forêt de Bemanateza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, -23.99222, 43.88067, 90 m, spiny forest/thicket, (Fisher, Griswold *et al.*) (CASC); Andohahela National Park, Tsimelaha, -24.93683, 46.62667, 180 m, transition forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Ihazofotsy - Parcel III, Andohahela National Park, transition forest, Tulear Province, -24.83483, 46.48683, 80 m, tropical dry forest, transition between spiny and dry deciduous forests, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Tsimelaha - Parcel II, Andohahela National Park, transition forest, Tulear Province, -24.93683, 46.62667, 180 m, transition forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC).

Camponotus niveosetosus species group

Camponotus descarpentriasi Santschi

(Figures 6C–D, 15, 23)

Camponotus descarpentriasi Santschi, 1926: 263. Lectotype minor worker, **present designation**, Madagascar, Province Antananarivo, Massif de l'Ankaratra, Ambahona, -20.04, 47.19165, 1800 m (J. Descarpentries), AntWeb CASENT0101206 (NHMB) [examined]. Paralectotypes: 2 major workers, 1 queen and 1 male with same data as lectotype but with specimen codes: CASENT0101202, CASENT0101205; CASENT0101203 (queen), CASENT0101204 (male) (NHMB).

Diagnosis. Body color generally black; posterior portion of head, dorsum of mesosoma, and lateral margin of propodeal declivity with randomly scattered, whitish, erect hairs; with head in full-face view, erect hairs absent immediately behind lateral margin of clypeus, whitish erect hairs posteriorly confined to posterolateral angle of head, median clypeal carina not visible, eyes located in posterior fifth of head; in lateral view, mesosoma long and low; propodeal dorsum longer than declivitous face; fewer whitish erect hairs present on dorsum of body, only one row of hairs present from upper half to apex of petiolar node; transverse light strip on posterior margin of abdominal tergites narrow, width 1/8 the visible width of tergite.

Description. Minor worker. In full-face view head elongate (CWb/CL: 0.86–0.90), lateral borders straight, feebly diverging posteriorly; posterior margin broadly convex. Eyes protruding, located roughly at posterior fifth of head (PoOc/CL: 0.18±0.01, 0.17–0.19) and rarely breaking lateral outlines of head (CWb/CL: 0.86–0.90; CW/CL, 0.85–0.91). With head in full-face view, anteromedian margin of clypeus bluntly angulate, anterolateral corner rounded; median portion convex, making longitudinal, median carina faintly visible; posterior border feebly notched medially. Mandible subtriangular, masticatory margins equipped with six teeth. Antennal scape long (SL/CS: 1.14±0.02, 1.11–1.17), approximately its distal portion extending beyond posterior cephalic margin, its basal half cylindrical. In lateral view, mesosoma long and low (MPH/ML: 0.40±0.01, 0.39–0.42); promesonotum more or less convex; propodeal dorsum slightly decreasing in height posteriorly, with transverse concavity at midlength, longer than declivitous face. In dorsal view, metanotal groove slightly impressed. Propodeal spiracle opening slitlike. Petiolar node compressed anteroposteriorly and tapering dorsally; anterior face generally convex and

posterior face straight. Tibia of middle and hind legs with pectinate spurs. Transverse strip on posterior margin of gastral tergites narrow, maximum width roughly 1/10 the visible width of second tergite.

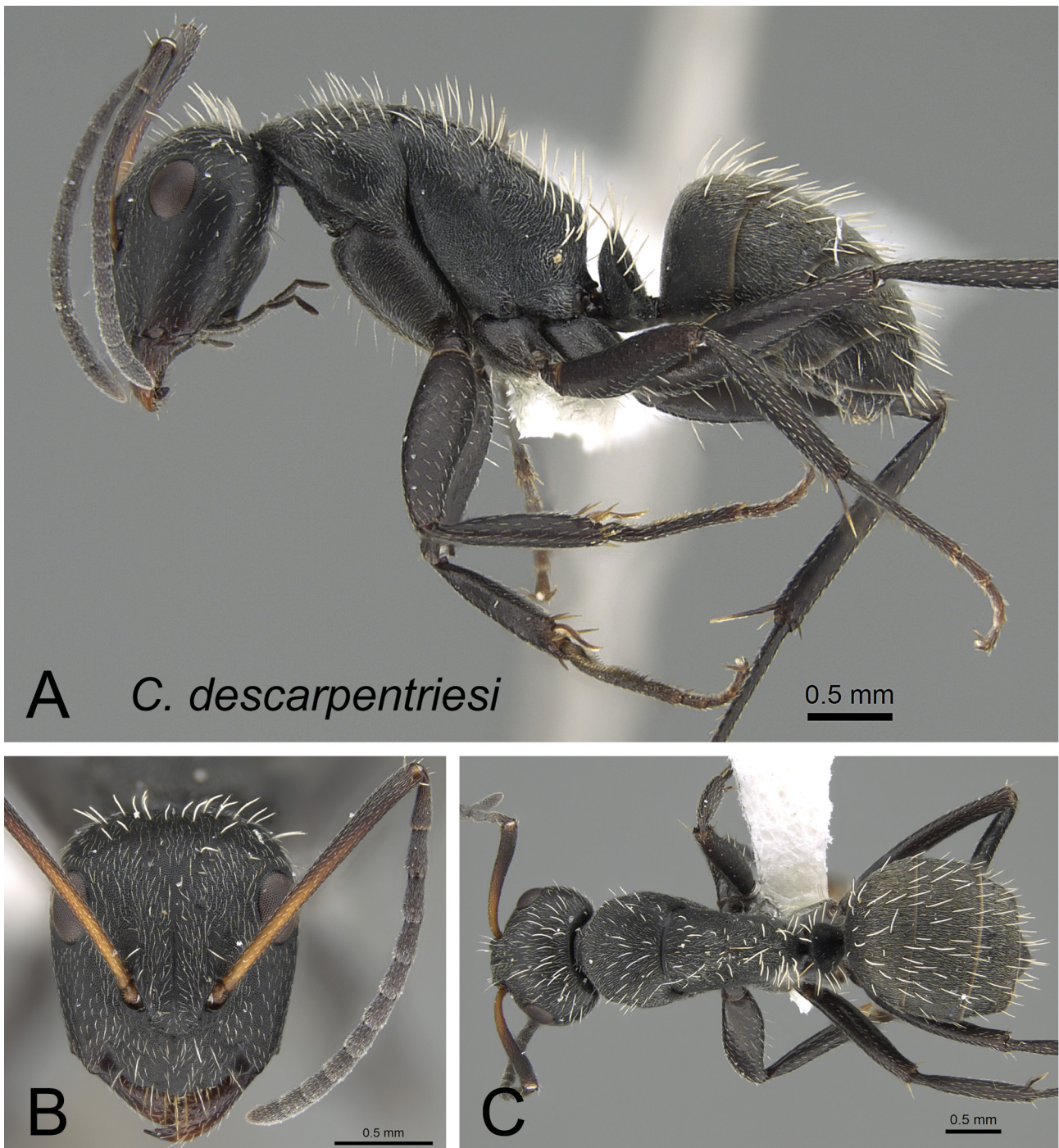


FIGURE 15. *Camponotus descarpentriesi* minor worker CASENT0763876. A: lateral view. B: head in full-face view. C: dorsal view.

Head and mesosoma finely and densely reticulate punctate; their lateral portion with much larger punctures. Gastral tergites finely imbricate. Mandible coriaceous with sparse piligerous punctures. Whitish erect hairs randomly spread along median section of head capsule to its posterior fourth portion, where they are transversally scattered to the posterolateral corner of head. Erect hairs lacking immediately behind lateral clypeal margin. Anteromedian portion of head dorsum and gastral tergites covered with hairs thinner than those of posterior cephalic margin and dorsum of body. Petiolar node and posterior portion of propodeum with several hairs at least twice as long as those on promesonotum. Pubescence whitish yellow, sparse on dorsum of head and becoming

increasingly abundant toward gastral tergites. Body color black and matte; basal portion of antennal scape, tip of mandible, and legs brown.

Major worker. Characteristics of minor worker, except: head much larger (CS: 1.94 ± 0.09 , 1.88–2.01; CWb/CL: 0.98 ± 0.02 , 0.97–1); lateral margins broadly convex and gradually converging towards base of mandibles. Mandibles more powerful, apical margin armed with seven teeth. Clypeus short and trapezoid (ClyL/GPD: 0.56 ± 0.06 , 0.51–0.60), length roughly one fourth length of head (ClyL/CL: 0.23 ± 0.01 , 0.23–0.23), its anterolateral angle more rounded and anteromedian margin generally convex. Eyes located more in front of head capsule (CWb/CL: 0.98 ± 0.02 , 0.97–1; CW/CL: 0.87 ± 0.02 , 0.85–0.87), level of posterior margin at posterior fourth of head capsule (PoOc/CL: 0.24 ± 0.02 , 0.23–0.25). Apical fourth of antennal scape surpassing posterior cephalic margin (SL/CS: 0.85 ± 0.1 , 0.78–0.92). In dorsal view, metanotal groove obsolete; metanotum indistinct; in lateral view, propodeum feebly at lower level with respect to promesonotum. In lateral view, petiolar apex higher and node more flattened anteroposteriorly. Head capsule finely and densely reticulate punctate to finely imbricate; sparse pubescence arises from middle of two to five smaller punctures embedded in one larger areole on lateral portion anterior to level of anterior margin of eye.

Discussion. *Camponotus descarpentriesi* and *C. madagascarensis* look very similar, but the latter has a higher and more robust mesosoma (MW/ML: 0.51 ± 0.02 , 0.47–0.58; MPH/ML: 0.41 ± 0.03 , 0.35–0.47), while the former is characterized by a lower, more slender mesosoma (MW/ML: 0.49 ± 0.01 , 0.47–0.50; MPH/ML: 0.40 ± 0.01 , 0.39–0.42). In lateral view, the propodeal dorsum is straight in *C. madagascarensis* while with a transverse concavity at midlength in *C. descarpentriesi*. Also, *C. madagascarensis* has a visible longitudinal carina on the clypeus, but in *C. descarpentriesi* this longitudinal carina is indistinct, and the clypeus is only evenly convex medially. The pubescence is much denser and the transverse light strip on posterior margin of each gastral segment is narrower than in *C. madagascarensis*.

In the present study, the definition of *C. descarpentriesi* according to the qualitative morphology-based study is congruent with the study based on multivariate morphometric analysis. The existence of the species, which is supported by the grouping obtained from the clustering and the partitioning methods, is confirmed by shape PCA, and the samples are correctly identified by cumulative LDA at 100% success.

Distribution and biology. This species is unique to Madagascar and found only in the grassland and ericoid thickets of the central highlands. The species has been collected from Ambahona forest of Ankaratra massif in the north, Ankazomivady forest near Ambositra, and Andringitra National Parc in the south. The search for food is carried out terrestrially on the ground and through leaf litter, and arboreally on lower vegetation.

Additional material examined. MADAGASCAR: Province **Toliara:** 28 km SSW Ambositra, Ankazomivady, -20.775, 47.16833, 1670 m, grassland, (B.L. Fisher) (CASC); Parc National d'Andringitra, Plateau d'Andohariana, 35.9 km 205° Ambalavao, -22.15233, 46.89917, 2000 m, ericoid thicket, (B.L. Fisher *et al.*) (CASC).

***Camponotus madagascarensis* Forel stat. rev.**

(Figures 4A, 5A, 6A–B, 16, 24)

Camponotus niveosetosus madagascarensis Forel, 1886: 4. Lectotype minor worker, **present designation**, Madagascar (Grandidier), AntWeb CASENT0101383 (MHNG) [examined].

Subspecies of *Camponotus niveosetosus*: Dalla Torre, 1893: 245; Emery, 1896: 377, 1925: 129; Wheeler, 1922a: 1052; Bolton, 1995: 110. Status as species and description of queen: Santschi, 1926: 262. Combination in *Camponotus (Myrmopiromis)*: Wheeler, 1922a: 1052; Emery, 1925: 129.

[Note: *Mayria madagascarensis* Forel: 1886: 4, (same publication, same page as Forel 1886 above), is a junior secondary homonym of *Camponotus niveosetosus madagascarensis* Forel, 1886: 4; replacement name *Camponotus repens* Forel, 1897: 187)].

Diagnosis. Body color black; posterior portion of head, mesosoma dorsum, and lateral margin of propodeal declivity with randomly scattered, whitish, erect hairs; with head in full-face view, erect hairs lacking immediately behind lateral margin of clypeus, whitish erect hairs on posterior cephalic portion scattered laterally to level of anterior margin of eyes, median clypeal carina visible, eyes located in posterior fourth of head; in lateral view, mesosoma long and low; propodeal dorsum longer than declivitous face; numerous whitish erect hairs present on

dorsum of body; petiolar node with two rows of hairs from its upper half to apex; transverse light strip on posterior margin of abdominal tergites large, width 1/5 the visible width of tergite.

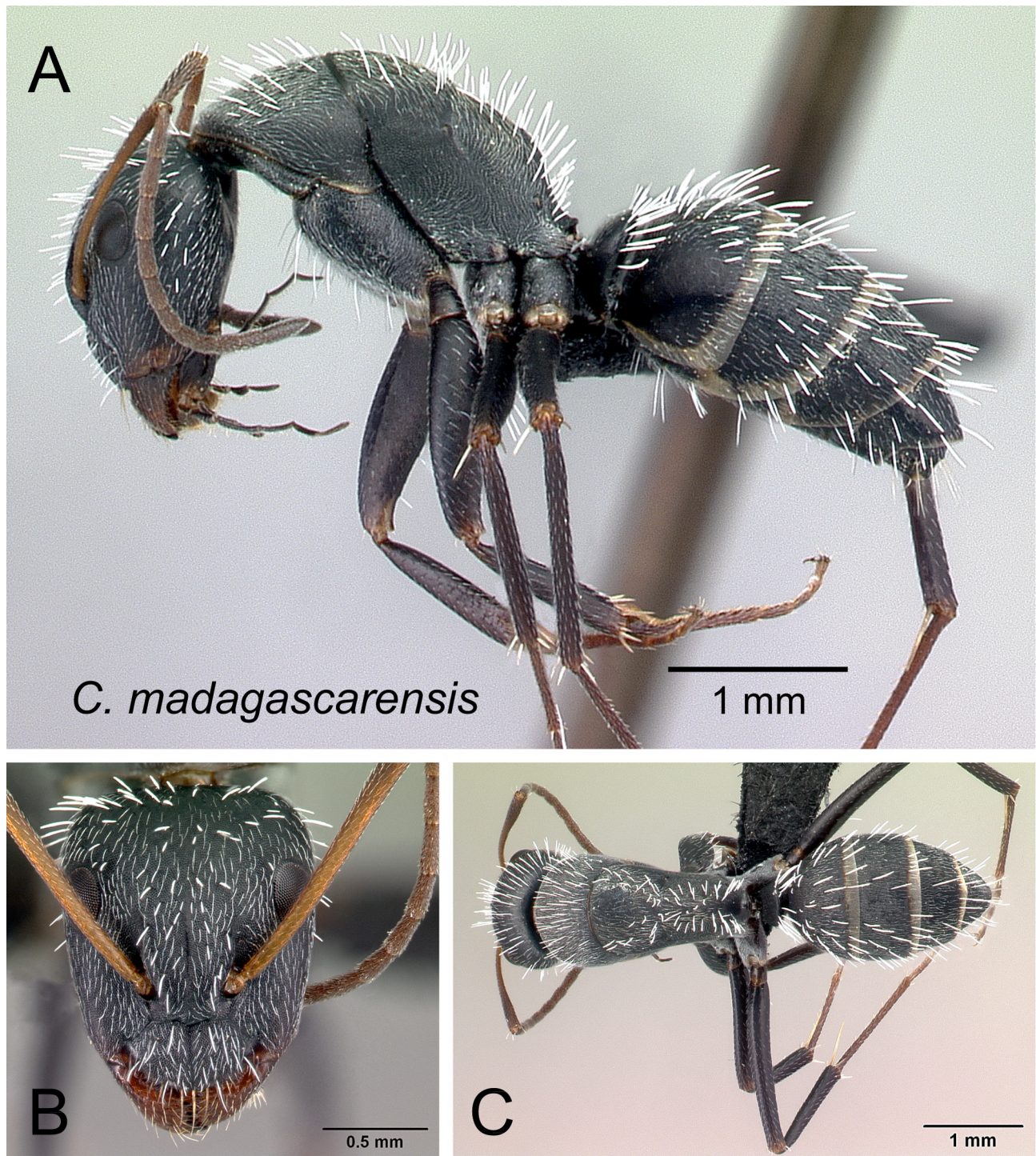


FIGURE 16. *Camponotus madagascarensis* minor worker CASENT0125551. A: lateral view; B: head in full-face view. C: dorsal view.

Description. Minor worker. In full-face view head elongate and rectangular (CWb/CL: 0.76–0.89), lateral border straight and slightly diverging posteriorly and joining the more or less convex posterior margin in a rounded angle. Eyes protruding, located at posterior fourth of head (PoOC/CL: 0.24 ± 0.02 ; 0.21–0.27) and occasionally breaking lateral outlines of head (CWb/CL: 0.76–0.89; CW/CL: 0.78–1.05). Clypeus truncate anteriorly, with bluntly rounded anterolateral angle; longitudinally median, blunt carina present; posterior margin feebly notched

medially. Mandible subtriangular, apical margins with six teeth. Antennal scape long, its distal portion extending beyond posterior margin of head. In lateral view, mesosoma long and low (MPH/ML: 0.41 ± 0.03 , 0.35–0.47), with broadly convex dorsal outline, distinctly decreasing in height toward posteriormost portion of the straight propodeal dorsum. In dorsal view, metanotal groove obsolete, slightly impressed or characterized by a simple shiny line. Propodeal declivity slightly inclined posteriorly and somewhat concave toward junction to petiolar node. Propodeal spiracle opening elongate or slitlike. Petiolar node scalelike, anterior and posterior faces parallel to each other from base to upper half from level of spiracle and then anterior face posteriorly inclined to reach the dorsalmost portion of posterior margin. Tibial spurs of middle and hind legs pectinate. Transverse light strip on posterior margin of gastral tergites wide, maximum width roughly 1/5 of the visible width of second tergite.

Head and mesosoma finely and densely reticulate punctate. Gastral tergites finely coriarius or finely strigulate. Mandible imbricate with sparse piligerous punctures. Numerous whitish erect hairs randomly scattered along median portion to posterior fifth portion of head, where they are transversally scattered to the lateral cephalic margin down to the level of compound eyes; erect hairs absent immediately behind lateral clypeal margin. Hairs on anteromedian portion of head and gastral sternites thinner than those from near posterior cephalic margin to gastral tergites. Some hairs on petiolar node and posterior portion of propodeum at least twice as long as those on promesonotum. Pubescence on dorsum of body sparse, but denser on gastral tergites. Body color black and matte; legs basally reddish black to reddish brown, tarsus and antennal scape yellowish brown, and funiculus dark brown.

Major worker. Characteristics of minor worker, except: head much larger (CS: 2.44 ± 0.24 , 2.05–2.76; CWb/CL: 0.89 ± 0.03 , 0.86–0.95); lateral margins either broadly convex or straight and abruptly converging towards base of mandibles. Mandibles more robust, apical margin more elongate and armed with seven to eight teeth. Median portion of clypeus elongate (ClyL/GPD: 0.89 ± 0.04 , 0.81–0.95; ClyL/CL: 0.32 ± 0.00 , 0.32–0.33), with more rounded anterolateral angle and more flat median portion. Eyes located more in front of head capsule (CWb/CL: 0.89 ± 0.03 , 0.86–0.95; CW/CL: 0.78 ± 0.02 , 0.75–0.82), level of their posterior margin at posterior third of head capsule (PoOc/CL: 0.30 ± 0.01 , 0.29–0.32). Antennal scape barely surpassing posterior cephalic margin. In dorsal view, metanotal groove impressed; metanotum not visible; in lateral view, propodeum feebly at lower level with respect to promesonotum. In lateral view, petiolar node higher and more flattened anteroposteriorly. Head capsule finely and densely reticulate punctate; sparse appressed hair arises from middle of two to five smaller punctures embedded in one larger puncture on lateral portion.

Discussion. See discussion under *C. descarpentriasi*.

The conventional taxonomic delimitation of *C. madagascarensis* is corroborated by the combination of the NC-clustering method and partitioning technique. Further, recognition of the species is corroborated by confirmatory LDA at 100% identification success and supported by shape PCA.

Distribution and biology. *Camponotus madagascarensis* is an endemic, widespread species of Madagascar. It is known to occupy western dry forest habitats, the north central and south central portions of eastern rainforests, savannah woodland of the central highland, and subhumid gallery forests of the southern high plateau. The species is absent from spiny bush and thicket in the southwest and southernmost portions of the island. The species is sympatric with *C. grandidieri*, *C. mita*, and *C. voeltzkowii*. Members of *C. madagascarensis* forage either terrestrially on the forest floor, through leaf mold and rotten wood, or on low vegetation. Nests are constructed not only under rocks and rootmats and litter on rocks or rotten logs, and in the ground, but also in dead tree stumps, dead branches, and twigs above the ground.

Additional material examined. MADAGASCAR: Madagascar (MHNG); Province **Antananarivo:** Andohony I Non Protected Area, 22.62 km SW Antsirabe, -20.06784, 46.99068, 1451 m, savannah grassland, (A. Ravelomanana) (CASC); Andohony IV Non Protected Area, 22.51 km SW Antsirabe, -20.06718, 46.99274, 1526 m, Uapaca woodland, (A. Ravelomanana) (CASC); Kaloy, -18.59568, 47.65333, 1338 m, grassland, (B.L. Fisher *et al.*) (CASC); Antsiranana, 7 km N Joffre Ville [camp 2 of Fisher], -12.33333, 49.25, 360 m, in forest, (Irwin, Schlinger, Harin'Hala) (CASC); Ambanja, -13.68268, 48.45245, 30 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Forêt 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); Nosy Faly, -13.36435, 48.49137, 40 m, open secondary vegetation, (B.L. Fisher *et al.*) (CASC); Réserve Analamerana, 28.4 km 99° Anivorano-Nord, -12.74667, 49.49483, 60 m, tropical dry forest, (B.L. Fisher) (CASC); Réserve Spéciale d'Ambre, 3.5 km 235° SW Sakaramy, -12.46889, 49.24217, 325 m, cultivated land, (Fisher, Griswold *et al.*) (CASC); Sakaramy, -12.44071, 49.23061, 350 m, grassland, (B.L. Fisher *et al.*) (CASC); Taizambato, 22.9 km NE Ambanja, -13.5092, 48.56722, 16 m, coconut plantation, (B.L. Fisher *et*

al.) (CASC); Province **Fianarantsoa**: Ambalavao, -21.83267, 46.93867, 1020 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Ambalavao, -21.83267, 46.93867, 1020 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Amoron'i Mania Region, District of Ambositra, Itaviana Uapaca forest, 135 km SE of Antsirabe, -20.17333, 47.086, 1359 m, Uapaca forest, (Rin'ha, Mike) (CASC); Ampanenitra Non Protected Area, 41.19 km SE Ambalavao, -21.9652, 47.31001, 1010 m, savannah grassland, (A. Ravelomanana) (CASC); Ampotoampoto II National Parc, 8.07 km NW Ilakaka, -22.62806, 45.18843, 919 m, savannah woodland, (A. Ravelomanana) (CASC); Ampotoampoto IV National Parc, 7.83 km NW Ilakaka, -22.62944, 45.1912, 923 m, savannah woodland, (A. Ravelomanana) (CASC); Antohatsahomby II Non Protected Area, 23.38 km NW Itremo, -20.55444, 46.58438, 1640 m, Uapaca woodland, (A. Ravelomanana) (CASC); 1 km E of Isalo National Park Interpretive Center, Fianarantsoa Prov., -22.62667, 45.35817, 885 m, dry wash, (R. Harin'Hala) (CASC); Forêt d'Analalava, 29.6 km 280° W Ranohira, -22.59167, 45.12833, 700 m, Uapaca woodland, (Fisher, Griswold *et al.*) (CASC); Forêt d'Analalava, 29.6 km 280° W Ranohira, -22.59167, 45.12833, 700 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, -20.59333, 46.56333, 1550 m, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Horombe Region, District of Ihosy, Isalo National Park, 900 m E of ANGAP Interpretation Center, -22.62667, 45.35817, 701 m, open area near stream, (Rin'ha, Mike) (CASC); Horombe Region, District of Ihosy, Betapia (Border of Fianarantsoa and Tulear): 9 km SW of Ilakaka Saphir town, -22.62883, 45.36117, 1036 m, Uapaca forest, (Rin'ha, Mike) (CASC); Isalo III National Parc, 12.02 km SW Ranohira, -22.61583, 45.31084, 870 m, Bismarckia woodland, (A. Ravelomanana) (CASC); Manandriana III Non Protected Area, 27.25 km SW Ambositra, -20.73333, 47.09391, 1578 m, savannah grassland, (A. Ravelomanana) (CASC); Parc National d'Andringitra, Plateau d'Andohariana, 35.9 km 205° Ambalavao, -22.15233, 46.89917, 2000 m, ericoid thicket, (B.L. Fisher *et al.*) (CASC); Parc National d'Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, -22.29833, 45.35167, 990 m, Uapaca woodland, (Fisher, Griswold *et al.*) (CASC); Parc National d'Isalo, Sahanafa River, 29.2 km 351° N Ranohira, -22.31333, 45.29167, 500 m, gallery forest, (Fisher, Griswold *et al.*) (CASC); stream area, 900 m E of Isalo National Park Interpretive Center, Fianarantsoa Prov., -22.62667, 45.35817, 750 m, open area near stream, (R. Harin'Hala) (CASC); Tsaranoro, 32.8 km 230° Ambalavao, -22.08317, 46.774, 975 m, savannah woodland, (B.L. Fisher *et al.*) (CASC); Province **Mahajanga**: Maevatanana, Le Moul (NHMB); Ambolomaiky, 48.1 km SE Mahajanga, -15.8541, 46.74663, 77 m, disturbed dry forest, (B.L. Fisher *et al.*) (CASC); Mahavavy River, 10.6 km 148° SSE Mitsinjo, -16.08167, 45.935, 50 m, tropical dry 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); Maropapango, 52.3 km N Antsohihy, -14.32043, 48.03058, 18 m, mangrove, (B.L. Fisher *et al.*) (CASC); Parc National de Namoroka, 17.8 km 329° WNW Vilanandro, -16.37667, 45.32667, 100 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National de Namoroka, 9.8 km 300° WNW Vilanandro, -16.46667, 45.35, 140 m, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, -18.70944, 44.71817, 150 m, tropical dry forest on Tsingy, (Fisher, Griswold *et al.*) (CASC); Réserve forestière Beanka, 50.7 km E Maintirano, -17.8873, 44.47113, 160 m, savannah woodland, (B.L. Fisher *et al.*) (CASC); Réserve forestière Beanka, 50.7 km E Maintirano, -17.8873, 44.47113, 160 m, savannah shrubland, (B.L. Fisher *et al.*) (CASC); Toamasina, Manakambahiny Atsinanana, -17.75, 48.71667 primary forest, (A. Pauly) (CASC); Province **Toliara**: Forêt Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition, (B.L. Fisher *et al.*) (CASC); Forêt Vohidava 89.2 km N Amboasary, -24.239, 46.28233, 850 m, tropical dry forest, (B.L. Fisher *et al.*) (CASC); Ivahona, -23.45591, 46.17376, 820 m, village/park/garden, (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.26215, 45.17004, 505 m, barren rock with sparse vegetation, burned grass, (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.31334, 45.14525, 575 m, burned savannah, (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., -21.34109, 45.18054, 500 m, barren rock with sparse vegetation, burned grass, (B.L. Fisher *et al.*) (CASC); Makay Mts., -21.26215, 45.17004, 505 m, barren rock with sparse vegetation, burned grass, (B.L. Fisher *et al.*) (CASC); Makay, -21.3133, 45.14788, 520 m, gallery forest, (J.M. Bichain) (CASC); Southern Isoky-Vohimena Forest, -22.68333, 44.83333, 730 m, (Sylvain) (CASC).

***Camponotus mita* Rakotonirina, Csősz & Fisher sp. n.**

(Figures 5B, 7A, 17, 25)

Holotype worker. MADAGASCAR: Province **Antsiranana:** Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, -13.11833, 49.23, 425 m, rainforest, beating low vegetation, 15–17 Dec 2003 (B.L. Fisher *et al.*) collection code: BLF10326, specimen code: CASENT0498906 (CASC).

Paratypes. 3 workers with same data as holotype but with specimen codes: CASENT0498907, CASENT0763884, CASENT0763884 (CASC, MHNG).

Diagnosis. Integument black; posterior portion of head, dorsum of mesosoma, and lateral margin of propodeal declivity with randomly scattered, whitish, erect hairs; basal half of antennal scape flattened dorsoventrally; in lateral view, mesosoma short and high, propodeal dorsum shorter than declivitous face; scattered erect hairs present immediately behind lateral margin of clypeus; dorsum of body with a few scattered, erect hairs and thin, short, and sparse pubescence; tibiae without suberect hairs.

Description. Minor worker. In full-face view head elongate, subrectangular (CWb/CL: 0.81–0.84), with straight and parallel lateral margins which join the slightly broadly convex posterior margin at a blunt angle. With head in lateral view, posterior corner of head bluntly angulate, not extending into a lobe. Eyes weakly protruding, not breaking the outline of lateral cephalic margin (CWb/CL: 0.83±0.01, 0.81–0.84; CW/CL: 0.80±0.01, 0.78–0.82), located at posterior fifth of head (PoOc/CL: 0.20±0.01, 0.18–0.21). In full-face view, clypeus transversely trapezoidal, its anteromedian margin projecting into a blunt triangular lobe, anterolateral angle lacking, median portion with blunt longitudinal carina, posterior margin medially notched. Mandible subtriangular, armed with six teeth. Antennal scape long, less than its distal portion surpassing posterior cephalic border; basal half strongly flattened dorsoventrally, width greatest near basal condyle. In lateral view, mesosoma short and high (MPH/ML: 0.49±0.02, 0.46–0.53); promesonotum convex and domelike, its level separately higher than that of propodeum; propodeal dorsum short, rounding to steeply sloping propodeal declivity; metanotal groove obsolete. Opening of propodeal spiracle elongate or slitlike. In lateral view, petiolar node scalelike and short, petiolar spiracle located roughly at midheight of node; anterior face sloping posteriorly at dorsal fourth portion of node to reach the straight posterior face dorsally. Middle and hind legs with one pectinate tibial spur. Transverse light strip on posterior margin of gastral tergites wide, maximum width roughly 1/6 of the visible width of second tergite.

Head finely and densely reticulate punctate to finely imbricate; promesonotum finely and densely reticulate punctate, propodeum finely and densely reticulate rugulose; lateral portion of mesosoma with effaced fine and dense reticulate punctures anteriorly and areolate sculpture posteriorly; gastral tergites with fine, transverse strigulae. Mandibles coriarius interspersed with piligerous punctures. Whitish erect hairs randomly scattered from median portion of head to near its posterior margin, where they are transversally spread to near the lateral cephalic margin and down anteriorly to near base of mandible and behind lateral margin of clypeus. Head, pronotum, and anterior section of mesonotum covered with hairs thinner and more erect than remaining posterior portion of body; lateral margin of propodeum with more than one row of hairs; suberect hairs lacking on tibiae. Pubescence short and sparse, distance between some of them greater than their length. Body color black and matte; appendages dark reddish black, basal portion of antennal scape, tip of mandible, and leg brown to dark brown.

Major worker. Unknown.

Discussion. *Camponotus mita* may be confused with *C. voeltzkowii* because both have the propodeal dorsum shorter than the declivitous face, and there are scattered erect hairs immediately behind the lateral margin of the clypeus. However, the basal half of the antennal scape in *C. voeltzkowii* is cylindrical and without a lobe-like leading edge. In addition, the dorsum of the body of the latter species is covered with numerous erect hairs and abundant pubescence.

The identity of *C. mita* based on conventional qualitative taxonomy is also recognized by multivariate morphometric analysis. The cluster of the samples of the species created by NC-clustering and partitioning methods is corroborated by shape PCA and confirmed by cumulative LDA with an identification success of 100%.

Distribution and biology. *Camponotus mita* is endemic to Madagascar and occurs only in the northern part of the island. While some workers of this species have been collected by litter sifting and Malaise traps from dry forest habitats with altitudes ranging from 60 m to 90 m, others were found foraging on the forest floor and on low vegetation in the humid forests of Andavakoera and Ambato between 150 m and 425 m in altitude.

Additional material examined. MADAGASCAR: Province **Antsiranana:** Forêt Ambato, 26.6 km 33° Ambanja, -13.4645, 48.55167, 150 m, rainforest, (B.L. Fisher) (CASC); Forêt 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); Réserve Analamerana, 28.4 km 99° Anivorano-Nord, -12.74667, 49.49483, 60 m, tropical dry forest, (B.L. Fisher) (CASC); SAVA Region, District of Vohemar, Andranotsimaty dry forest, 9 km NE of Daraina, -13.1695, 49.70067, 90 m, dry dense forest, (Mike, Rinha) (CASC).

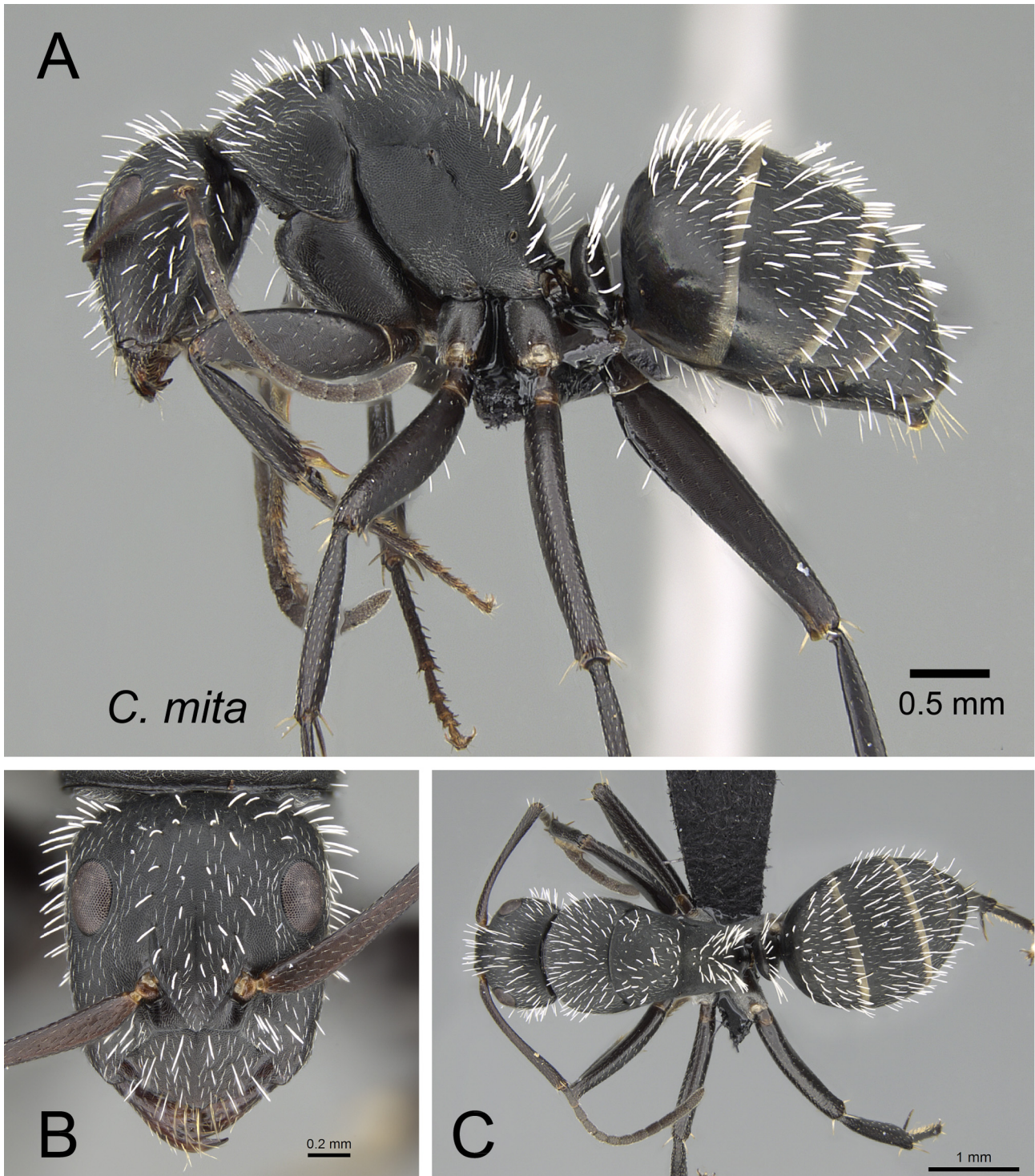


FIGURE 17. *Camponotus mita* minor worker CASENT0498906. A: lateral view. B: head in full-face view. C: dorsal view.

Camponotus voeltzkowii Forel

(Figures 7B, 18, 26)

Camponotus voeltzkowii Forel, 1894: 226. Lectotype minor worker, **present designation**, Madagascar, Mahajanga (Voeltzkow), AntWeb CASENT0101376 (MHNG) [examined]. Paralectotype minor worker, same data as lectotype but with specimen code CASENT0101377 (MHNG) [examined]. [Combination in *Camponotus (Myrmoturba)*: Forel, 1914: 271. Combination in *Camponotus (Myrmopirromis)*: Wheeler, 1922a: 1052; Emery 1925: 129; Bolton, 1995: 129, 131].

Diagnosis. Integument black; posterior portion of head, dorsum of mesosoma, and lateral margin of propodeal declivity with randomly scattered, whitish, erect hairs; basal half of antennal scape flattened dorsoventrally; in lateral view, mesosoma short and high, propodeal dorsum shorter than declivitous face; few scattered erect hairs present immediately behind lateral margin of clypeus; dorsum of body with numerous, randomly scattered, long, erect hairs and abundant long pubescence; tibiae with sparse suberect hairs.

Description. Minor worker. In full-face view head slightly longer than wide (CWb/CL: 0.91 ± 0.03 , 0.87–1.07), lateral borders straight and diverging posteriorly and joining the more or less posterior margin in a distinct angle. In lateral view, posterior cephalic margin extending backward into a rounded lobe. Eyes protruding, almost breaking lateral borders of head (CWb/CL: 0.91 ± 0.03 , 0.87–1.07; CW/CL: 0.89 ± 0.03 , 0.86–1.04), located at posterior sixth to fifth portion of head (PoOc/CL: 0.17 ± 0.01 , 0.15–0.23). With head in full-face view, clypeus trapezoidal; anteromedian margin projecting into a triangular lobe; anterolateral portion bluntly angulate; median portion convex, with visible longitudinal carina. Mandible triangular, apical margin equipped with six teeth. Antennal scape long, roughly distal portion extending beyond posterior margin of head (SL/CS: 1.10 ± 0.05 , 1.01–1.19); basal portion cylindrical, not flattened dorsoventrally. In lateral view, mesosoma short and high (MPH/ML: 0.54 ± 0.05 , 0.46–0.71), dorsal outline of promesonotum domelike, its level higher than that of propodeum; anterodorsal portion of pronotum angulate; propodeal dorsum short, joining the sharply inclined propodeal declivity into a blunt angle; metanotal groove obsolete. Opening of propodeal spiracle circular or elongate to slitlike. In lateral view, petiolar node scalelike and high, petiolar spiracle located at level lower than midheight of node; anterior face starting to incline posteriorly at dorsal third portion of node to reach the straight posterior face dorsally. Middle and hind legs with single pectinate tibial spur. Transverse light strip on posterior margin of gastral tergites wide, maximum width roughly 1/8 the visible width of second tergite.

Head dorsum finely and densely reticulate punctate to finely areolate, becoming finely imbricate posteriorly; pronotum finely and densely reticulate punctate to finely imbricate, mesonotum and propodeum finely and densely reticulate rugulose. Lateral portion of head and mesosoma finely imbricate. Gastral tergites finely and transversely strigulate anteriorly and finely imbricate posteriorly. Mandible with coriarius punctulate sculpture. Whitish erect hairs randomly scattered from median portion of head to near its posterior margin, where they spread transversally to near the lateral margin and down anteriorly to near base of mandible and behind lateral margin of clypeus. Head, pronotum, anterior section of mesonotum, and posterior section of gastral tergites covered with hairs thinner and more erect than posterior portion of mesonotum, propodeum, petiolar node, and first gastral tergite; tibiae covered with scattered suberect hairs. Pubescence long and quite dense, distance between them smaller than their length; pubescence more abundant on gaster than mesosoma and head.

Major worker. With characteristics of minor worker, but head subquadrate (CWb/CL: 0.97 ± 0.02 , 0.94–0.99) to cordate in full-face view, posterior cephalic margin slightly broadly excised. Eyes placed more interior relative to head capsule (CWb/CL: 0.97 ± 0.02 , 0.94–0.99; CW/CL: 0.84 ± 0.01 , 0.81–0.85). Mandibles more robust, masticatory margin with more than six teeth. Clypeus with elongate median portion (ClyL/GPD: 0.78 ± 0.02 , 0.73–0.81), anteromedian margin straight to slightly broadly convex. Antennal scape short, barely extending beyond posterior cephalic border (SL/CS: 0.76 ± 0.01 , 0.75–0.79). Dorsal outline of mesosoma forming a continuous convexity; metanotal groove a slightly impressed line. Lateral portion of head finely and densely reticulate punctate to finely areolate, with scattered groups of two to seven areoles surrounding the base of an appressed or erect hair; each group of these areoles is sometimes embedded in a poorly defined puncture. Lateral portion of mesosoma finely areolate to finely imbricate.

Discussion. See discussion under *C. mita*.

For *C. voeltzkowii*, the conclusions drawn from qualitative morphology-based taxonomy agree with the classification hypothesis provided by the exploratory data analysis and the confirmatory technique of the multivariate morphometrics. The combination of this information strengthens the status of *C. voeltzkowii* as a species.

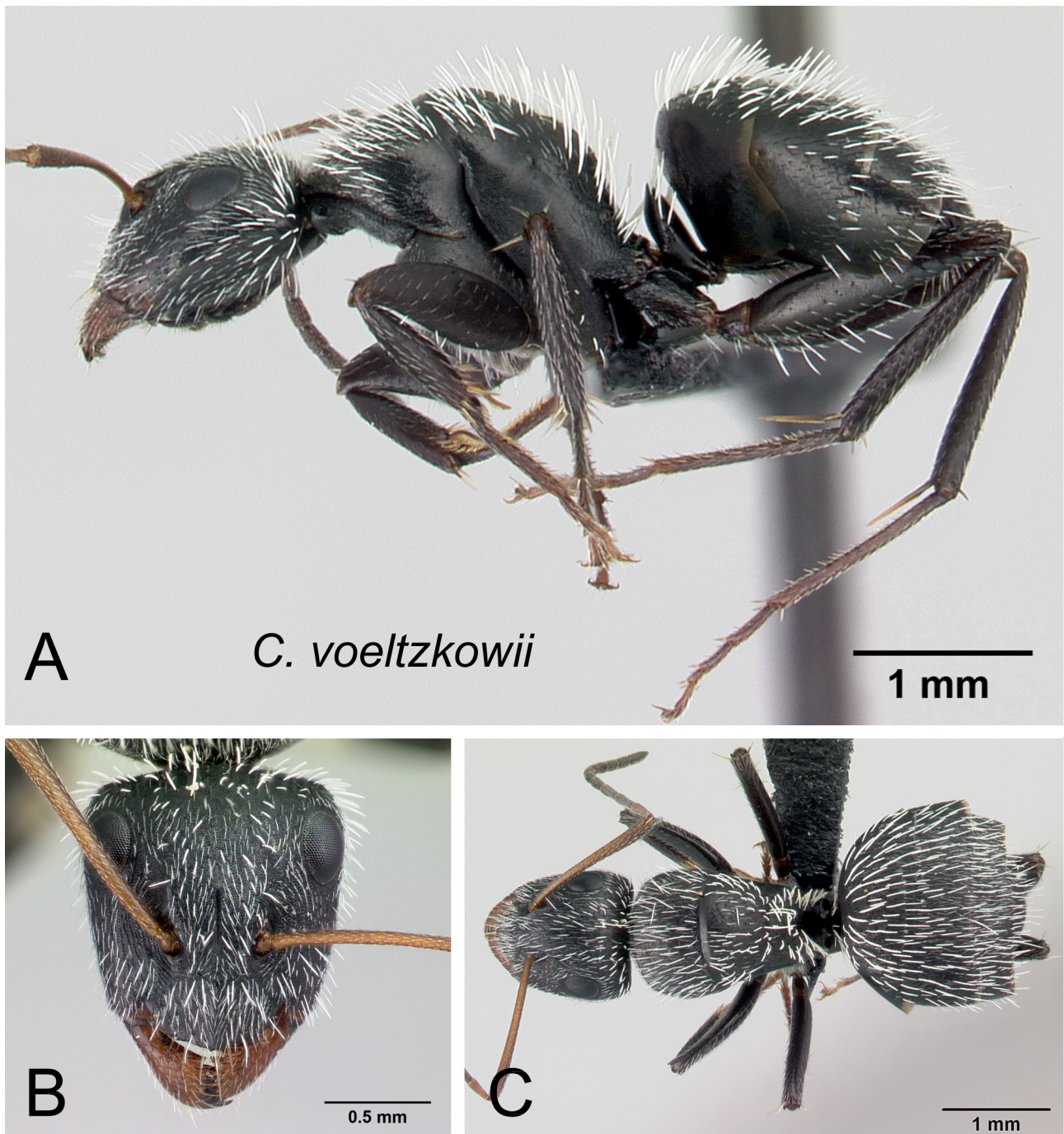
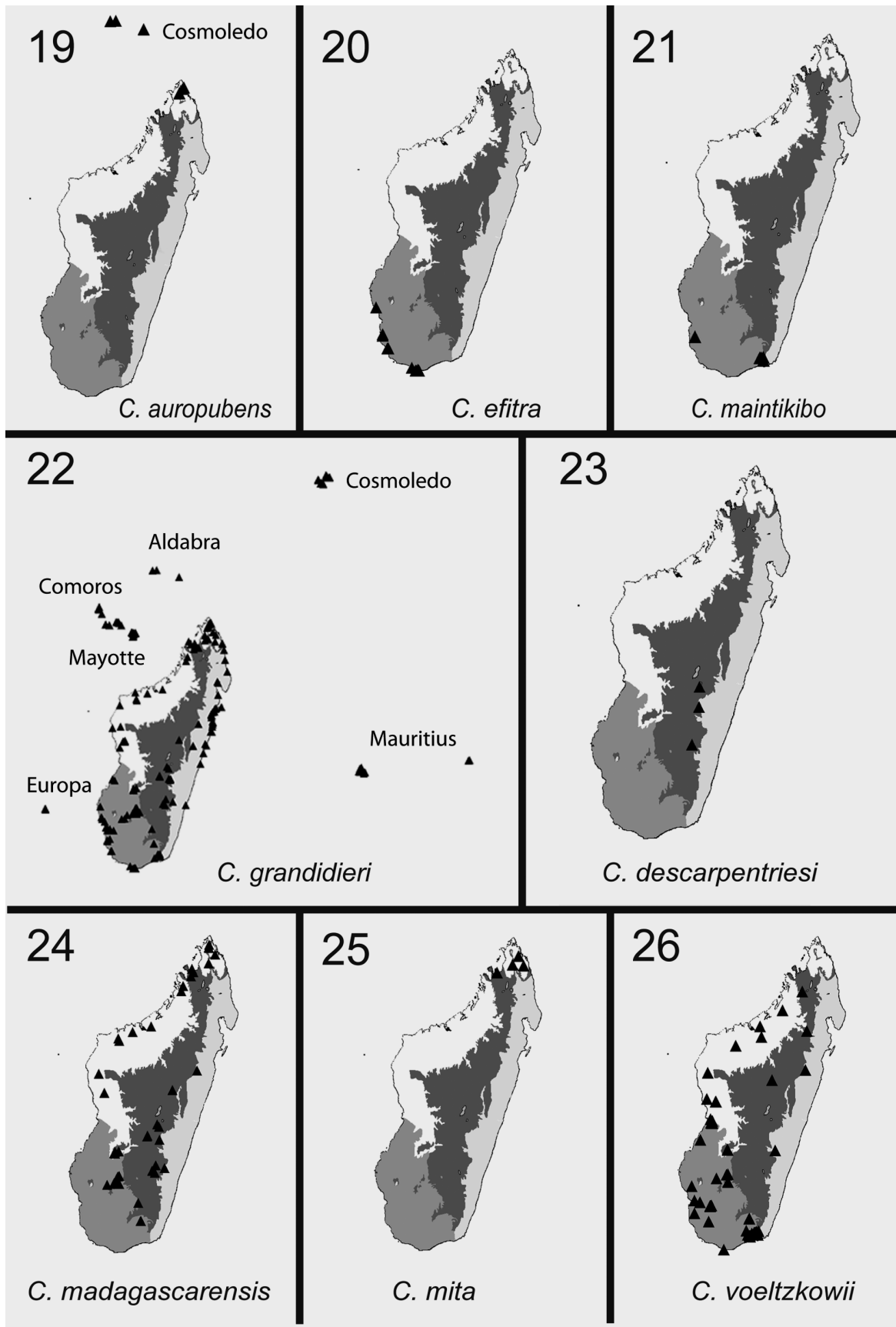


FIGURE 18. *Camponotus voeltzkowii* minor worker CASENT0121619. A: lateral view. B: head in full-face view. C: dorsal view.

Distribution and biology. *Camponotus voeltzkowii* is one of the most common species within the *niveosetosus* species group of the Malagasy region. In Madagascar, it is widespread in the west but absent in the northernmost region. To the north, its geographic distribution is limited to montane rainforest of the northern highland. Along the western portion of the island, the distributional range of *C. voeltzkowii* consists of the dry forest on Tsingy, gallery forest, littoral forest habitats in the north to southwest, as well as spiny bush and thicket in the extreme south of the island. The species is also known to occur in Uapaca woodland of the central high plateau region, and in the northern-and southern-central portions of the island's eastern rainforests. The species also can occupy anthropogenic habitats such as disturbed and degraded forests and urban gardens. Colony nests are found either on the forest floor under stones or in rotten logs, or in the dead branches or twigs of trees. Foraging activity is carried out on the ground and through leaf litter or on lower vegetation.



FIGURES 19–26. Distribution maps of the *Camponotus grandidieri* and *niveosetosus* species groups in the Malagasy region. Fig. 19: *C. auropubens*; Fig. 20: *C. efitra*; Fig. 21: *C. maintikibo*; Fig. 22: *C. grandidieri*; Fig. 23: *C. descarpentriesi*, Fig. 24: *C. madagascarensis*, Fig. 25: *C. mita*, Fig. 26: *C. voeltzkowii*.

Camponotus voeltzkowii is sympatric with *C. madagascarensis* and *C. grandidieri*.

Additional material examined. MADAGASCAR: Madagascar (MHNG); Province **Antananarivo:** Analamanga Region, District of Ankazobe, Ambohitantely, 46 km NE of Ankazobe, -18.198, 47.2815, 701 m, sclerophyll forest, (Rin'ha, Mike) (CASC); Province **Fianarantsoa:** Fitovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, -21.25083, 47.40717, 1127 m, forest edge, open area, (Rin'ha, Mike) (CASC); Parc National d'Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, -22.29833, 45.35167, 990 m, Uapaca woodland, (Fisher, Griswold *et al.*) (CASC); Parc National d'Isalo, Sahanafa River, 29.2 km 351° N Ranohira, -22.31333, 45.29167, 500 m, gallery forest, (Fisher, Griswold *et al.*) (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); stream area, 900 m E of Isalo National Park Interpretive Center, Fianarantsoa Prov., -22.62667, 45.35817, 750 m, open area near stream, (R. Harin'Hala) (CASC); Province **Mahajanga:** [Majanga] (MHNG); Ambolomaiky, 48.1 km SE Mahajanga, -15.8541, 46.74663, 77 m, disturbed dry forest, (B.L. Fisher *et al.*) (CASC); Ampijoroa National Park, 160 km N Maevatanana, Mahajanga Prov., deciduous forest, -16.31944, 46.81333, 43 m, deciduous forest, (M. Irwin, R. Harin'Hala) (CASC); Boeny Region, District of Soalala, Beaboaly Bamboo forest, 10 km SW of Soalala, 4 km from Baly village, -16.04533, 48.804, 9 m, bamboo forest, (M. Irwin, R. Harin'Hala) (CASC); Boeny Region, District of Marovoay, Ampijoroa National Park, 160 km N of Maevatanana on RN 04, -16.31933, 46.81333, 42 m, deciduous forest, (M. Irwin, R. Harin'Hala) (CASC); Boeny Region, District of Soalala Analamanitra forest, 14 km SW of Mitsinjo, -16.7, 45.7, 19 m, dense dry forest, (M. Irwin, R. Harin'Hala) (CASC); Forêt de Tsimembo, 8.7 km 336° NNW Soatana, -19.02139, 44.44067, 20 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Parc National 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); Parc National 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); Region Sofia, Bemanevika, -14.337, 48.58874, 1606 m, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve forestière Beanka, 50.7 km E Maintirano, -17.88021, 44.46877, 140 m, tropical dry forest on tsingy, (B.L. Fisher *et al.*) (CASC); Sofia Region, District of Sofia, Anjiamangirana 45 km S Antsohihy, Analagnambe galleryforest, 5 km W Anjiamangirana, -15.157, 47.73417, 97 m, low degraded dry forest, (M. Irwin, R. Harin'Hala) (CASC); Station Forestiere Ampijoroa, -16.31667, 46.81667, 80 m, tropical dry forest, (P.S. Ward) (PSWC); Province **Toamasina:** Parc National de Zahamena, Tetezambatana forest, near junction of Nosivola and Manakambahiny Rivers, -17.74298, 48.72936, 860 m, rainforest, (B.L. Fisher *et al.*) (CASC); Province **Toliara:** [Fort Dauphin; Museum Paris Collection, Ernest André 1914] (MNHN); 18.4 km N Amboasary, -24.87367, 46.39767, 85 m, spiny forest/thicket, (B.L. Fisher *et al.*) (CASC); 2 km SW Mahamavo, Rés.Andohahela, -24.78333, 46.7, 320 m, tropical dry forest, (P.S. Ward) (PSWC); 45 km NE Morondava, -20.05, 44.61667, 30 m, tropical dry forest, (P.S. Ward) (PSWC); 55 km NE Morondava, -19.9, 44.6, 25 m, tropical dry forest, (P.S. Ward) (PSWC); Ambohimahavelona village 33 km NE of Tulear, Andoharano dry forest, -23.44083, 43.89967, 46 m, dry forest, (M. Irwin, R. Harin'Hala) (CASC); Androy Region, District of Tsihombe, 74 km S of Tsihombe, Cap Ste Marie Reserve, -25.58767, 45.163, 36 m, spiny bush, (Rin'ha, Mike) (CASC); Anosy Region, District of Amboasary, 58 km SW of Fort Dauphin, 8 km NW of Amboasary, Berenty Special Reserve, -25.00667, 46.30333, 85 m, galleryforest, (Rin'ha, Mike) (CASC); Anosy Region, District of Amboasary, Andohaela National Park Parcelle III, Ihazofotsy, 32 km NE Amboasary, -24.83083, 46.53617, 58 m, dry forest, spiny forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Anosy Region, District of Amboasary, 58 km SW of Fort Dauphin, 8 km NW of Amboasary, Berenty Special Reserve, -25.021, 46.3055, 36 m, spiny forest, (Rin'ha, Mike) (CASC); Anosy Region, District of Fort-Dauphin, Andohaela National Park Parcelle II, Tsimela, 42 km W of Fort-Dauphin, -24.93683, 46.62667, 177 m, transition forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Anosy Region, Parc National d'Andohahela, Forêt de Manatalinjo, -24.82505, 46.57811, 90 m, spiny forest/thicket, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Parc National d'Andohahela, Forêt de Manatalinjo, -24.82466, 46.60111, 100 m, spiny forest/thicket, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Berenty Reserve, -24.98333, 46.3, 30 m, gallery forest, (D.M. Olson) (PSWC), Berenty Special Reserve, 8 km NW Amboasary, 58 km SW of Fort Dauphin, Tulear Province, -25.00667, 46.30333, 85 m, gallery forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Ejeda, -24.3505, 44.516, 250 m, urban/garden, (B.L. Fisher *et al.*) (CASC); Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, -20.06915, 44.66041667, 30 m, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, -20.045, 44.66222, 100 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de

Kirindy, 15.5 km 64° ENE Marofandilia, -20.045, 44.66222, 100 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Mahavelo, Isantoria River, -24.75833, 46.15717, 110 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Mahavelo, Isantoria River, 5.5 km 37° NE Ifotaka, -24.75361, 46.1515, 115 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Mite, 20.7 km 29° WNW Tongobory, -23.52417, 44.12133, 75 m, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt Vohidava 88.9 km N Amboasary, -24.24067, 46.28783, 500 m, spiny forest/dry forest transition, (B.L. Fisher *et al.*) (CASC); Forêt Vohidava 89.2 km N Amboasary, -24.239, 46.28233, 850 m, tropical dry forest, (B.L. Fisher *et al.*) (CASC); Forêt Vohidava 89.2 km N Amboasary, -24.239, 46.28233, 850 m, tropical dry forest, (B.L. Fisher *et al.*) (CASC); Forêt Vohidava 89.6 km N Amboasary, -24.23333, 46.30167, 230 m, spiny forest/thicket, (B.L. Fisher *et al.*) (CASC); Ihazofotsy - Parcel III, Andohahela National Park, transition forest, Tulear Province, -24.83483, 46.48683, 80 m, transition between spiny and dry deciduous forests, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Kirindy, 47.3 km NE Morondava, -20.07125, 44.6655, 60 m, tropical dry forest, (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., -21.21985, 45.32396, 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); Manombo, -22.80707, 43.76375, 222 m, gallery forest, TS1, (Frontier Wilderness Project) (CASC); Menabe Region, District of Morondava, Beroboka village 45 km NE of Morondava, Antsarongaza, dry forest 7.5 km E of Beroboka, -19.9775, 44.66633, 50 m, dry forest, (Michael Irwin, Rin'ha) (CASC); Menabe Region, District of Morondava, Beroboka village, 45km NE of Morondava, Antsarongaza, gallery forest, 7 km E of Beroboka, -19.9775, 44.66533, 45 m, gallery forest, (Michael Irwin, Rin'ha) (CASC); Parc National d'Andohahela, Forêt d'Ambohibory, 1.7 km 61° ENE Tsimelahy, 36.1 km 308° NW Tolagnaro, -24.93, 46.6455, 300 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Parc National d'Andohahela, Forêt de Manatalinjo, 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, -24.81694, 46.61, 150 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Parc National de Kirindy Mite, 16.3 km 127° SE Belo sur Mer, -20.79528, 44.147, 80 m, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Parc National de Tsimanampetsotsa, Forêt de Bemanateza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, -23.99222, 43.88067, 90 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Parcel I, Beza Mahafaly Reserve, near research station, Tulear Province, -23.6865, 44.591, 165 m, dry deciduous forest, (R. Harin'Hala) (CASC); Parcel II, Beza Mahafaly Reserve, near Bellevue, Tulear Province, -23.68983, 44.5755, 180 m, spiny forest, (R. Harin'Hala) (CASC); Res. Beza Mahafaly, Parcel 1, -23.65, 44.63333, 130 m, tropical dry forest, (P.S. Ward) (PSWC); Rés. Beza Mahafaly, Parcel 2, -23.68333, 44.56667, 200 m, spiny forest/thicket, (P.S. Ward) (PSWC); Réserve Privé Berenty, Forêt d'Anjapolo, 21.4 km 325° NW Amboasary, -24.92972, 46.20967, 65 m, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); southern Isoky-Vohimena Forest, 59 km NE Sakaraha, -22.46667, 44.85, 730 m, tropical dry forest, (B.L. Fisher) (CASC).

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Supplementary material

Basic measurements of individual specimens of the Malagasy *Camponotus grandidieri* and *niveosetosus* species groups arranged by species code, collection code, and specimen code (unique identification number). See text for abbreviations.

The supplementary material can be accessed from the Dryad Repository using the link <http://dx.doi.org/10.5061/dryad.1vh64>