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Taxonomic revision of the Malagasy *Camponotus* subgenus *Mayria* (Hymenoptera, Formicidae) using qualitative and quantitative morphology

JEAN CLAUDE RAKOTONIRINA[1,2] & BRIAN L. FISHER[3]

[1]*Madagascar Biodiversity Center, BP 6257, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar.*
[2]*Département d'Entomologie, Faculté des Sciences, BP 906, Université d'Antananarivo, Madagascar.*
E-mail: jcrakoto25@yahoo.com
[3]*Entomology, California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, U.S.A.*
E-mail: bfisher@calacademy.org

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Abstract

The *Camponotus* subgenus *Mayria* is revised based on the analysis of both qualitative morphological characters and morphometric traits. The multivariate analysis combined the Nest Centroid (NC)-clustering method and Partitioning Algorithm based on Recursive Thresholding (PART) function to generate species hypotheses based on 19 continuous morphological traits of minor workers. The proposed species hypotheses were confirmed by cumulative Linear Discriminant Analysis (LDA). Morphometric ratios for the subsets of minor and major workers were used in species descriptions and redefinitions. In this study, 14 species are recognized, of which seven are newly described: *C. lamosy* **sp. n.**, *C. liandia* **sp. n.**, *C. mainty* **sp. n.**, *C. manabo* **sp. n.**, *C. raina* **sp. n.**, *C. sada* **sp. n.**, *C. tanosy* **sp. n.** Four species are redescribed: *C. christi* Forel, *C. dromedarius* Forel, *C. lubbocki* Forel, and *C. repens* Forel. The following are raised to species and redescribed: *C. foersteri* Forel **stat. n.**, *C. maculiventris* Emery **stat. n.**, and *C. pulcher* **stat. n.** The following are synonymized under *C. foersteri*: *Camponotus cambouei* Forel, **syn. n.**; *C. christi ambustus* Forel, **syn. n.**; *C. christi ferrugineus* Emery, **syn. n.** and *C. pictipes* Forel, **syn. n**. The following are synonymized under *C. lubbocki*: *Camponotus lubbocki christoides*

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Forel, **syn. n.** and *C. lubbocki rectus* Forel, **syn. n.** Also included in this revision are an illustrated species identification key, taxonomic discussions, images, and distribution maps for each species superimposed with the ecoregions of Madagascar.

Key words: taxonomy, morphometry, subgenus *Mayria*, Madagascar, species delimitation

Introduction

Camponotus is one of the hyper-diverse and ecologically important genera in the Malagasy region (Fisher 1997; Rakotonirina *et al.* 2016). Based on the new collections estabilished by the intensive research surveys of ants in the region (Fisher 2005), the majority of the species have yet to be described. Recently, Rakotonirina *et al.* revised the taxonomy of the *C. edmondi* species group (2016), which recognizes 15 species, and the *C. grandidieri* and *niveosetosus* species groups (2017), which together include eight species. Rasoamanana *et al.* (2017) studied the taxonomy of the *Camponotus* subgenus *Myrmopytia* (*imitator* species group), which contains four species. As part of an ongoing project aiming at revising the entire genus in the Malagasy region, the present contribution revises the taxonomy of the *Camponotus* subgenus *Mayria*.

The subgenus *Mayria* is distributed across the Afrotropical region, but the present study focuses on the Malagasy members of the subgenus only. The Malagasy *Mayria* initially contained just two species, *C. repens* and *C. lubbocki,* which were originally described by Forel in1886. Subsequently, 10 other species and subspecies from Madagascar were described initially under two different subgenera (*Myrmocamelus*, *Myrmosaga*), but later placed in the *Mayria* subgenus by Emery (1925) and Bolton (1995); they are still placed in *Mayria* in the present contribution. Generally, members of this subgenus are characterized by a narrow frontal lobe, which partially covers the antennal insertion, an S-shaped frontal carina, which is strongly divergent posteriorly, a procoxa of normal size, a laterally narrow and low petiolar node, an elongate and narrow gaster, which is generally low and short anteriorly, and body sculpture varying from smooth and shiny to finely and densely imbricate.

In recent taxonomic revisions, species delimitation and identification has been facilitated by a combination of information from multivariate statistical methods for analyzing morphometric data, qualitative morphological characters, and biological and distributional data (e.g. Rakotonirina *et al.* 2016, 2017). We apply similar methods in the present revision, which recognizes 14 species. This revision is accompanied by an illustrated species-level identification key, and the description of each species is complemented by high-resolution montage images and a geographic distribution map.

Materials and methods

Abbreviation of depositories

CASC	California Academy of Sciences, San Francisco, CA, USA
MHNG	Musée d'Histoire Naturelle, Geneva, Switzerland
MNHN	Musée National d'Histoire Naturelle, Paris, France
MSNG	Museo de Storia Naturele, Genoa, Italy
NHMB	Naturhistorisches Museum, Basel, Switzerland
PBZT	Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar
PSWC	P.S. Ward Collection, University of California at Davis, CA, USA
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany

Materials. The present study includes all specimens of the subgenus *Mayria* collected by the members of the Madagascar Biodiversity Center and other ant researchers. Most of these collections were sampled from 1992 through 2016. Data of the pinned specimens examined during this revision are available on AntWeb (www.antweb.org) and can be accessed using the unique identifying specimen code (CASENT number) affixed to each pin.

A total of 392 specimens from 158 collecting events were measured in this study (see Suppl. material 1). Collection codes with prefix ANTC, ARA, BLF, HJR or MG, indicate distinct collecting events, and were used as grouping factors in the NC-clustering method.

Methods. 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. Information about the biology of each species was based on the data obtained from specimen sampling (the nest series and isolated worker specimens) in the field.

The designation of a lectotype from syntype specimens, which directly match the original description of a named species, is desirable to create a stable nomenclature based on article 74 of the ICZN code. 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.

Qualitative morphological characters were observed using a Leica MZ 12.5 binocular microscope. Minor and major workers were evaluated for patterns of morphological discontinuities. Observed discontinuities in morphological space could indicate reproductive boundaries between populations and as such were used to infer potential species limits. Species limits based on qualitative morphological characters were compared with the species hypothesis derived from the quantitative analysis of measurements.

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; ranges are shown as minimum and maximum values. 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, 2017). The following characters were evaluated in the present revision:

CL (Maximum cephalic length): 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.

ClyL (Clypeal length): 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. Median concavity on either or both margins reduces the length of the clypeus.

CS (Cephalic size): The arithmetic mean of CL and CWb. CS is used to indicate the general body size of the ant.

CW (Maximum cephalic width): The maximum distance between the lateral margins of the compound eyes in full-face view.

CWb (Maximum head capsule width): The maximum width of the head excluding the compound eyes.

EL (Eye length): Maximum diameter of the compound eye.

FR (Frontal carina distance): The maximum distance between the frontal carinae.

GPD (Maximum tentorial pit distance): The longest distance between the centers of the fossae located at or very close to the posterolateral margin of the clypeus.

HTL (Maximum hind tibia length): 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.

ML (Mesosoma length): 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.

MPD (Mesothoracico-propodeal distance): 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. 01, Rakotonirina *et al*. 2016).

MPH (Mesothoracico-propodeal height): 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.

MW (Mesosoma width): 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").

NOH (Petiolar node height): The maximum distance between the petiolar spiracle and the dorsalmost point of the petiolar node.

OMD (Oculo-mandibular distance): The smallest distance between the anterior margin of the compound eye and the mandibular insertion to the head.

PEW (Petiolar width): The maximum width of the petiole in dorsal view.

PoOc (Postocular distance): 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.

PrOc (Preocular distance): 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.

SL (Scape length): Straight line length of the first antennal segment excluding the basal condyle.

TCD (Torular carina distance): The minimum distance between the torular arches that surround the antennal insertion.

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 minor worker specimens), and (2) the ratios (indices) of measurements of one measured trait (variable) to another to calculate the body proportions (Table 1). In Table 1, the ratios of measurements for minor and major workers of each species are presented as arithmetic means with standard deviation in the upper line and as ranges in square brackets in the lower line.

TABLE 1. Ratios of morphometric data for minors and majors of every species treated in this revision. Upper line: mean of ratios ± standard deviation, lower line in square brackets: minimum and maximum values.

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
christi	minor (N=28)	1.01±0.09	0.76±0.03	0.72±0.02	0.34±0.01
		[0.87, 1.17]	[0.69, 0.83]	[0.69, 0.74]	[0.31, 0.36]
	major (N=3)	1.53±0.05	0.94±0.01	0.78±0.01	0.31±0.01
		[1.48, 1.58]	[0.93, 0.95]	[0.78, 0.79]	[0.30, 0.32]
dromedarius	minor (N=37)	1.22±0.10	0.80±0.07	0.78±0.07	0.34±0.02
		[1.04, 1.45]	[0.72, 1.05]	[0.73, 1.05]	[0.31, 0.39]
	major (N=6)	1.64±0.12	0.93±0.04	0.83±0.03	0.33±0.01
		[1.48, 1.82]	[0.86, 0.98]	[0.79, 0.85]	[0.31, 0.35]
foersteri	minor (N=34)	1.00±0.11	0.77±0.03	0.75±0.02	0.33±0.01
		[0.75, 1.23]	[0.71, 0.85]	[0.70, 0.78]	[0.31, 0.35]
	major (N=3)	1.42±0.17	0.95±0.03	0.83±0.00	0.31±0.01
		[1.30, 1.62]	[0.91, 0.98]	[0.82, 0.83]	[0.30, 0.32]
lamosy	minor (N=20)	1.09±0.10	0.77±0.03	0.77±0.02	0.34±0.01
		[0.85, 1.22]	[0.73, 0.82]	[0.72, 0.79]	[0.31, 0.37]
	major (N=2)	1.82±0.04	1.01±0.02	0.86±0.03	0.30±0.00
		[1.79, 1.85]	[0.99, 1.03]	[0.84, 0.87]	[0.30, 0.31]
liandia	minor (N=13)	0.85±0.09	0.78±0.02	0.77±0.02	0.26±0.01
		[0.73, 1.11]	[0.73, 0.82]	[0.73, 0.79]	[0.24, 0.27]
	major (N=2)	1.41±0.07	0.88±0.02	0.79±0.03	0.28±0.00
		[1.36, 1.46]	[0.87, 0.90]	[0.77, 0.81]	[0.27, 0.28]

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
lubbocki	minor (N=16)	1.10±0.08	0.84±0.02	0.80±0.01	0.27±0.01
		[1.00, 1.32]	[0.81, 0.88]	[0.77, 0.81]	[0.25, 0.30]
	major (N=3)	1.85±0.22	1.00±0.03	0.86±0.01	0.28±0.01
		[1.59, 2.01]	[0.96, 1.03]	[0.85, 0.87]	[0.27, 0.29]
maculiventris	minor (N=51)	0.94±0.16	0.81±0.06	0.78±0.03	0.32±0.01
		[0.72, 1.50]	[0.74, 1.03]	[0.74, 0.87]	[0.29, 0.36]
	major (N=10)	1.29±0.10	0.93±0.09	0.81±0.06	0.31±0.02
		[1.14, 1.42]	[0.78, 1.01]	[0.69, 0.92]	[0.28, 0.34]
mainty	minor (N=38)	0.95±0.09	0.79±0.03	0.77±0.02	0.30±0.03
		[0.76, 1.11]	[0.72, 0.86]	[0.73, 0.81]	[0.23, 0.36]
	major (N=10)	1.43±0.25	0.95±0.09	0.82±0.04	0.29±0.02
		[1.08, 1.80]	[0.80, 1.07]	[0.75, 0.87]	[0.27, 0.32]
manabo	minor (N=17)	1.24±0.08	0.84±0.02	0.81±0.02	0.27±0.01
		[1.10, 1.37]	[0.80, 0.88]	[0.79, 0.84]	[0.25, 0.28]
pulcher	minor (N=7)	1.05±0.09	0.84±0.05	0.81±0.02	0.33±0.01
		[0.98, 1.24]	[0.81, 0.94]	[0.79, 0.86]	[0.31, 0.35]
	major (N=2)	1.50±0.11	1.00±0.04	0.87±0.01	0.31±0.01
		[1.42, 1.58]	[0.97, 1.03]	[0.86, 0.88]	[0.31, 0.32]
raina	minor (N=16)	0.97±0.08	0.71±0.04	0.70±0.02	0.35±0.02
		[0.92, 1.26]	[0.67, 0.85]	[0.68, 0.76]	[0.31, 0.37]
	major (N=6)	1.60±0.06	0.95±0.01	0.81±0.01	0.30±0.01
		[1.53, 1.67]	[0.93, 0.97]	[0.79, 0.83]	[0.29, 0.31]
repens	minor (N=22)	0.85±0.09	0.81±0.03	0.82±0.02	0.27±0.01
		[0.70, 1.13]	[0.75, 0.92]	[0.79, 0.85]	[0.25, 0.29]
	major (N=5)	1.35±0.11	0.94±0.02	0.84±0.01	0.27±0.01
		[1.20, 1.43]	[0.90, 0.97]	[0.83, 0.85]	[0.26, 0.29]
sada	minor (N=20)	0.82±0.04	0.68±0.01	0.68±0.01	0.33±0.01
		[0.73, 0.94]	[0.66, 0.69]	[0.67, 0.70]	[0.31, 0.35]
	major (N=3)	1.67±0.06	0.89±0.001	0.79±0.001	0.30±0.01
		[1.62, 1.73]	[0.89, 0.89]	[0.78, 0.79]	[0.29, 0.31]
tanosy	minor (N=4)	0.91±0.04	0.71±0.02	0.77±0.03	0.30±0.01
		[0.87, 0.96]	[0.69, 0.74]	[0.75, 0.81]	[0.28, 0.31]
	major (N=3)	1.25±0.06	0.83±0.03	0.80±0.02	0.31±0.01
		[1.21, 1.33]	[0.80, 0.87]	[0.78, 0.82]	[0.30, 0.32]
christi	minor (N=28)	0.44±0.01	0.33±0.02	0.23±0.01	0.26±0.01
		[0.42, 0.48]	[0.30, 0.43]	[0.22, 0.25]	[0.25, 0.29]
	major (N=3)	0.49±0.01	0.31±0.01	0.22±0.01	0.29±0.01
		[0.48, 0.50]	[0.30, 0.31]	[0.21, 0.23]	[0.28, 0.30]
dromedarius	minor (N=37)	0.43±0.01	0.35±0.02	0.25±0.01	0.27±0.01
		[0.42, 0.46]	[0.28, 0.37]	[0.20, 0.27]	[0.25, 0.29]
	major (N=6)	0.45±0.02	0.33±0.01	0.24±0.01	0.27±0.01
		[0.43, 0.48]	[0.32, 0.35]	[0.23, 0.25]	[0.26, 0.29]

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
foersteri	minor (N=34)	0.43±0.02	0.33±0.01	0.23±0.01	0.27±0.01
		[0.39, 0.47]	[0.31, 0.36]	[0.21, 0.27]	[0.24, 0.28]
	major (N=3)	0.47±0.01	0.30±0.01	0.23±0.00	0.28±0.01
		[0.47, 0.48]	[0.30, 0.31]	[0.22, 0.23]	[0.27, 0.29]
lamosy	minor (N=20)	0.42±0.01	0.36±0.01	0.25±0.01	0.26±0.01
		[0.41, 0.45]	[0.34, 0.38]	[0.22, 0.27]	[0.25, 0.27]
	major (N=2)	0.48±0.01	0.32±0.00	0.22±0.00	0.28±0.00
		[0.48, 0.49]	[0.32, 0.32]	[0.22, 0.22]	[0.28, 0.29]
liandia	minor (N=13)	0.52±0.02	0.29±0.01	0.24±0.01	0.29±0.01
		[0.48, 0.54]	[0.27, 0.30]	[0.22, 0.26]	[0.28, 0.31]
	major (N=2)	0.54±0.01	0.30±0.01	0.24±0.00	0.31±0.01
		[0.53, 0.55]	[0.29, 0.30]	[0.23, 0.24]	[0.30, 0.32]
lubbocki	minor (N=16)	0.52±0.01	0.32±0.01	0.26±0.01	0.33±0.01
		[0.50, 0.54]	[0.30, 0.35]	[0.24, 0.27]	[0.31, 0.34]
	major (N=3)	0.53±0.01	0.33±0.00	0.25±0.01	0.34±0.02
		[0.52, 0.54]	[0.32, 0.33]	[0.24, 0.26]	[0.32, 0.37]
maculiventris	minor (N=51)	0.44±0.02	0.34±0.01	0.23±0.01	0.26±0.01
		[0.40, 0.47]	[0.31, 0.36]	[0.21, 0.25]	[0.25, 0.29]
	major (N=10)	0.47±0.02	0.33±0.02	0.24±0.02	0.28±0.02
		[0.42, 0.50]	[0.29, 0.37]	[0.22, 0.26]	[0.26, 0.30]
mainty	minor (N=38)	0.46±0.03	0.35±0.02	0.25±0.01	0.28±0.01
		[0.40, 0.51]	[0.31, 0.39]	[0.23, 0.28]	[0.26, 0.30]
	major (N=10)	0.49±0.02	0.32±0.01	0.23±0.01	0.29±0.01
		[0.44, 0.51]	[0.31, 0.34]	[0.22, 0.26]	[0.27, 0.32]
manabo	minor (N=17)	0.49±0.01	0.33±0.01	0.25±0.01	0.30±0.01
		[0.47, 0.52]	[0.31, 0.34]	[0.24, 0.28]	[0.29, 0.31]
pulcher	minor (N=7)	0.43±0.01	0.37±0.01	0.25±0.01	0.26±0.01
		[0.41, 0.44]	[0.36, 0.38]	[0.24, 0.27]	[0.24, 0.28]
	major (N=2)	0.45±0.01	0.34±0.00	0.24±0.00	0.28±0.01
		[0.44, 0.45]	[0.34, 0.34]	[0.24, 0.25]	[0.27, 0.28]
raina	minor (N=16)	0.40±0.01	0.32±0.01	0.23±0.01	0.27±0.01
		[0.39, 0.44]	[0.30, 0.33]	[0.22, 0.25]	[0.25, 0.29]
	major (N=6)	0.47±0.01	0.33±0.01	0.25±0.01	0.31±0.01
		[0.45, 0.48]	[0.32, 0.35]	[0.24, 0.26]	[0.29, 0.32]
repens	minor (N=22)	0.48±0.02	0.44±0.01	0.31±0.01	0.29±0.01
		[0.44, 0.53]	[0.41, 0.47]	[0.30, 0.33]	[0.27, 0.32]
	major (N=5)	0.50±0.01	0.40±0.01	0.29±0.01	0.31±0.03
		[0.49, 0.51]	[0.38, 0.42]	[0.28, 0.30]	[0.25, 0.33]
sada	minor (N=20)	0.43±0.01	0.29±0.01	0.22±0.01	0.26±0.01
		[0.40, 0.45]	[0.27, 0.32]	[0.21, 0.24]	[0.24, 0.30]
	major (N=3)	0.51±0.02	0.31±0.00	0.24±0.00	0.30±0.00
		[0.50, 0.53]	[0.31, 0.31]	[0.24, 0.24]	[0.30, 0.30]

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
tanosy	minor (N=4)	0.44±0.01	0.34±0.02	0.26±0.01	0.29±0.00
		[0.43, 0.45]	[0.32, 0.37]	[0.25, 0.27]	[0.29, 0.30]
	major (N=3)	0.44±0.02	0.33±0.02	0.25±0.01	0.31±0.01
		[0.42, 0.46]	[0.30, 0.35]	[0.24, 0.26]	[0.30, 0.32]
christi	minor (N=28)	0.64±0.03	1.53±0.09	0.26±0.01	0.48±0.02
		[0.60, 0.72]	[1.35, 1.70]	[0.23, 0.29]	[0.44, 0.51]
	major (N=3)	0.77±0.03	1.06±0.03	0.22±0.02	0.46±0.01
		[0.73, 0.79]	[1.03, 1.08]	[0.20, 0.24]	[0.45, 0.47]
dromedarius	minor (N=37)	0.67±0.03	1.34±0.08	0.26±0.01	0.45±0.03
		[0.62, 0.71]	[1.16, 1.48]	[0.23, 0.29]	[0.37, 0.57]
	major (N=6)	0.69±0.02	1.07±0.06	0.23±0.01	0.44±0.01
		[0.67, 0.73]	[1.01, 1.19]	[0.22, 0.24]	[0.43, 0.45]
foersteri	minor (N=34)	0.64±0.02	1.44±0.07	0.27±0.01	0.46±0.01
		[0.61, 0.71]	[1.29, 1.58]	[0.24, 0.32]	[0.44, 0.48]
	major (N=3)	0.69±0.02	1.06±0.07	0.24±0.01	0.44±0.01
		[0.67, 0.71]	[0.98, 1.11]	[0.23, 0.25]	[0.43, 0.45]
lamosy	minor (N=20)	0.62±0.02	1.30±0.06	0.28±0.01	0.44±0.01
		[0.57, 0.68]	[1.22, 1.42]	[0.26, 0.31]	[0.42, 0.46]
	major (N=2)	0.75±0.01	0.94±0.03	0.22±0.00	0.45±0.01
		[0.74, 0.76]	[0.92, 0.96]	[0.22, 0.22]	[0.44, 0.46]
liandia	minor (N=13)	0.65±0.04	1.19±0.04	0.26±0.02	0.47±0.01
		[0.57, 0.72]	[1.08, 1.25]	[0.22, 0.28]	[0.45, 0.49]
	major (N=2)	0.81±0.00	0.84±0.03	0.20±0.01	0.47±0.02
		[0.81, 0.81]	[0.82, 0.87]	[0.19, 0.20]	[0.46, 0.48]
lubbocki	minor (N=16)	0.76±0.12	1.20±0.06	0.24±0.01	0.48±0.01
		[0.65, 1.18]	[1.08, 1.26]	[0.23, 0.27]	[0.46, 0.50]
	major (N=3)	0.87±0.07	0.84±0.06	0.19±0.02	0.46±0.00
		[0.79, 0.92]	[0.80, 0.91]	[0.18, 0.21]	[0.45, 0.46]
maculiventris	minor (N=51)	0.62±0.03	1.34±0.15	0.28±0.02	0.45±0.01
		[0.55, 0.68]	[0.83, 1.60]	[0.23, 0.30]	[0.42, 0.48]
	major (N=10)	0.70±0.04	1.06±0.14	0.24±0.02	0.44±0.02
		[0.65, 0.75]	[0.90, 1.29]	[0.21, 0.28]	[0.41, 0.47]
mainty	minor (N=38)	0.65±0.03	1.42±0.10	0.27±0.01	0.47±0.02
		[0.59, 0.71]	[1.28, 1.86]	[0.25, 0.29]	[0.44, 0.50]
	major (N=10)	0.72±0.04	1.11±0.21	0.23±0.02	0.46±0.03
		[0.65, 0.78]	[0.89, 1.44]	[0.21, 0.28]	[0.43, 0.51]
manabo	minor (N=17)	0.70±0.03	1.38±0.05	0.26±0.01	0.51±0.01
		[0.64, 0.73]	[1.28, 1.46]	[0.24, 0.28]	[0.49, 0.54]
pulcher	minor (N=7)	0.61±0.03	1.35±0.07	0.27±0.01	0.43±0.01
		[0.57, 0.65]	[1.20, 1.41]	[0.26, 0.28]	[0.41, 0.45]
	major (N=2)	0.71±0.03	1.00±0.05	0.24±0.02	0.42±0.00
		[0.70, 0.73]	[0.97, 1.04]	[0.23, 0.25]	[0.42, 0.42]

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
raina	minor (N=16)	0.64±0.04	1.36±0.11	0.29±0.02	0.42±0.01
		[0.60, 0.74]	[1.02, 1.47]	[0.25, 0.31]	[0.40, 0.44]
	major (N=6)	0.78±0.03	0.79±0.03	0.24±0.01	0.40±0.01
		[0.73, 0.81]	[0.74, 0.81]	[0.22, 0.25]	[0.38, 0.41]
repens	minor (N=22)	0.67±0.05	0.99±0.06	0.29±0.01	0.46±0.01
		[0.62, 0.83]	[0.78, 1.06]	[0.25, 0.31]	[0.43, 0.49]
	major (N=5)	0.83±0.08	0.70±0.04	0.24±0.02	0.45±0.01
		[0.69, 0.89]	[0.67, 0.77]	[0.22, 0.27]	[0.42, 0.46]
sada	minor (N=20)	0.62±0.03	1.38±0.04	0.30±0.01	0.42±0.01
		[0.57, 0.67]	[1.30, 1.49]	[0.28, 0.33]	[0.41, 0.47]
	major (N=3)	0.72±0.02	0.77±0.01	0.22±0.00	0.43±0.00
		[0.70, 0.74]	[0.76, 0.78]	[0.21, 0.22]	[0.43, 0.44]
tanosy	minor (N=4)	0.68±0.01	1.38±0.04	0.33±0.01	0.44±0.00
		[0.67, 0.70]	[1.32, 1.41]	[0.31, 0.34]	[0.43, 0.44]
	major (N=3)	0.76±0.01	1.11±0.03	0.27±0.01	0.42±0.01
		[0.75, 0.77]	[1.08, 1.15]	[0.27, 0.28]	[0.41, 0.42]
christi	minor (N=28)	0.42±0.01	0.28±0.01	0.75±0.01	1.47±0.07
		[0.39, 0.44]	[0.25, 0.30]	[0.72, 0.77]	[1.29, 1.59]
	major (N=3)	0.44±0.02	0.24±0.00	0.76±0.01	1.15±0.03
		[0.43, 0.46]	[0.24, 0.25]	[0.75, 0.77]	[1.11, 1.18]
dromedarius	minor (N=37)	0.47±0.01	0.27±0.02	0.80±0.01	1.37±0.08
		[0.45, 0.49]	[0.23, 0.30]	[0.79, 0.83]	[1.20, 1.53]
	major (N=6)	0.47±0.00	0.26±0.03	0.79±0.01	1.18±0.05
		[0.47, 0.48]	[0.20, 0.27]	[0.78, 0.81]	[1.14, 1.27]
foersteri	minor (N=34)	0.43±0.02	0.26±0.01	0.75±0.04	1.33±0.06
		[0.41, 0.55]	[0.24, 0.29]	[0.73, 0.96]	[1.20, 1.46]
	major (N=3)	0.49±0.04	0.26±0.00	0.81±0.09	1.09±0.05
		[0.46, 0.53]	[0.25, 0.26]	[0.76, 0.92]	[1.05, 1.15]
lamosy	minor (N=20)	0.45±0.01	0.27±0.01	0.78±0.01	1.26±0.05
		[0.42, 0.47]	[0.25, 0.29]	[0.76, 0.80]	[1.19, 1.37]
	major (N=2)	0.46±0.02	0.25±0.01	0.80±0.00	1.03±0.01
		[0.45, 0.47]	[0.25, 0.26]	[0.80, 0.80]	[1.02, 1.04]
liandia	minor (N=13)	0.44±0.01	0.25±0.01	0.73±0.01	1.24±0.05
		[0.43, 0.46]	[0.24, 0.27]	[0.72, 0.77]	[1.15, 1.31]
	major (N=2)	0.48±0.02	0.24±0.00	0.75±0.01	0.97±0.05
		[0.47, 0.50]	[0.24, 0.25]	[0.74, 0.76]	[0.94, 1.00]
lubbocki	minor (N=16)	0.43±0.01	0.26±0.01	0.74±0.01	1.27±0.04
		[0.41, 0.46]	[0.24, 0.29]	[0.72, 0.76]	[1.19, 1.33]
	major (N=3)	0.47±0.01	0.24±0.02	0.76±0.00	0.98±0.07
		[0.46, 0.47]	[0.22, 0.25]	[0.75, 0.76]	[0.92, 1.06]

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
maculiventris	minor (N=51)	0.45±0.01	0.27±0.02	0.75±0.01	1.21±0.12
		[0.42, 0.49]	[0.21, 0.33]	[0.71, 0.78]	[0.86, 1.35]
	major (N=10)	0.47±0.02	0.26±0.02	0.77±0.02	1.07±0.14
		[0.43, 0.49]	[0.23, 0.30]	[0.74, 0.80]	[0.92, 1.28]
mainty	minor (N=38)	0.44±0.01	0.27±0.02	0.74±0.01	1.34±0.08
		[0.42, 0.46]	[0.22, 0.31]	[0.71, 0.78]	[1.02, 1.45]
	major (N=10)	0.45±0.01	0.25±0.02	0.75±0.01	1.18±0.17
		[0.43, 0.46]	[0.23, 0.31]	[0.73, 0.77]	[1.03, 1.49]
manabo	minor (N=17)	0.47±0.01	0.32±0.01	0.77±0.01	1.50±0.04
		[0.46, 0.50]	[0.30, 0.34]	[0.75, 0.79]	[1.42, 1.58]
pulcher	minor (N=7)	0.49±0.01	0.25±0.01	0.80±0.01	1.26±0.03
		[0.48, 0.51]	[0.24, 0.26]	[0.79, 0.81]	[1.20, 1.30]
	major (N=2)	0.51±0.01	0.24±0.01	0.81±0.00	1.04±0.04
		[0.50, 0.51]	[0.23, 0.25]	[0.80, 0.81]	[1.02, 1.07]
raina	minor (N=16)	0.43±0.01	0.31±0.01	0.77±0.02	1.26±0.09
		[0.42, 0.46]	[0.30, 0.33]	[0.71, 0.80]	[1.02, 1.37]
	major (N=6)	0.47±0.01	0.33±0.01	0.79±0.01	0.87±0.02
		[0.46, 0.48]	[0.31, 0.35]	[0.78, 0.80]	[0.84, 0.89]
repens	minor (N=22)	0.48±0.01	0.28±0.01	0.72±0.01	1.05±0.05
		[0.45, 0.50]	[0.26, 0.31]	[0.69, 0.74]	[0.90, 1.10]
	major (N=5)	0.49±0.02	0.28±0.01	0.73±0.02	0.79±0.03
		[0.47, 0.51]	[0.27, 0.29]	[0.70, 0.74]	[0.73, 0.82]
sada	minor (N=20)	0.41±0.05	0.28±0.01	0.74±0.08	1.30±0.05
		[0.38, 0.55]	[0.26, 0.30]	[0.70, 0.97]	[1.16, 1.41]
	major (N=3)	0.47±0.01	0.32±0.02	0.76±0.01	0.91±0.01
		[0.46, 0.48]	[0.30, 0.35]	[0.75, 0.77]	[0.91, 0.92]
tanosy	minor (N=4)	0.42±0.01	0.31±0.02	0.75±0.00	1.39±0.04
		[0.40, 0.43]	[0.30, 0.34]	[0.74, 0.76]	[1.36, 1.45]
	major (N=3)	0.44±0.00	0.31±0.01	0.75±0.01	1.18±0.03
		[0.43, 0.44]	[0.29, 0.32]	[0.73, 0.76]	[1.15, 1.20]
christi	minor (N=28)	1.78±0.06	0.39±0.01	0.25±0.01	*christi*
		[1.65, 1.89]	[0.36, 0.42]	[0.22, 0.28]	
	major (N=3)	1.46±0.04	0.41±0.02	0.20±0.03	
		[1.41, 1.50]	[0.40, 0.44]	[0.17, 0.22]	
dromedarius	minor (N=37)	1.74±0.08	0.46±0.01	0.24±0.02	*dromedarius*
		[1.51, 1.89]	[0.42, 0.48]	[0.20, 0.28]	
	major (N=6)	1.54±0.07	0.45±0.01	0.22±0.03	
		[1.45, 1.62]	[0.44, 0.46]	[0.19, 0.25]	
foersteri	minor (N=34)	1.73±0.09	0.38±0.03	0.24±0.02	*foersteri*
		[1.27, 1.81]	[0.35, 0.50]	[0.21, 0.27]	
	major (N=3)	1.37±0.15	0.43±0.04	0.20±0.01	
		[1.20, 1.48]	[0.40, 0.47]	[0.20, 0.21]	

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TABLE 1. (Continued)

Species	Castes	CS	CWb/CL	CW/CL	PoOC/CL
lamosy	minor (N=20)	1.79±0.03	0.44±0.01	0.29±0.01	*lamosy*
		[1.74, 1.87]	[0.41, 0.47]	[0.27, 0.31]	
	major (N=2)	1.41±0.03	0.45±0.01	0.23±0.01	
		[1.39, 1.43]	[0.44, 0.45]	[0.23, 0.24]	
liandia	minor (N=13)	1.62±0.05	0.38±0.02	0.24±0.02	*liandia*
		[1.51, 1.68]	[0.36, 0.41]	[0.20, 0.26]	
	major (N=2)	1.33±0.08	0.42±0.00	0.20±0.01	
		[1.27, 1.39]	[0.41, 0.42]	[0.19, 0.21]	
lubbocki	minor (N=16)	1.64±0.05	0.38±0.02	0.20±0.02	*lubbocki*
		[1.55, 1.74]	[0.36, 0.42]	[0.17, 0.23]	
	major (N=3)	1.32±0.06	0.43±0.02	0.18±0.01	
		[1.27, 1.38]	[0.42, 0.45]	[0.17, 0.19]	
maculiventris	minor (N=51)	1.66±0.10	0.41±0.02	0.23±0.02	*maculiventris*
		[1.34, 1.85]	[0.38, 0.44]	[0.17, 0.28]	
	major (N=10)	1.48±0.17	0.42±0.03	0.24±0.04	
		[1.34, 1.80]	[0.38, 0.46]	[0.18, 0.31]	
mainty	minor (N=38)	1.69±0.07	0.40±0.01	0.24±0.02	*mainty*
		[1.32, 1.76]	[0.36, 0.43]	[0.20, 0.28]	
	major (N=10)	1.48±0.12	0.40±0.02	0.21±0.02	
		[1.33, 1.70]	[0.37, 0.43]	[0.18, 0.24]	
manabo	minor (N=17)	1.63±0.05	0.43±0.01	0.22±0.01	*manabo*
		[1.54, 1.70]	[0.41, 0.46]	[0.19, 0.24]	
pulcher	minor (N=7)	1.76±0.06	0.47±0.01	0.24±0.02	*pulcher*
		[1.63, 1.81]	[0.45, 0.49]	[0.21, 0.25]	
	major (N=2)	1.44±0.03	0.46±0.01	0.19±0.00	
		[1.42, 1.46]	[0.45, 0.46]	[0.19, 0.19]	
raina	minor (N=16)	1.89±0.09	0.45±0.01	0.28±0.02	*raina*
		[1.62, 1.99]	[0.44, 0.47]	[0.24, 0.30]	
	major (N=6)	1.43±0.04	0.46±0.01	0.23±0.02	
		[1.37, 1.46]	[0.45, 0.47]	[0.20, 0.25]	
repens	minor (N=22)	1.66±0.05	0.38±0.01	0.22±0.01	*repens*
		[1.50, 1.74]	[0.35, 0.40]	[0.19, 0.25]	
	major (N=5)	1.37±0.06	0.41±0.01	0.22±0.01	
		[1.31, 1.45]	[0.39, 0.42]	[0.21, 0.23]	
sada	minor (N=20)	1.79±0.16	0.37±0.04	0.25±0.02	*sada*
		[1.35, 2.04]	[0.34, 0.50]	[0.23, 0.30]	
	major (N=3)	1.34±0.01	0.36±0.09	0.20±0.01	
		[1.33, 1.35]	[0.26, 0.41]	[0.19, 0.22]	
tanosy	minor (N=4)	1.81±0.05	0.41±0.01	0.28±0.01	*tanosy*
		[1.76, 1.89]	[0.40, 0.42]	[0.27, 0.30]	
	major (N=3)	1.57±0.03	0.40±0.01	0.24±0.01	
		[1.53, 1.59]	[0.40, 0.41]	[0.23, 0.26]	

Data preparation. Minor and major workers have a broken scaling relationship among the measured characters and have different allometric properties (see Rakotonirina *et al.* 2016, 2017). To address this, we used only minor workers in the multivariate statistical analysis. We used minor workers because they were more abundant in the material examined.

Generation of species hypotheses. Species hypotheses were generated using the Nest Centroid clustering (NC-clustering) technique (Seifert *et al.* 2014) via the packages CLUSTER (Maechler *et al.* 2014) and MASS (Venables & Ripley 2002), and Partitioning Algorithm based on Recursive Thresholding (PART) method via the package "clusterGenomics" (Nilsen & Lingjaerde 2013) and the function PART. The procedure followed Csősz and Fisher (2016) and Rakotonirina *et al.* (2017).

Testing species hypotheses. To validate the species recognized by exploratory analyses, the confirmatory linear discriminant analysis (LDA) was conducted repeatedly until the final classification, exhibiting the highest posterior probability values, was achieved (Csősz *et al*. 2014).

Results and discussion

Multivariate statistical analysis of morphometric data. The NC-clustering dendrogram revealed 14 clusters, also recognized by both "hclust" and "kmeans"clustering methods in the partitioning process (PART) (Fig. 1). The clusters are interpreted as 14 species.

The 14 species hypothesis proposed by the exploratory analysis was supported by the cumulative LDA, with 98.75% identification success (Table 2). Three specimens of *C. foersteri* were misidentified, two as *C. maculiventris* and one as *C. mainty*. These misidentifications may be ascribed to similar morphology displayed by the three species. Morphologically similar species frequently exhibit overlapping ranges of quantitative measurements and share qualitative morphological characters (Table 2).

Morphological diagnosis of the worker castes of the Malagasy *Camponotus* subgenus *Mayria*. As for most *Camponotus* species, minor and major worker castes exist within a colony of the subgenus *Mayria*. There are also various worker forms presenting continuous morphological variation between these two castes. The following combination of characters can be employed to reliably distinguish the subgenus *Mayria* from other Malagasy subgenera and species groups of *Camponotus.*

Minor worker

- Head elongate in full-face view, lateral margins slightly diverging posteriorly and start rounding at about posterior third of head; posterior margins more or less straight.
- Mandible triangular, basal margin as long as apical margin, which most frequently has six (or very rarely five) sharp teeth.
- Palp formula: 6,4.
- Clypeus most frequently with broadly convex anterior margin, occasionally straight (*C. dromedarius, C. lubbocki, C. pulcher*), projecting into triangular lobe (*C. liandia*). Sometimes anterior margin bordered by lamella (*C. raina, C. sada*).
- Antenna with 12 antennomeres, with elongate flagellomeres; apical antennomere slightly longer than other flagellomeres; antennal scape long, generally its distal half surpassing the posterior cephalic margin.
- Frontal lobe narrow and partially covering the antennal insertion; frontal carina S-shaped, strongly divergent posteriorly.
- Compound eye large, protruding, its posterior margin usually located about one-half to one-third of the cephalic length from the posterior margin of the head.
- Mesosoma in lateral view, ranging from strongly arched to flat or with pronotum and mesonotum weakly convex, mesonotum and propodeum almost straight.
- Promesonotal suture visible.
- Pronotum with rounded humeral angle, without sharp margination between its dorsum and lateral face.
- Mesopleuron and propodeal surface together clearly longer than lateral portion of pronotum in lateral view.
- Metapleural gland lacking.
- Metanotal groove inconspicuous to clearly visible.

- Procoxa of normal size, maximum width as large as, or smaller than the width of mesopleuron.
- Middle and hind tibiae with single pectinate spur.
- Petiolar node laterally narrow and low.
- Gaster generally elongate and narrow, anteriorly low and short.
- Sculpture varying from smooth and shiny to finely and densely imbricate.

TABLE 2. Classification matrix of species showing the identification success (percentage), the observed identification (rows) against the predicted identification (columns) based on cumulative LDA. Numbers in the matrix are specimen counts.

Observed species	Predicted species														
	christi	*dromedarius*	*foersteri*	*lamosy*	*liandia*	*lubbocki*	*maculiventris*	*mainty*	*manabo*	*pulcher*	*raina*	*repens*	*sada*	*tanosy*	Identification success (%)
christi	28	0	0	0	0	0	0	0	0	0	0	0	0	0	100
dromedarius	0	37	0	0	0	0	0	0	0	0	0	0	0	0	100
foersteri	0	0	31	0	0	0	2	1	0	0	0	0	0	0	91.18
lamosy	0	0	0	20	0	0	0	0	0	0	0	0	0	0	100
liandia	0	0	0	0	13	0	0	0	0	0	0	0	0	0	100
lubbocki	0	0	0	0	0	16	0	0	0	0	0	0	0	0	100
maculiventris	0	0	0	0	0	0	53	0	0	0	0	0	0	0	100
mainty	0	0	1	0	0	0	0	32	0	0	0	0	0	0	96.97
manabo	0	0	0	0	0	0	0	0	17	0	0	0	0	0	100
pulcher	0	0	0	0	0	0	0	0	0	7	0	0	0	0	100
raina	0	0	0	0	0	0	0	0	0	0	16	0	0	0	100
repens	0	0	0	0	0	0	0	0	0	0	0	22	0	0	100
sada	0	0	0	0	0	0	0	0	0	0	0	0	20	0	100
tanosy	0	0	0	0	0	0	0	0	0	0	0	0	0	4	100
Total	28	37	32	20	13	16	55	33	17	7	16	22	20	4	98.75

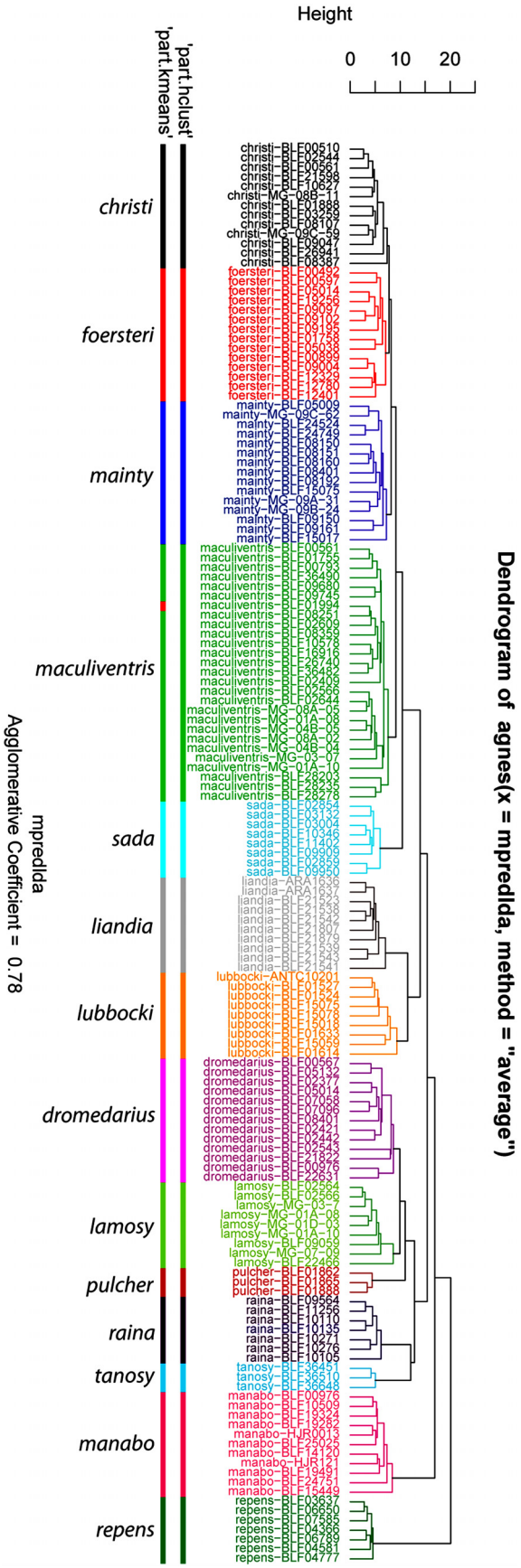


FIGURE 1. Dendrogram of NC-PART-clustering of the 14 species recognized in the *Camponotus* subgenus *Mayria*. Color bars represent the species hypothesis generated by PART using "hclust" and "kmeans" clustering methods. The corresponding label on the tip of the branch (the species name followed by the collection code) is given the same color code.

Major worker

Major worker similar to minor worker, but differing by the following distinctive traits: larger head and mesosoma, antennal scape shorter, at most apical third extending beyond posterior margin of head, petiolar node much higher than long (flattened anteroposteriorly), lateral portion of head with scattered shallow punctures superimposed on finely and densely imbricate sculpture (*C. lubbocki, C. liandia,* and *C. repens*).

Synoptic list of the Malagasy *Camponotus* subgenus *Mayria* recognized in the study

christi Forel, 1886b
dromedarius Forel, 1891
foersteri Forel, 1886b **stat. n.**
= *camboui* Forel, 1891 **syn. n.**
= *christi ambustus* Forel, 1892 **syn. n.**
= *christi ferrugineus* Emery, 1899 **syn. n.**
= *pictipes* Forel, 1891 **syn. n**
lamosy Rakotonirina & Fisher, **sp. n.**
liandia Rakotonirina & Fisher, **sp. n.**
lubbocki Forel, 1886b
= *lubbocki christoides* Forel, 1891 **syn. n.**
= *lubbocki rectus* Forel, 1891 **syn. n.**
maculiventris Emery, 1895 **stat. n.**
mainty Rakotonirina & Fisher, **sp. n.**
manabo Rakotonirina & Fisher, **sp. n.**
pulcher Forel, 1892 **stat. n.**
raina Rakotonirina & Fisher, **sp. n.**
repens Forel, 1897
sada Rakotonirina & Fisher, **sp. n.**
tanosy Rakotonirina & Fisher, **sp. n**

Identification key to worker caste of the Malagasy *Camponotus* subgenus *Mayria*

1. Median portion of clypeus with longitudinal carina (Fig. 2A) 2
- Median portion of clypeus without longitudinal carina (Fig. 2B). 6

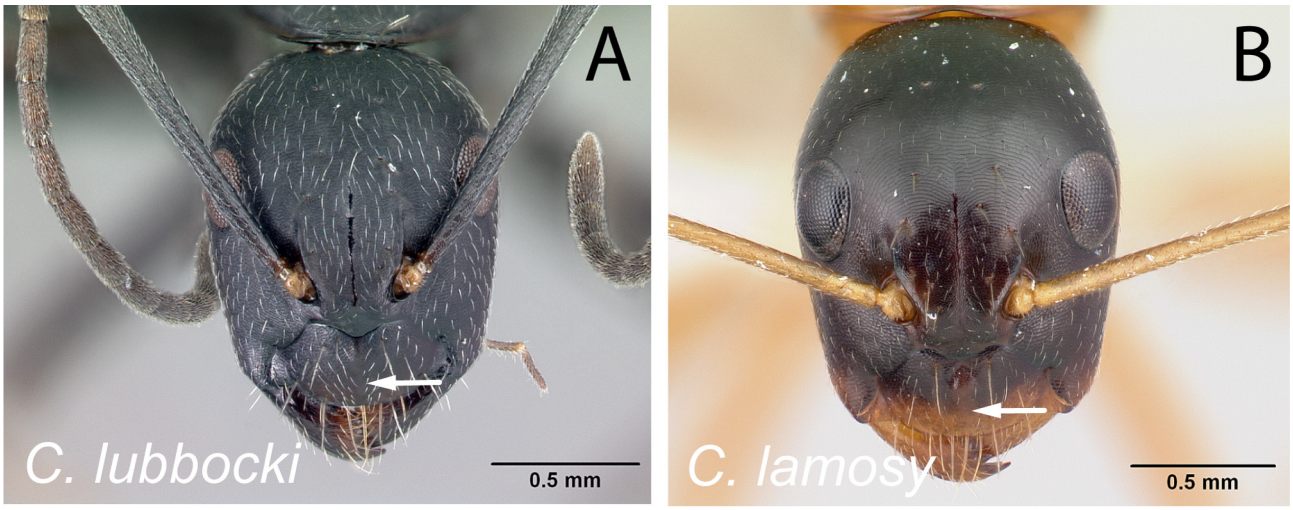


FIGURE 2. Head in full-face view. A: *C. lubbocki* (CASENT0486998). B: *C. lamosy* (CASENT0408976).

2. Smaller species (minor: CS: 0.70–1.26; major: 1.20–1.67); distal portion of procoxa white (Fig. 3A). 3
- Larger species (minor: CS: 0.73–1.37; major: CS: 1.39–2.1); procoxa without white patch (Fig. 3B) 4

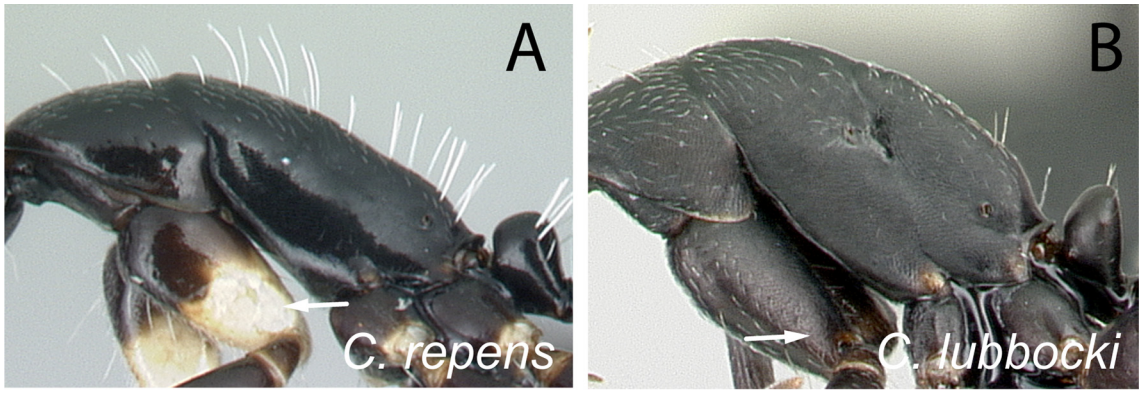


FIGURE 3. Mesosoma and petiolar node in lateral view. A: *C. repens* (CASENT0217300). B: *C. lubbocki* (CASENT0486998).

3. Dorsum of mesosoma covered with numerous slender erect hairs and elongate appressed hairs; in lateral view, petiolar node higher than long (Fig. 4A). . . . . ***repens***
- Pronotum, junction of dorsum and declivity surface of propodeum and posterodorsal margin of petiole each with one pair of elongate, stout erect hairs; a few short appressed hairs present on dorsum of mesosoma; in lateral view, petiolar node longer than high (Fig. 4B) . . . . . ***raina***

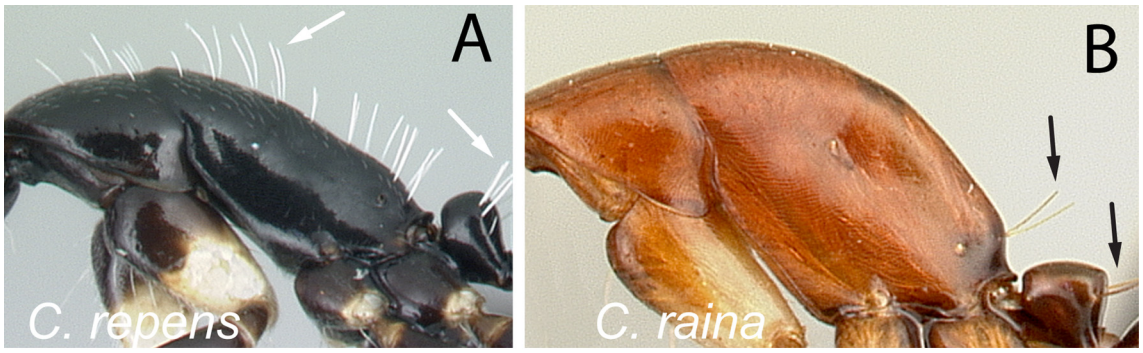


FIGURE 4. Mesosoma and petiolar node in lateral view. A: *C. repens* (CASENT0217300). B: *C. raina* (CASENT0499051).

4. In lateral view, mesosoma short and high; dorsal margin of petiolar node convex; dorsum of mesosoma covered with numerous (15-20) long erect hairs and a scattered short pubescence (Fig. 5A) . . . . . ***manabo***
- In lateral view, mesosoma long and low, petiolar node tapered dorsally; dorsum of mesosoma covered with few (6-10) short erect hairs and abundant long pubescence (Fig. 5B). 5

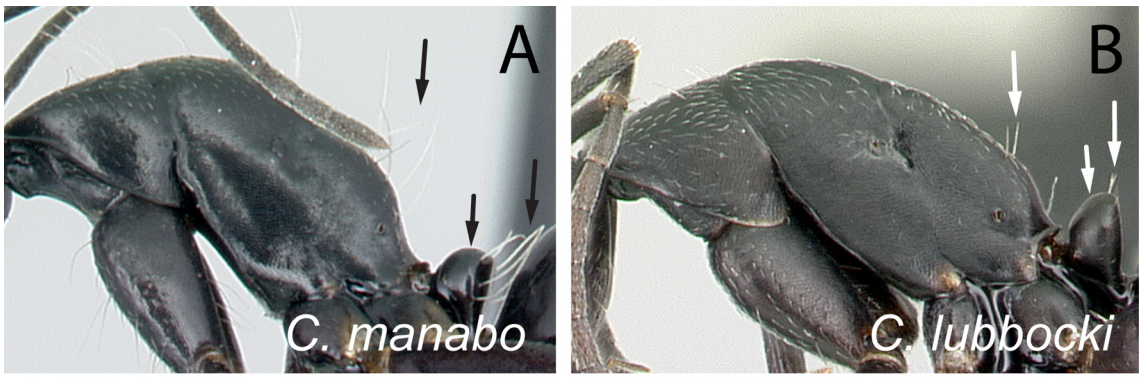


FIGURE 5. Mesosoma and petiolar node in lateral view. A: *C. manabo* (CASENT0496383). B: *C. lubbocki* (CASENT0486998).

5. Anteromedian clypeal margin projecting into an obtusely triangular lobe (Fig. 6A) . . . . . ***liandia***
- Anteromedian clypeal margin broadly rounded, almost truncate (Fig. 6B) . . . . . ***lubbocki***

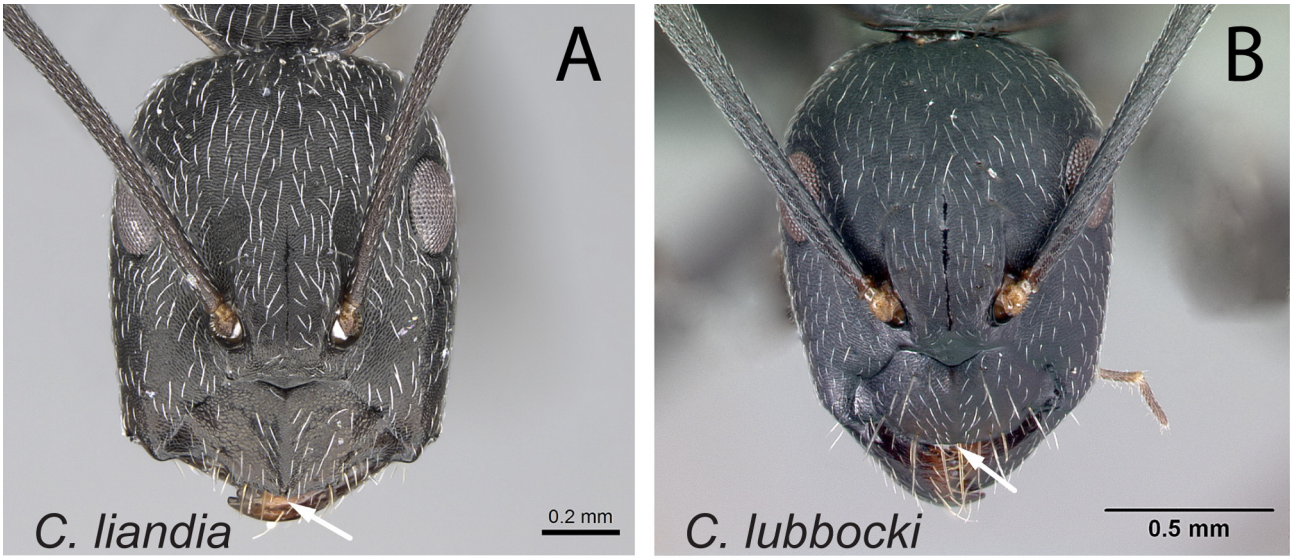


FIGURE 6. Head in full-face view. A: *C. liandia* (CASENT0803904). B: *C. lubbocki* (CASENT0486998).

6. Apical margin of mandible armed with five teeth (Fig. 7A). . . . . ***tanosy***
- Apical margin of mandible armed with six teeth (Fig. 7B). 7

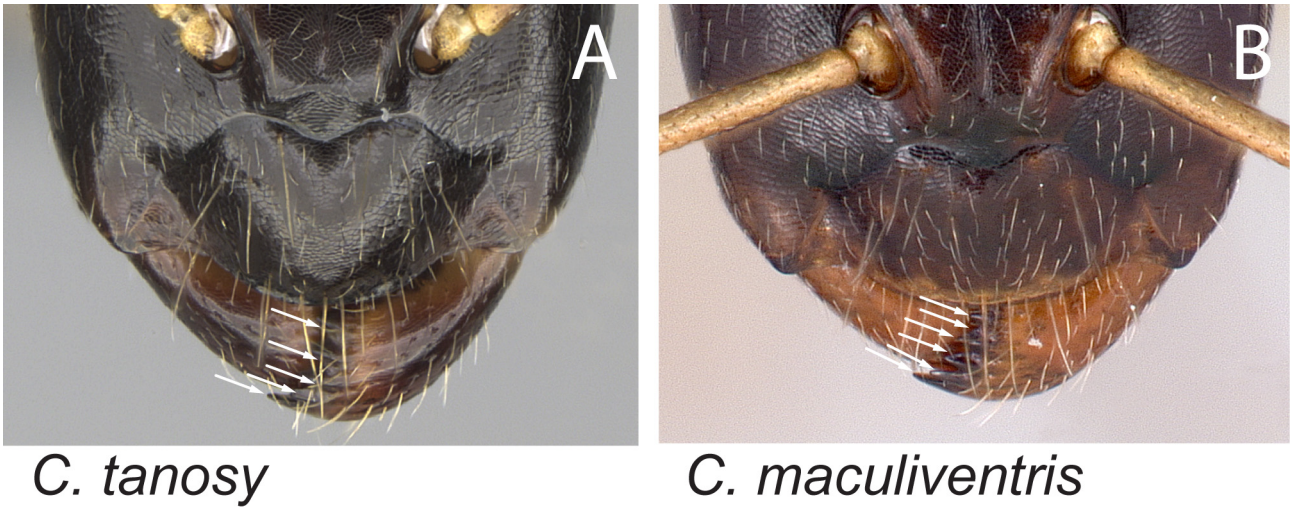


FIGURE 7. Anterior portion of the head in full-face view. A: *C. tanosy* (CASENT0803890). B: *C. maculiventris* (CASENT0082042).

7. Anteromedian margin of clypeus bordered by a lamella; in full-face view, head distinctly longer than broad (CWb/CL: minor: 0.68±0.01; major: 0.89±0.001) (Fig. 8A); in lateral view, junction of dorsal and declivity surfaces of propodeum broadly rounded . . . . . ***sada***
- Anteromedian margin of clypeus not bordered by a lamella; in full-face view, head not strongly longer than broad (CWb/CL: minor: 0.76±0.03–0.84±0.02; major: 0.93±0.04–1.01±0.02) (Fig. 8B); in lateral view, junction of propodeal dorsum and declivity surface with a distinct angle 8

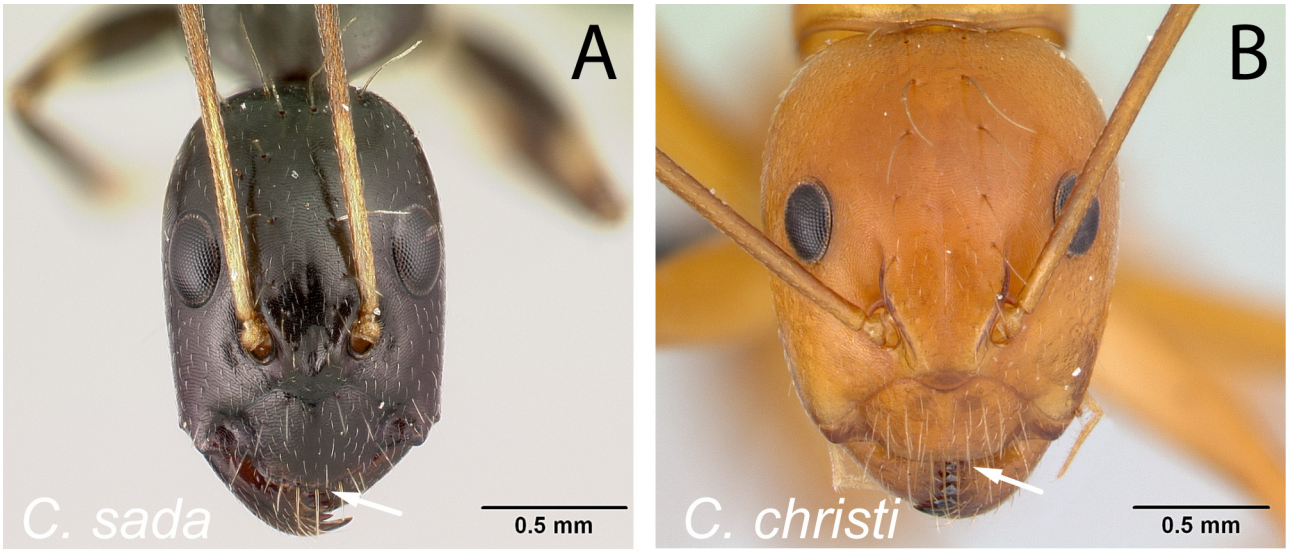


FIGURE 8. Head in full-face view. A: *C. sada* (CASENT0498916). B: *C. christi* (CASENT0129791).

8. In lateral view, mesosoma short and high, its dorsal outline continuously arched and dome-like in structure; propodeal declivity inclined posteriorly (Fig. 9A). 9
- In lateral view, mesosoma long and low, its dorsal outline not dome-like in structure; propodeal declivity inclined anteriorly (Fig. 9B) 11

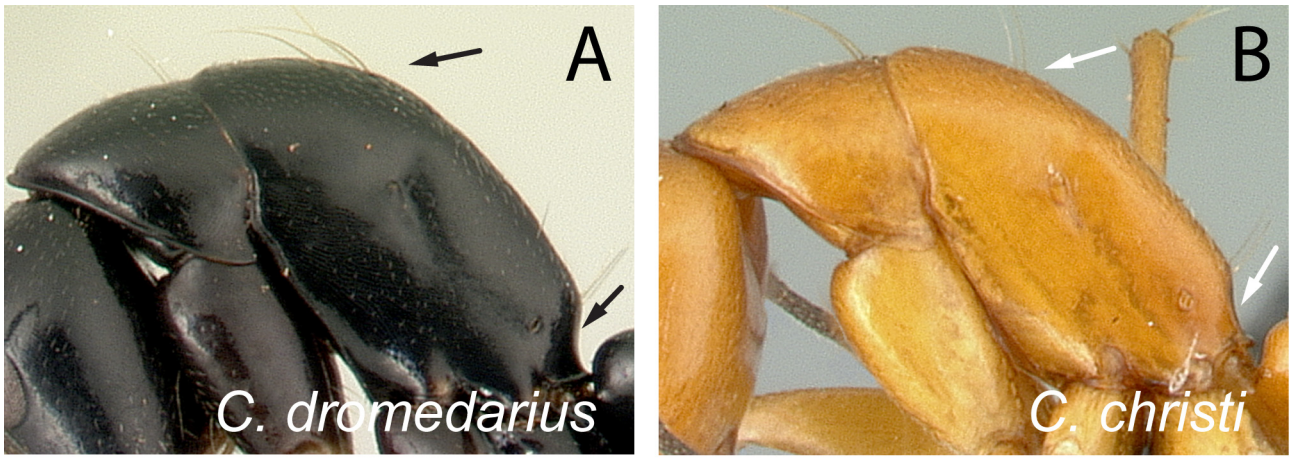


FIGURE 9. Mesosoma in lateral view. A: *C. dromedarius* (CASENT0496817). B: *C. christi* (CASENT0129791).

9. In lateral view, propodeal dorsum slightly excised medially, petiole node longer than high (Fig. 10A) . . . . . ***lamosy***
- In lateral view, propodeal dorsum smooth, without excision or concavity (Fig. 10B); petiole node as long as high or higher than long 10

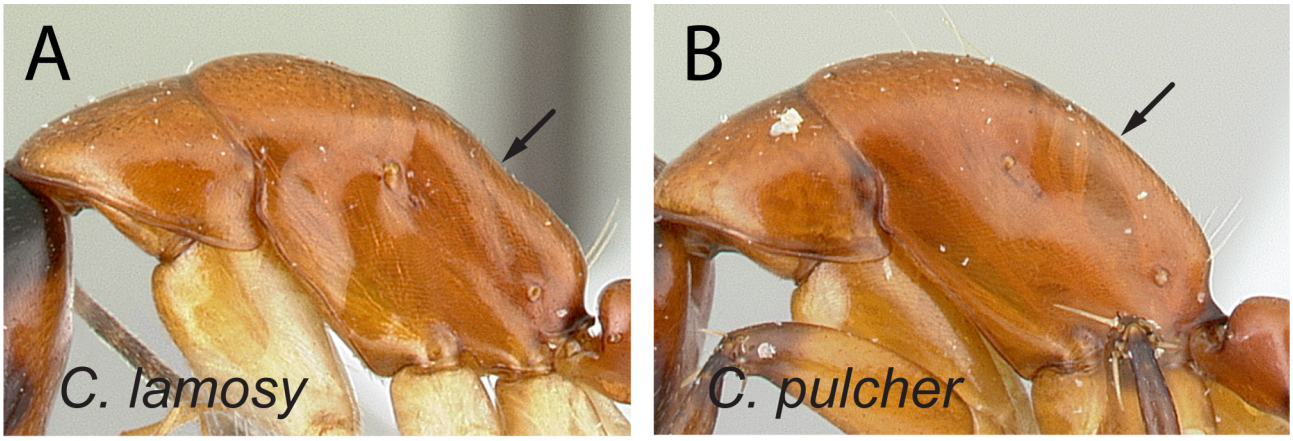


FIGURE 10. Mesosoma in lateral view. A: *C. lamosy* (CASENT0408976). B: *C. pulcher* (CASENT0191639).

10. Larger species (CS: minor: 1.22±0.10; major: 1.64±0.12); in lateral view, petiole node distinctly higher than long (Fig. 11A); anteromedian margin of clypeus broadly convex (Fig. 16B) . . . . . ***dromedarius***
- Smaller species (CS: minor: 1.05±0.09; major: 1.50±0.11); in lateral view, petiole node as long as high (Fig. 11B); anteromedian margin of clypeus slightly concave medially (Fig. 30B) . . . . . ***pulcher***

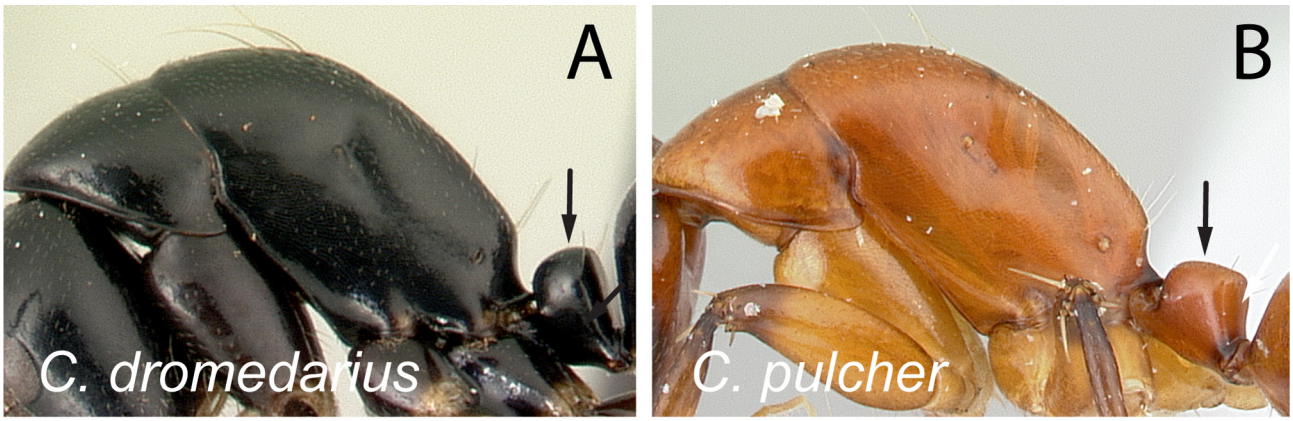


FIGURE 11. Mesosoma and petiole node in lateral view. A: *C. dromedarius* (CASENT0496817). B: *C. pulcher* (CASENT0191639).

11. Color of legs as the same as color of body, trochanters and distal portions of coxae yellow, reddish-black or dark brown; petiole node flattened anteroposteriorly (Fig. 12A, 12B) 12
- Legs with at least trochanters and distal portions of coxae yellowish to white, not as the same as color of body; petiole node not flattened anteroposteriorly, its dorsal margin distinctly broadly convex (Fig. 12C). 13

FIGURE 12. Head, mesosoma and petiolar node in lateral view. A: *C. christi* (CASENT0129791). B: *C. mainty* (CASENT0487002). C: *C. foersteri* (CASENT0179450).

12. Body entirely yellow to light brown, antenna becoming dark brown toward its apex (Fig. 13A) . . . . . ***christi***
- Body entirely or mostly black to reddish-black; antenna brown to dark brown basally and becoming dark brown to black toward its apex (Fig. 13B). . . . . ***mainty***

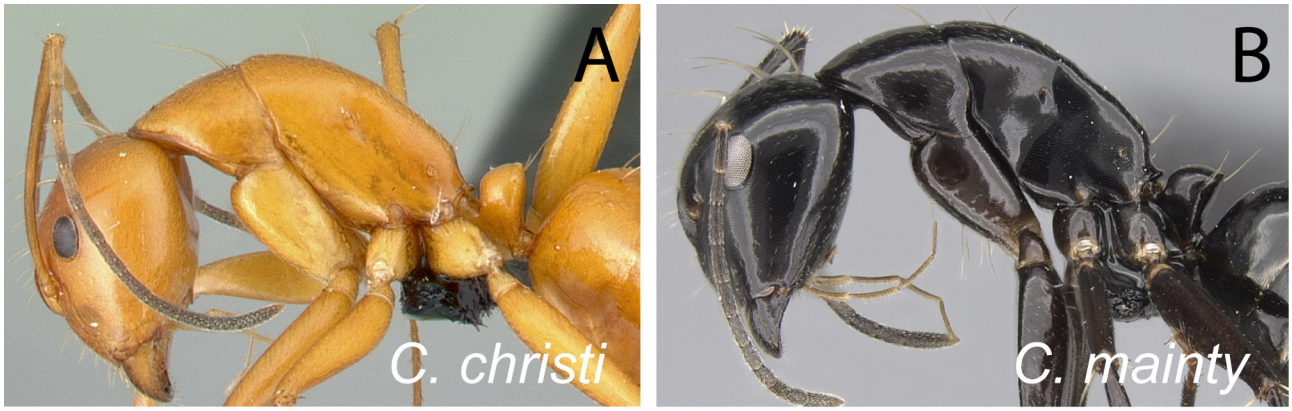


FIGURE 13. Head, mesosoma, petiolar node and part of the first gastral segment in lateral view. A: *C. christi* (CASENT0129791). B: *C. mainty* (CASENT0497845).

13. In lateral view, length of posterior portion of propodeal dorsum measured from the end of line connecting anteriormost point of pronotal shield and metathoracic spiracle as long as height of declivity (Fig. 14A); hind tibia shorter than hind femur; hind tibia shorter (HTL/CS: minor: 1.21±0.12; major: 1.07±0.14). . . . . ***maculiventris***
- In lateral view, length of posterior portion of propodeal dorsum measured from the end of line connecting anteriormost point of pronotal shield and metathoracic spiracle roughly twice as long as height of declivity (Fig. 14B); hind tibia as long as hind femur; hind tibia longer (HTL/CS: minor: 1.33±0.06; major: 1.09±0.05) . . . . . ***foersteri***

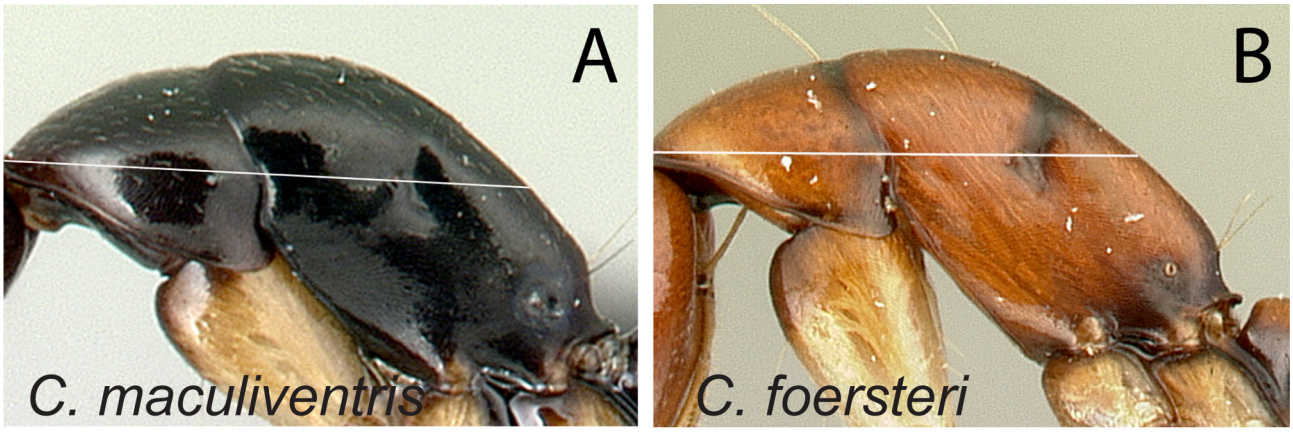


FIGURE 14. Mesosoma in lateral view. A: *C. maculiventris* (CASENT0082042). B: *C. foersteri* (CASENT0179450).

Species accounts of the Malagasy *Camponotus* subgenus *Mayria*

Camponotus christi Forel
(Figures 8B, 9B, 12A, 13A, 15, 21)

Camponotus christi Forel, 1886b: 184. Lectotype minor worker, **present designation**, Centre de Madagascar [Ambatomanjaka, Miarinarivo, -18.766947, 46.869107, 1344 m] (Hildebrandt), AntWeb CASENT0101544 (MHNG). Paralectotype: 1 minor worker with same data as lectotype but specimen coded: CASENT0101435 (Camboué) (MNHN) [examined]. [Combination in *Camponotus (Myrmocamelus):* Forel, 1914: 270; in *Camponotus (Myrmosaga):* Wheeler, 1922: 1045; in *Camponotus (Mayria):* Emery, 1925: 122; Bolton, 1995: 92, 131].

Diagnosis. Median portion of clypeus without longitudinal carina; mandible with six teeth; anteromedian margin of clypeus not bordered by a lamella; in lateral view, mesosoma long and low, its dorsal outline not a dome-like

structure; propodeal declivity inclined anteriorly; body color entirely yellow to light brown, legs with same color as body.

FIGURE 15. *Camponotus christi* minor worker CASENT0129791. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Minor worker. In full-face view, head elongate (CWb/CL: 0.76±0.03; 0.69–0.83), lateral margins straight and more or less parallel to each other, rounding broadly to the slightly, medially excised posterior

margin. Anterior clypeal margin straight, with broadly angulate junction to lateral margin; median longitudinal carina absent. Eyes not breaking lateral outlines of head; their posterior margin located approximately at posterior third portion of head (PoOc/CL: 0.34±0.01; 0.31–0.36). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, more than its distal half extending beyond posterior cephalic border. In lateral view, pronotum and anterior half of mesonotum forming feeble convexity, posterior half of mesonotum and propodeal dorsum straight and long, joining declivity surface with noticeable angle. Propodeal dorsum roughly three times as long as height of declivity; propodeal spiracle circular. Petiolar node as high as or higher than long, its dorsal margin rounding to anterior face and joining posterior face at an angle.

Dorsum of head covered with numerous yellowish, elongate, erect hairs; pronotum and mesonotum each with a pair of erect hairs, propodeum with a pair of hairs found on junction to declivity; sparse, short pubescence present on dorsum of body. Body color entirely yellowish-orange to orange-brown and funicular segments becoming dark brown toward the apex.

Major worker. Differing from minor worker in the following characters: enlarged head, with markedly concave posterior margin; apical third of antennal scape surpassing posterior cephalic margin; robust mesosoma, metanotum distinctly visible, propodeal dorsum rounding to declivity and twice as long as height of declivity; petiolar node tapering dorsally. More pairs of erect hairs on junction of propodeal dorsum and declivity and on posterodorsal margin of petiolar node.

Discussion. Workers of *C. christi* are similar to those of *C. mainty, C. foersteri* and *C. maculiventris* in that their clypeus lacks a median longitudinal carina, and in lateral view, their mesosoma is long and low. However, *C. christi* workers are easily separable by their entirely yellow to light brown body color and legs. In the members of *C. mainty*, their body is entirely black to reddish-black. In the two latter species, at least the trochanters and the distal portion of the coxa are yellowish to white.

The cluster of *C. christi* shown by the dendrogram of NC-PART clustering is confirmed by the cumulative LDA at 100% identification success, indicating the support of the species hypothesized by qualitative morphology-based taxonomy. The cluster for *C. christi* is located next to that of *C. foersteri* and *C. mainty*, which suggests that the three species are more similar to each other than other species. This finding corroborates their close morphological similarity as detected by the qualitative analysis.

Distribution and biology. *Camponotus christi* is widely distributed across Madagascar. It occupies sclerophyll forests of the central high plateau, tropical dry forests in the west to coastal scrub and littoral rainforests, as well as montane rainforests in the east. While its workers have been found foraging on the forest floor and the lower portions of vegetation, their nest sites have been located in root mats in the ground layer, rotten logs, rotting tree stumps, rotten pockets above the ground, dead branches and bamboo above the ground, and in canopy moss and leaf litter.

Additional material examined. 'Andrangoloaka], (Sikora) (MHNG); [antananarivo, Museum Paris, Grandidier 1893], (Camboué) (MNHN); [Divers, tous les Divers sont de la Forêt d'Andrangoloaka, 20, Museum Paris, Grandidier 1899] (MNHN); [Forêt d'Analamanita Province Antananarivo], (Camboué) (MHNG); 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m, -18.47333, 47.96, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Analamanga Region, District of Ankazobe, Ambohitantely, 46 km NE of Ankazobe, 701 m, -18.198, 47.2815, sclerophyll forest, (Mike, Rinha) (CASC); Forêt de galerie, Andranorovitra, 24.0 km NNE Ankazobe, 1491 m, -18.11243, 47.19757, disturbed gallery montane forest, (B.L. Fisher *et al.*) (CASC); Mandraka, 1312 m, -18.91813, 47.91717, montane rainforest, (B.L. Fisher *et al.*) (CASC); Mandraka Park, 1360 m, -18.9019, 47.90786, montane shrubland, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale d'Ambohitantely, Forêt d Ambohitantely, 20.9 km 72° NE d Ankazobe, 1410 m, -18.22528, 47.28683, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale d'Ambohitantely, 1580 m, -18.18762, 47.28576, montane forest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale d'Ambohitantely, 1490 m, -18.22444, 47.2774, montane forest, (B.L. Fisher *et al.*) (CASC); Tananarive, (Waterlot) (MNHN); Province **Antsiranana:** [Diego Suarez], (Ch. Alluaud) (MHNG); 11.0 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1565 m, -14.75, 49.45, montane rainforest, (B.L. Fisher) (CASC); 6.5 km SSW Befingotra, Réserve Anjanaharibe-Sud, 875 m, -14.75, 49.5, rainforest, (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1280 m, -14.75, 49.46667, montane rainforest, (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1200 m, -14.75, 49.46667, montane rainforest, (B.L. Fisher) (CASC); Ampasindava, Andranomatavy Forest, 543 m, -13.66296, 47.97936, disturbed dry forest, (B.L. Fisher *et al.*) (CASC); Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, -

13.79861, 48.16167, rainforest, (Fisher, Griswold *et al.*) (CASC); Antsiranana II Pref: Antsahampano S.-Pref: Montagne d'Ambre. Site MD1, 1049 m, -12.52765, 49.17235, in *Commelina* regrowth on path next to degraded primary riparian rainforest, (D. Lees, R. Ranaivosolo & P. Razafindraibe) (CASC); Betaolana Forest, along Bekona River, 880 m, -14.52996, 49.44039, rainforest, (B.L. Fisher *et al.*) (CASC); Forêt de Binara, 9.1 km 233° SW Daraina, 725 m, -13.26333, 49.60333, rainforest, (B.L. Fisher) (CASC); Galoko chain, Mont Galoko, 520 m, -13.58487, 48.71818, rainforest, (B.L. Fisher *et al.*) (CASC); Galoko chain, Mont Galoko, 980 m, -13.5888, 48.72864, montane forest, (B.L. Fisher *et al.*) (CASC); Galoko chain, Mont Galoko, 1100 m, -13.59358, 48.73157, montane forest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 415 m, -14.17066, 49.95409, rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 715 m, -14.16666, 49.95, rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 390 m, -14.10295, 50.01984, rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 715 m, -14.16666, 49.95, rainforest, (B.L. Fisher *et al.*) (CASC); Montagne d'Ambre National Park, Roussette Camp 7 km SW Park entrance, 960 m, -12.51444, 49.18139, rainforest, (Mike, Frank, Rin'ha) (CASC); Parc National de Marojejy, 25.7 km 32° NNE Andapa, 10.3 km 314° NW Manantenina, 1575 m, -14.445, 49.74167, montane rainforest, (B.L. Fisher) (CASC); Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 1325 m, -14.44333, 49.74333, montane rainforest, (B.L. Fisher) (CASC); Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, -14.435, 49.76, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Montagne d'Ambre, 1100 m, -12.52306, 49.17901, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 925 m, -12.53444, 49.1795, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Parc National Montagne d'Ambre, Mahasarika, 1135 m, -12.53176, 49.17662, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Montagne d'Ambre, Roussettes, 1025 m, -12.52574, 49.17238, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Manongarivo, 12.8 km 228° SW Antanambao, 780 m, -13.97667, 48.42333, rainforest, (B.L. Fisher) (CASC); SAVA Region, District of Sambava, Marojejy National Park, 5 km W of Manantenina village, 1st Camp site (Mantella), 487 m, -14.43817, 49.774, Low altitude rainforest, (Rin'ha, Mike) (CASC); 3 km W Sakalava Beach [white dunes site], 40 m, -12.28617, 49.36667, white dunes in littoral forest, (Harin'Hala, Irwin, Schlinger) (CASC); Montaigne Français, 150 m, -12.325, 49.33333, along forested limestone ridge, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [Petit Lac road], 1125 m, -12.52028, 49.17917, rainforest, (R. Harin'Hala) (CASC); Sakalava Beach [vegetated beach dunes], 10 m, -12.26278, 49.3975, across sandy trail in dwarf littoral forest, (R. Harin'Hala) (CASC); Province **Fianarantsoa:** [Imerina], (Camboué) (MHNG); [Nosi be Imerina], (Sikora) (MHNG); 3 km W Ranomafana, nr. Ifandiana, 950 m, -21.25, 47.41667, rainforest, (P.S. Ward) (PSWC); 38 km S Ambalavao, Réserve Andringitra, 1680 m, -22.2, 46.96667, montane rainforest, (B.L. Fisher) (CASC); 40 km S Ambalavao, Réserve Andringitra, 1275 m, -22.21667, 46.96667, montane rainforest, (B.L. Fisher) (CASC); 7.6 km 122º Kianjavato, Forêt Classée Vatovavy, 175 m, -21.4, 47.94, rainforest, (B.L. Fisher *et al.*) (CASC); 8.0 km NE Ivohibe, 1200 m, -22.42167, 46.89833, montane rainforest, (B.L. Fisher & Sylvain) (CASC); 9.0 km NE Ivohibe, 900 m, -22.42667, 46.93833, rainforest, (B.L. Fisher & Sylvain) (CASC); Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 1020 m, -21.2665, 47.42017, mixed tropical forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Fitovavy Fitovinany Region, District of Ifanadiana Belle vue area1200 m S of Ranomafana National Park entrance, 1018 m, -21.2665, 47.42017, rainforest, (Rin'ha, Mike) (CASC); Fitovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, 1127 m, -21.25083, 47.40717, forest edge, open area, (Rin'ha, Mike) (CASC); Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 1550 m, -20.59333, 46.56333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Forêt de Vevembe, 66.6 km 293° Farafangana, 600 m, -22.791, 47.18183, rainforest, transition to montane forest, (B.L. Fisher *et al.*) (CASC); JIRAMA water works near river, Ranomafana National Park, Fianarantsoa Prov., 690 m, -21.2485, 47.45217, open area near stream, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Réserve Spéciale Manombo, 32 km SE of Farafangana, 36 m, -23.02183, 47.72, Lowland rainforest, (Rin'ha, Mike) (CASC); Miandritsara Forest, 40 km S of Ambositra, 822 m, -20.79267, 47.17567, Low altitude rainforest, (Rin'ha, Mike) (CASC); Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, 940 m, -23.83517, 46.96367, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1250 m, -23.84083, 46.9575, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 1100 m, -21.29, 47.43333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale Ivohibe 8.0 km E Ivohibe, 1200 m, -22.48333, 46.96833, montane rainforest, (B.L. Fisher & Sylvain) (CASC); Réserve Spéciale Ivohibe, 7.5 km ENE Ivohibe, 900 m, -22.47, 46.96, rainforest, (B.L.

Fisher & Sylvain) (CASC); Réserve Spéciale Manombo 24.5 km 228° Farafangana, 30 m, -23.01583, 47.719, rainforest, (B.L. Fisher *et al.*) (CASC); radio tower, Ranomafana National Park, Fianarantsoa Prov., 1130 m, -21.25083, 47.40717, forest edge, mixed tropical forest, open area, (M. Irwin, R. Harin'Hala) (CASC); Ranomafana National Park, Talatakely area, 0.4 km WSW of Park Entrance, 900 m, -21.41667, 47.68333, mixed tropical forest, (D. H. & K.M. Kavanaugh) (CASC); stream area, 900 m E of Isalo National Park Interpretive Center, Fianarantsoa Prov., 750 m, -22.62667, 45.35817, open area near stream, (R. Harin'Hala) (CASC); Vohiparara, -21.23333, 47.36667, (A. Pauly) (CASC); Vohiparara broken bridge, Fianarantsoa Prov., 1110 m, -21.22617, 47.36983, high altitude rainforest, (R. Harin'Hala) (CASC); Province **Mahajanga:** Forêt de Tsimembo, 8.7 km 336° NNW Soatana, 20 m, -19.02139, 44.44067, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m, -16.28322, 48.81443, transition humid forest, (B.L. Fisher *et al.*) (CASC); Region Sofia, Bemanevika, 1606 m, -14.337, 48.58874, montane rainforest, (B.L. Fisher *et al.*) (CASC); Region Sofia, Bemanevika, 1657 m, -14.32826, 48.58406, montane rainforest, (B.L. Fisher *et al.*) (CASC); Province **Toamasina:** Baie d'Antongil (Mocquerys) (MSNG); 19 km ESE Maroantsetra, 250 m, -15.48333, 49.9, rainforest, (P.S. Ward) (PSWC); 1 km SSW Andasibe (= Perinet), 920 m, -18.93333, 48.41667, rainforest, (P.S. Ward) (PSWC); 5.3 km SSE Ambanizana, Andranobe, 600 m, -15.66667, 49.96667, rainforest, (B.L. Fisher) (CASC); 5.3 km SSE Ambanizana, Andranobe, 425 m, -15.67133, 49.97395, rainforest, (B.L. Fisher) (CASC); 6.3 km S Ambanizana, Andranobe, 25 m, -15.6813, 49.958, rainforest, (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, 825 m, -15.58506, 50.00952, rainforest, (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, 1000 m, -15.56667, 50, montane rainforest, (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, 1080 m, -15.56667, 50, montane rainforest, (B.L. Fisher) (CASC); 6 km ESE Andasibe (= Perinet), 900 m, -18.95, 48.46667, rainforest, (P.S. Ward) (PSWC); 7 SE Andasibe National Park Headquarters, 1050 m, -18.96278, 48.45267, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); Ambalahasina, 62.4 km 19° Toamasina, 15 m, -17.59452, 49.46785, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Ambatovy, 12.4 km NE Moramanga, 1010 m, -18.84963, 48.2947, montane rainforest, (B.L. Fisher *et al.*) (CASC); Ambatovy, 12.4 km NE Moramanga, 1000 m, -18.84773, 48.29568, montane rainforest, (B.L. Fisher *et al.*) (CASC); Ambatovy, 12.4 km NE Moramanga, 1080 m, -18.83937, 48.30842, montane rainforest, (B.L. Fisher *et al.*) (CASC); Analamay, 1068 m, -18.80623, 48.33707, montane rainforest, (Malagasy ant team) (CASC); Andasibe National Park, botanic garden near entrance, west of ANGAP office, 1025 m, -18.92639, 48.40783, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); Ankerana, 865 m, -18.40062, 48.81311, rainforest, (B.L. Fisher *et al.*) (CASC); Ankerana, 750 m, -18.40829, 48.82107, rainforest, (B.L. Fisher *et al.*) (CASC); Ankerana, 1035 m, -18.4017, 48.80605, montane forest, (B.L. Fisher *et al.*) (CASC); Bevolota 17.1 km N Andasibe, 995 m, -18.77071, 48.43164, montane rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1016 m, -18.79944, 48.40375, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1013 m, -18.80388, 48.40506, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1064 m, -18.80398, 48.40358, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 960 m, -18.80438, 48.40735, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 1044 m, -18.76087, 48.37128, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 983 m, -18.76131, 48.36437, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 918 m, -18.77898, 48.36375, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 983 m, -18.76131, 48.36437, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 984 m, -18.76369, 48.4203, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1039 m, -18.76465, 48.41938, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1018 m, -18.75737, 48.42302, rainforest, (B.L. Fisher *et al.*) (CASC); F.C. Andriantantely, 530 m, -18.695, 48.81333, rainforest, (H.J. Ratsirarson) (CASC); F.C. Didy, 960 m, -18.19833, 48.57833, rainforest, (H.J. Ratsirarson) (CASC); F.C. Sandranantitra, 450 m, -18.04833, 49.09167, rainforest, (H.J. Ratsirarson) (CASC); Forêt Ambatovy, 14.3 km 57° Moramanga, 1075 m, -18.85083, 48.32, montane rainforest, (Malagasy ant team) (CASC); Manakambahiny Atsinanana, -17.75, 48.71667, Primary forest, (A. Pauly) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, -15.28833, 49.54833, rainforest, (Fisher, Griswold *et al.*)

(CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, -15.18833, 49.615, rainforest, (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m, -15.17833, 49.635, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Nosy Mangabe, 300 m, -15.5, 49.76667, rainforest, (P.S. Ward) (PSWC); Nosy Mangabe, 5 m, -15.5, 49.76667, littoral vegetation, (P.S. Ward) (PSWC); Nosy Mangabe, 7.43 km S Maroantsetra, 3 m, -15.4973, 49.76223, littoral rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Masoala, 39.4 km 150° SSE Maroantsetra, 200 m, -15.71, 49.97, rainforest, (B.L. Fisher, H.J. Ratsirarson) (CASC); Parc National Mananara-Nord, 7.1 km 261° Antanambe, 225 m, -16.455, 49.7875, rainforest, (B.L. Fisher *et al.*) (CASC); Parcelle K7 Tampolo, 10 m, -17.28333, 49.41667, littoral forest, (Malagasy ant team) (CASC); Réserve Nationale Integrale Betampona, Betampona 35.1 km NW Toamasina, 500 m, -17.91801, 49.20074, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 450 m, -16.77274, 49.26551, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 475 m, -16.76912, 49.26704, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 520 m, -16.7633, 49.26692, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 470 m, -16.7702, 49.26638, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 360 m, -16.81753, 49.29498, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 425 m, -16.8162, 49.29202, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 460 m, -16.81209, 49.29216, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 480 m, -16.80561, 49.29507, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Ambodiriana, 4.8 km 306°Manompana, along Manompana river, 125 m, -16.67233, 49.70117, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Perinet-Analamazaotra, 950 m, -18.93333, 48.43333, rainforest, (D. M. O lson) (PSWC); Réserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 390 m, -17.924, 49.19967, rainforest, (B.L. Fisher *et al.*) (CASC); S.F. Tampolo, 10 km NNE Fenoarivo Atn., 10 m, -17.2825, 49.43, littoral rainforest, (B.L. Fisher) (CASC); Tampolo, Masoala Peninsula, 40.4 km 154° SSE Maroantsetra, 30 m, -15.73, 49.96, rainforest, (B.L. Fisher, H.J. Ratsirarson) (CASC); Torotorofotsy, 1005 m, -18.77048, 48.43043, montane rainforest, (B.L. Fisher *et al.*) (CASC); Torotorofotsy, 1070 m, -18.87082, 48.34737, montane rainforest, marsh edge, (Malagasy ant team) (CASC); Province **Toliara:** 10 km NW Enakara, Res Andohahela, 420 m, -24.56667, 46.81667, rainforest, (B.L. Fisher) (CASC); 13 km NW Enakara, Réserve Andohahela, 1250 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 13 km NW Enkara, Res Andohahela, 1140 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 6 km ESE Imonty, Réserve Andohahela, 1200 m, -24.85, 46.75, rainforest, (P.S. Ward) (PSWC); Anosy Region, Anosyenne Mts, 29.9 km NW Manantenina, 750 m, -24.13894, 47.06804, montane rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1125 m, -24.13894, 47.06804, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1315 m, -24.13632, 47.05485, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Parc National Andohahela, Col de Tanatana, 400 m, -24.74969, 46.84949, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Forêt Ivohibe 55.0 km N Tolagnaro, 200 m, -24.569, 47.204, rainforest, (B.L. Fisher *et al.*) (CASC); Forêt Ivohibe 55.6 km N Tolagnaro, 650 m, -24.56167, 47.20017, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 275 m, -24.7585, 46.85367, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Andohahela, Manangotry, 33.8 km NW Tolagnaro, 575 m, -24.75117, 46.85783, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, -24.76389, 46.75167, montane rainforest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Privée Berenty, Forêt de Bealoka, Mandrare River, 14.6 km 329° NNW Amboasary, 35 m, -24.95694, 46.2715, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Spéciale Kalambatritra, 1365 m, -23.4185, 46.4583, grassland, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ambinanitelo, 1325 m, -23.4502, 46.45658, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ampanihy, 1270 m, -23.4635, 46.4631, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ampanihy, 1269 m, -23.463, 46.47057, montane rainforest, (B.L. Fisher *et al.*) (CASC); [Central Madagascar], (MHNG); [Central Madagascar], (MHNG); [de Diversa, Museum Paris, Grandidier 1899], (MNHN); [Madagasc.], (MHNG); 11 km SE Ampasimanolotra (=Brickaville), 5 m, -18.9, 49.13333, littoral rainforest, (P.S. Ward) (PSWC); massif du Tsaratanana (versant Sud), Andohanambatoafo, 2030 m, (P. Soga) (MNHN).

Camponotus dromedarius Forel

(Figures 9A, 11A, 16, 22)

Camponotus dromedarius Forel, 1891: 65 (minor worker), 66 (major worker), 67 (m.), 72 (key). Lectotype minor worker, **present designation**, Madagascar, Imerina et environs d'Antananarivo, Forêt d'Analamainty, ex bamboo internodium (Camboué), AntWeb CASENT0101534 (MHNG). Paralectotype worker and male of same data as lectotype but with respective specimen codes: CASENT0101531 (MHNG), CASENT0101422 (MNHN) [examined]. [Combination in *Camponotus (Myrmocamelus*): Forel, 1914: 270; in *Camponotus (Myrmosaga):* Emery, 1920: 257; in *Camponotus (Mayria):* Emery, 1925: 122].

Diagnosis. Median portion of clypeus not longitudinally carinate; mandible with six teeth; in lateral view, mesosoma short and high, its dorsal outline continuously arched in a dome-like structure; propodeal declivity inclined posteriorly; in lateral view, propodeal dorsum straight, without excision; petiolar node higher than long; anterior clypeal margin broadly convex.

Description. Minor worker. In full-face view, head longer than broad (CWb/CL: 0.80±0.07; 0.72–1.05), lateral margins roughly straight and slightly converging anteriorly; posterior margin more or less straight. Anteromedian clypeal margin straight with broadly convex lateral angle. Eyes not breaking lateral outlines of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.34±0.02; 0.31–0.39). Mandible triangular, masticatory margin with six sharp teeth. Antennal scape long, roughly its distal half extending beyond posterior cephalic border. In lateral view, mesosoma evenly convex, its dorsal outline continuously arched in a dome-like structure; pronotum with anterodorsal margin; pronotum and mesonotum separated by a shallow, broad angle; junction of propodeal dorsum and declivity round. Petiolar node higher than long.

Whitish, erect, filiform hairs abundant and pubescence present on dorsum of head, mesosoma, petiolar node, and gastral segments. Body color generally black or mesosoma dark brown with orange spots.

Major worker. Characteristics the same as minor worker, except the enlarged head (CS: 1.64±0.12; 1.48–1.82; CWb/CL: 0.93±0.04; 0.86–0.98); the more strongly built mandible; apical third of antennal scape surpassing posterior cephalic margin; metanotum visible; propodeal dorsum convex and its junction to declivity broadly angulate; petiolar node much higher than long.

Discussion. Members of *C. dromedarius* can be separated from similar species in the group such as *C. pulcher* and *C. lamosy* by its larger body size (CL: 1.19–1.84), the straight propodeal dorsum, and the higher than long petiolar node. It can be distinguished from other species by the absence of a median longitudinal carina on its clypeus, the dome-like structure of its mesosoma, and the generally black body color which occasionally has a dark brown mesosoma with orange spots.

The taxonomic categorization of *C. dromedarius* based on study of qualitative morphology is supported by the NC-clustering. Separation of this species is confirmed by LDA with 100%.

Distribution and biology. *Camponotus dromedarius* is only known from Madagascar. Members of the species have been found mostly at altitudes between 800–1400 m in the central region, relict montane rainforest in the central west, and eastern montane rainforests. The species nests in rotten logs and rotting tree stumps and forages on the ground and low vegetation in these habitats.

Additional material examined. Province **Antananarivo:** [Antananarivo, Museum Paris, Grandidier 1893], Ambatomanjaka, Miarinarivo, 1398 m, -18.705147, 46.825284, (Camboué) (MNHN); [Madagascar], Ambatomanjaka, Miarinarivo, 1344 m, -18.766947, 46.869107 (NHMB); 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m, -18.47333, 47.96, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Province **Antsiranana:** Galoko chain, Mont Galoko, 980 m, -13.5888, 48.72864, montane forest, (B.L. Fisher *et al.*) (CASC); Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 1325 m, -14.44333, 49.74333, montane rainforest, (B.L. Fisher) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Province **Fianarantsoa:** [Imerina], Fahizay, Ambositra, 1317 m, -20.5, 47.333332, (Camboué) (MHNG); 2 km W Andrambovato, along river Tatamaly, 1075 m, -21.51167, 47.41, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1250 m, -23.84083, 46.9575, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 1100 m, -21.29, 47.43333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Province **Toamasina:** [Nosi be (Imerina)], Anosibe An'ala, Anosibe, 660 m, -19.433332, 48.216667, (Sikora) (MHNG); 6.9 km NE Ambanizana,

Ambohitsitondroina, 825 m, -15.58506, 50.00952, rainforest, (B.L. Fisher) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1013 m, -18.80388, 48.40506, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*)

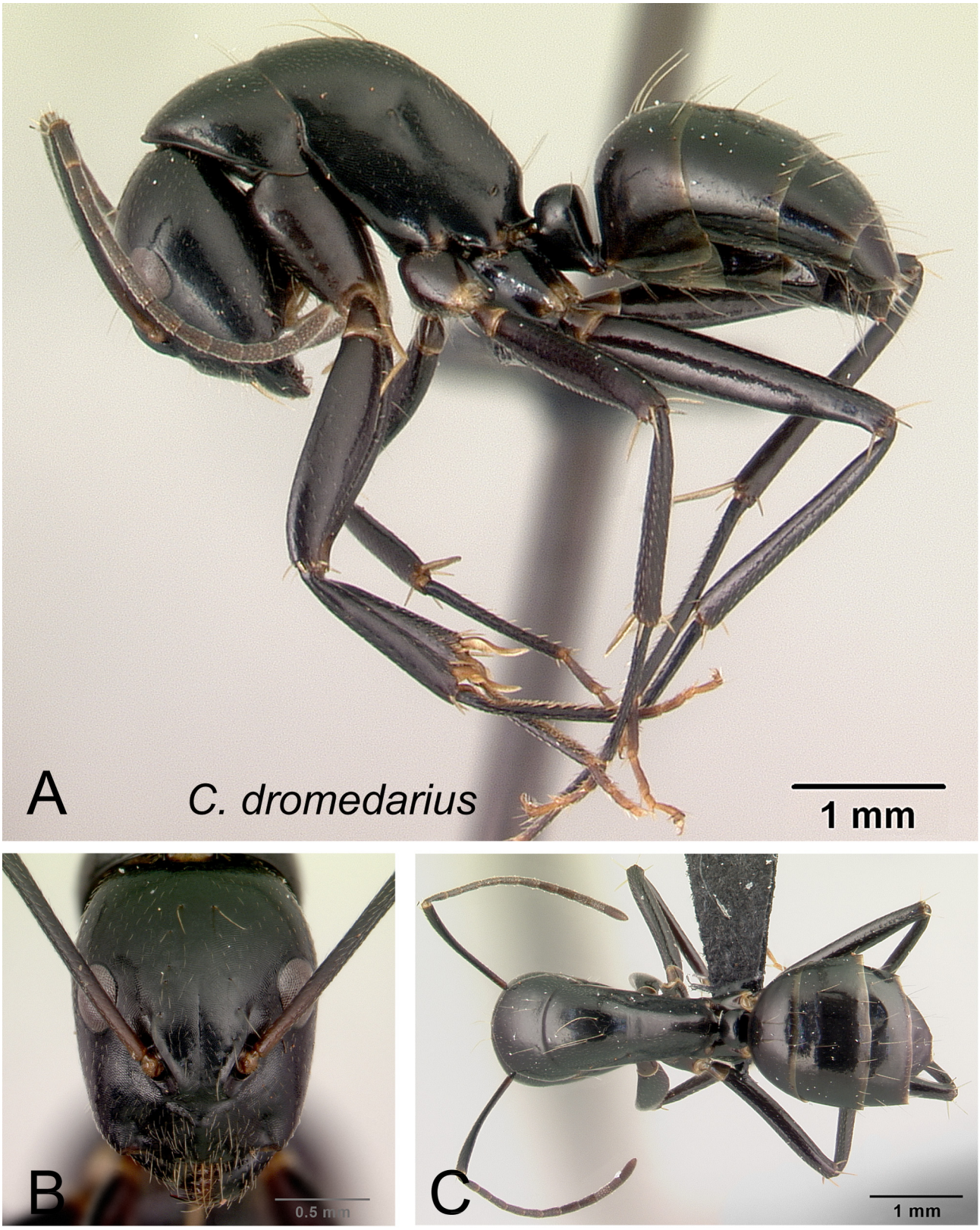


FIGURE 16. *Camponotus dromedarius* minor worker CASENT0496817. A: lateral view. B: head in full-face view. C: dorsal view.

(CASC); Province **Toliara:** 13 km NW Enkara, Res Andohahela, 1140 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 13 km NW Enkara, Res Andohahela, 1280 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 13 km NW Enkara, Res Andohahela, 1300 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 6 km ESE Imonty, Réserve Andohahela, 1200 m, -24.85, 46.75, rainforest, (P.S. Ward) (PSWC); Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, -24.76389, 46.75167, montane rainforest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 35.2 km 312° NW Ambaravaranala, 1050 m, -18.26667, 45.40667, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ambinanitelo, 1325 m, -23.4502, 46.45658, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ampanihy, 1270 m, -23.4635, 46.4631, montane rainforest, (B.L. Fisher *et al.*) (CASC).

Camponotus foersteri Forel stat. n.

(Figures 12C, 14B, 17, 23)

Camponotus christi foersteri Forel, 1886b: 185. Lectotype minor worker, **present designation**, Centre de Madagascar (Hildebrandt), AntWeb CASENT0101543 (MHNG). Paralectotype: 1 major worker, Forêt d'Analamainty, Antananarivo (Camboué), Antweb CASENT0101545 (MHNG) [examined]. Raised to species by Dalla Torre, 1893: 231. As subspecies of *christi,* Emery, 1896: 771; Wheeler, 1922: 1045. [Combination in *Camponotus (Mayria):* Emery, 1925: 122]. **Stat. n.**

Camponotus cambouei Forel, 1891: 68. Lectotype minor worker, **present designation**, Madagascar, Imerina, Antananarivo (Camboué), AntWeb CASENT0101523 (MHNG). Paralectotypes of 3 major workers and 2 minor workers with same data as lectotype but specimen coded respectively as: CASENT0101530, CASENT0101433, CASENT0101108 (MHNG, MNHN, NHMB); CASENT0101529, CASENT0104624 (MHNG, ZMHB) [examined]. [Combination in *Camponotus (Camponotus):* Forel, 1914: 266; in *Camponotus (Myrmosaga):* Emery, 1920: 257; in *Camponotus (Mayria):* Emery, 1925: 122]. **Syn. n.**

Camponotus christi var. *ambustus* Forel, 1892: 233. Lectotype minor worker, **present designation**, Madagascar, Forêt d'Andrangoloaka (Sikora), AntWeb CASENT0101535 (MHNG). Paralectotype: 1 dealate queen with same data as lectotype but specimen coded: CASENT0101546 (MHNG) [examined]. [Combination in *Camponotus (Mayria):* Emery, 1925: 122]. **Syn. n.**

Camponotus christi var. *ferrugineus* Emery, 1899: 290. Lectotype minor worker, **present designation**, Madagascar, Antongil [Toamasina, Maroantsetra, -15.43333, 49.75, 12 m] (Mocquerys), AntWeb CASENT0102102 (MSNG). Paralectotypes: 2 major workers with same data as lectotype but specimen coded: CASENT0102100, CASENT0102101 (MSNG). [examined]. [Combination in *Camponotus (Myrmosaga):* Wheeler, 1922: 1045; in *Camponotus (Mayria):* Emery, 1925: 122; Bolton, 1995: 99]. **Syn. n.**

Camponotus pictipes Forel, 1891: 217. Lectotype minor worker, **present designation**, Madagascar, Forêt d'Andrangoloaka [Antananarivo, Manjakandriana, Mantasoa, -19.033333, 47.916668, 1409 m] (Sikora). Antweb CASENT0102422 (MHNG). Paralectotype: 2 major workers with same data as lectotype but specimen coded: CASENT0102421, CASENT0102423 (MHNG) [examined]. [Combination in *Camponotus (Myrmosaga):* Wheeler, 1922: 1045; in *Camponotus (Mayria):* Emery, 1925: 123; Bolton, 1995: 117, 131]. **Syn. n.**

Diagnosis. Median portion of clypeus without longitudinal carina; mandible with six teeth; anteromedian margin of clypeus not bordered by a lamella; in lateral view, mesosoma long and low, its dorsal outline not a dome-like structure; propodeal declivity inclined anteriorly; in lateral view, length of posterior portion of propodeal dorsum measured from the end of line connecting anteriormost point of pronotal shield and metathoracic spiracle roughly twice as long as height of declivity; hind tibia as long as hind femur; petiolar node not flattened anteroposteriorly, its dorsal margin distinctly broadly convex; trochanters and distal portions of coxae yellowish to white.

Description. Minor worker. In full-face view, head longer than high, lateral margin straight, weakly diverging posteriorly and rounding to the more or less straight posterior margin. Anteromedian clypeal margin straight, with broadly angulate junction to lateral margin; median longitudinal carina absent. Eyes not breaking lateral outlines of head; their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.33±0.01; 0.31–0.35). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, generally its distal half extending beyond posterior cephalic border. In lateral view, pronotum and mesonotum weakly convex, separated by a shallow suture, posterior half of mesonotum and propodeal dorsum straight and long, junction between propodeal dorsum and declivity surface broadly angulate; propodeal dorsum about three times as long as height of declivity; height of mesosoma taken from posteroventral corner of pronotum to highest point of mesonotum more than twice the height to level of metathoracic spiracle; propodeal spiracle circular. Hind tibia roughly as long as hind femur. Petiolar node as high as long, anterior face rounding to dorsal margin; posterodorsal portion angulate.

Dorsum of head covered with numerous yellowish, elongate, erect hairs; pronotum, mesonotum, and posterodorsal angle of propodeum with a pair of erect hairs; petiolar node with two pairs of erect hairs; pubescence short and sparse. Head and gastral segments darker in color relative to mesosoma and appendages: head and gaster either black to dark brown or dark brown to orange brown with yellow spots on tergites and mesosoma dark brown to yellow-orange with dark spot on metanotal groove and propodeal declivity. Appendages: coxa dark brown basally and whitish-yellow apically; trochanter whitish-yellow; femur and tibia whitish-yelllow with dark brown spots on proximal and apical portion; tarsus dark brown basally and lighter in color apically.

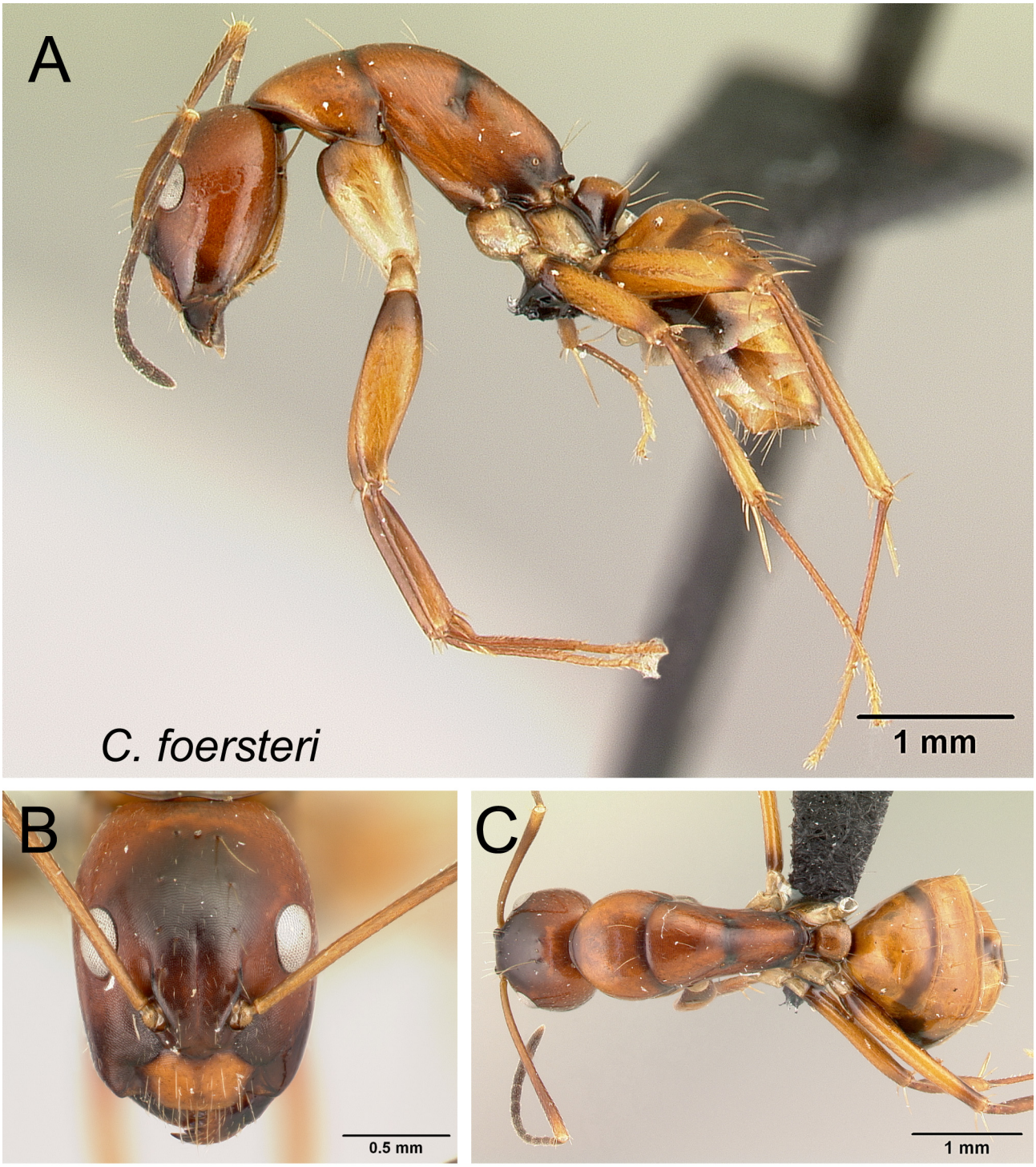


FIGURE 17. *Camponotus foersteri* minor worker CASENT0179450. A: lateral view. B: head in full-face view. C: dorsal view.

Major worker. Differing from minor worker in the following characters: enlarged head, with markedly concave posterior margin; apical fourth of antennal scape surpassing posterior cephalic margin; robust mesosoma, metanotum distinctly visible, propodeal dorsum rounding to declivity and twice as long as height of declivity; dorsal margin of petiolar node inclined posteriorly from shorter anterior face towards much longer posterior face. More pairs of erect hairs on junction of propodeal dorsum and declivity and on posterodorsal margin of petiolar node.

Discussion. *Camponotus foersteri* may be confused with *C. maculiventris* in that both species have legs that are characterized by at least the trochanters and the distal portions of coxae yellowish to white. However, in *C. maculiventris* the length of the propodeal dorsum is twice as the height of the declivity surface and the hind tibia is shorter than the hind femur. See also discussion under *C. christi* and *C. mainty.*

The relatively high 8.8% error rate in classification of *C. foersteri* achieved by LDA covers a misclassification of a single minor worker (as *C. mainty*), owing to the small range of minor worker forms of *C. foersteri* available for this study. The definition of *C. foersteri* based on traditional qualitative morphology is congruent with the results obtained from the exploratory analysis using a combination of NC-clustering and partitioning methods.

Distribution and biology. *Camponotus foersteri* is an endemic species to Madagascar where it is broadly distributed across ecosystems ranging from tropical dry forests to transitional humid forests, coastal scrub and littoral rainforests through montane rainforests, and the grasslands of the central high plateau and the eastern region of the island. Its members forage through leaf litter, on forest floor, and on low vegetation. Colony nests are found in root mats in the ground, rotten logs, rotting tree stumps, under root mats and on rock litter, under root mats on dead trees, and in dead twigs or branches above the ground.

Additional material examined. Province **Antananarivo:** [Forêt d'Analamanita P. Antananarivo], (Camboué) (MHNG); [Andrangoloaka], (Sikora) (MHNG); [Central Madagascar], 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m, -18.47333, 47.96, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Mandraka, 1312 m, -18.91813, 47.91717, montane rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale d'Ambohitantely, Forêt d Ambohitantely, 20.9 km 72° NE d Ankazobe, 1410 m, -18.22528, 47.28683, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Province **Antsiranana:** Montaigne Français, 150 m, -12.325, 49.33333, along forested limestone ridge, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Galoko chain, Mont Galoko, 520 m, -13.58487, 48.71818, rainforest, (B.L. Fisher *et al.*) (CASC); 11.0 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1565 m, -14.75, 49.45, montane rainforest, (B.L. Fisher) (CASC); 6.5 km SSW Befingotra, Réserve Anjanaharibe-Sud, 875 m, -14.75, 49.5, rainforest, (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1280 m, -14.75, 49.46667, montane rainforest, (B.L. Fisher) (CASC); 9.2 km WSW Befingotra, Réserve Anjanaharibe-Sud, 1200 m, -14.75, 49.46667, montane rainforest, (B.L. Fisher) (CASC); Betaolana Forest, along Bekona River, 880 m, -14.52996, 49.44039, rainforest, (B.L. Fisher *et al.*) (CASC); Binara Forest, 559 m, -13.26206, 49.60672, degraded rainforest, (B.L. Fisher *et al.*) (CASC); Foret de Binara, 9.1 km 233° SW Daraina, 725 m, -13.26333, 49.60333, rainforest, (B.L. Fisher) (CASC); Galoko chain, Mont Galoko, 980 m, -13.5888, 48.72864, montane forest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 415 m, -14.17066, 49.95409, rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 550 m, -14.16044, 49.95216, rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 415 m, -14.17066, 49.95409, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Marojejy, 25.7 km 32° NNE Andapa, 10.3 km 314° NW Manantenina, 1575 m, -14.445, 49.74167, montane rainforest, (B.L. Fisher) (CASC); Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 1325 m, -14.44333, 49.74333, montane rainforest, (B.L. Fisher) (CASC); Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, -14.435, 49.76, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Marojejy, Manantenina River, 28.0 km 38° NE Andapa, 8.2 km 333° NNW Manantenina, 450 m, -14.43667, 49.775, rainforest, (B.L. Fisher *et al.*) (CASC); R. N.I. Marojejy, 11 km NW Manantenina, 1225 m, -14.43333, 49.75, montane rainforest, (E.L. Quinter) (CASC); Prov. Antsiranana Réserve Spéciale Manongarivo 17.3 km 218° SW Antanambao, 1580 m, -14.02167, 48.41833, montane rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo, 14.5 km 220° SW Antanambao, 1175 m, -13.99833, 48.42833, montane rainforest, (B.L. Fisher) (CASC); Montaigne Français, 150 m, -12.325, 49.33333, along forested limestone ridge, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [lemur trail], 975 m, -12.51667, 49.18333, rainforest, (Irwin, Schlinger, Harin'H) (CASC); Parc National Montagne d'Ambre [Petit Lac road], 1125

m, -12.52028, 49.17917, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre, Roussettes, 1025 m, -12.52574, 49.17238, montane rainforest, (B.L. Fisher *et al.*) (CASC); Province **Fianarantsoa:** 2 km W Andrambovato, along river Tatamaly, 1075 m, -21.51167, 47.41, montane rainforest, (B.L. Fisher *et al.*) (CASC); 38 km S Ambalavao, Réserve Andringitra, 1680 m, -22.2, 46.96667, montane rainforest, (B.L. Fisher) (CASC); 40 km S Ambalavao, Réserve Andringitra, 1275 m, -22.21667, 46.96667, montane rainforest, (B.L. Fisher) (CASC); 7.6 km 122º Kianjavato, Forêt Classée Vatovavy, 175 m, -21.4, 47.94, rainforest, (B.L. Fisher *et al.*) (CASC); 8.0 km NE Ivohibe, 1200 m, -22.42167, 46.89833, montane rainforest, (B.L. Fisher & Sylvain) (CASC); 9.0 km NE Ivohibe, 900 m, -22.42667, 46.93833, montane rainforest, (B.L. Fisher & Sylvain) (CASC); 7.6 km 122º Kianjavato, Forêt Classée Vatovavy, 175 m, -21.4, 47.94, rainforest, (B.L. Fisher *et al.*) (CASC); 3 km W Ranomafana, near Ifandiana, 950 m, -21.25, 47.41667, rainforest, (P.S. Ward) (PSWC); Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 1020 m, -21.2665, 47.42017, mixed tropical forest, (R. Harin'Hala) (CASC); Fitovavy Fitovinany Region, District of Ifanadiana Belle vue area 1200 m S of Ranomafana National Park entrance, 1018 m, -21.2665, 47.42017, rainforest, (Rin'ha, Mike) (CASC); Fitovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, 1127 m, -21.25083, 47.40717, forest edge, open area, (Rin'ha, Mike) (CASC); Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 1550 m, -20.59333, 46.56333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); JIRAMA water works near river, Ranomafana National Park, Fianarantsoa Prov., 690 m, -21.2485, 47.45217, open area near stream, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Miandritsara Forest, 40 km S of Ambositra, 822 m, -20.79267, 47.17567, Low altitude rainforest, (Rin'ha, Mike) (CASC); Parc National Befotaka-Midongy, Papango 27.7 km S Midongy-Sud, Mount Papango, 940 m, -23.83517, 46.96367, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1250 m, -23.84083, 46.9575, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 1100 m, -21.29, 47.43333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale Ivohibe 8.0 km E Ivohibe, 1200 m, -22.48333, 46.96833, montane rainforest, (B.L. Fisher & Sylvain) (CASC); radio tower, Ranomafana National Park, Fianarantsoa Prov., 1130 m, -21.25083, 47.40717, forest edge, mixed tropical forest, open area, (M. Irwin, R. Harin'Hala) (CASC); Ranomafana National Park, Talatakely area, 0.4 km WSW of Park Entrance, 900 m, -21.41667, 47.68333, mixed tropical forest, (D. H. & K.M. Kavanaugh) (CASC); Vohiparara broken bridge, Fianarantsoa Prov., 1110 m, -21.22617, 47.36983, high altitude rainforest, (R. Harin'Hala) (CASC); Province **Mahajanga:** Réserve Spéciale Marotandrano, Marotandrano 48.3 km S Mandritsara, 865 m, -16.28322, 48.81443, transition humid forest, (B.L. Fisher *et al.*) (CASC); Province **Toamasina:** [Baie d'Antongil], Andasibe National Park, botanic garden near entrance, West of ANGAP office, 1025 m, -18.92639, 48.40783, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); 19 km ESE Maroantsetra, 250 m, -15.48333, 49.9, rainforest, (P.S. Ward) (PSWC); 5.3 km SSE Ambanizana, Andranobe, 425 m, -15.67133, 49.97395, rainforest, (B.L. Fisher) (CASC); 6.3 km S Ambanizana, Andranobe, 125 m, -15.6813, 49.958, rainforest, (B.L. Fisher) (CASC); 6.3 km S Ambanizana, Andranobe, 25 m, -15.6813, 49.958, rainforest, (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, 1080 m, -15.56667, 50, montane rainforest, (B.L. Fisher) (CASC); Ambalahasina, 62.4 km 19° Toamasina, 15 m, -17.59452, 49.46785, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Ambatovy, 12.4 km NE Moramanga, 1010 m, -18.84963, 48.2947, montane rainforest, (B.L. Fisher *et al.*) (CASC); Ambatovy, 12.4 km NE Moramanga, 1000 m, -18.84773, 48.29568, grassland, (B.L. Fisher *et al.*) (CASC); Ambatovy, 12.4 km NE Moramanga, 1080 m, -18.83937, 48.30842, montane rainforest, (B.L. Fisher *et al.*) (CASC); Ankerana, 1035 m, -18.4017, 48.80605, montane forest, (B.L. Fisher *et al.*) (CASC); Andasibe National Park, botanic garden near entrance, West of ANGAP office, 1025 m, -18.92639, 48.40783, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); 6 km ESE Andasibe (=Perinet), 900 m, -18.95, 48.46667, rainforest, (P.S. Ward) (PSWC); Analamay, 1068 m, -18.80623, 48.33707, montane rainforest, (Malagasy ant team) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1016 m, -18.79944, 48.40375, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1013 m, -18.80388, 48.40506, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 968 m, -18.80424, 48.40081, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 960 m, -18.80438, 48.40735, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 984 m, -18.76369, 48.4203, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1039 m, -18.76465, 48.41938, rainforest, (B.L. Fisher *et al.*) (CASC); F.C.

Sandranantitra, 450 m, -18.04833, 49.09167, rainforest, (H.J. Ratsirarson) (CASC); Forêt Ambatovy, 14.3 km 57° Moramanga, 1075 m, -18.85083, 48.32, montane rainforest, (Malagasy ant team) (CASC); Parc National de Masoala, 39.4 km 150° SSE Maroantsetra, 200 m, -15.71, 49.97, rainforest, (B.L. Fisher, H.J. Ratsirarson) (CASC); Réserve Perinet-Analamazaotra, 950 m, -18.93333, 48.43333, rainforest, (D. M. O lson) (PSWC); Torotorofotsy, 1070 m, -18.87082, 48.34737, montane rainforest, marsh edge, (Malagasy ant team) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1016 m, -18.79944, 48.40375, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 1044 m, -18.76087, 48.37128, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 939 m, -18.76124, 48.42134, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Tsaravoniana, 1018 m, -18.75737, 48.42302, rainforest, (B.L. Fisher *et al.*) (CASC); F.C. Andriantantely, 530 m, -18.695, 48.81333, rainforest, (H.J. Ratsirarson) (CASC); F.C. Sandranantitra, 450 m, -18.04833, 49.09167, rainforest, (H.J. Ratsirarson) (CASC); Forêt Ambatovy, 14.3 km 57° Moramanga, 1075 m, -18.85083, 48.32, montane rainforest, (B.L. Fisher) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, -15.28833, 49.54833, rainforest, (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, -15.18833, 49.615, rainforest, (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m, -15.17833, 49.635, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Parc National Mananara-Nord, 7.1 km 261° Antanambe, 225 m, -16.455, 49.7875, rainforest, (B.L. Fisher *et al.*) (CASC); Parcelle K7 Tampolo, 10 m, -17.28333, 49.41667, littoral forest, (Malagasy ant team) (CASC); Réserve Nationale Integrale Betampona, Betampona 35.1 km NW Toamasina, 500 m, -17.91801, 49.20074, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Ambodiriana, 4.8 km 306° Manompana, along Manompana river, 125 m, -16.67233, 49.70117, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Betampona, Camp Rendrirendry 34.1 km 332° Toamasina, 390 m, -17.924, 49.19967, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Betampona, Camp Vohitsivalana, 37.1 km 338° Toamasina, 520 m, -17.88667, 49.2025, rainforest, (B.L. Fisher *et al.*) (CASC); S.F. Tampolo, 10 km NNE Fenoarivo Atn., 10 m, -17.2825, 49.43, littoral rainforest, (B.L. Fisher) (CASC); Torotorofotsy, 1005 m, -18.77048, 48.43043, montane rainforest, (B.L. Fisher *et al.*) (CASC); Torotorofotsy, 1070 m, -18.87082, 48.34737, montane rainforest, marsh edge, (Malagasy ant team) (CASC); Province **Toliara:** 6 km ESE Imonty, Réserve Andohahela, 1200 m, -24.85, 46.75, rainforest, (P.S. Ward) (PSWC); Anosy Region, Anosyenne Mts, 29.9 km NW Manantenina, 750 m, -24.13894, 47.06804, montane rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Parc National Andohahela, Col de Tanatana, 400 m, -24.74969, 46.84949, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); [Madagascar], (MHNG); 11 km SE Ampasimanolotra (=Brickaville), 5 m, -18.9, 49.13333, littoral rainforest, (P.S. Ward) (PSWC); 10 km NW Enakara, Res Andohahela, 420 m, -24.56667, 46.81667, rainforest, (B.L. Fisher) (CASC); 11 km NW Enakara, Réserve Andohahela, 800 m, -24.56667, 46.83333, rainforest, (B.L. Fisher) (CASC); 13 km NW Enakara, Réserve Andohahela, 1250 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 13 km NW Enkara, Res Andohahela, 1140 m, -24.55, 46.8, montane rainforest, (B.L. Fisher) (CASC); 13 km NW Enkara, Res Andohahela, 850 m, -24.56667, 46.81667, rainforest, (B.L. Fisher) (CASC); Anosy Region, Anosyenne Mts, 29.33 km NW Manantenina, 540 m, -24.13993, 47.07418, montane rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Anosyenne Mts, 29.9 km NW Manantenina, 750 m, -24.13894, 47.06804, montane rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Foret Ivohibe 55.0 km N Tolagnaro, 200 m, -24.569, 47.204, rainforest, (B.L. Fisher *et al.*) (CASC); Foret Ivohibe 55.6 km N Tolagnaro, 650 m, -24.56167, 47.20017, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Andohahela, Col de Tanatana, 33.3 km NW Tolagnaro, 275 m, -24.7585, 46.85367, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National Andohahela, Manangotry, 33.8 km NW Tolagnaro, 575 m, -24.75117, 46.85783, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, -24.76389, 46.75167, montane rainforest, (Fisher-Griswold Arthropod Team) (CASC); Parc National d'Andohahela, Manampanihy River, 5.4 km 113° ESE Mahamavo, 36.7 km 343° NNW Tolagnaro, 650 m, -24.76389, 46.76683, rainforest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Privée Berenty, Foret de Bealoka, Mandrare River, 14.6 km 329° NNW Amboasary, 35 m, -24.95694, 46.2715, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Spéciale Kalambatritra, 1365 m, -23.4185, 46.4583, grassland, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, 1365 m, -23.4185, 46.4583, grassland, (B.L. Fisher *et al.*) (CASC); massif du Tsaratanana (versant Sud), Andohanambatoafo, 2030, (P. Soga) (MNHN).

Camponotus lamosy **Rakotonirina & Fisher sp. n.**
(Figures 2B, 10A, 18, 24)

Holotype worker. Madagascar: Province Antsiranana, Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, -12.53444, 49.1795, 925 m, transect subsample #08, Beat 25 sample transect, 10 m, beating low vegetation montane rainforest, 20–26 Jan 2001 (Fisher, Griswold *et al.*) collection code: BLF02566, specimen code: CASENT0408976 (CASC).

Paratypes. 11 workers with same data as holotype but with specimen codes: CASENT0408963, CASENT0408965, CASENT0408966, CASENT0408968, CASENT0408970, CASENT0408971, CASENT0408972, CASENT0408973, CASENT0408974, CASENT0408975, CASENT0408977 (CASC, BMNH, MHNG, PBZT).

Diagnosis. Clypeus without median longitudinal carina; mandible with six teeth; anteromedian margin of clypeus not lamellate; in lateral view, mesosoma short and high, its dorsal outline continuously arched in a dome-like structure; propodeal declivity inclined posteriorly; in lateral view, propodeal dorsum slightly excised medially, petiolar node longer than high.

Description. Minor worker. In full-face view head longer than broad (CWb/CL: 0.77±0.03; 0.73–0.82), lateral margins roughly straight and slightly converging anteriorly and posteriorly; posterior margin more or less straight. Clypeus with straight anteromedian margin and rounded anterolateral angle. Eyes sometimes breaking the lateral outlines of the head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.34±0.01; 0.31–0.37). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its apical third surpassing posterior margin of head. In lateral view, outline of pronotum more or less straight and mesonotum forming a separate convexity; propodeum slightly concave anteriorly and weakly convex posteriorly; its junction to declivity angulate; declivity inclined posteriorly. Petiolar node longer than high.

Dorsum of head and gastral segments with abundant erect filiform hairs; pronotum with 2 pairs, mesonotum, propodeum and petiolar node with one pair of erect hairs. Pubescence short and sparse on gastral segments. Head black, mesosoma, petiolar node, gaster and legs yellow-orange with black to dark brown spot on lower level of lateral surface of pronotum, propodeum and petiole. Coxa and trochanter whitish-yellow, base and apical portion of femur dark brown.

Major worker. Differing from minor worker in having larger heart-shaped head, apical fourth of antennal scape surpassing posterior cephalic margin; robust mesosoma with distinct metanotum, and as high as long petiolar node. Other characters as in minor worker.

Discussion. *Camponotus lamosy* is similar to *C. dromedarius* and *C. pulcher*, but can be distinguished by its slightly excised propodeal dorsum.

The definition of *Camponotus lamosy* based on qualitative morphological analysis and multivariate morphometry is congruent. Recognition of the species is supported by the clustering shown by the dendrogram (Fig. 1) and confirmed by LDA at a 100% classification success.

Distribution and biology. *Camponotus lamosy* occupies the littoral forest habitats of the north, the rainforests of the northeast, and the montane rainforests of the central high plateau and the southeast of Madagascar. Endemic to the island, the species is found foraging both on the ground and through the leaf litter or on the lower portions of vegetation, and its nests are located in rotten logs or in dead branches above ground.

Additional material examined. Province **Antsiranana:** 6.5 km SSW Befingotra, Réserve Anjanaharibe-Sud, 875 m, -14.75, 49.5, rainforest, (B.L. Fisher) (CASC); Betaolana Forest, along Bekona River, 880 m, -14.52996, 49.44039, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, -14.435, 49.76, rainforest, (B.L. Fisher) (CASC); Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 925 m, -12.53444, 49.1795, (Joy Boutin) (CASC); Parc National Montagne d'Ambre, Crête, 1110 m, -12.58132, 49.13368, montane rainforest, (B.L. Fisher *et al.*) (CASC); 3 km W Sakalava Beach [white dunes site], 40 m, -12.28617, 49.36667, white dunes in littoral forest, (Harin'Hala, Irwin, Schlinger) (CASC); 7 km N Joffreville [camp 2 of Fisher], 360 m, -12.33333, 49.25, in dry forest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [Petit Lac road], 1125 m, -12.52028, 49.17917, rainforest, (R. Harin'Hala) (CASC).

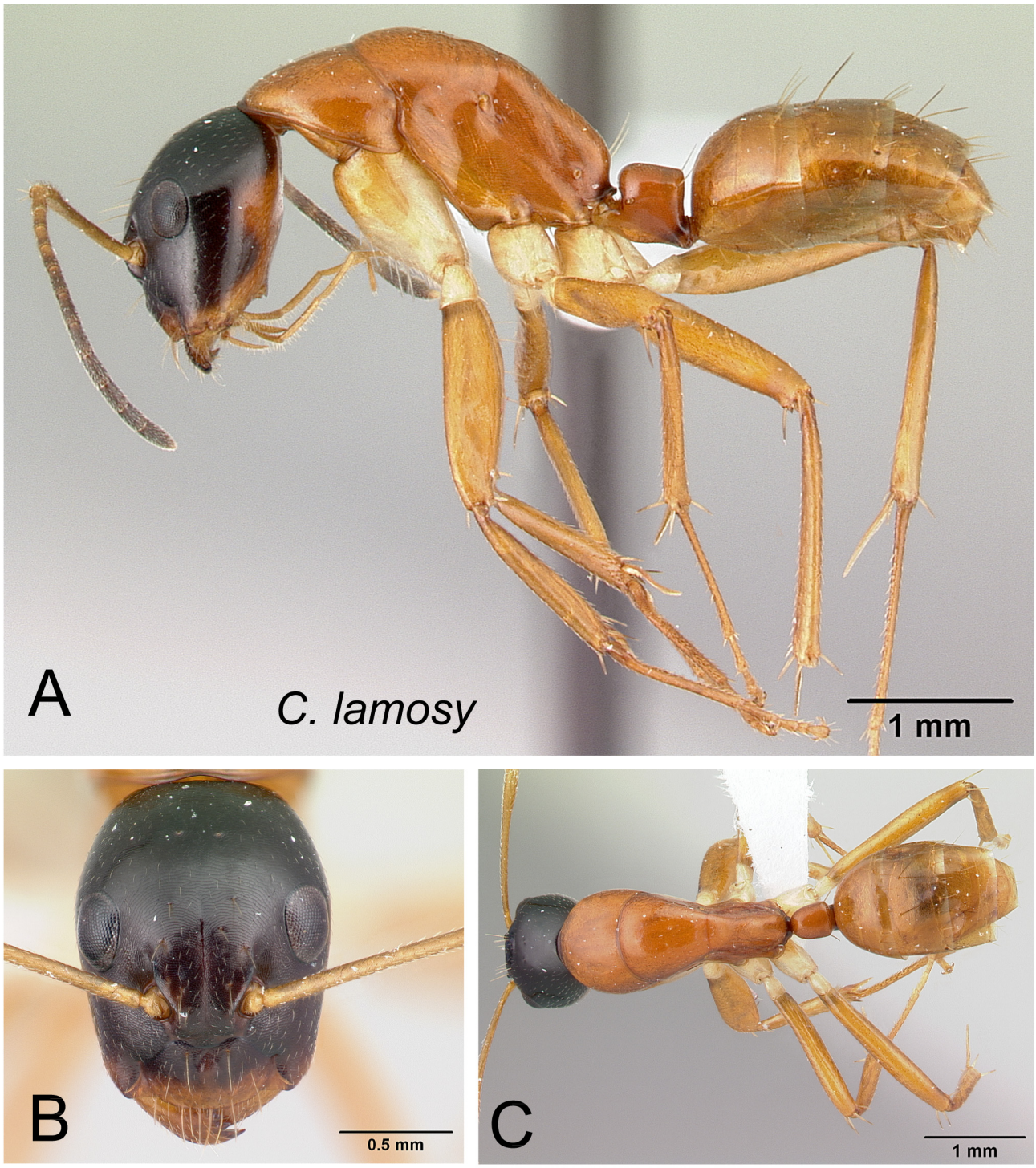


FIGURE 18. *Camponotus lamosy* minor worker CASENT0408976. A: lateral view. B: head in full-face view. C: dorsal view.

Camponotus liandia **Rakotonirina & Fisher sp. n.**
(Figures 6A, 19, 25)

Holotype worker. Madagascar: Province Antananarivo, Andohony I Non Protected Area, 22.62 km SW Antsirabe, -20.06784, 46.99068, 1451 m, transect subsample #16, soil digging 20 sample transect, 10 m, ex soil, Savannah grassland, 6–7 Mar 2012 (A. Ravelomanana) collection code: ARA1637, specimen code: CASENT0803903 (CASC).

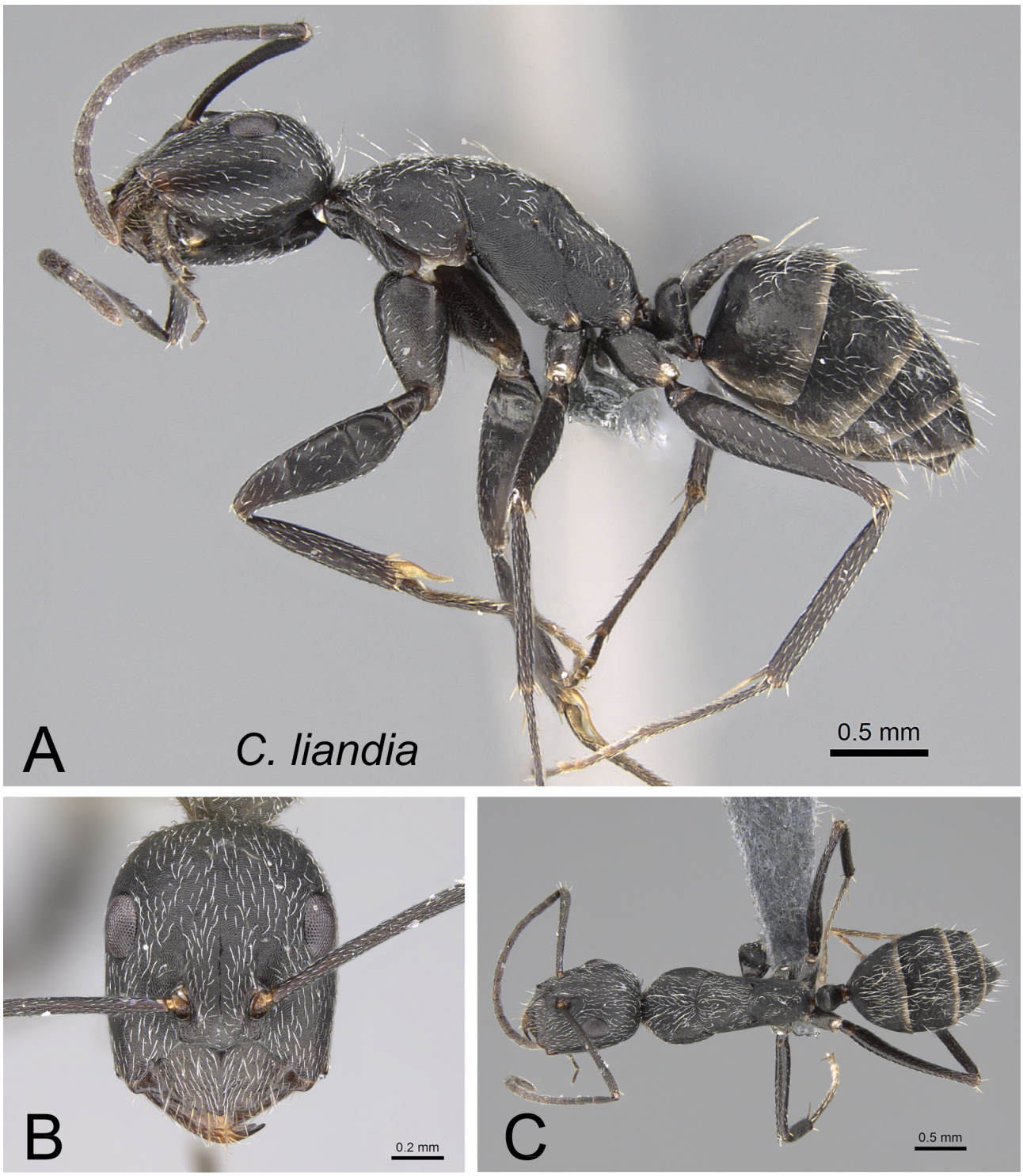


FIGURE 19. *Camponotus liandia* minor worker CASENT0803903. A: lateral view. B: head in full-face view. C: dorsal view.

Paratypes. 4 workers with same data as holotype but with specimen codes: CASENT0803901, CASENT0803902, CASENT0803904, CASENT0803905; 4 workers with collection code: ARA1636, specimen codes: CASENT0803900, CASENT0803897, CASENT0803898, CASENT0803899 (CASC, BMNH, MHNG, PBZT).

Diagnosis. Median portion of clypeus with longitudinal carina; anteromedian margin of clypeus projecting into an obtuse triangular lobe; in lateral view, mesosoma long and low; petiolar node tapered dorsally; body entirely dark brown to black, coxa without white color; dorsum of mesosoma covered with 6 to 10 short erect hairs and abundant and long pubescence.

Description. Minor worker. In full-face view, head elongate and rectangular, lateral margins parallel, posteriorly rounding to a more or less straight posterior margin. Anterior clypeal margin projecting into obtusely angulate lobe. Eyes not breaking lateral outlines of head, their posterior margins located far behind the mid-length of the head (PoOc/CL: 0.26±0.01; 0.24–0.27). Mandible triangular, masticatory margin with six teeth. Antennal scape long, roughly its distal half surpassing posterior cephalic margin. In lateral view, pronotum and mesonotum convex; propodeal dorsum slightly concave medially; junction of propodeal dorsum and declivity surface broadly rounded; propodeal dorsum approximately three times longer than height of declivity; propodeal spiracle slit-like. Petiolar node tapering dorsally.

Dorsum of head, mesosoma, petiole, and gaster covered with scattered erect hairs, shorter than height of propodeal declivity, and abundant, long pubescence. Body color reddish-black to black

Major worker. Differing from minor worker in the following characters: larger head, with slight medial concavity on posterior margin; more or less straight anterior clypeal margin; antennal scape barely surpassing posterior cephalic margin; in lateral view, mesosoma characterized by even convexity of pronotum and mesonotum, separated from propodeum by distinct metanotum.

Discussion. *Camponotus liandia* is similar to *C. lubbocki* with respect to the shape of the body, but *C. lubbocki* is characterized by its broadly rounded anteromedian clypeal margin.

The grouping of the *C. liandia* samples in the same cluster presented by the dendrogram of multivariate morphometric analysis is supported by the cumulative LDA at 100% identification success. This finding is congruent with that of the qualitative morphology-based study. Also, the location of the *C. liandia* cluster next to that of *C. lubbocki* proves the close qualitative morphological similarity between these two species.

Distribution and biology. This species has only been collected in the grasslands of the central and the southern high plateaux of Madagascar. While its workers forage either on the ground or on low vegetation, nest sites are under stones and branches on the ground.

Additional material examined. Province **Antananarivo:** Andohony I Non Protected Area, 22.62 km SW Antsirabe, 1451 m, -20.06784, 46.99068, Savannah grassland, (A. Ravelomanana) (CASC); Province **Toliara:** Réserve Spéciale Kalambatritra, 1365 m, -23.4185, 46.4583, grassland, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Kalambatritra, Ambinanitelo, 1345 m, -23.45373, 46.45773, grassland, (B.L. Fisher *et al.*) (CASC).

Camponotus lubbocki **Forel**

(Figures 2A, 3B, 5B, 6B, 20, 26)

Camponotus lubbocki Forel, 1886b: 186. Lectotype minor worker, **present designation**, Madagascar, Imerina Antananarivo [Fianarantsoa, Amoron'I Mania, Ambositra, Fahizay, -20.5, 47.333332, 1317 m] (Camboué), AntWeb CASENT0101518 (MHNG). [examined]. Paralectotypes. 1 major worker and 1 alate queen with same data as lectotype but with specimen codes: CASENT0101516, CASENT0101515 (MHNG). [Combination in *Camponotus (Myrmosaga):* Forel, 1912: 92; Emery, 1920: 257; Wheeler, 1922: 1046; in *Camponotus (Mayria):* Emery, 1925: 123; Bolton, 1995: 109, 131].

Camponotus lubbocki var. *christoides* Forel, 1891: 61. Holotype minor worker, Madagascar, Antsiranana Province, Lokobe (O'Swald) [not examined]. Raised to species by Dalla Torre, 1893:224. As subspecies of *lubbocki,* Emery, 1896: 772; Wheeler, 1922: 1046. [Combination in *Camponotus (Mayria):* Emery, 1925: 123]. **Syn. n.**

Camponotus lubbocki var. *rectus* Forel, 1891: 217. Lectotype minor worker, **present designation**, Süd Central Madagascar [Fianarantsoa Urban, Haute Matsiatra, 2eme Arrondissement, -21.433332, 47.083332, 1160 m] (Hildebrandt), AntWeb CASENT0101512 (MHNG) [examined]. Paralectotypes. 1 worker of same data as lectotype but with specimen code: CASENT0101514 (MHNG); 2 minor workers from Forêt d'Andrangoloaka [Mantasoa, Manjakandriana, -19.033333, 47.916668, 1409 m] (Sikora), with specimen codes: CASENT0101105, CASENT0101106 (NHMB) [examined]. [Combination in *Camponotus (Myrmosaga)*: Wheeler, 1922: 1046; in *Camponotus (Mayria):* Emery, 1925: 123; Bolton, 1995: 109, 120]. **Syn. n.**

Diagnosis. Median portion of clypeus with longitudinal carina; anteromedian margin of clypeus broadly rounded; in lateral view, mesosoma long and low; petiolar node tapered dorsally; body entirely dark brown to black, coxa without white color; dorsum of mesosoma covered with 6 to 10 short erect hairs and abundant and long pubescence.

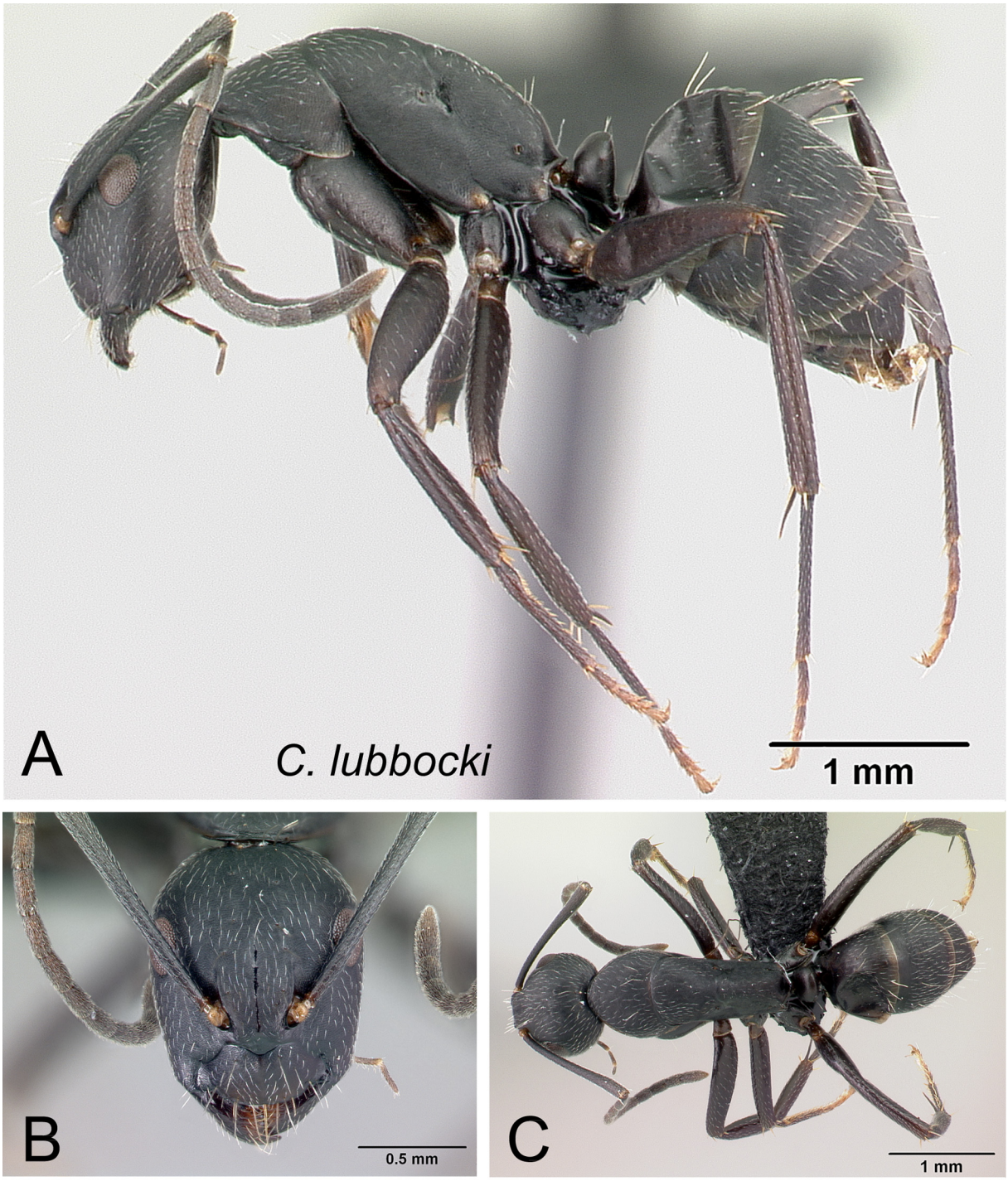


FIGURE 20. *Camponotus lubbocki* minor worker CASENT0486998. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Minor worker. In full-face view, head elongate and rectangular, posterolateral margin rounding to the roughly straight posterior margin. Clypeus with broadly rounded anterior margin and remarkable anterolateral angles; median carina visible and fully developed. Eyes not breaking lateral outlines of head, their posterior margins located far behind the midlength of the head (PoOc/CL: 0.27±0.01; 0.25–0.30). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, its basal half nearly reaching posterior cephalic border. In lateral view, pronotum and anterior portion of mesonotum noticeably convex; posterior portion of mesonotum and propodeal dorsum straight; junction of propodeal dorsum and declivity surface broadly angulate; propodeal dorsum roughly three times longer than height of declivity; propodeal spiracle slit-like. Petiolar node higher than long and tapering dorsally.

Sparse, erect hairs, shorter than height of propodeal declivity and abundant, long pubescence present on dorsum of head, mesosoma, petiole and gaster; body color entirely reddish-black to black.

Major worker. With characteristics of minor worker, except for the following characters: enlarged head, with slight medial excision on posterior margin; medially concave anterior clypeal margin; apical third of antennal scape surpassing posterior cephalic margin; pronotum and mesonotum forming an even convexity and separated from propodeum by distinct metanotum.

Discussion. *Camponotus lubbocki* is morphologically similar to *C. liandia* and *C. manabo* but the anteromedian clypeal margin projects into an obtuse triangular lobe in *C. liandia*. In *C. manabo,* the dorsal margin of the petiolar node is convex in lateral view and the mesosomal dorsum is covered with numerous erect hairs and sparse, short pubescence.

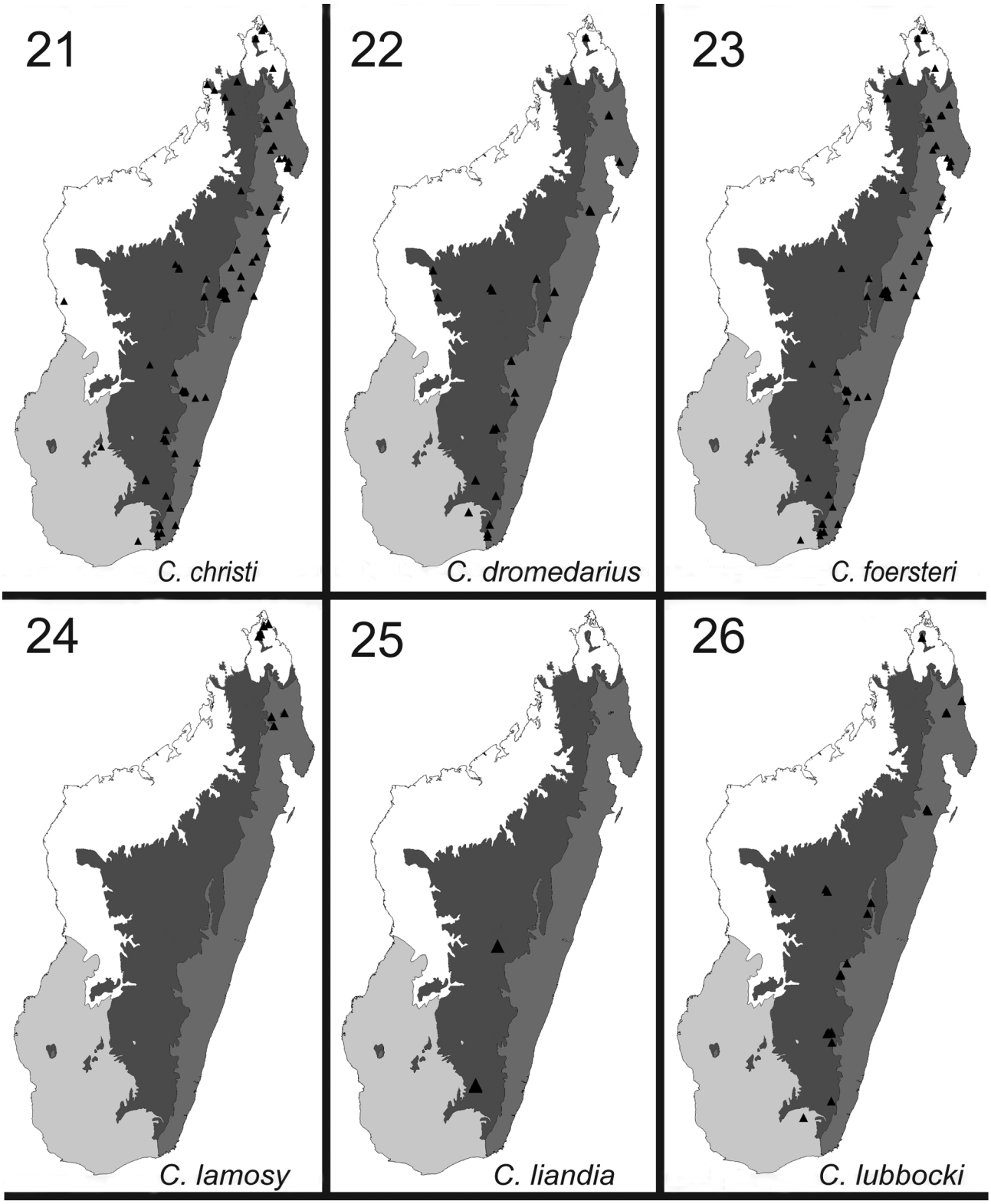
We were not able to examine the type specimen of *C. lubbocki* var. *christoides*, but based on the original description the distinctive characters that were used to differentiate it from *C. lubbocki* vary within and across the populations of *C. lubbocki.* Thus, the synonymy of *C. lubbocki* var. *christoides* under *C. lubbocki.*

The qualitative morphological distinction between *C. lubbocki* and *C. liandia* has been confirmed by multivariate analyses of quantitative morphology. The cluster of *C. lubbocki* samples in the NC-clustering dendrogram is supported by LDA with a classification success of 100%.

Distribution and biology. *Camponotus lubbocki* commonly occurs in montane shrubland and montane rainforests in the northeast, central, and southern high plateau of Madagascar. The species is rarely known from rainforests and the transitional forest between spiny and dry forests. Across this mountainous region, the species nests mostly in the ground, in root mats in the ground, and under moss on the ground, but occasionally nests in rotten logs and under stones.

Additional material examined. Province **Antananarivo:** [Andrangloaka], Mantasoa, Manjakandriana, 1409 m, -19.03333, 47.91667 (Sikora), (NHMB), [Antananarivo, Museum Paris, Grandidier 1899], Ambatomanjaka, Miarinarivo, 1398 m, -18.705147, 46.825284, (MNHN); [Central Madagascar], Ambatomanjaka, Miarinarivo, 1344 m,-18.766947, 46.869107 (MHNG); [Env. de Tananarive], Ambatomanjaka, Miarinarivo, 1399 m, -18.705147, 46.825284, (MNHN); [Imerina], Fahizay, Ambositra, 1317 m, -20.5, 47.33333, (MHNG); [Madagascar, Museum Paris, Grandidier 1899], Ambatomanjaka, Miarinarivo, 1344 m,-18.766947, 46.869107, (MNHN); [Sud Central Madagascar], 2eme Arrondissement, Fianarantsoa Urban; 1160 m, -21.433332, (MHNG); Tsimbazaza, Antananarivo renivohitra, 1275 m, -18.93, 45.52611, (MNHN); [Tananarive], Ambatomanjaka, Miarinarivo, 1398 m, -18.705147, 46.825284, (MNHN); Ankatso, Tankafatra, Andramasina, 1519 m, -19.3, 47.83333, 20 Fev., (MNHN); Province **Antsiranana:** Montagne d'Ambre, Mosorolava, Antsiranana Rural; 1113 m, -12.616667, 49.15, (MNHN); Parc National de Marojejy, 25.4 km 30° NNE Andapa, 10.9 km 311° NW Manantenina, 2000 m, -14.445, 49.735, montane shrubland, (B.L. Fisher) (CASC); R. N.I. Marojejy, 11 km NW Manantenina, 1875 m, -14.45, 49.73333, montane rainforest, (E.L. Quinter) (CASC); Province **Fianarantsoa:** 27.4 km SSW Ambositra, 1600 m, -20.77, 47.18667, (CASC); 28 km. SSW Ambositra, Ankazomivady, 1670 m, -20.775, 47.16833, (CASC); 36 km S Ambalavao, Réserve Andringitra, 900 m, -22.2, 46.93833, W 1 large mixed sample, (CASC); 8.0 km NE Ivohibe, 1200 m, -22.42167, 46.96833, gc#135-173. general collecting, (Sylvain) (CASC); 8.5 km SE Antanitotsy, Anjavidilava Forest, 1990 m, -22.16667, 46.96667, MW 25 sample transect, 5m, (CASC); 36 km S Ambalavao, Réserve Andringitra, 1900 m, -22.2, 46.96667, montane rainforest, (B.L. Fisher) (CASC); Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1250 m, -23.84083, 46.9575, montane rainforest, (B.L. Fisher *et al.*) (CASC); Miandritsara Forest, 40 km S of Ambositra, 822 m, -20.79267, 47.17567, Malaise, (CASC); Parc National Andringitra, Forêt Ravaro 12.5 km SW Antanifotsy, 1500–1800 m, -22.21167, 46.845, Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1500 m, -22.21167, 46.845, (CASC); Parc naturel communautaire, 29.3 km SW Ambositra, 1250 m, -23.84083, 46.9575, (CASC); Réserve Andringitra, cuvette du Pic Boby, 2500 m, -22.18333, 46.9, (CASC); Réserve Andringitra, Plateau d'Andohariana, base of Pic d'Ivangomena, 2450 m, -22.2, 46.9, (CASC); Réserve Andringitra, 8.5 km SE Antanitotsy, 1990 m, -22.16667, 46.96667, (CASC); Province **Mahajanga:** Prov. d'Analalava, Maromandia, Bemanevika, Sambava, 26 m, -14.15, 50.11667, (MNHN); Province **Toamasina:** Réserve Spéciale Ambatovaky, Sandrangato river, 475 m, -16.76912, 49.26704, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 355 m, -16.77468, 49.26551, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 360 m, -16.81753, 49.29498, yellow pan trap, YP 25 trap transect, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 400 m, -16.81745, 49.2925, (CASC); Réserve Spéciale Ambatovaky, Sandrangato

river, 480 m, -16.80561, 49.29507, (CASC); RNI Marojejy, 10.5 km NW Manantenina, 1625 m, -14.43333, 49.75, yellow pan trap, (CASC); Province **Toliara:** Forêt Vohidava, 88.9 km N Amboasary, 500 m, -24.24067, 46.28783, spiny forest/dry forest transition, (B.L. Fisher *et al.*) (CASC).



FIGURES 21–26. Distribution maps of *Camponotus* subgenus *Mayria* in Madagascar. Fig. 21: *C. christi;* Fig. 22: *C. dromedarius;* Fig. 23: *C. foersteri;* Fig. 24: *C. lamosy;* Fig. 25: *C. liandia,* Fig. 26: *C. lubbocki.*

Camponotus maculiventris Emery

(Figures 7B, 14A, 27, 35)

Camponotus christi maculiventris Emery, 1895: 337, 344 (worker minor, major, dq.). Lectotype minor worker, **present designation**, Madagascar, Antsiranana (Diego-Suarez), (Alluaud, 1893), AntWeb CASENT0102104 (MSNG). Paralectotypes. 1 minor worker, 2 major workers and 1 dealate queen with same data as lectotype but with specimen codes: CASENT0101539, CASENT0101540 (MHNG); CASENT0102103, CASENT0102105 (dealate queen) (MSNG). [Combination in *Camponotus (Myrmosaga):* Wheeler, 1922: 1045; in *Camponotus (Mayria):* Emery, 1925: 122; Bolton, 1995: 110].

Diagnosis. Median portion of clypeus without median longitudinal carina; mandible armed with six teeth; anteromedian margin of clypeus not bordered by a lamella; in lateral view, length of posterior portion of propodeal dorsum measured from the end of line connecting anteriormost point of pronotal shield and metathoracic spiracle as long as height of declivity; petiole node not flattened anteroposteriorly, its dorsal margin distinctly broadly convex; body mostly black, legs with at least trochanters and distal portions of coxae yellowish to white; hind tibia shorter than hind femur.

Description. Minor worker. In full-face view, head elongate, lateral margin slightly convex and weakly diverging posteriorly, rounding to a more or less straight posterior margin. Anterior margin of clypeus broadly convex, angle absent between lateral and anteromedian margins; median longitudinal carina lacking. Eyes not breaking lateral outlines of head; their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.32±0.01; 0.29–0.36). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, about its apical half surpassing the posterior cephalic margin. In lateral view, either pronotum, mesonotum, and propodeal dorsum forming even convexity or pronotum and mesonotum forming separate convexity and propodeal dorsum straight, joining declivity surface at a broad angle. Propodeal dorsum about twice as long as height of declivity; height of mesosoma taken from posteroventral corner of pronotum to highest point of mesonotum less than twice the height to level of metathoracic spiracle; propodeal spiracle rounded. Hind tibia shorter than hind femur. Petiolar node as high as long, dorsal margin forming broad angle with anterior and posterior faces.

Dorsum of head covered with numerous yellowish, elongate, erect hairs; pronotum, mesonotum, and posterodorsal angle of propodeum each with a pair of erect hairs; petiolar node with two pairs of erect hairs near its posterodorsal angle; pubescence short and sparse. Head mesosoma, petiole, and gastral segments black to brown and darker in color relative to appendages. Anterior half of second gastral tergite and first three sternites with lighter spot; trochanter and at least distal half of coxa whitish-yellow; femur and tibia whitish-yellow with dark brown spots on proximal and apical portion; tarsus and antennae dark brown basally and lighter in color apically.

Major worker. With characteristics of minor worker, except: enlarged head, with concave posterior margin; apical fourth of antennal scape surpassing posterior cephalic margin; robust mesosoma, metanotum distinctly visible; petiolar node higher than long, its dorsal margin inclined posteriorly from shorter anterior face towards much longer posterior face.

Discussion. *Camponotus maculiventris* may be difficult to differentiate from *C. pulcher* in that both species have a short and high mesosoma and lack the median longitudinal carina on the clypeus, the straight propodeal dorsum, and the shape of the petiolar node. But in *C. pulcher* the anteromedian margin of the clypeus is slightly concave medially, the head is black, abdominal segments 3 and 4 are yellow-orange with remaining segments mostly black, and the mesosoma is reddish-orange. Workers of *C. maculiventris* can also be confounded with those of *C. foersteri* and *C. mainty,* but in *C. foersteri* the propodeal dorsum is three times as long as the height of the declivity and the hind tibia is as long as hind femur. Members of *C. mainty* have an entirely black to reddish-black body and legs, and a flattened petiolar node.

Camponotus maculiventris is one of the most widespread species in the subgenus *Mayria* and shows important morphological variation in the form of the mesosoma, overall body size, and leg color. The variants however cannot be distinguished according to the qualitative morphology-based study and they gradually merge into one another across the distribution of the species. The existence of discrete variants was not supported by the NC-clustering and partitioning approaches. The samples from each of the variants are scattered across the *C. maculiventris* cluster and these samples were correctly identified by LDA at 100% success.

Distribution and biology. Samples for *C. maculiventris* have been generally recorded from the rainforests of the east and the montane rainforests of the center and east of Madagascar and are occasionally found in the littoral

rainforest of the northeast. Along its eastern distribution, the geographic range is from Sakalava Beach in the northernmost to the Parc National Andasibe in the center and down to Anosyenne Montain in the southernmost region. *Camponotus maculiventris* forages most frequently on lower vegetation and in leaf litter but rarely on the forest floor. Nest series have been collected frequently from dead branches above the ground and rotten logs but occasionally from under stones and root mats in the ground or on rocks.

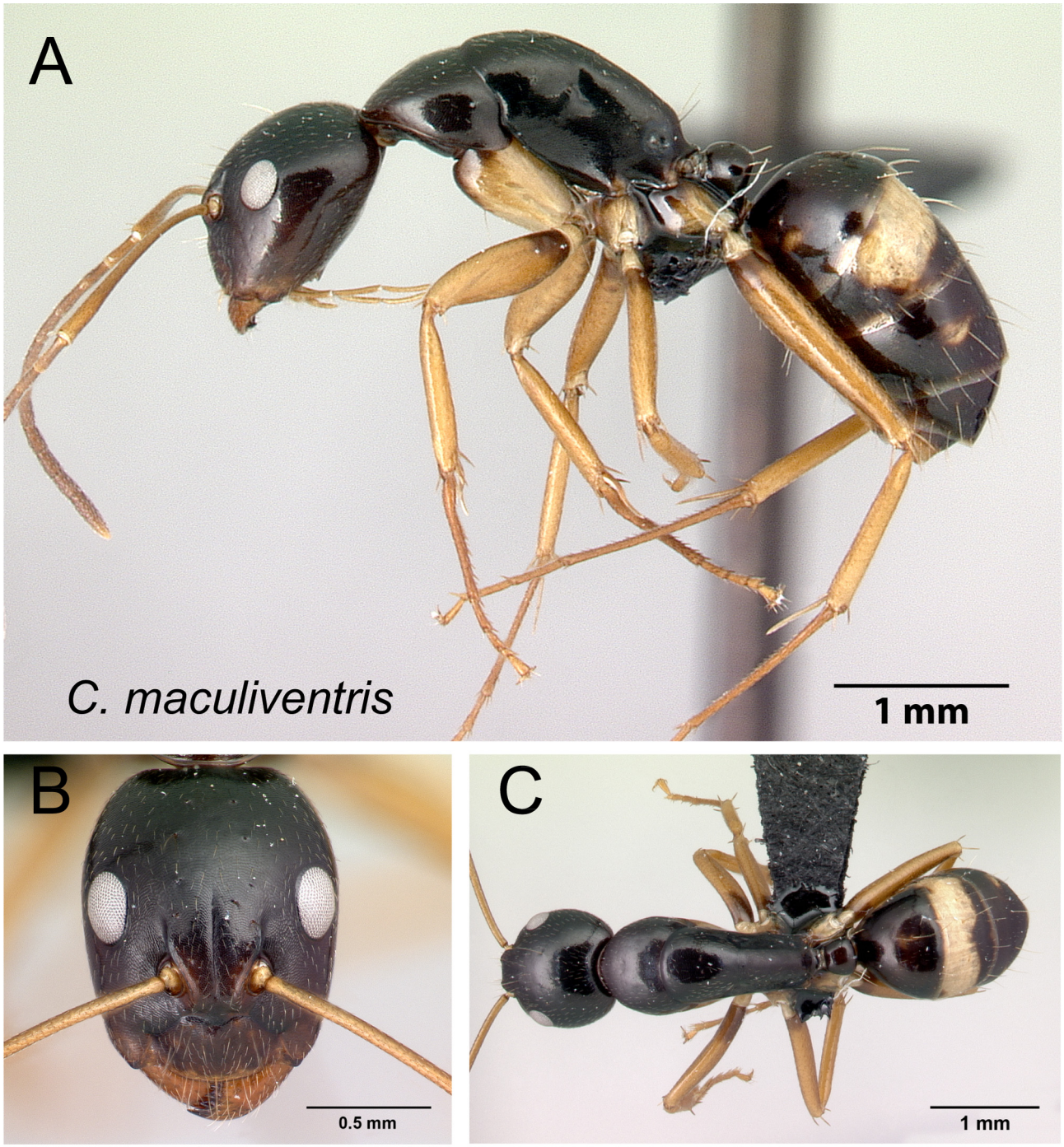


FIGURE 27. *Camponotus maculiventris* minor worker CASENT0082042. A: lateral view. B: head in full-face view. C: dorsal view.

Additional material examined. Province **Antananarivo:** Réserve Spéciale d'Ambohitantely, 1580 m, -18.18762, 47.28576, montane forest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale d'Ambohitantely, 1490 m, -18.22444, 47.2774, montane forest, (B.L. Fisher *et al.*) (CASC); Province **Antsiranana:** 6.5 km SSW Befingotra, Réserve Anjanaharibe-Sud, 875 m, -14.75, 49.5, rainforest, (B.L. Fisher) (CASC); Antsiranana II Pref:

Antsahampano S.-Pref: Montagne d'Ambre. Site MD1, 1049 m, -12.52765, 49.17235, in *Commelina* regrowth on path next to degraded primary riparian rainforest, (D. Lees, R. Ranaivosolo & P. Razafindraibe) (CASC); Forêt de Binara, 9.1 km 233° SW Daraina, 725 m, -13.26333, 49.60333, rainforest, (B.L. Fisher) (CASC); Makirovana forest, 900 m, -14.16506, 49.9477, montane rainforest, (B.L. Fisher *et al.*) (CASC); Makirovana forest, 715 m, -14.16666, 49.95, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Marojejy, Manantenina River, 27.6 km 35° NE Andapa, 9.6 km 327° NNW Manantenina, 775 m, -14.435, 49.76, rainforest, (B.L. Fisher) (CASC); Parc National Montagne d'Ambre, 3.6 km 235° SW Joffreville, 925 m, -12.53444, 49.1795, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Prov. Antsiranana Réserve Spéciale Manongarivo 17.3 km 218° SW Antanambao, 1580 m, -14.02167, 48.41833, montane rainforest, (B.L. Fisher) (CASC); 3 km W Sakalava Beach [white dunes site], 40 m, -12.28617, 49.36667, white dunes in littoral forest, (Harin'Hala, Irwin, Schlinger) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Sakalava Beach [vegetated beach dunes], 10 m, -12.26278, 49.3975, across sandy trail in dwarf littoral forest, (R. Harin'Hala) (CASC); Province **Toamasina:** 7 km SE Andasibe National Park Headquarters, 1050 m, -18.96278, 48.45267, tropical forest, (M.E. Irwin, R. Harin'Hala) (CASC); Ambatovy, 12.4 km NE Moramanga, 1080 m, -18.83937, 48.30842, montane rainforest, (B.L. Fisher *et al.*) (CASC); Analamay, 1068 m, -18.80623, 48.33707, montane rainforest, (Malagasy ant team) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, -15.28833, 49.54833, rainforest, (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 18.0 km 21° NNE Ambinanitelo, 470 m, -15.18833, 49.615, rainforest, (Fisher, Griswold *et al.*) (CASC); Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m, -15.17833, 49.635, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Ambodiriana, 4.8 km 306° Manompana, along Manompana river, 125 m, -16.67233, 49.70117, rainforest, (B.L. Fisher *et al.*) (CASC); Torotorofotsy, 1005 m, -18.77048, 48.43043, montane rainforest, (B.L. Fisher *et al.*) (CASC); Province **Toliara:** Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1125 m, -24.13894, 47.06804, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1315 m, -24.13632, 47.05485, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Parc National Andohahela, Col de Tanatana, 400 m, -24.74969, 46.84949, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC).

Camponotus mainty **Rakotonina & Fisher sp. n.**
(Figures 12B, 13B, 28, 36)

Holotype worker. Madagascar: Province Toamasina, Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, -15.17833, 49.635, 1100 m, ex rotten log, montane rainforest, 12–16 Mar 2003 (Fisher, Griswold *et al.*) collection code: BLF08192, specimen code: CASENT0497845 (CASC).

Paratypes. 6 minor and 8 major workers with same data as holotype but with specimen codes: minors: CASENT0497841, CASENT0497844, CASENT0804669, CASENT0804670, CASENT0804671, CASENT0804672; majors: CASENT0497842, CASENT0497843, CASENT0804673, CASENT0804674, CASENT0804675, CASENT0804676, CASENT0804677, CASENT0804678 (CASC, BMNH, MHNG, PBZT).

Diagnosis. Median portion of clypeus without longitudinal carina; mandible with six teeth; anteromedian margin of clypeus not bordered by a lamella; in lateral view, mesosoma long and low, its dorsal outline not a dome-like structure; propodeal declivity inclined anteriorly and not perpendicular to ventral face of propodeum; petiolar node more or less flattened anteroposteriorly; body entirely or mostly black to reddish-black; appendages reddish-black or dark brown.

Description. Minor worker. In full-view, head elongate, lateral margin straight and diverging posteriorly, rounding to the slightly convex posterior margin. Anterior clypeal margin straight, rounding to lateral margin; median longitudinal carina absent. Eyes either breaking the lateral outlines of head or not, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.30±0.03; 0.23–0.36). Mandible triangular, masticatory margin with six teeth. Antennal scape long, roughly its distal half surpassing posterior cephalic border. In lateral view, pronotum slightly convex, mesonotum and propodeal dorsum straight and elongate, joining declivity surface at broad angle. Propodeal dorsum roughly three times as long as height of declivity; propodeal spiracle round. Petiolar node higher than long, junction of dorsal margin to anterior face rounded and angulate to posterior face.

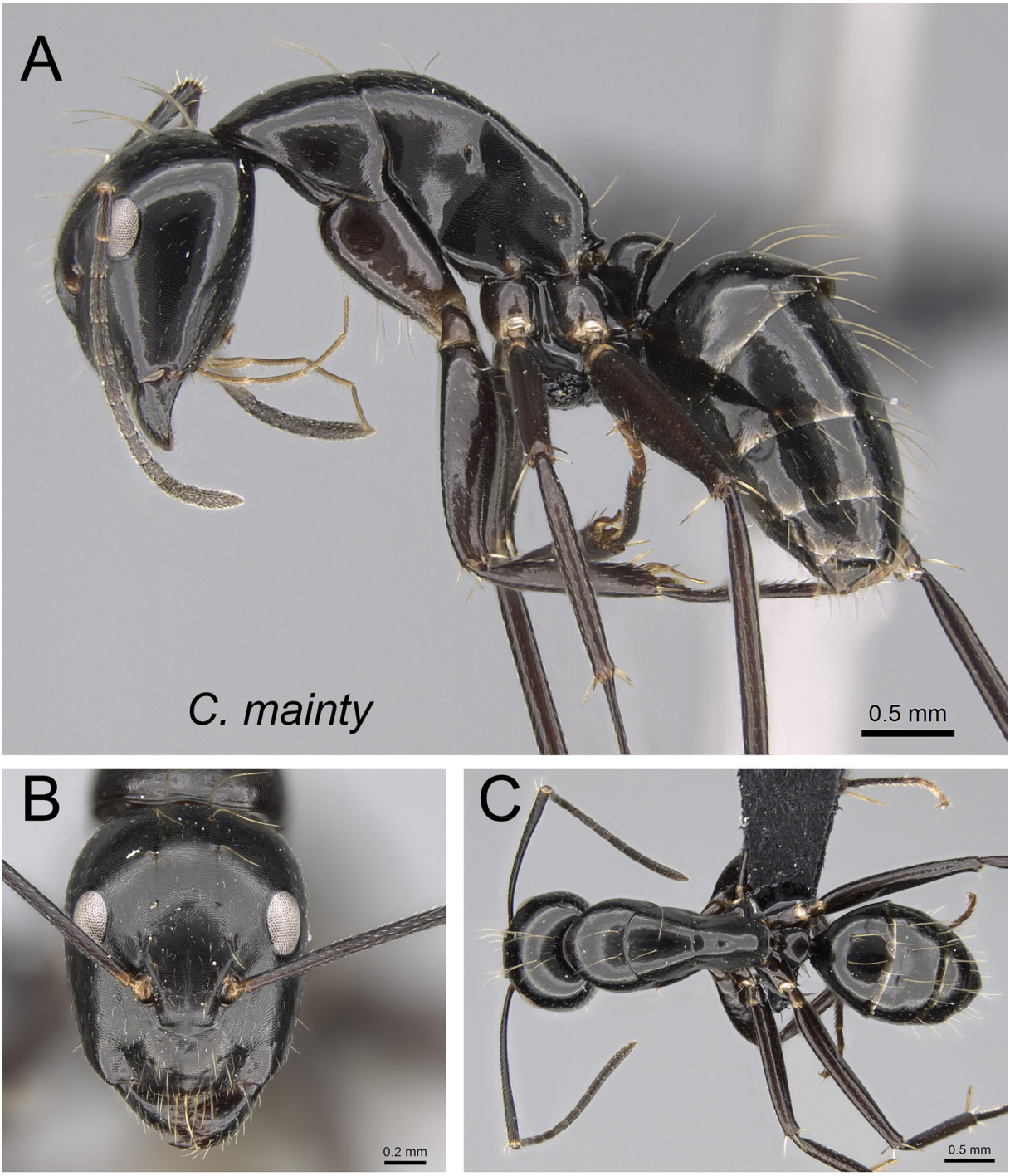


FIGURE 28. *Camponotus mainty* minor worker CASENT0497845. A: lateral view. B: head in full-face view. C: dorsal view.

Dorsum of head covered with numerous whitish, elongate erect hairs; pronotum, mesonotum and junction of propodeal dorsum and declivity with a pair of erect hairs; pubescence short and sparse on dorsum of body; petiolar node with at least two pairs of erect hairs on its posterodorsal margin. Body and appendages entirely black, or head, mesosoma, and gaster black and legs with funicular segments reddish-brown.

Major worker. Differing from minor worker in the following characters: enlarged head with markedly concave posterior margin; apical fourth of antennal scape surpassing posterior cephalic margin; robust mesosoma, with pronotum and mesonotum convex, metanotum distinct, propodeal dorsum straight and forming broad angle with declivity and twice as long as height of declivity; petiolar node tapering dorsally.

Discussion. *Camponotus mainty* can be confused with *C. maculiventris* and with *C. foersteri*, but in both latter

species the trochanter and the distal portion of the coxa is yellowish to white in color and also the petiolar node is not flattened anteroposteriorly, but its dorsal margin is distinctly broadly convex. *Camponotus christi* can be separable from *C. mainty* by the yellow to light brown color of its body.

The species definition for *C. mainty* is supported by the congruence between the results of traditional qualitative morphology and the NC-clustering technique combined with the partitioning method. However, identification success is only 96.97%, because its one minor worker is misclassified as *C. foersteri* by the LDA. This suggests that the entire range of minor worker forms of these species might not have been measured, and both species are closely related and have similar quantitative and qualitative morphology. In addition, one minor worker of *C. foersteri* is misclassified as *C. mainty* by the cumulative LDA, confirming their close morphological similarity. The two are distinguished by morphological traits not easily incorporated into the morphometric approach. The legs of *C. mainty* are entirely black to dark brown and its petiolar node is higher than long whereas in *C. foersteri* the trochanter and the distal portion of the coxa is yellowish to white and its petiolar node is at least as long as high.

Distribution and biology. *Camponotus mainty* is an endemic species of Madagascar, generally distributed in the mountainous regions of the northeast and southeast, as well as the central high plateau of the island. This species is known to nest frequently in rotten logs and rotting tree stumps and rarely in root mats in the ground layer. Foraging occurs on the ground and on lower vegetation.

Additional material examined. Province **Antananarivo:** 25 km NNE Ankazobe, 1500 m, -18.1, 47.18333, rainforest, (P.S. Ward) (PSWC); Station Forestière Manjakatompo, 1600 m, -19.35, 47.31667, montane rainforest, (P.S. Ward) (PSWC); Province **Antsiranana:** Parc National de Marojejy, 25.4 km 30° NNE Andapa, 10.9 km 311° NW Manantenina, 2000 m, -14.445, 49.735, montane shrubland, (B.L. Fisher) (CASC); Parc National de Marojejy, Antranohofa, 26.6 km 31° NNE Andapa, 10.7 km 318° NW Manantenina, 1325 m, -14.44333, 49.74333, montane rainforest, (B.L. Fisher) (CASC); Prov. Antsiranana Réserve Spéciale Manongarivo 17.3 km 218° SW Antanambao, 1580 m, -14.02167, 48.41833, montane rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo, 20.4 km 219° SW Antanambao, 1860 m, -14.04667, 48.40167, montane rainforest, (B.L. Fisher) (CASC); Province **Fianarantsoa:** 29 km SSW Ambositra, Ankazomivady, 1700 m, -20.77667, 47.165, Border of disturbed forest, (H.G.Robertson) (CASC); Belle Vue trail, Ranomafana National Park, Fianarantsoa Prov., 1020 m, -21.2665, 47.42017, mixed tropical forest, (R. Harin'Hala) (CASC); Fitovavy Fitovinany Region, District of Ifanadiana, 12 km W of Ranomafana, 1127 m, -21.25083, 47.40717, forest edge, open area, (Rin'ha, Mike) (CASC); Forêt d'Atsirakambiaty, 7.6 km 285° WNW Itremo, 1550 m, -20.59333, 46.56333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); JIRAMA water works near river, Ranomafana National Park, Fianarantsoa Prov., 690 m, -21.2485, 47.45217, open area near stream, (R. Harin'Hala) (CASC); Parc National Befotaka-Midongy, Papango 28.5 km S Midongy-Sud, Mount Papango, 1250 m, -23.84083, 46.9575, montane rainforest, (B.L. Fisher *et al.*) (CASC); Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 1100 m, -21.29, 47.43333, montane rainforest, (Fisher, Griswold *et al.*) (CASC); radio tower, Ranomafana National Park, Fianarantsoa Prov., 1130 m, -21.25083, 47.40717, forest edge, mixed tropical forest, open area, (M. Irwin, R. Harin'Hala) (CASC); Vohiparara broken bridge, Fianarantsoa Prov., 1110 m, -21.22617, 47.36983, high altitude rainforest, (R. Harin'Hala) (CASC); Province **Toamasina:** Réserve Spéciale Ambatovaky, Sandrangato river, 355 m, -16.77468, 49.26551, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 430 m, -16.7755, 49.26427, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 360 m, -16.81753, 49.29498, beating low vegetation, (CASC); Ambalahasina, 62.4 km 19° Toamasina, 15 m, -17.59452, 49.46785, coastal scrub, (B. Blaimer, F.N. Raharimalala) (CASC); Montagne d'Anjanaharibe, 19.5 km 27° NNE Ambinanitelo, 1100 m, -15.17833, 49.635, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Province **Toliara:** Forêt Ivohibe, 55.0 km N Tolagnaro, 200 m, -24.569, 47.204, rainforest, (B.L. Fisher *et al.*) (CASC); Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 900 m, -24.76389, 46.75167, montane rainforest, (Fisher-Griswold Arthropod Team) (CASC); 1 km NE Ambalavao, nr. Antananarivo, 1350 m, -19.08333, 47.53333, roadside, (P.S. Ward) (CASC).

Camponotus manabo **Rakotonirina & Fisher sp. n.**
(Figures 5A, 29, 37)

Holotype worker. Madagascar: Province Toamasina, Bevolota 17.1 km N Andasibe, -18.77071, 48.43164, 995 m,

ex rotten log, montane rainforest, 12 Dec 2007 (B.L. Fisher *et al.*) collection code: BLF19324, specimen code: CASENT0135055 (CASC).

Paratype. 1 worker with same data as holotype but with specimen code: CASENT0135056 (CASC).

Diagnosis. Median portion of clypeus with a longitudinal carina; in lateral view, mesosoma short and high; body entirely dark brown to black without any white spots, dorsum of mesosoma covered with 15 to 20 long erect hairs and scattered short pubescence; anteromedian margin of clypeus broadly convex; dorsal margin of petiolar node convex.

Description. Minor worker. In full-face view, head elongate, lateral margin straight and diverging posteriorly, rounding to the slightly medially excised posterior margin. Anterior clypeal margin broadly convex; median carina short and located in its posterior quarter. Eyes not breaking lateral outlines of head; their posterior margins located far behind the mid-length of the head (PoOc/CL: 0.27±0.01; 0.25–0.28). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its distal half extending beyond posterior cephalic border. In lateral view, dorsal outline of mesosoma a continuous convexity; propodeal dorsum rounding to declivity surface; propodeal dorsum roughly twice as long as the declivity is high; propodeal spiracle slit-like. Petiolar node higher than long, its dorsal margin convex.

Dorsum of mesosoma covered with whitish, elongate, erect hairs of the same height as propodeal declivity and sparse short pubescence. Body color entirely black and appendages reddish-black.

Major worker. Differing from minor worker in the following characters: enlarged head with noticeably concave posterior margin; robust mesosoma, with distinct metanotum, propodeal dorsum twice as long as height of declivity; petiolar node tapering dorsally.

Discussion. *Camponotus manabo* can be distinguished from the other species in the *Mayria* group by the presence of median longitudinal carina on its clypeus, the short and high mesosoma, and the existence of numerous erect hairs and a small quantity of short pubescence on the dorsum of the mesosoma.

The qualitative, morphology-based study of *C. matsilo* is in agreement with the multivariate morphometric technique and both methods support the taxonomic delimitation for this species. The validity of the species, which is supported by the grouping obtained from NC-clustering and partitioning methods, is confirmed by LDA with an identification success of 100%.

Distribution and biology. Endemic to Madagascar, *C. manabo* is geographically recorded from the eastern rainforests and montane rainforests of Madagascar. Its distribution ranges from Ambanizana in the north to the Corridor Forestier Analamay-Mantadia, Ambatoharanana in the center through the Vevembe Forest and down to Ivohibe Forest in the south. Worker specimens have been found foraging mostly on the ground and in leaf litter, and nest sites are in rotten logs.

Additional material examined. Province **Fianarantsoa:** Forêt de Vevembe, 66.6 km 293° Farafangana, 600 m, -22.791, 47.18183, rainforest, transition to montane forest, (B.L. Fisher *et al.*) (CASC); Province **Toamasina:** Réserve Spéciale Ambatovaky, Sandrangato river, 360 m, -16.81753, 49.29498, rainforest, (CASC); Réserve Spéciale Ambatovaky, Sandrangato river, 480 m, -16.80561, 49.29507, rainforest, (CASC); 5.3 km SSE Ambanizana, Andranobe, 425 m, -15.67133, 49.97395, rainforest, (B.L. Fisher) (CASC); 6.9 km NE Ambanizana, Ambohitsitondroina, 825 m, -15.58506, 50.00952, rainforest, (B.L. Fisher) (CASC); Bevolota 17.1 km N Andasibe, 995 m, -18.77071, 48.43164, montane rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambatoharanana, 1058 m, -18.79956, 48.4028, rainforest, (B.L. Fisher *et al.*) (CASC); Corridor Forestier Analamay-Mantadia, Ambohibolakely, 918 m, -18.77898, 48.36375, rainforest, (B.L. Fisher *et al.*) (CASC); F.C. Andriantantely, 530 m, -18.695, 48.81333, rainforest, (H.J. Ratsirarson) (CASC); Forêt Ambatovy, 14.3 km 57° Moramanga, 1075 m, -18.85083, 48.32, montane rainforest, (Malagasy ant team) (CASC); Montagne d'Akirindro 7.6 km 341° NNW Ambinanitelo, 600 m, -15.28833, 49.54833, rainforest, (Fisher, Griswold *et al.*) (CASC); *PARC NATIONAL* Mantadia, 895 m, -18.79167, 48.42667, rainforest, (H.J. Ratsirarson) (CASC); Réserve Naturelle Betampona, 34.08 km 332° Toamasina, 525 m, -17.91977, 49.20039, rainforest, (B.L. Fisher) (CASC); Sahafina forest 11.4 km W Brickaville, 140 m, -18.81445, 48.96205, rainforest, (B.L. Fisher *et al.*) (CASC); Station Forestière Analamazaotra, Analamazaotra 1.3 km S Andasibe, 980 m, -18.38466, 48.41271, montane rainforest, (B.L. Fisher *et al.*) (CASC); Province **Toliara:** Forêt Ivohibe 55.0 km N Tolagnaro, 200 m, -24.569, 47.204, rainforest, (B.L. Fisher *et al.*) (CASC).

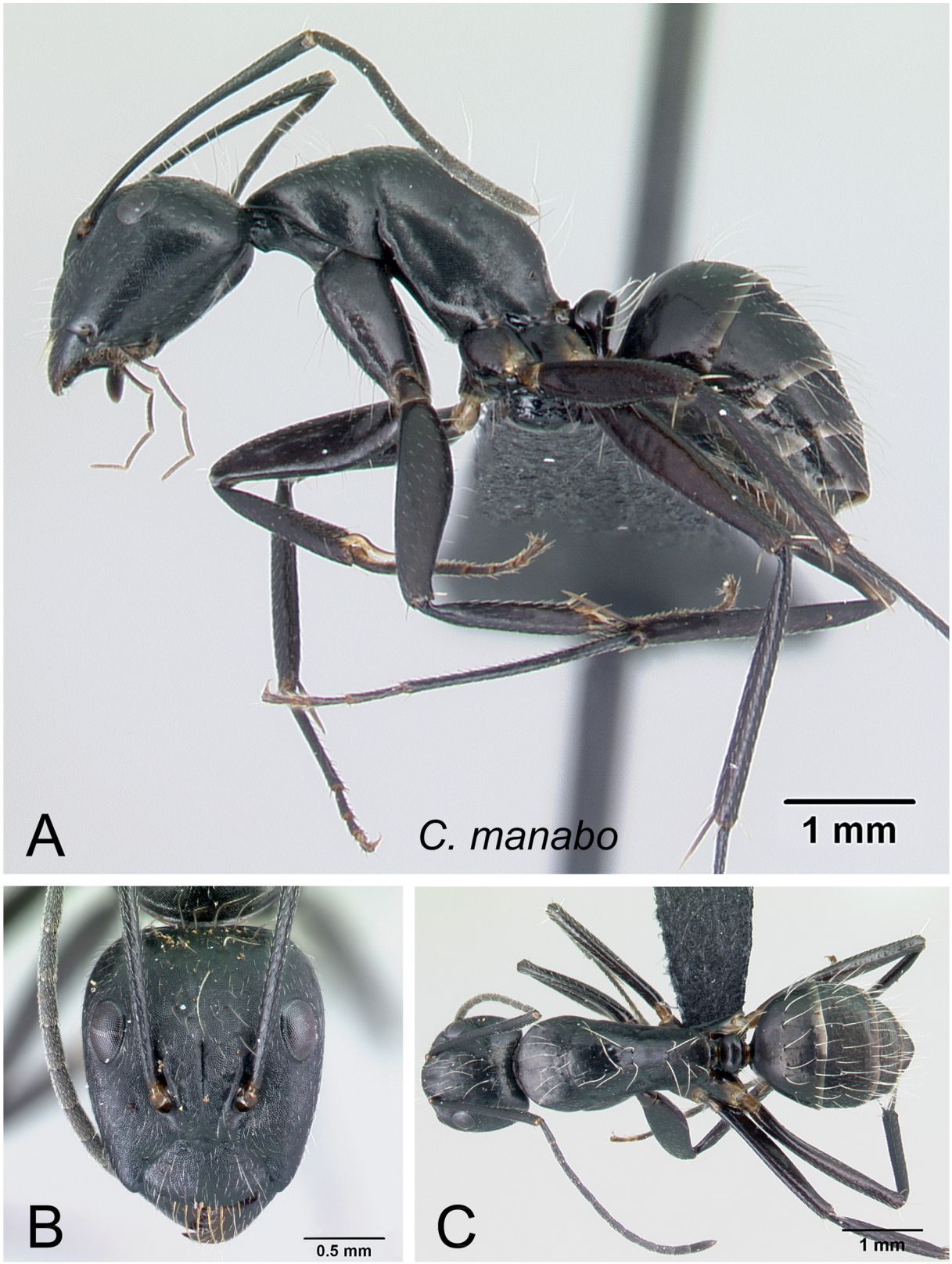


FIGURE 29. *Camponotus manabo* minor worker CASENT0496383. A: lateral view. B: head in full-face view. C: dorsal view.

***Camponotus pulcher* Forel Stat. n.**
(Figures 10B, 11B, 12B, 30, 38)

Camponotus dromedarius var. *pulcher* Forel, 1892: 234. Lectotype minor worker, **present designation**, Madagascar, Imerina ville d'Anosibe [Toamasina, Anosibe an'Ala, -19.433332, 48.216667, 660 m] (Sikora), AntWeb CASENT0101533 (MHNG) [examined]. [Combination in *Camponotus (Myrmosaga):* Wheeler, 1922: 1045; in *Camponotus (Mayria):* Emery, 1925: 122; Bolton, 1995: 119]. **Stat. n.**

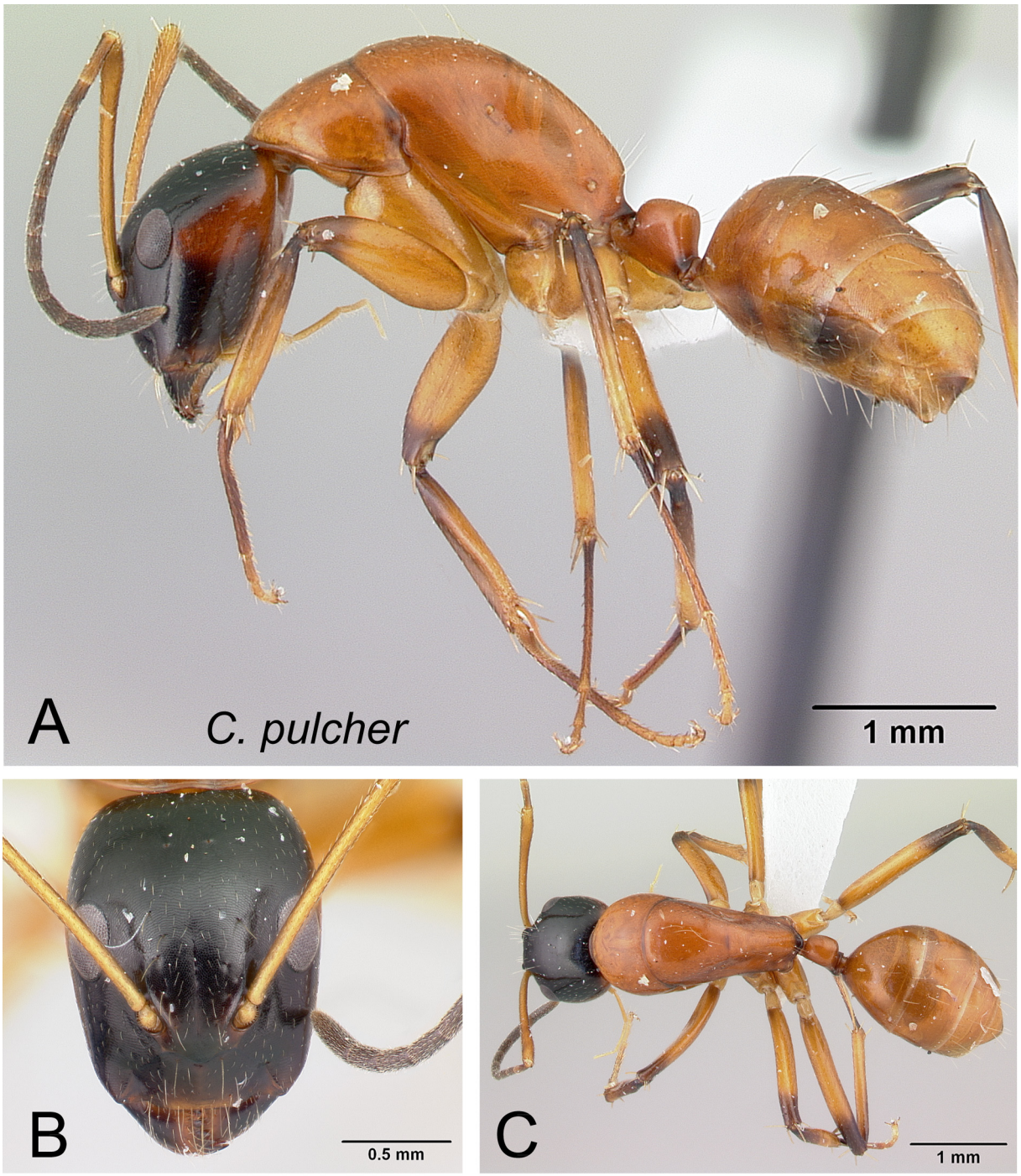


FIGURE 30. *Camponotus pulcher* minor worker CASENT0191639. A: lateral view. B: head in full-face view. C: dorsal view.

Diagnosis. Median longitudinal carina of clypeus lacking; anteromedian margin of clypeus slightly concave medially; mandible with six teeth; in lateral view, mesosoma short and high, propodeal dorsum straight, not excised medially; petiolar node as long as high.

Description. Minor worker. In full-face view, head longer than broad (CWb/CL: 0.84±0.05; 0.81–0.94), lateral margin straight anterior to the eye and convex posteriorly; posterior margin slightly excised medially. Clypeus with feebly concave anteromedian margin and broadly angulate lateral margin. Eyes not breaking lateral outlines of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.33±0.01; 0.31–0.35). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its distal half surpassing posterior margin of head. With mesosoma in lateral view, dorsal outline forming an even continuous convexity, joining declivity in a broad angle; propodeal declivity straight and inclined posteriorly. Petiolar node as high as long.

Dorsum of head, mesosoma, and gastral segments with scattered, erect, slender hairs and sparse pubescence. Head black, mesosoma and petiole orange and black spot sometimes present along metanotal suture; gastral segments generally orange, posterior portion of second gastral tergite and remainder of sternite and tergite patchily or entirely dark brown to black; scape and other appendages generally yellow to light orange, flagellum and junction of femur and tibia and proximal portion of basitarsus brown to dark brown.

Major worker. With characteristics of minor worker, except for the typically broader head, much higher petiolar node, and more dark brown to black spots on dorsum of mesosoma and gastral segments.

Discussion. *Camponotus pulcher* is similar to *C. dromedarius* and *C. lamosy.* See discussion sections under *C. dromedarius* and *C. lamosy* where the comparisons of these species are provided.

Two syntype specimens were designated by Forel to represent *C. pulcher* in his original description, but after careful observations, only one specimen, which is presently designated as a lectotype of the species, matches this description. The second specimen, with AntWeb CASENT0101532, has been removed from *C. pulcher* and is currently placed in *C. foersteri* in the present revision.

The qualitative morphology-based delimitation of *C. pulcher* is confirmed by multivariate statistical analysis. The validity of the species is also confirmed by LDA at 100% classification success.

Distribution and biology. This species is distributed along the rainforest and montane rainforest habitats of the north and northeast as well as the central east of Madagascar. In the Réserve Spéciale Manongarivo, where both forest habitats are found, the members of *C. pulcher* have been known to nest in rotting tree stumps and forage in leaf litter and on low vegetation. In the rainforests of the Parc National Masoala and the montane rainforest of Torotorofotsy, colonies have been collected from rotten logs.

Additional material examined. Province **Antsiranana:** Masoala National Park, 280 m, -15.3014, 50.22776, rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale Manongarivo, 12.8 km 228° SW Antanambao, 780 m, -13.97667, 48.42333, rainforest, (B.L. Fisher) (CASC); Réserve Spéciale Manongarivo, 14.5 km 220° SW Antanambao, 1175 m, -13.99833, 48.42833, montane rainforest, (B.L. Fisher) (CASC); Province **Toamasina:** Torotorofotsy, 1070 m, -18.87082, 48.34737, montane rainforest, marsh edge, (Malagasy ant team) (CASC); Torotorofotsy, 1070 m, -18.87082, 48.34737, montane rainforest, marsh edge, (Malagasy ant team) (CASC).

Camponotus raina Rakotonirina & Fisher sp. n.

(Figures 5B, 6A, 31, 39)

Holotype worker. Madagascar: Province Antsiranana, Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, -13.11833, 49.23, 425 m, ex rotten log, rainforest 16 Dec 2003 (B.L. Fisher *et al.*) BLF10292, CASENT0499051 (CASC).

Paratypes. 8 minor and 6 major workers with same data as holotype but with specimen codes: minors: CASENT0499049, CASENT0499050, CASENT0804659, CASENT0804660, CASENT0804661, CASENT0804662, CASENT0804663, CASENT0804664; majors: CASENT0499052, CASENT0499053, CASENT0804665, CASENT0804666, CASENT0804667, CASENT0804668 (CASC, BMNH, MHNG, MSNG, PBZT).

Diagnosis. Median portion of clypeus with longitudinal carina; anteromedian margin of clypeus covered with lamella; pronotum, junction of dorsum and declivity surface of propodeum and posterodorsal margin of petiole each with one pair of elongate, stout erect hairs; in lateral view, petiolar node longer than high; distal portion of procoxa white.

Description. Minor worker. In full-face view, head longer than wide, lateral margin straight and slightly

converging posteriorly; posterior margin more or less straight. Anteromedian clypeal margin broadly convex and with broadly rounded, translucent lamella. Eyes breaking lateral outlines of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.35±0.02; 0.31–0.37). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its distal half extending beyond posterior cephalic margin. In lateral view, promesonotum flat and becoming curved toward junction to propodeum; propodeal dorsum straight, propodeal declivity inclined posteriorly; petiolar node longer than high.

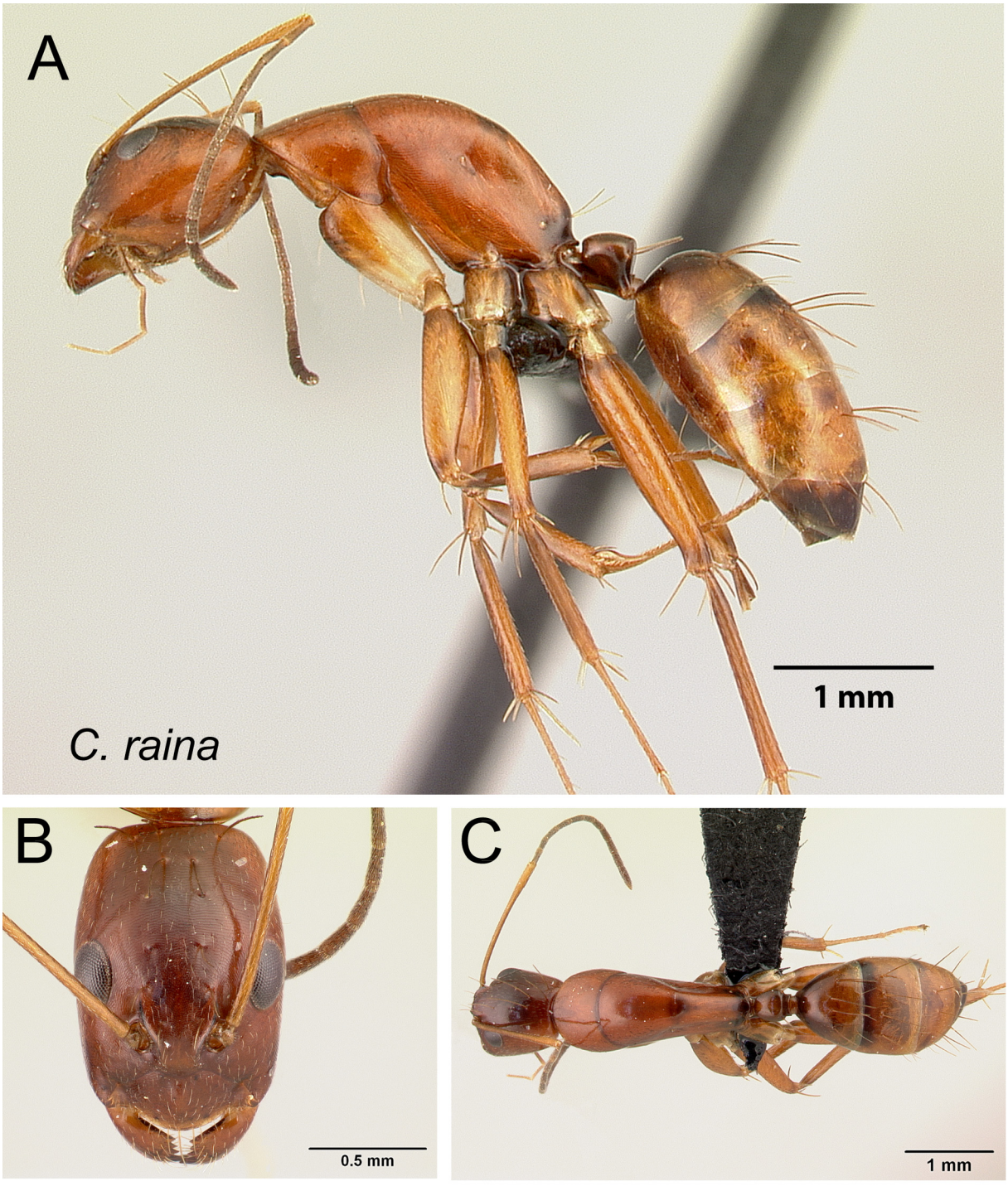


FIGURE 31. *Camponotus raina* minor worker CASENT0499051. A: lateral view. B: head in full-face view. C: dorsal view.

Blunt, elongate, erect brown hairs and short and sparse pubescence present on dorsum of head, petiolar node, and gastral segments. Head reddish-orange laterally and reddish-black to dark brown frontally, petiole reddish-black to dark brown; trochanter and distal portion of coxae whitish-yellow; abdominal segments yellow-orange

with black patches in anterolateral portions of 3 and 4 and darker color from segment 6; scape, femur, and tarsus a lighter color.

Major worker. With characterisitics of minor worker, except for the following divergent features: enlarged head, apical fifth of antennal scape surpassing posterior cephalic margin, much more robust mesosoma, pronotum and mesonotum forming a convexity, separated from propodeum by a distinct metanotum; propodeal dorsum rounding to declivity; petiolar node tapering dorsally; larger dark brown to black spots on gastral tergites, sometimes on mesosoma and head.

Discussion. In the *Camponotus* subgenus *Mayria*, *C. raina* can be confused with *C. tanosy*, but in the latter the anteromedian margin of the clypeus is not bordered by a lamella, the masticatory margin of the mandible is armed with five teeth, and the petiolar node is higher than long. *Camponotus raina* may also be confounded with *C. sada* but the latter has an elongate but low mesosoma and a black to dark brown head and mesosoma.

The taxonomic identity of *C. raina* based on conventional qualitative morphology is supported by multivariate morphometric analysis. The grouping of the samples of this species obtained from the NC-clustering and partitioning methods is confirmed by LDA with an identification success of 100%.

Distribution and biology. This species is limited to the littoral and rainforests as well as the tropical dry forests of northeastern Madagascar. Members of *C. raina* have been found nesting in rotten logs and rotten sticks on the ground and foraging in leaf litter, on forest floors, and on low vegetation.

Additional material examined. Province **Antsiranana:** Ambondrobe, 41.1 km 175° Vohemar, 10 m, -13.71533, 50.10167, littoral rainforest, (B.L. Fisher) (CASC); Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe, 4.6 km 356° N Betsiaka, 425 m, -13.11833, 49.23, rainforest, (B.L. Fisher) (CASC); Forêt d'Antsahabe, 11.4 km 275° W Daraina, 550 m, -13.21167, 49.55667, tropical dry forest, (B.L. Fisher) (CASC); Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, -12.97, 49.7, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Binara, 7.5 km 230° SW Daraina, 375 m, -13.255, 49.61667, tropical dry forest, (B.L. Fisher) (CASC).

Camponotus repens **Forel**

(Figures 3A, 4A, 32, 40)

Camponotus repens Forel, 1897: 187. Lectotype minor worker, **present designation**, Mojanga, West Madagascar [Mahajanga, Ambatoboeny, Madirovalo, -16.523884, 46.516262, 23 m] (Grandidier), AntWeb CASENT0102437 (MHNG) [examined]. Paralectotypes. 3 minor workers of same data as lectotype but with specimen code: CASENT0102434, CASENT0102438 (MHNG), CASENT0101175 (NHMB). [Combination in *Camponotus (Mayria):* Forel, 1897: 187. Replacement name of *Mayria madagascarensis* Forel, 1886a: 4, a junior secondary homonym of *Camponotus niveosetosus madagascarensis* Forel, 1886a: 4].

Diagnosis. Median portion of clypeus with longitudinal carina; dorsum of mesosoma covered with numerous slender erect hairs and elongate appressed hairs; in lateral view, petiolar node higher than long; distal portion of procoxa white.

Description. Minor worker. In full-face view, head elongate, oval, with broadly convex posterior margin. Clypeus with truncate anteromedian margin, its junction to lateral margin broadly angulate; clypeal lamella absent. Eyes breaking lateral outlines of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.27±0.01; 0.25–0.29). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its apical third extending beyond posterior cephalic border. In lateral view, pronotum weakly convex; mesonotum and propodeum more or less straight; propodeal angle roughly rounded; propodeal dorsum roughly one and a half times longer than height of declivity. Petiolar node about as high as long.

Dorsum of body covered with numerous slender, whitish, erect hairs and abundant elongate pubescence. Head, mesosoma, and gaster black; legs generally much lighter in color than body: trochanter, apical portion of coxa and femur whitish-yellow; rest of leg dark brown basally and becoming light brown toward the apex; antennal scape and apical portion of funiculus dark brown and basal portion of funiculus light brown to brown.

Major worker. With characteristics of minor worker except for the following divergent characters: larger head; antennal scape barely surpassing posterior cephalic margin; longitudinal median cariana on posterior half of clypeus; pronotum weakly convex; mesonotum and propodeal dorsum more or less straight and separated by a shallow metanotum; declivity surface rounding to propodeal dorsum.

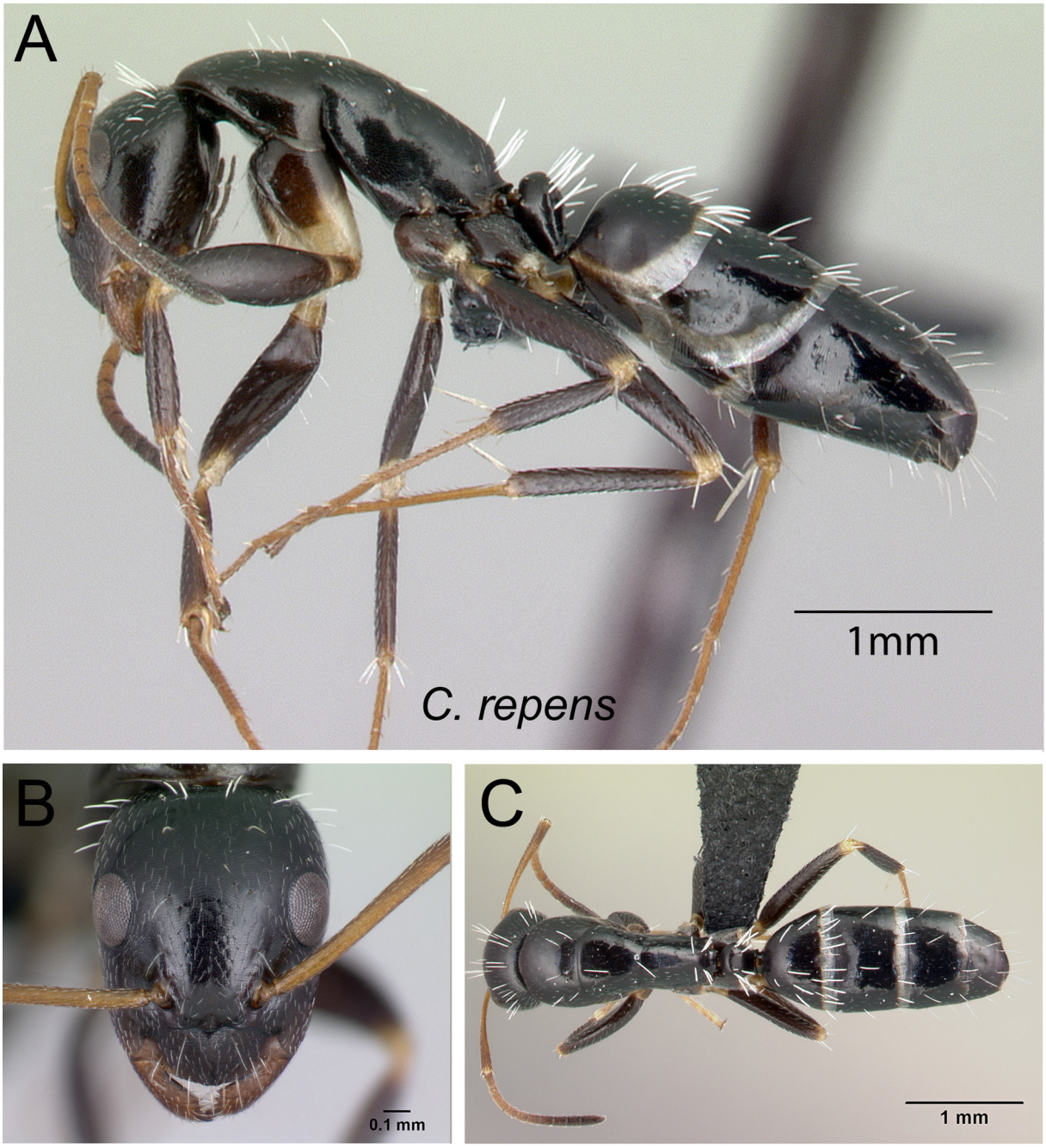


FIGURE 32. *Camponotus repens* minor worker CASENT0491267. A: lateral view. B: head in full-face view. C: dorsal view.

Discussion. One of the smallest species (CL: 0.8–1.18; PW: 0.54–0.83) in the subgenus *Mayria*, *C. repens* can be recognized by its mesosoma dorsum covered with numerous slender erect hairs and elongate appressed hairs, the convex median portion of the clypeus and the white color of the distal portion of the procoxa.

Species delimitation of *C. repens* on the basis of traditional taxonomic study is congruent with the grouping generated by NC-clustering combined with the PART method. The species was also classified correctly at 100% by the confirmatory LDA.

Distribution and biology. *Camponotus repens* is an endemic, widespread species distributed across the littoral forests and rainforests of the north, the tropical dry forests of the northwest and west, the gallery forests of the central south and southeast, and the spiny forests and thickets in the south of Madagascar. In open habitats like *Uapaca* woodland, spiny forests and thickets, and a few tropical forests, the nests are found either in the ground or under stones, whereas in most of the dry habitats and the gallery forests the species nests in rotten logs, rot pockets, and rotting tree stumps. Workers have been found foraging in the leaf litter, on the ground and on the lower parts of

the vegetation.

Additional material examined. Province **Antananarivo:** Analamanga Region, District of Ankazobe, Ambohitantely, 46 km NE of Ankazobe, 701 m, -18.198, 47.2815, Forêt sclerophylle, (Rin'ha, Mike) (CASC); Province **Antsiranana:** Ampasindava, Forêt d'Ambilanivy, 3.9 km 181° S Ambaliha, 600 m, -13.79861, 48.16167, rainforest, (Fisher, Griswold *et al.*) (CASC); Forêt d'Analabe, 30.0 km 72° ENE Daraina, 30 m, -13.08333, 49.90833, littoral rainforest, (B.L. Fisher *et al.*) (CASC); Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m, -12.86361, 49.22583, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m, -12.90889, 49.10983, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National Montagne d'Ambre [1st campsite], 960 m, -12.51444, 49.18139, rainforest, (R. Harin'Hala) (CASC); Parc National Montagne d'Ambre [Petit Lac road], 1125 m, -12.52028, 49.17917, rainforest, (R. Harin'Hala) (CASC); Sakalava Beach [vegetated beach dunes], 10 m, -12.26278, 49.3975, across sandy trail in dwarf litoral forest, (R. Harin'Hala) (CASC); Province **Fianarantsoa:** Amoron'i Mania Region, District of Ambositra, Italaviana *Uapaca* forest, 135 km SE of Antsirabe, 1359 m, -20.17333, 47.086, *Uapaca* forest, (Rin'ha, Mike) (CASC); Parc National d'Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, 990 m, -22.29833, 45.35167, *Uapaca* woodland, (Fisher, Griswold *et al.*) (CASC); Parc National d'Isalo, Sahanafa River, 29.2 km 351° N Ranohira, 500 m, -22.31333, 45.29167, gallery forest, (Fisher, Griswold *et al.*) (CASC); stream area, 900 m E of Isalo National Park Interpretive Center, Fianarantsoa Prov., 750 m, -22.62667, 45.35817, open area near stream, (R. Harin'Hala) (CASC); Province **Mahajanga:** Ampijoroa National Park, 160 km N Maevatanana, Mahajanga Prov., deciduous forest, 43 m, -16.31944, 46.81333, deciduous forest, (Michael Irwin, Rin'ha) (CASC); Boeny Region, District of Soalala, Beaboaly Bamboo forest, 10 km SW of Soalala, 4 km of Baly village, 9 m, -16.04533, 48.804, bamboo forest, (Mike, Rinha) (CASC); Boeny Region, District of Marovoay, Ampijoroa National Park, 160 km North of Maevatanana on RN 04, 42 m, -16.31933, 46.81333, deciduous forest, (Mike, Rinha) (CASC); Boeny Region; District of Soalala, Namoroka 53 km of Soalala, Ambatofolaka dry forest, 3 km N of Vilanandro villlage, 105 m, -16.47333, 45.39133, dense dry forest in the mud, (Mike, Rinha) (CASC); Forêt Ambohimanga, 26.1 km 314° Mampikony, 250 m, -15.96267, 47.43817, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Tsimembo, 8.7 km 336° NNW Soatana, 20 m, -19.02139, 44.44067, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Melaky Region, District of Besalampy, Marofototra palm forest, 17 km W of Besalampy, 10 m, -16.72167, 44.42367, palm trees on sand, (Irwin, Rin'ha) (CASC); Parc National d'Ankarafantsika, Ampijoroa Station Forestière, 40 km 306° NW Andranofasika, 130 m, -16.32083, 46.81067, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National de Baie de Baly, 12.4 km 337° NNW Soalala, 10 m, -16.01, 45.265, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 100 m, -16.40667, 45.31, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National de Namoroka, 9.8 km 300° WNW Vilanandro, 140 m, -16.46667, 45.35, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Réserve d'Ankoririka, 10.6 km 13° NE de Tsaramandroso, 210 m, -16.26722, 47.04861, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Réserve forestière Beanka, 50.2 km E Maintirano, 250 m, -18.02649, 44.05051, tropical dry forest on tsingy, (B.L. Fisher *et al.*) (CASC); Réserve forestière Beanka, 50.2 km E Maintirano, 153 m, -17.88756, 44.47265, tropical dry forest on tsingy, (B.L. Fisher *et al.*) (CASC); Réserve forestière Beanka, 50.7 km E Maintirano, 140 m, -17.88021, 44.46877, tropical dry forest on tsingy, (B.L. Fisher *et al.*) (CASC); Sofia Region, District of Port-Berger, Ambovomamy 20 km N of Port-Berger, 86 m, -15.45117, 47.61333, secondary forest on white sandy area, (Mike, Frank, Rin'ha) (CASC); Station Forestière Ampijoroa, 80 m, -16.31667, 46.81667, tropical dry forest, (P.S. Ward) (PSWC); Province **Toliara:** 50 km N Morondava, -20.06667, 44.58333, in primary dry forest, (A. Pauly) (CASC); Anosy Region, District of Amboasary, 58 km SW of Fort Dauphin, 8 km NW of Amboasary, Berenty Special Réserve, 85 m, -25.00667, 46.30333, gallery forest, (Mike, Frank Parker, Rin'ha) (CASC); Anosy Region, District of Amboasary, 58 km SW of Fort Dauphin, 8 km NW of Amboasary, Berenty Special Réserve, 36 m, -25.021, 46.3055, spiny forest, (Mike, Rinha) (CASC); Anosy Region, District of Fort-Dauphin, Andohaela National Park Parcelle II, Tsimela,42 km W of Fort-Dauphin, 176 m, -24.93683, 46.62667, transition forest, (Michael Irwin, Frank Parker, Rin'ha) (CASC); Anosy Region, Parc National d'Andohahela, Forêt de Manatalinjo, 100 m, -24.82466, 46.60111, spiny forest/thicket, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Parc National d'Andohahela, Forêt de Manatalinjo, 90 m, -24.82505, 46.57811, spiny forest/thicket, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Atsimo Andrefana Region, District of Betioky, 30 km E Betioky, Beza Mahafaly Special Reserve (Around Research Station); 165 m, -23.6865, 44.591, dry deciduous gallery forest, (Rin'ha, Mike) (CASC); Fiherenana, 65 m, -23.22252, 43.88088, gallery forest,

degraded, (Frontier Project) (CASC); Forêt de Beroboka, 5.9 km 131° SE Ankidranoka, 80 m, -22.23306, 43.36633, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, 30 m, -20.06855, 44.659565, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Kirindy, 15.5 km 64° ENE Marofandilia, 100 m, -20.045, 44.66222, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Mahavelo, Isantoria River, 110 m, -24.75833, 46.15717, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Mite, 20.7 km 29° WNW Tongobory, 75 m, -23.52417, 44.12133, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Forêt de Tsinjoriaky, 6.2 km 84° E Tsifota, 70 m, -22.80222, 43.42067, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Forêt Vohidava 88.9 km N Amboasary, 500 m, -24.24067, 46.28783, spiny forest/dry forest transition, (B.L. Fisher *et al.*) (CASC); Makay Mts., 570 m, -21.29961, 45.12919, dry forest edge and burned savannah, (B.L. Fisher *et al.*) (CASC); Makay Mts., 620 m, -21.31664, 45.1296, dry forest on sandy soil, (B.L. Fisher *et al.*) (CASC); Makay Mts., 525 m, -21.31364, 45.14782, gallery forest on sandy soil, (B.L. Fisher *et al.*) (CASC); Makay Mts., 500 m, -21.25864, 45.16412, gallery forest with bamboo, (B.L. Fisher *et al.*) (CASC); Manderano, 70 m, -23.52722, 44.0875, gallery forest, (Frontier Project) (CASC); Manderano, 80 m, -23.52333, 44.09444, spiny thicket, (Frontier Project) (CASC); Menabe Region, District of Morondava, Beroboka village 45 km NE of Morondava, Antsarongaza dry forest 7.5 km E of Beroboka, 50 m, -19.9775, 44.66633, dry forest, (Michael Irwin, Rin'ha) (CASC); Menabe Region, District of Morondava, Beroboka village 45 km NE of Morondava, Antsarongaza gallery forest 7 km E of Beroboka, 45 m, -19.9775, 44.66533, 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, 300 m, -24.93, 46.6455, 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, 150 m, -24.81694, 46.61, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Parc National de Kirindy Mite, 16.3 km 127° SE Belo sur Mer, 80 m, -20.79528, 44.147, tropical dry forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Berenty, 25 m, -25.01667, 46.3, tropical dry forest, (P.S. Ward) (PSWC); Réserve Privée Berenty, Forêt d'Anjapolo, 21.4 km 325° NW Amboasary, 65 m, -24.92972, 46.20967, spiny forest/thicket, (Fisher-Griswold Arthropod Team) (CASC); Réserve Privée Berenty, Forêt de Bealoka, Mandrare River, 14.6 km 329° NNW Amboasary, 35 m, -24.95694, 46.2715, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); Réserve Privée Berenty, Forêt de Malaza, Mandrare River, 8.6 km 314° NW Amboasary, 40 m, -25.00778, 46.306, gallery forest, (Fisher-Griswold Arthropod Team) (CASC); 3 km E Itampolo, Malaise across path of lower bench of Andrimpano Forest, 45 m, -24.65783, 43.95617, dry forest, (ME Irwin, Rin'ha) (CASC); 5 km N Ampotaka, Malaise on trail in Vitambany gallery forest, 86 m, -24.65033, 43.96317, gallery forest, (ME Irwin, Rin'ha) (CASC); Ambohimahavelona village 33 km NE of Tulear, Andoharano dry forest, 46 m, -23.44083, 43.89967, dry forest, (ME Irwin, Rin'ha) (CASC); Atsimo Andrefana Region, District of Tulear II, Tsifota 20 km N of Manombo, 15 m, -22.818, 43.37267, spiny forest, (ME Irwin, Rin'ha) (CASC); Mikea Forest, deciduous dry forest, Tulear Province, 30 m, -22.90367, 43.4755, deciduous dry forest, (M.E. Irwin, F.D. Parker, R. Harin'Hala) (CASC); Mikea Forest, spiny forest, Tulear Province, 37 m, -22.91333, 43.48222, spiny forest, (R. Harin'Hala) (CASC); Parcel I, Beza Mahafaly Réserve, near research station, Tulear Province, 165 m, -23.6865, 44.591, dry deciduous forest, (R. Harin'Hala) (CASC); Tsimanampetsotsa National Park, Mitoho Forest, malaise across trail at escarpment base, 120 m, -24.0485, 43.75233, dense dry forest, (ME Irwin, Rin'ha) (CASC); Riv: Menavava Behajomaty, Local: 5 km Mahatsinjo, PLS, (ORSTROM) (CASC).

Camponotus sada **Rakotonirina & Fisher sp. n.**
(Figures 8A, 33, 41)

Holotype worker. Madagascar: Province Antsiranana, Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, -13.11833, 49.23, 425 m, rainforest, under stone, 16 Dec 2003 (B.L. Fisher *et al.*) collection code: BLF10346, specimen code: CASENT0498916 (CASC).

Paratypes. 8 minor and 5 major workers with same data as holotype but with specimen codes: minors: CASENT0498917, CASENT0498918, CASENT0804651, CASENT0804652, CASENT0804654, CASENT0804655, CASENT0804657, CASENT0804658; majors: CASENT0498919, CASENT0498920, CASENT0498921, CASENT0804653, CASENT0804656 (CASC, BMNH, MHNG, MSNG, PBZT).

Diagnosis. Median portion of clypeus without longitudinal carina; anteromedian margin of clypeus covered

with lamella; mandible with six teeth; in full-face view, head distinctly longer than broad; antennal scape covered with appressed short hairs; in lateral view, junction of dorsal and declivity surfaces of propodeum broadly rounded; petiolar node longer than high.

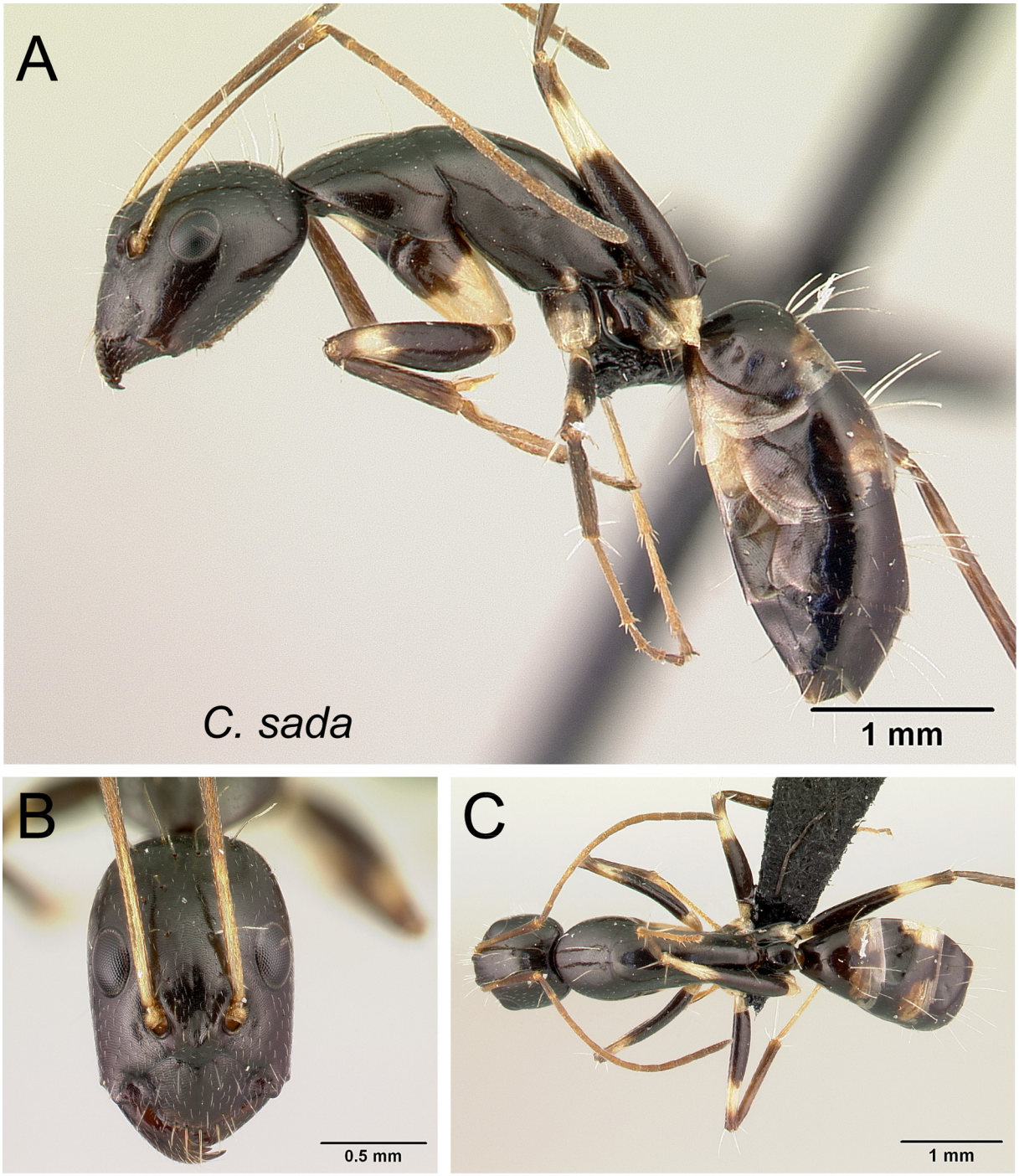


FIGURE 33. *Camponotus sada* minor worker CASENT0498916. A: lateral view. B: head in full-face view. C: dorsal view.

Description. Minor worker. In full-face view, head elongate, rectangular, with broadly convex posterior margin. Anteromedian clypeal margin broadly convex and with broadly rounded lamella. Eyes breaking lateral outlines of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.33±0.01; 0.31–0.35). Mandible triangular, apical margin with six sharp teeth. Antennal scape long, roughly its distal half extending beyond posterior cephalic border. In lateral view, promesonotum convex, propodeum straight, sometimes slightly concave, its dorsum joining the straight and anteriorly inclined declivity in a broad angle; propodeal dorsum approximately three times longer than height of declivity. Petiolar node longer than high and

inclined anteriorly.

More than one pair of elongate, stout, erect hairs near posterior border of head; pronotum, junction of dorsum and declivity of propodeum and posterodorsal margin of petiole each with one pair of elongate, stout erect hairs; few short appressed hairs present on dorsum of mesosoma. Antennal scape with abundant appressed short hairs. Body color generally black, with whitish distal portion of coxae, trochanter, femur and posterior portion of first gastral sternite; leg black on proximal portion and becoming progressively lighter in color toward its apex; first and second gastral tergite with pair of white spots; antennal scape and funiculus basally light brown and apically dark brown.

Major worker. Differing from minor worker in the following characters: larger head, absence of lamella on anterior clypeal margin, antennal scape barely surpassing posterior cephalic margin, much more robust mesosoma, with pronotum and mesonotum forming an even convexity, separated from propodeal dorsum by a shallow angle; higher than long petiolar node; much higher propodeal declivity; presence of at least three pairs of erect hairs on mesonotum. Other features as in minor worker.

Discussion. *Camponotus sada* and *C. raina* look similar but the latter has a short and high mesosoma and a generally reddish-orange head and mesosoma. *Camponotus sada* can be separated from *C. christi*, *C. foersteri,* and *C. maculiventris* by the presence of a median longitudinal carina on the clypeus. *Camponotus tanosy* differs from *C. sada* by the absence of a lamella on the anteromediam clypeal margin.

The NC-clustering showed quantitative morphological differences between *C. sada, C. foersteri*, *C. christi, C. mainty* and *C. maculiventris* that are confirmed by the partitioning method using hclust and kmeans algorithms. *Camponotus sada* is 100% successfully classified by LDA.

Distribution and biology. One of the *Mayria* group that occur only in the north of Madagascar, *C. sada* inhabits the montane rainforests of Parc National Ambre, the rainforests of Andavakoera, and the dry forests of Bekaraoka, Montagne des Français, Réserves Spéciales d'Analamerana and de l'Ankarana. Across these habitats, nests are built in the ground, under stones, or in root mats in the ground. Foraging behavior has been observed in leaf litter, on the forest floor, or on the lower parts of the vegetation.

Additional material examined. Province **Antsiranana:** Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe, 4.6 km 356° N Betsiaka, 425 m, -13.11833, 49.23, rainforest, (B.L. Fisher) (CASC); Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 175 m, -12.97, 49.7, tropical dry forest, (B.L. Fisher) (CASC); Forêt de Bekaraoka, 6.8 km 60° ENE Daraina, 150 m, -13.16667, 49.71, tropical dry forest, (B.L. Fisher) (CASC); Montagne des Français, 7.2 km 142° SE Antsiranana (=Diego Suarez), 180 m, -12.32278, 49.33817, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Parc National Montagne d'Ambre, 12.2 km 211° SSW Joffreville, 1300 m, -12.59639, 49.1595, montane rainforest, (Fisher, Griswold *et al.*) (CASC); Réserve Analamerana, 16.7 km 123° Anivorano-Nord, 225 m, -12.80467, 49.37383, tropical dry forest, (B.L. Fisher) (CASC); Réserve Analamerana, 28.4 km 99° Anivorano-Nord, 60 m, -12.74667, 49.49483, tropical dry forest, (B.L. Fisher) (CASC); Réserve Spéciale de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m, -12.86361, 49.22583, tropical dry forest, (Fisher, Griswold *et al.*) (CASC); Réserve Spéciale de l'Ankarana, 22.9 km 224° SW Anivorano Nord, 80 m, -12.90889, 49.10983, tropical dry forest, (Fisher, Griswold *et al.*) (CASC).

Camponotus tanosy Rakotonirina & Fisher sp. n.

(Figures 7A, 34, 42)

Holotype worker. Madagascar: Province Tokiara, Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, -24.13894, 47.06804, 1125 m, ex rotten log, rainforest, 26 Feb 2015, (B.L. Fisher, F.A. Esteves *et al.*), collection code: BLF36510, specimen code: CASENT0803890 (CASC).

Paratypes. 7 minor workers and 1 major worker with same data as holotype but with specimen codes: CASENT0803889, CASENT0803891, CASENT0803892, CASENT0803893, CASENT0803894 (major), CASENT0803895, CASENT0393312, CASENT0804650 (CASC, BMNH, MHNG, MSNG, PBZT).

Diagnosis. Median portion of clypeus without longitudinal carina; mandible with five teeth; anteromedian margin of clypeus not covered with lamella; antennal scape covered with sub-erect short hairs; in lateral view, petiolar node higher than long; junction of propodeal dorsum and declivity surface at an obtuse angle.

Description. Minor worker. In full-face view, head elongate, rectangular, with broadly convex posterior margin. Anteromedian clypeal margin broadly convex and not covered with lamella. Eyes breaking lateral outlines

of head, their posterior margins located well behind the mid-length of the head (PoOc/CL: 0.30±0.01; 0.28–0.31). Mandible triangular, apical margin with five sharp teeth. Antennal scape long, roughly its distal half extending beyond posterior cephalic border. In lateral view, pronotum and anterior portion of mesonotum slightly convex; posterior portion of mesonotum and propodeum more or less straight and rounding to the declivity surface; propodeal dorsum generally twice as long as height of declivity. Petiolar node higher than long, its dorsal margin rounding to anterior face.

One pair of elongate, stout, erect hairs near the posterior margin of head and a pair each on the pronotum, at the junction of propodeal dorsum & declivity and on the posterodorsal margin of the petiole; a few short appressed hairs present on mesosomal dorsum. Antennal scape with abundant sub-erect, short hairs. Head, mesosoma, petiole, gastral segments, and antennal scape generally black; trochanter and distal portion of coxa and first four gastral sternites whitish-yellow; femur, funiculus, tibia, and tarsus light brown to brown.

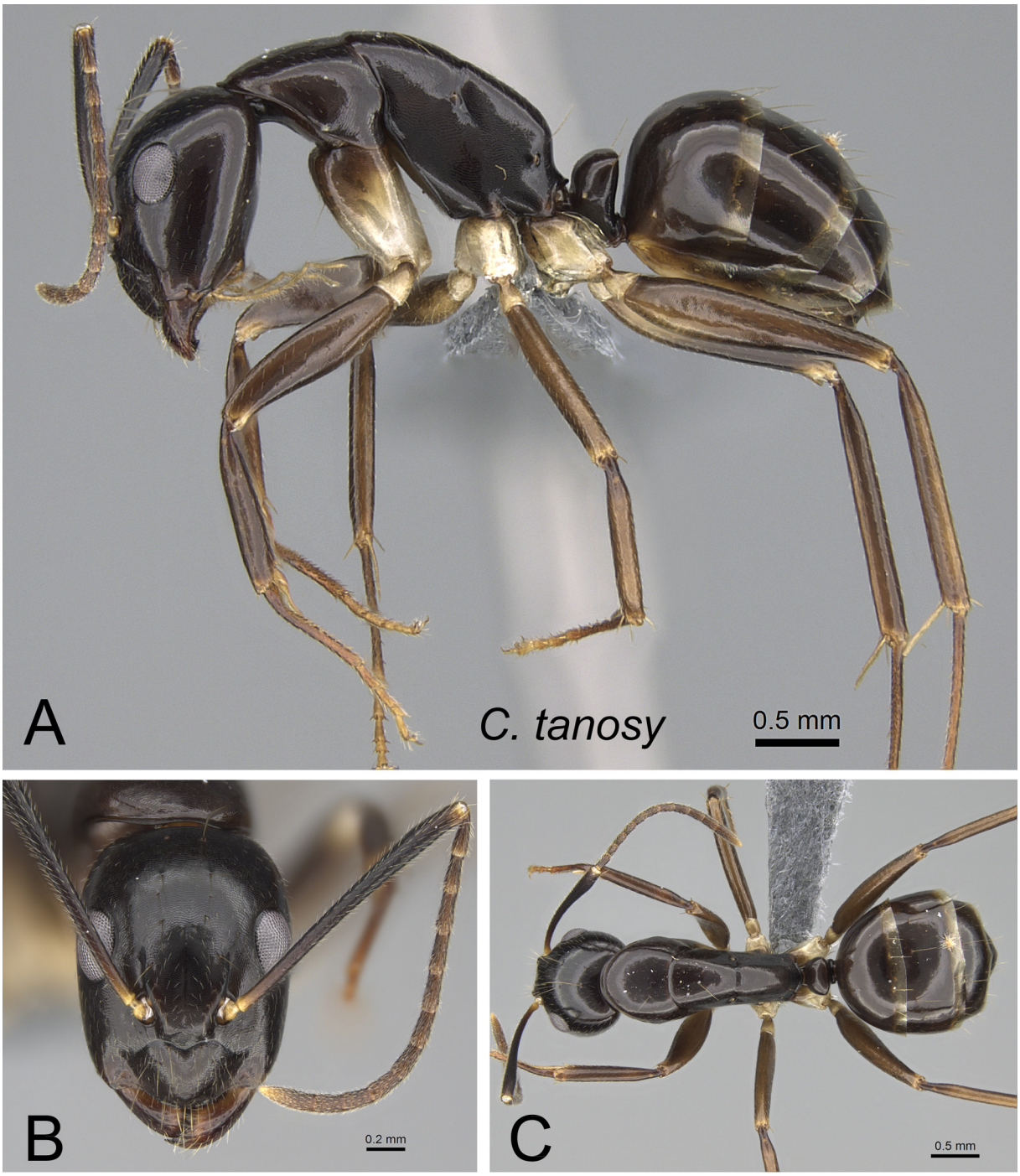
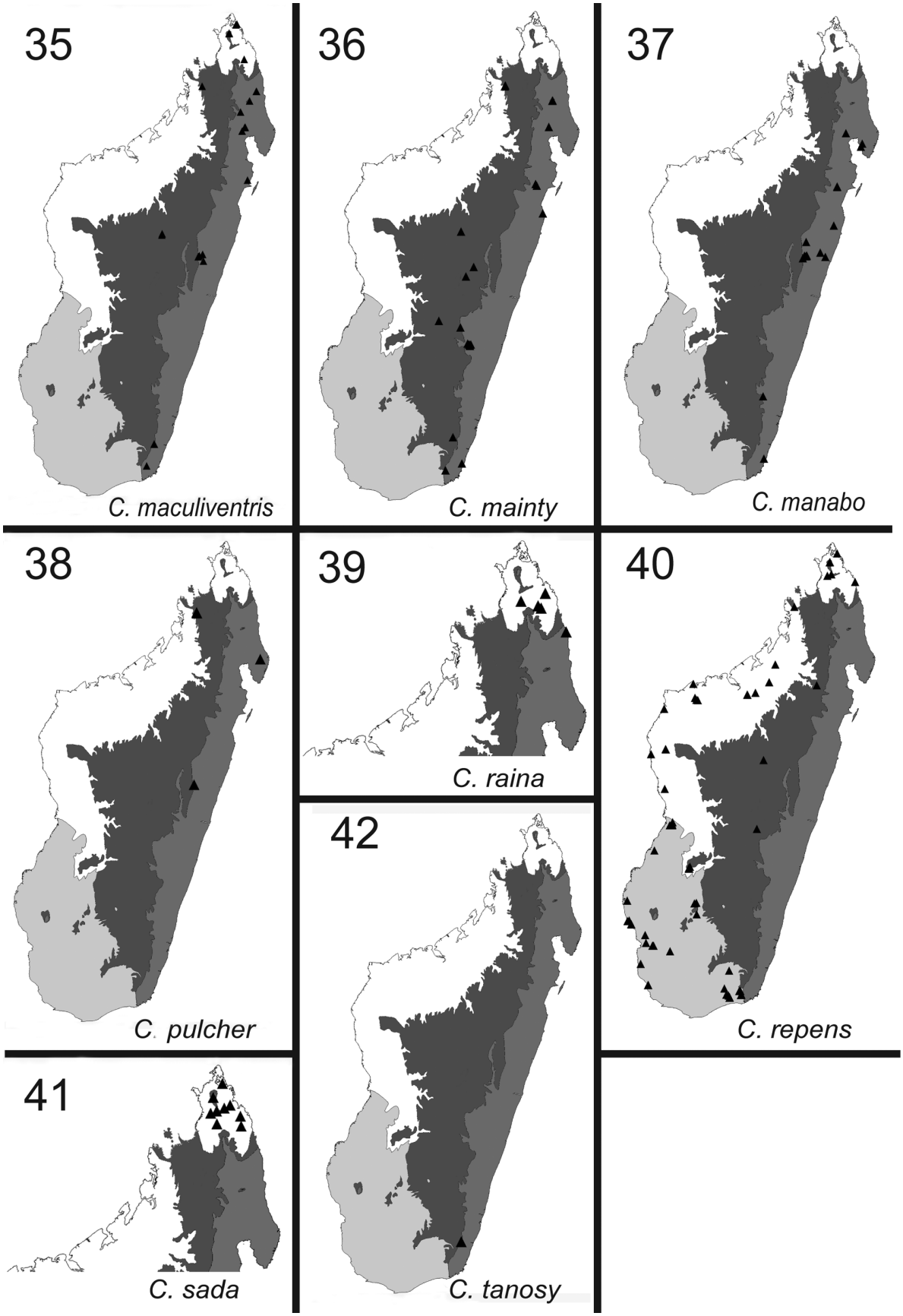


FIGURE 34. *Camponotus tanosy* minor worker CASENT0803890. A: lateral view. B: head in full-face view. C: dorsal view.



FIGURES 35–42. Distribution maps of *Camponotus* subgenus *Mayria* in Madagascar. Fig. 35: *C. maculiventris,* Fig. 36: *C. mainty,* Fig. 37: *C. manabo,* Fig. 38: *C. pulcher,* Fig. 39: *C. raina,* Fig. 40: *C. repens,* Fig. 41: *C. sada,* Fig. 42: *C. tanosy.*

Major worker. With characteristics of minor worker except: broader head, mesosoma much more robust with distinct metanotum; promesonotum slightly convex; propodeal dorsum more or less straight and rounding to the declivity surface; petiolar node tapering dorsally.

Discussion. See discussion under *C. raina* and *C. sada*.

The identification of *C. tanosy* based on conventional morphology-based taxonomy has been confirmed by multivariate morphometrics. The grouping of the samples of *C. tanosy* generated by the NC-clustering method is corroborated by LDA with a classification success of 100%.

Distribution and biology. *Camponotus tanosy* is only known from the rainforests of the Anosyenne Mountains in the Anosy region of Madagascar. Its nest sites are mostly in rotten logs and rarely under moss on live trees.

Additional material examined. Province **Toliara:** Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1125 m, -24.13894, 47.06804, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC); Anosy Region, Anosyenne Mts, 31.2 km NW Manantenina, 1315 m, -24.13632, 47.05485, rainforest, (B.L. Fisher, F.A. Esteves *et al.*) (CASC).

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Supplementary material

Basic measurements of individual minor workers of the Malagasy *Camponotus* subgenus *Mayria* 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. v280r0t