



<http://dx.doi.org/10.11646/zootaxa.3635.4.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:9DB4A023-F9B4-4257-900B-F672F93CD845>

A taxonomic revision of the *Meranoplus* F. Smith of Madagascar (Hymenoptera: Formicidae: Myrmicinae) with keys to species and diagnosis of the males

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ABSTRACT

The species-level taxonomy of the ant genus *Meranoplus* F. Smith from Madagascar is revised. Two new species, *M. cryptomys* **sp. n.** and *sylvarius* **sp. n.** are described from workers and queens; *M. mayri* Forel, 1910, and *M. radamae* Forel, 1891, are redescribed, and queens and males for these two species are described for the first time. The first diagnosis of *Meranoplus* males for any biogeographic region is provided based on Malagasy species. Illustrated keys to all known Malagasy castes and species are presented. Diagnoses are given for two species groups: the *M. mayri* group and the *M. nanus* group. The diagnosis of the *M. nanus* species group from Bolton (1981) is thereby expanded with six new characters. Two species are known from the *M. mayri* species group and seven described species are known for the *M. nanus* species group, including the two new species described herein. The mouthparts, genitalia, and all castes, where known, of Malagasy *Meranoplus* are illustrated.

Keywords: genitalia, gynes, Malagasy region, Meranoplinae, species groups, wing venation

INTRODUCTION

Meranoplus is a unique and charismatic myrmicine genus of hairy, slow-moving, and armored ants. The genus is currently classified in its own tribe, the Meranoplini, with one fossil genus, *Parameranoplus*, from Baltic amber (44.1 ± 1.1 mya; Bolton 2003; Engel 2001; Wheeler 1915). The historic shuffling of *Meranoplus* through higher taxa—Cryptoceridae, Cataulacinae, Tetramoriini, Meranoplini—reflects our poor understanding of the phylogenetic position of *Meranoplus* within the Formicidae. Brady *et al.* (2006) recovered a clade of *Meranoplus* and *Cataulacus*, although this relationship was not supported in Moreau *et al.* (2006). The extant species of *Meranoplus* are distributed throughout the Old World, absent only from the Palearctic and Oceania regions but with the exception of *M. levellei* Emery, 1883, from New Caledonia (Fisher 2010; Wheeler 1935).

The delineation of the genus *Meranoplus* is relatively straightforward; the genus is highly derived and unambiguously defined by several synapomorphies. The genus has been revised and reviewed across its entire distribution over the past few decades (Australasian region: Anderson 2006, Schödl 2004, 2007, Taylor 1990, 2006; Ethiopian region: Bolton 1981; and Oriental region: Schödl 1998, 1999). The genus is diagnosed by the compact mesosoma, which is dorsolaterally and often posterodorsally produced, and by the nine-segmented antenna with a three-segmented club (Bolton 2003). With over 80 valid species (Bolton 2012), it is predicted that over half of the *Meranoplus* diversity remains undescribed, most of these from Australia (Anderson 2006).

Species of this genus are predominantly ground-nesting and, when disturbed, will display thanatosis enhanced by crypsis, *i.e.*, individuals will accumulate dirt in their pilosity and play dead (Dornhaus & Powell 2010). With respect to diet, most species are omnivores and facultative granivores, while others, including the whole *M. diversus* species group, are specialist granivores (Anderson 2000, 2006). At least one species, the Malaysian rainforest-dwelling *M. mucronatus* F. Smith, 1857, is known to have a trophobiotic relationship with hemipterans (Maschwitz *et al.* 1987). *Meranoplus* species are known to be active both day and night (Gross *et al.* 1991), and to recruit via pheromone trails laid from the base of the sting using secretions from their extremely large Dufour glands (Hölldobler 1988; Billen *et al.* 2009; Billen & Taylor 1993). The function of the spatulate sting is still unknown (Kugler 1979). The only species of *Meranoplus* for which mating has been reported is *M. peringuiyi* Emery, 1886, in which mating swarms occurred after a rain and where males patrolled for the outnumbered females in a zig-zag manner (Robertson & Villet 1989; Schulmeister 2001).

Male *Meranoplus* descriptions are few, varied, and scattered throughout the literature and across the biogeographic regions (Donisthorpe 1949; Forel 1915; Smith 1876). None of these descriptions provide diagnosis of *Meranoplus* males for any biogeographic region or locale, and most do not provide sufficient detail for genus-level identification. Given the potential of male ants to clarify the natural history of ant reproductive biology (Kaspari *et al.* 2001), improve the discovery and definition of genera (Yoshimura & Fisher 2009, 2011, 2012a), and aid ant taxonomy and systematics (Brady & Ward 2005; LaPolla 2004; Song & Bucheli 2010; Yoshimura & Fisher 2012b), including descriptions of male ants is a research priority.

The biodiversity of Madagascar is exceptionally rich, with levels of endemism ranging from 65% for freshwater fish to 83–86% for non-marine plants, terrestrial vertebrates, and non-marine invertebrates (Goodman & Benstead 2005). Ants exhibit an endemism level of around 95% for the 1,300 Malagasy species, of which about 60% are undescribed (Fisher 2003, 2005; Hita Garcia & Fisher 2012). To this end, twenty-seven modern revisions in print or in press have contributed over 200 new species to the Malagasy ant fauna list. Here we present the first new species of Malagasy *Meranoplus* in over a century, with keys to all known castes, redescriptions of the workers of *M. mayri* Forel, 1910 and *M. radamae* Forel, 1891, the first descriptions of *Meranoplus* sexuals for Madagascar, and the first diagnosis of the male sex for the genus.

MATERIALS AND METHODS

Most specimens examined in this study were collected by Fisher *et al.* over the past two decades, provided with unique specimen identifiers affixed to each pin (*viz.* CASENT labels), and digitally databased. Every databased specimen record has been uploaded to AntWeb.org, a continuously updated resource that provides “living” distribution maps. Species distributions are illustrated in figs. 64–67.

Anatomical terminology predominantly follows prior authorities: mouthparts (Gotwald 1969), wing venation (Yoshimura & Fisher 2012b), setational stature (Wilson 1955), and sculpture (Harris 1979). An exception to

Yoshimura & Fisher's (2012b) venation terminology is the use of *costal cell* on the forewing, rather than costal+subcostal cell; no subcostal cell is present because of the fusion of the subcostal and radial veins in the Aculeata (Gauld & Bolton 1988). To summarize the sculptural terms: *areolate* is defined as raised ridges which connect to form polygons (cf. promesonotum in fig. 35); *costate* indicates linear, parallel raised ridges (cf. mesosomal pleurae in fig. 40); *dense-punctate* describes contiguous punctures (fig. 25); *rugose* describes non-linear raised ridges (fig. 51). *Stellate punctures* are defined as punctures having three or more radiating lines (fig. 26). In addition, many *Meranoplus* species have a carina on the ventral surface of the frontal carina above the scrobe, which is termed the *scrobal carina* (fig. 2). The term *torular lobe* is used as defined in Keller (2011), referring to the medial arch of the antennal socket torulus. The term *promesonotal shield* is unique to *Meranoplus*, and refers to the fused pro- and meso- segments of the mesosoma, which are often elongated as shelves laterally and posteriorly (Bolton 1981). Although abdominal segments IV–VII are distinctly constricted anteriorly in *Meranoplus*, we eschew the term gaster as it refers to different tagmata across the ant subfamilies (Keller 2011).

For genitalia, we follow the terminology of Boudinot (2013) which reflects the homologies of male ant genitalia with basal Hymenoptera; terms utilized by Yoshimura & Fisher (2011) are indicated in parentheses. The genitalia are composed of the *cupula* (= basal ring) and three paired valves: the *parameres*, *volsellae*, and *penisvalvae* (= aedeagal plates). The lateral-most valve, the paramere, is composed of the basal *basimere* and distal *telomere* (= harpago). The volsella, medial to the paramere and lateral to the penisvalva in situ, and is composed of the *basivolsella*, *cuspis*, and *digitus*. The cuspis and digitus are the distal elements of the volsella, and can be recognized by their position and shape: the cuspis is lateral (closest to the paramere), lobe-like, and extends anteriorly (basally) as a setose plate, while the digitus is medial (near the penisvalva) and finger-like with the apex often directed ventrally. The penisvalva is divided into the *valvura*, the anterior (basal) apodeme, and *valviceps*, the posterior (apical) broadened plate which often has teeth along the ventral margin.

Specimen preparation for mouthparts and male genitalia was done as follows. To soften specimens, point-mounted or in > 90% ethanol, specimens were placed in 70% ethanol at least overnight. To dissect mouthparts, the labiomaxillary complex was pulled somewhat out of the headcapsule with a no. 3 entomology pin with the tip bent into a hook. Using forceps, the labiomaxillary complex was grasped from the base and pulled out of the head capsule, then mounted on a glass slide with a drop of KY Personal Lubricant (Johnson & Johnson Inc., Markham, Canada). The labrum was removed by gently grasping the base of the sclerite and pulling. To dissect the genitalia from softened males, the entire genital capsule was removed from the metasoma, leaving behind sternum IX and tergum X. Observations on the intact genital capsule were made. The genital capsule was then grasped by the forceps and cut in half using a pin, after which the right penisvalva was removed. This penisvalva and its associated paramere and volsella were then mounted as two units on the same slide. The left half of the genitalia was placed in a ~4 mm cup-shaped piece of cotton and rolled in a 1 cm² piece of facial tissue. This was then inserted into a silicone-stoppered polyethylene microvial (BioQuip, Rancho Dominguez, California, U.S.A.) filled with 100% ethanol and placed upside-down in a vial of 100% ethanol with the voucher specimen. The slide mounts and voucher specimens were deposited in the CAS collection.

Montage images of point-mounted specimens were generated using Leica Application Software Version 3.8 from micrographs captured via a Leica DFC 450 camera attached to a Leica Z16 APO dissecting microscope. All montages are available on AntWeb.org (<http://www.AntWeb.org/>). Compound microscope images were captured with a Leica DFC 500 camera mounted on a Leica MZ 16A microscope using LAS V. 2.5.0 R1 software; montages were generated with Helicon Focus 4.70 software.

Measurements follow Schödl (2007) with additions and a few indicated acronym changes. Although of little value for delimiting *Meranoplus* species of Madagascar, measurements of the petiole and postpetiole are included for comparative purposes as they have previously been used for *Meranoplus* alpha taxonomy (Taylor 1996; Schödl 1998, 2007). Additionally, the scape index (SI) is conventionally calculated by dividing scape length by head length; we use a percentage representation of scape length divided by head length following Schödl (*ibid.*) to facilitate comparison to previous taxonomic works on the genus. Two systems were used to measure the spines to account for variation in the shape of the basal flanges of the propodeal spines. For workers, Longino's (2003) measure of propodeal spine length is followed (cf. SPL below). For gynes, the basal inflection point at the base of spine was used, as the spines of this caste do not have appreciably variable profiles.

Measurements were recorded in mm to three decimal places and were taken using two methods: with a digital Mitutoyo stage micrometer mounted on a Leica MZ 125 and an ocular cross-hair; or with an ocular micrometer

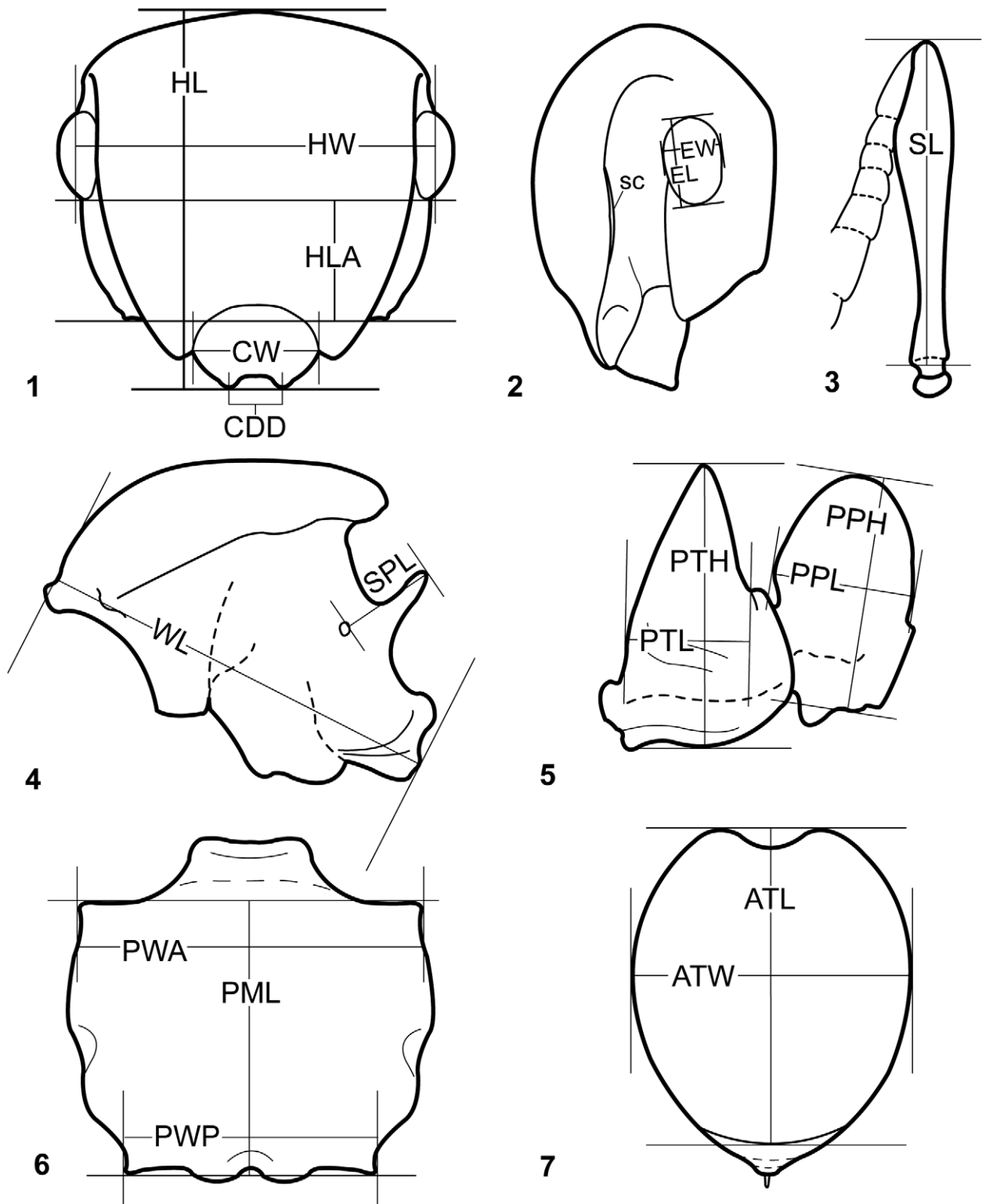
calibrated with a Leica standard (Art No. 10310345) which were either taken with a Leica MC165C or a Leica MC95. Only two significant figures are presented due to the use of the ocular micrometer, which reduced the precision of measurements. All measurements are illustrated (figs. 1–7).

Measurements

- ATL: *Abdominal Tergum IV Length*. Maximum length of fourth abdominal tergum measured with anterior and posterior margins in same plane of focus.
- ATW: *Abdominal Tergum IV Width*. Maximum width of fourth abdominal tergum with anterior, posterior, and lateral borders in same plane of focus.
- CDD: *Clypeal Denticle Distance*. Distance between clypeal denticle apices, measured in full-face view.
- CW: *Clypeus Width*. Distance between the apices of the frontal lobes across the clypeus.
- EL: *Eye Length*. Maximum eye length in profile view.
- EW: *Eye Width*. Maximum eye width in profile view.
- HL: *Head Length*. Maximum length of head capsule, excluding mandibles, measured from anterior margin of clypeus to nuchal carina, with both in same plane of focus.
- HLA: *Head Length, Anterior*. Distance between the anterior edges of the eyes to the mandible bases in full-face view.
- HW: *Head Width*. Maximum width of head capsule behind the eyes, in full-face view.
- PML: *Promesonotum Length*. Maximum length of promesonotum from posterior spine/denticle apices to anterolateral denticle apices; all four apices in same plane of focus. (= PMD, Schödl 2007)
- PPH: *Postpetiole Height*. Measured from sternal process base to postpetiole apex in lateral view.
- PPL: *Postpetiole Length*. Measured from anterior to posterior inflections of postpetiole node in lateral view.
- PWA: *Promesonotal Width, Anterior*. Maximum width of promesonotal shield between anterolateral denticle apices in dorsal view. (= PW, Schödl 2007)
- PWP: *Promesonotal Width, Posterior*. Distance between posterior-most promesonotal spine or denticle apices.
- PTH: *Petiole Height*. Measured from petiole sternum to apex in lateral view.
- PTL: *Petiole Length*. Measured from anterior to posterior inflections of petiole node.
- SL: *Scape Length*. Maximum length of the scape excluding basal constriction.
- SPL: *Propodeal Spine Length*. Workers: distance from inner posterior margin of propodeal spiracle to propodeal spine apex. Gynes: maximum propodeal spine length from basal inflection of spine, to spine apex.
- WL: *Weber's Length*. Maximum diagonal length of mesosoma from anterior inflection of pronotum to posterolateral corner of the metapleuron or the metapleural lobes, whichever is most distant.

Indices

- CDI: *Clypeal Denticle Index*. $CDD*100/CML$
- CI: *Cephalic Index*. $HW*100/HL$
- CS: *Cephalic Size*. $(HW+HL)/2$
- EYE: *Eye Index*. $100*(EL+EW)/CS$
- OMI: *Ocular-Mandibular Index*. $EL*100/HLA$
- PMI: *Promesonotum Index 1*. $PWA*100/PML$ (= PMI2, Schödl 2007)
- PPI: *Postpetiole Index*. $PPL*100/PPH$
- PTI: *Petiole Index*. $PTL*100/PTH$
- PWI: *Promesonotum Index 2*. $PWP*100/PML$
- SEI: *Scape-Eye Index*. $EL*100/SL$
- SI: *Scape Index*. $SL*100/HW$



FIGURES 1–7. Measurements of *Meranoplus* species. **1.** Measurements with head in full face view. **2.** Measurements of head in profile; scrobal carina indicated by “sc”. **3.** Scape length. **4.** Mesosoma profile measurements. **5.** Measurements of the petiole and postpetiole in profile. **6.** Promesonotal shield measurements, dorsal view. **7.** Abdominal tergum IV measurements, dorsal view.

Repositories

Collections which provided material for study or to which types have been distributed are abbreviated as follows:

BMNH	The Natural History Museum, London, U.K.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MHNG	Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
USNM	National Muséum of Natural History [Smithsonian], Washington, D.C., U.S.A.

SYNOPSIS OF MALAGASY SPECIES

Synopsis of *Meranoplus* species and species groups of Madagascar with known castes indicated in brackets (w, worker; q, queen; m, male):

Meranoplus mayri species group

mayri Forel, 1910. MADAGASCAR [w, q, m]

Meranoplus nanus species group

cryptomys sp. n. MADAGASCAR [w, q]

radamae Forel, 1891. MADAGASCAR [w, q, m]

sylvarius sp. n. MADAGASCAR [w, q]

DIAGNOSIS OF MALAGASY *MERANOPLUS* MALES

Without a global or regional assessment of Myrmicine males, an indication of synapomorphies is not possible. For a diagnosis of the worker refer to Bolton (2003).

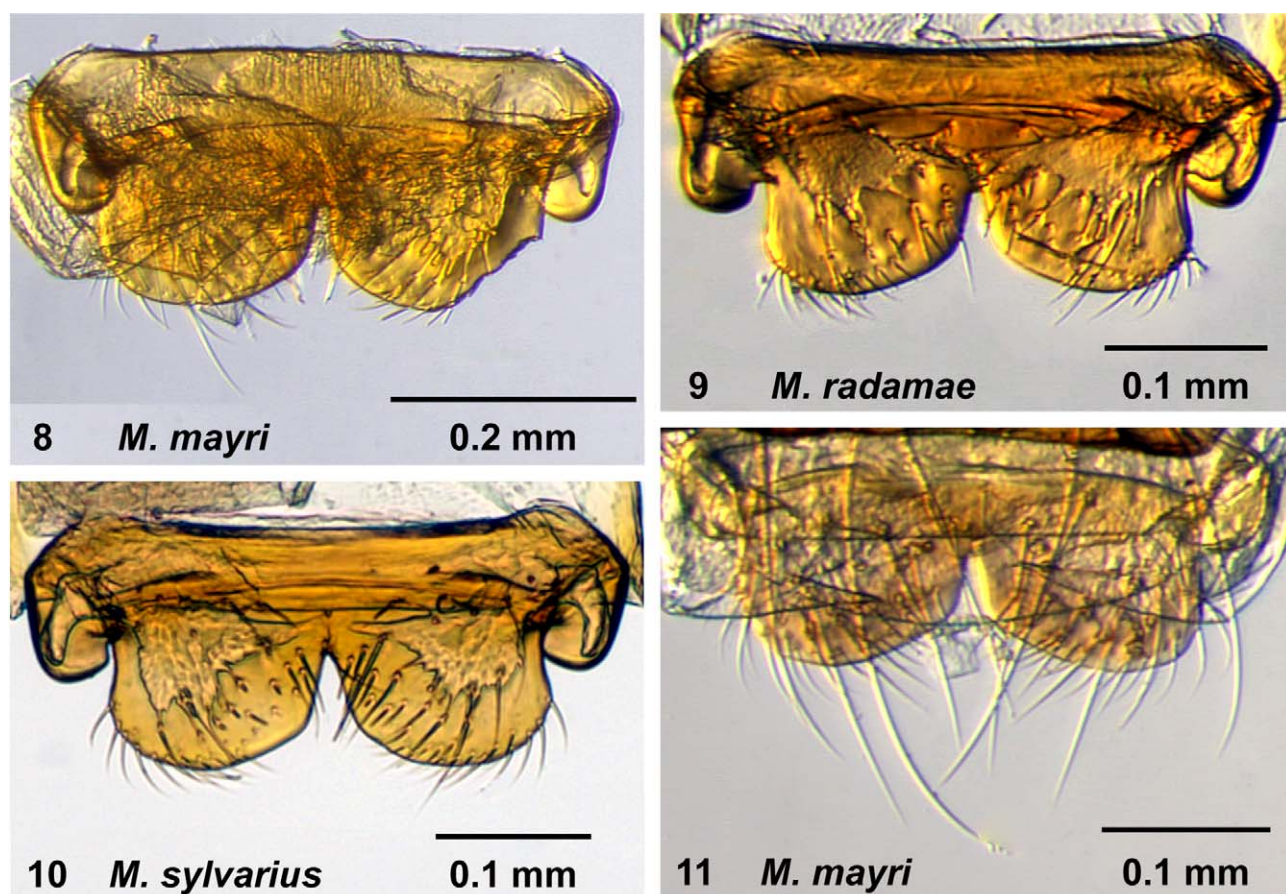
1. Labrum cleft medially (fig. 11).
2. Palpal formula 5,3 (fig. 12).
3. Cardo with egg-shaped lacuna (fig. 12).
4. Mandibles poorly developed, infrequently reaching midline of head when closed; spatulate to bladelike (figs. 31, 32, 48).
5. Antenna with 13 segments; antennomeres 5-13 swollen.
6. Scape short (SI < 33; figs. 31, 32, 48).
7. Eyes large (EL/HW 0.30-0.45; figs. 31, 32).
8. Ocelli present, about as large as antennal sockets (figs. 31, 32, 48).
9. Clypeus not produced posteriorly between antennal sockets (figs. 31, 32, 48).
10. Frontal lobes absent (figs. 31, 32, 48).
11. Frontal carinae distinct to absent (figs. 31, 32, 48).
12. Torular lobe present, raised.
13. Head with raised nuchal carina (figs. 46, 55).
14. Notaulus present (figs. 47, 56).
15. Parapsidal line present (figs. 47, 56).
16. Meso- and metatibial spurs present, single.
17. Forewing (FW) pterostigma present (fig. 17).
18. FW vein Rs+M splits distal to crossvein 1m-cu (fig. 17).
19. FW crossvein cu-a occurs about 2/3 along length of M+Cu (fig. 17).
20. FW crossvein 2rs-m absent (fig. 17).
21. Hindwing (HW): terminal segments of veins Sc+R1 and Rs with bases contiguous (fig. 18).
22. HW cell formed by the veins Sc+R, M+Cu and crossvein M+1rs-m narrow, apex acute (fig. 18).
23. HW cell formed by the veins 1A, M+Cu and crossvein cu-a less than 1/3 the length of the larger cell (fig. 18).
24. Petiole without pedicel (figs. 46, 55).
25. Postpetiole globose in lateral view; constricted posteriorly (figs. 46, 55).
26. Abdominal sternum XIII broadly emarginate.

27. Abdominal sternum IX about as long as broad; narrowed apically.
28. Pygostyles present.
29. Telomere separated from basimere by a suture (figs. 13, 14).
30. Digitus long, fingerlike; apex curved or bent ventrally (figs. 13, 14).
31. Penisvalva subrectangular with serrate ventral margin (figs. 15, 16).

Comments

Comments correspond to character numbers as above.

4. Male mandibles vary, with some specimens having two denticles on the masticatory margin, some specimens having one denticle—variably in the basal or apical position—and some specimens edentate. Any combination of the above characters may be found differing between the left and right mandibles of the same specimen.
16. Meso- and metatibial spurs may be absent in the unknown male of *Meranoplus sylvarius*, for which the females lack these spurs.
25. The petiolar node varies much more than the postpetiole in development within populations, varying from subnodiform (posterior face somewhat distinct) to globose.



FIGURES 8–11. Labrum of *Meranoplus* species, ectal view. **8.** *Meranoplus mayri* worker (CASENT0317545). **9.** *Meranoplus radamae* worker (CASENT0317561). **10.** *Meranoplus sylvarius* worker (CASENT0317566). **11.** *Meranoplus mayri* male (CASENT0317565).

SPECIES GROUPS

All four Malagasy species of *Meranoplus* are endemic and conform to Bolton's (1981, 2003) diagnosis of the genus. Two additional shared traits potentially diagnostic for the genus but not mentioned in Bolton (2003) are the spatulate sting (Kugler 1978) and the presence of a denticle or strong swelling on the ventral side of the mandible beneath the third tooth from the masticatory margin apex. The Malagasy species may be split into the *M. mayri* and *M. radamae* groups with south Indian and Afrotropical affinities, respectively. Further characters shared by all

Malagasy *Meranoplus* but varying elsewhere (and used by Bolton [1981] to diagnose species groups) are four mandibular teeth; posterior margin of promesonotum overhanging posterior face of propodeum; propodeal spines well-developed; petiole cuneate; petiole dorsal margin without teeth or spines; and postpetiole nodiform and without a posteriorly projecting process.

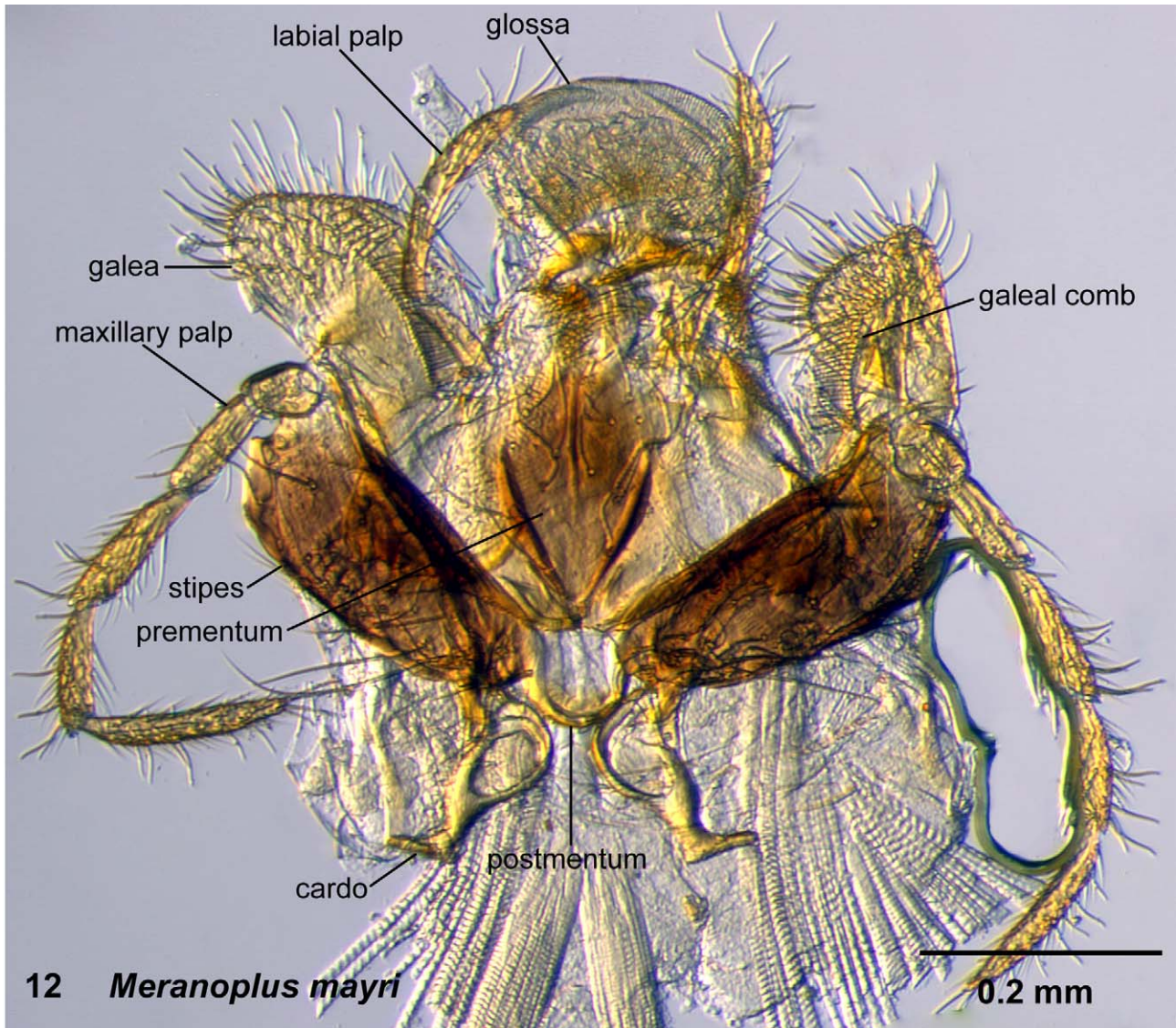
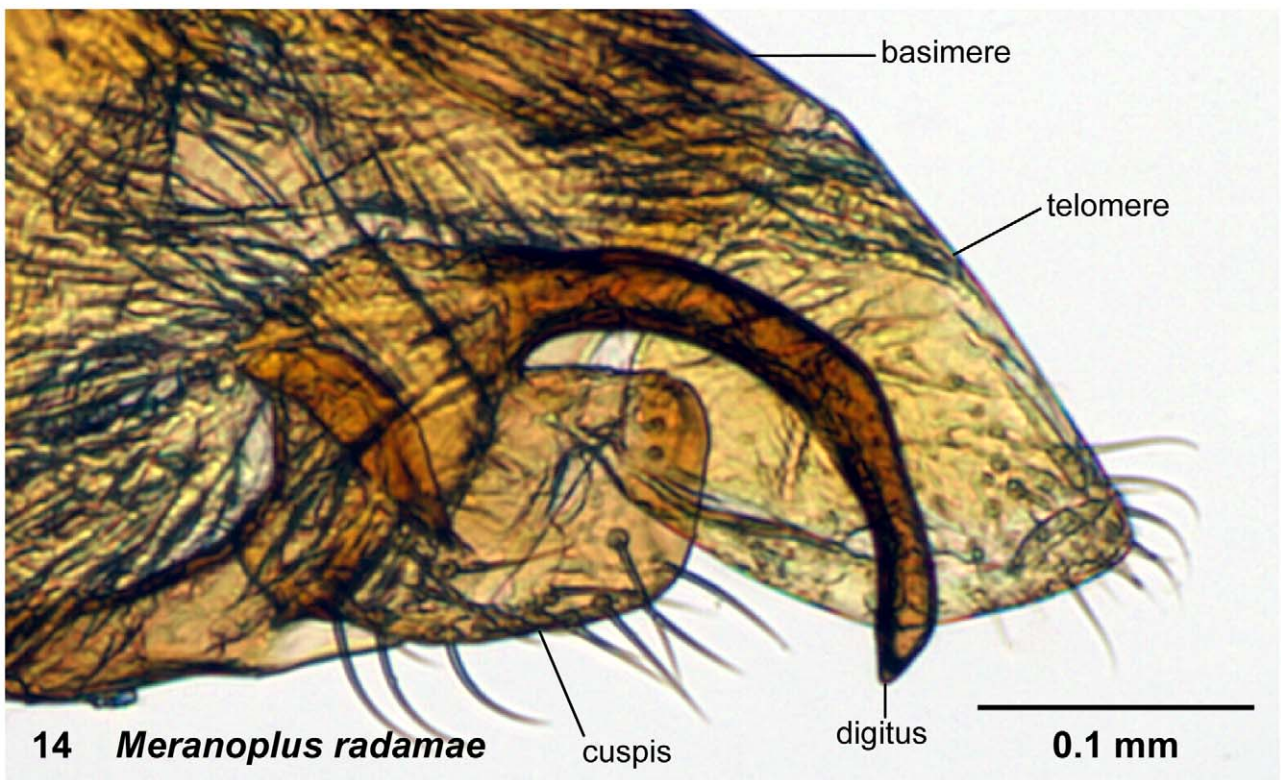
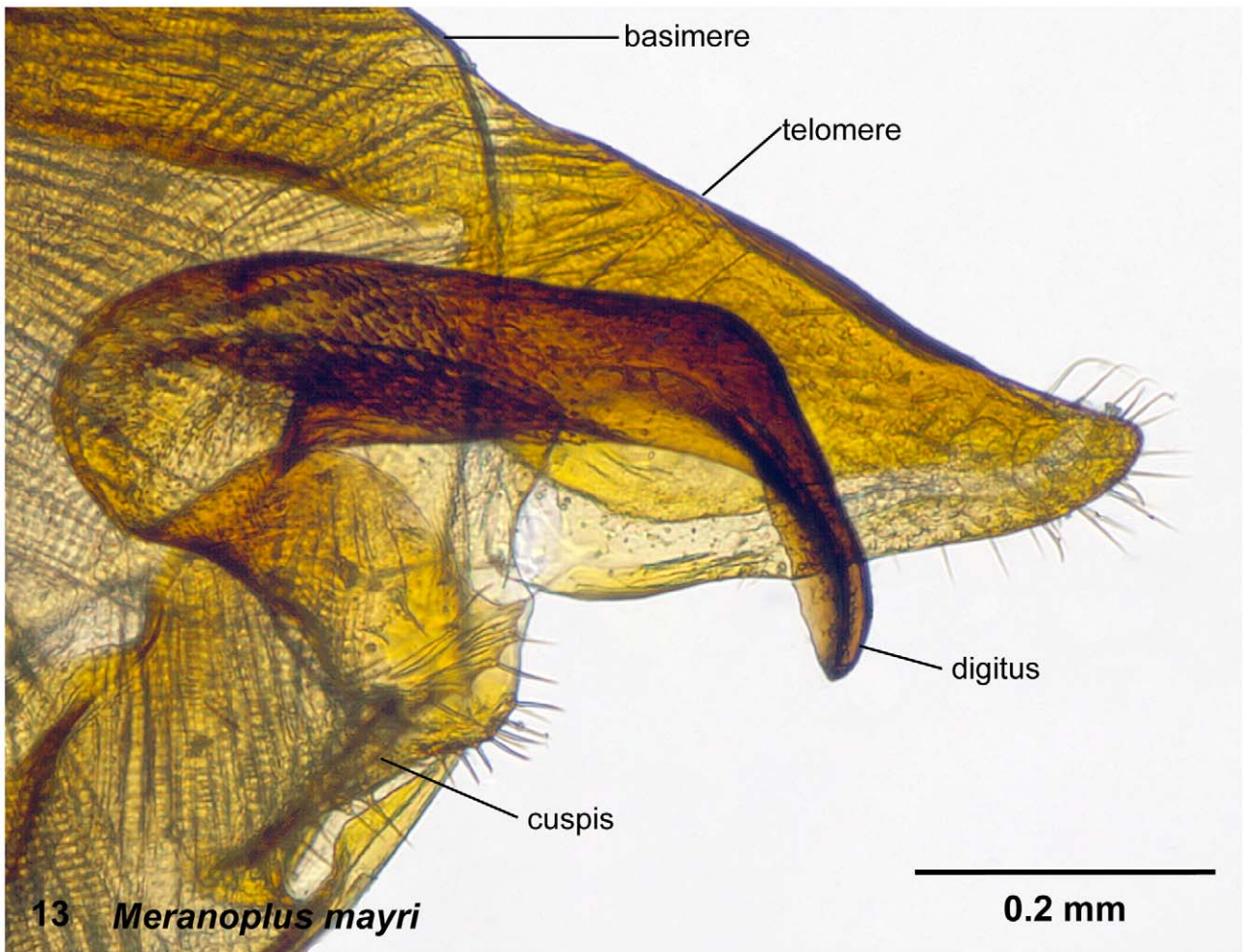


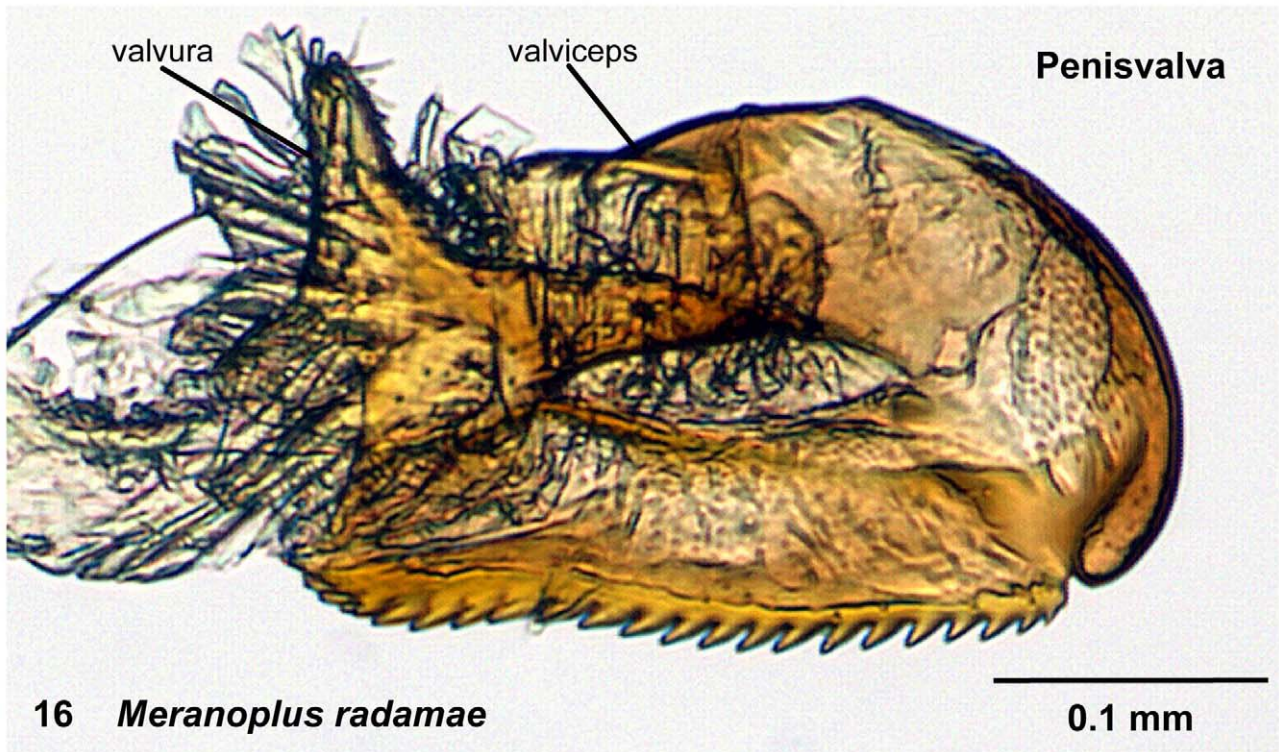
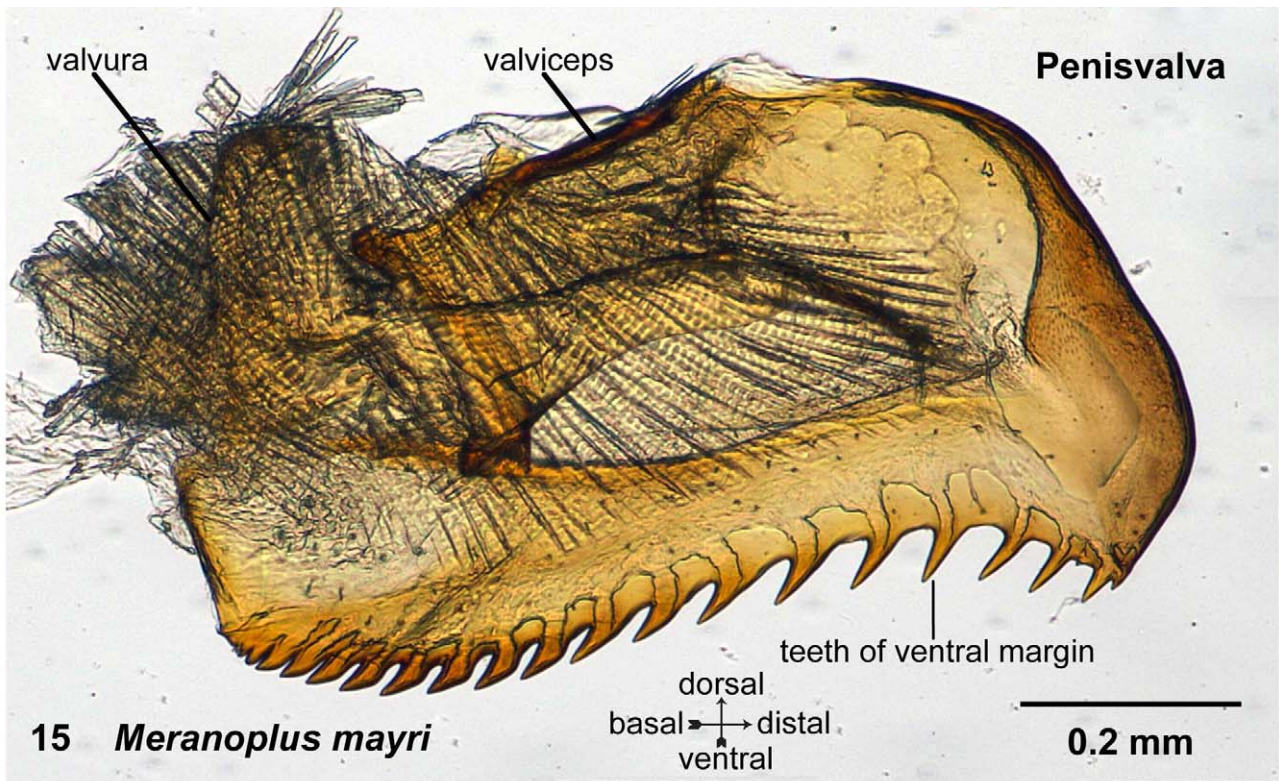
FIGURE 12. Labiomaxillary complex of a male *M. mayri*, ectal view (CASENT0317565).

Non-Malagasy *Meranoplus* species examined—in addition to literature descriptions or figures—to construct the diagnoses are as follows:

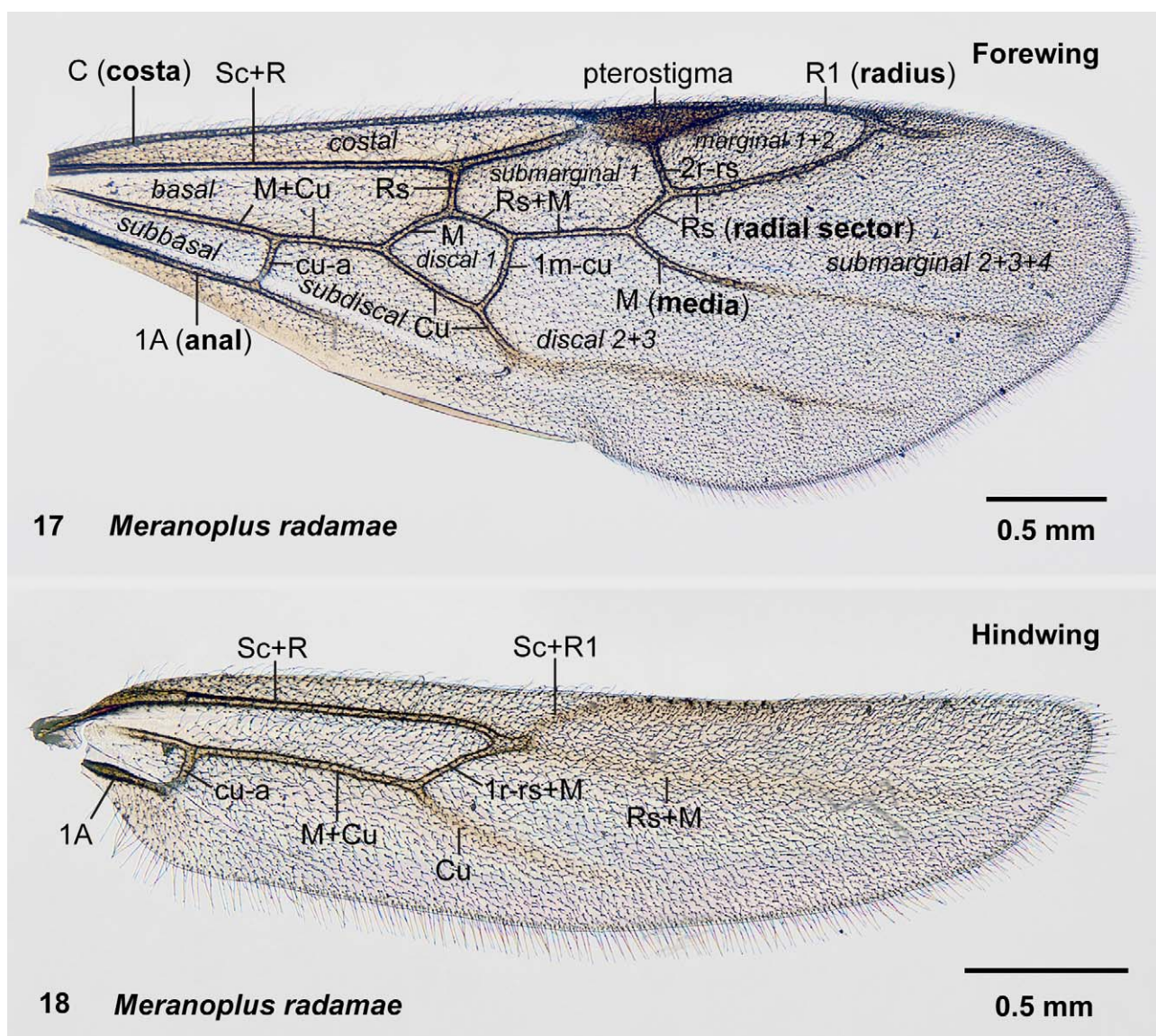
Meranoplus ajax Forel [Australia]; *armatus* Smith [S.E. Asia]; *asteriscus* Donisthorpe [S.E. Asia]; *atronitodus* Schödl MS-name [S.E. Asia]; *aurealus* Crawley [Australia]; *bellii* Forel [India]; *bicolor* (Guérin-Méneville) [India, S.E. Asia]; *biliran* Schödl [S.E. Asia]; *birmanus* Schödl [S.E. Asia]; *boltoni* Schödl [Sri Lanka]; *borneensis* Schödl [S.E. Asia]; *castaneus* Smith [S.E. Asia]; *clypeatus* Bernard [Afrotropical region]; *dimidiatus* Smith [Australia]; *diversus* Smith [Australia]; *fenestratus* Smith [Australia]; *ferrugineus* Crawley [Australia]; *glaber* Arnold [Afrotropical region]; *hirsutus* Mayr [Australia]; *inermis* Emery [Afrotropical region]; *laeviventris* Emery [S.E. Asia]; *levis* Donisthorpe [India]; *loebli* Schödl [Sri Lanka]; *magrettii* André [Afrotropical region]; *malaysianus* Schödl [S.E. Asia]; *mucronatus* Smith [S.E. Asia]; *nanus* André [Afrotropical region]; *nepalensis* Schödl [Indian region]; *niger* Donisthorpe [S.E. Asia]; *oceanicus* Smith [Australia]; *peringueyi* Emery [Afrotropical region]; *pubescens* (Smith) [Australia]; *rarpilis* Donisthorpe [S.E. Asia]; *rothneyi* Forel [India]; *rugosus* Crawley [Australia]; *sabronensis* Donisthorpe [S.E. Asia]; *spininodis* Arnold [Afrotropical region]; *sthenus* Bolton [Afrotropical region]; *vestigator* Smith [S.E. Asia].



FIGURES 13–14. Right volsella and paramere of *Meranoplus* species, in mesal view displaying the digitus, cuspis, basimere, and telomere. **13.** *Meranoplus mayri* (CASENT0317564). **14.** *Meranoplus radamae* (CASENT0115117).



FIGURES 15–16. Right penisvalva of *Meranoplus* species, ectal view. **15.** *Meranoplus mayri* (CASENT0317564). **16.** *Meranoplus radamae* (CASENT0115117).



FIGURES 17–18. Right fore- and hindwings of a *M. radamae* gyne, dorsal view (CASENT0317562). Fused veins are indicated by a plus sign, “+”, and crossveins by a dash, “-”. Cell names are indicated in *italics*. **17.** Forewing. **18.** Hindwing.

Diagnosis of the *M. mayri* species group (worker)

The *Meranoplus mayri* group consists of *M. mayri*, from Madagascar, and *M. levis* Donisthorpe, 1942, from South India and Sri Lanka. This group was proposed by Schödl (1998) based on the arcing costate sculpture of the promesonotal shield and longitudinal costate sculpture of the head. On the basis of examination of the *M. levis* holotype and the morphometrics provided by Schödl (1998), we concur and provide additional characters in the *M. mayri* species group diagnosis. Diagnosis of the sexuals of this species group would be premature, however, as gynes and males of *M. levis* are unknown.

The following characters set the species of the *M. mayri* group apart among the Afrotropical species-group schemata of Bolton (1981) and the Oriental species from Schödl (1998, 1999); unique character states for the *M. mayri* group among the Afrotropical and Oriental species are *italicized*:

1. Bicolored: head through postpetiole dark to bright orange, abdominal segments IV–VII piceous to black.
2. Face with longitudinal costae.
3. *Frontal carina laminate and broadly translucent, at least until midlength of eye.*
4. Head broader than long (CI > 100).
5. *Dorsum of promesonotal shield with numerous concentric costae arcing anteriorly from one posterolateral spine to the other.*

6. Lateral and posterior margins of promesonotal shield distinctly laminate and concealing pleurae and propodeum in dorsal view.
7. *Lateral margins of promesonotal shield translucent from anterolateral corners to bases of posterolateral spines.*
8. *Posterolateral promesonotal spines somewhat dorsoventrally flattened, with one or two ventrolateral longitudinal carinae.*
9. Petiolar apex acute in profile view.
10. Petiole anterior and posterior faces smooth.
11. Lateral face of petiole with one to many longitudinal costae or carinae.
12. Petiole dorsal margin straight to convex in posterior view; without spines or teeth near mid-line.
13. Postpetiole nodiform, strongly sculptured.
14. External (dorsal) tibial faces roughened with sculpture.
15. Fourth abdominal tergum dense-punctate, at least posteriorly.

Diagnosis of the *M. nanus* species group (worker)

The *Meranoplus nanus* group (Bolton 1981) is herein expanded to six species, with the inclusion of *M. radamae*, *M. cryptomys*, and *M. sylvarius*, in addition to the three Afrotropical species *M. clypeatus* Bernard, 1953, *M. inermis* Emery, 1895, and *M. nanus* Emery, 1895. Two characters from Bolton's (1981) diagnosis of the *M. nanus* group must be expanded: postpetiole squamiform to nodiform, rather than squamiform to anteroposteriorly compressed; and propodeal spines absent, short, or well-developed. Otherwise characters used by Bolton (1981) to diagnose the *M. nanus* group stand, and six additional characters are provided in the species group diagnosis. Although a few males of the African *M. nanus* group species have been examined for this study, a diagnosis of males or gynes of this species group would be premature until a larger sample size is available.

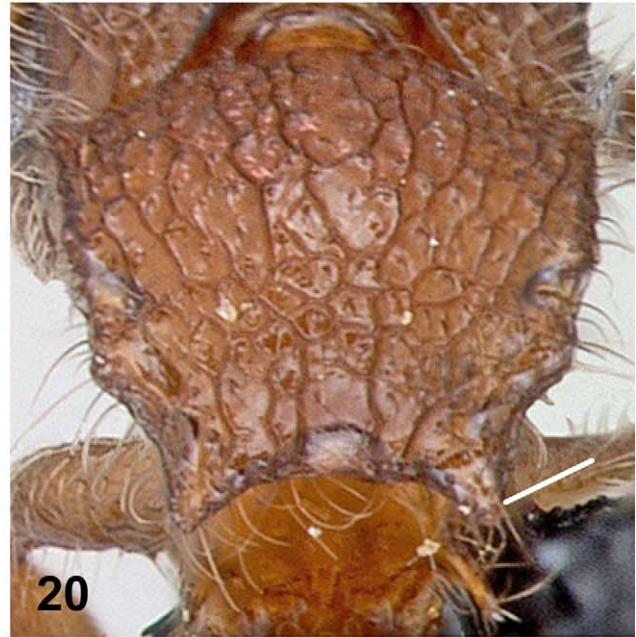
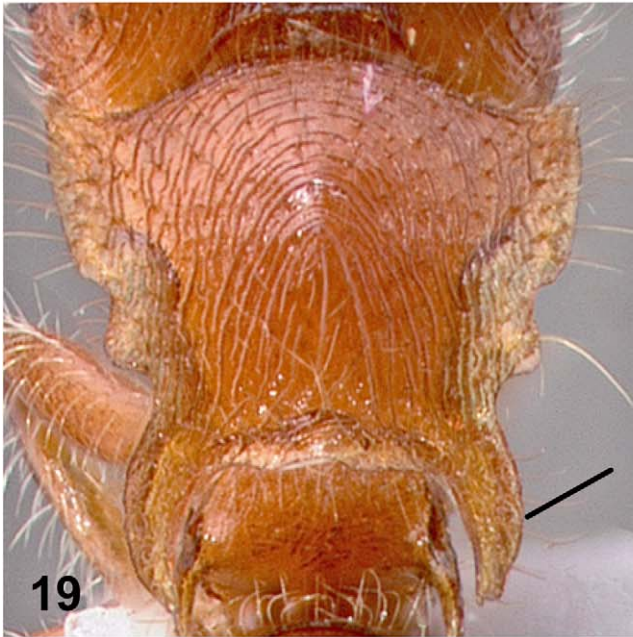
The following characters set the species of the *M. nanus* group apart among the Afrotropical species-group schemata of Bolton (1981) and the Oriental species from Schödl (1998, 1999); unique character states for the *M. nanus* group among the Afrotropical and Oriental species are italicized:

1. Four mandibular teeth.
2. Promesonotum broader than long, with length measured from apices of anterolateral to posterolateral denticles.
3. Promesonotal shield overhanging pleurae laterally.
4. Promesonotal shield overhanging propodeum posteriorly.
5. Promesonotal-propodeal suture distinct and strongly arched medially.
6. Propodeal spines absent through well-developed.
7. Petiole narrow-cuneate; without spines or teeth dorsally.
8. Anterior and posterior faces of petiole smooth and shining.
9. Lateral face of petiole with one or two longitudinal curvaceous carinae which extend posteriorly from above the spiracle and join with the posterior collar.
10. Postpetiole squamiform to nodiform; never cuboid nor with a posteriorly-directed process.
11. *Fourth abdominal sclerites with stellate setiferous punctures.*

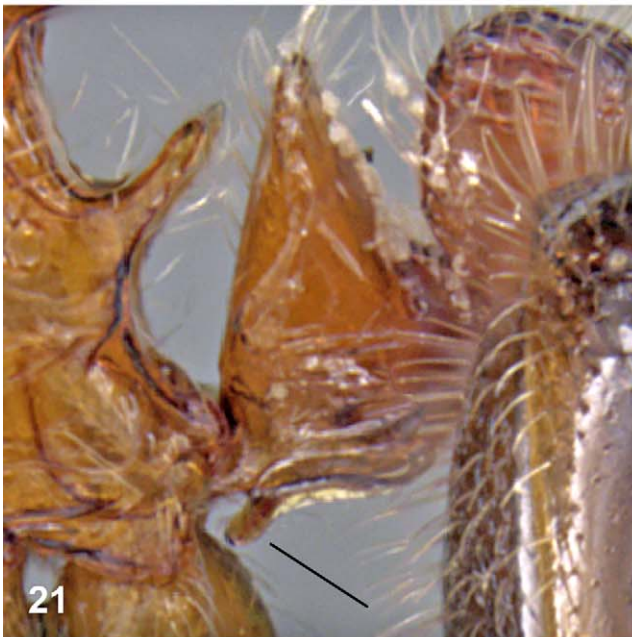
KEY TO SPECIES

Key to workers

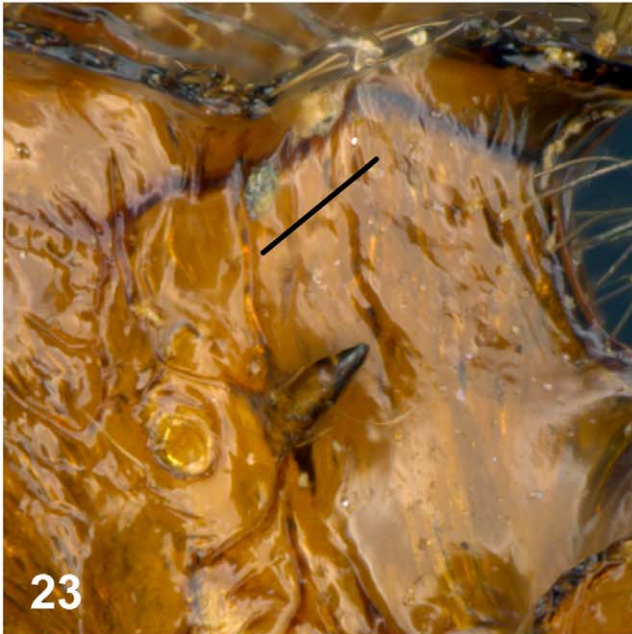
- 1 In dorsal view, posterolateral corners of promesonotal shield with spines produced beyond the posterior margin a distance greater than their width (fig. 19) *Meranoplus mayri*
- In dorsal view, posterolateral corners of promesonotal shield with denticles that never project beyond the posterior margin more than the width of their bases (fig. 20) 2
- 2 Bicolored: head through postpetiole orange, abdominal segments IV–VII dark brown to black. Petiolar sternum with finger-shaped anterior-projecting process (fig. 21) *M. cryptomys*
- Unicolorous; if somewhat bicolored, abdominal segments IV–VII never black. Petiolar sternum without finger-shaped anterior-projecting process (fig. 22) 3
- 3 Yellow to brown; occasionally darker brown, but never black. Propodeal spine with carina extending dorsally to promesonotal shield base (fig. 23). Middle and hind tibiae with a thin subapical spur *M. radamae*
- Unicolorous chocolate brown to black. Propodeal spine without carina extending dorsally to promesonotal shield base (fig. 24). Both middle and hind tibiae without subapical spur *M. sylvarius*



FIGURES 19–20. Promesonota of *Meranoplus* workers in dorsal view. **19.** *Meranoplus mayri*: promesonotum with posterolateral spines (CASENT0430421; anon.). **20.** *Meranoplus radamae*: promesonotum with posterolateral denticles (CASENT0486686; A. Nobile 2007).



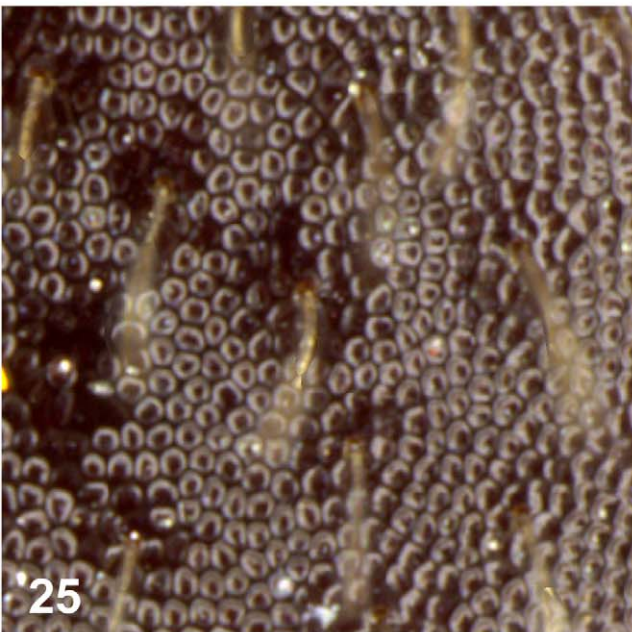
FIGURES 21–22. Petioles and postpetioles of *Meranoplus* workers in profile. **21.** *Meranoplus cryptomys*: subpetiolar process fingerlike (CASENT0440939). **22.** *Meranoplus radamae*: subpetiolar process produced as denticle (CASENT0486686; A. Nobile 2007).



FIGURES 23–24. Mesosomata of *Meranoplus* workers in oblique posterolateral view. **23.** *Meranoplus radamae*: propodeal spine with dorsomedian costa reaching notopropodeal suture (CASENT0486686; A. Nobile 2007). **24.** *Meranoplus sylvarius*: propodeal spine without dorsomedian costa reaching notopropodeal suture (CASENT0317529).

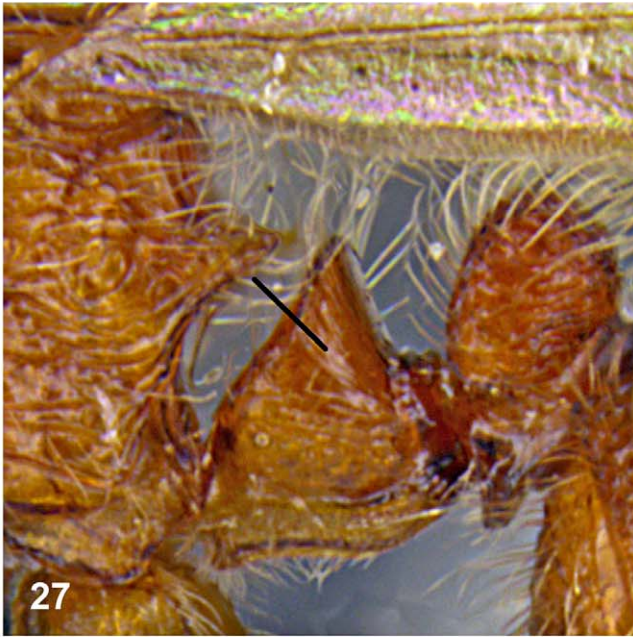
Key to queens

- 1 Setae on fourth abdominal tergum (ATIV) set in circular to oval punctures (fig. 25). ATIV dense-punctate (fig. 25). Larger species (WL > 1.85) *M. mayri*
- Setae on ATIV set in stellate punctures (fig. 26). ATIV not dense-punctate, but rather shining between setiferous punctures, at least in posterior half (fig. 26). Smaller species (WL < 1.70) 2



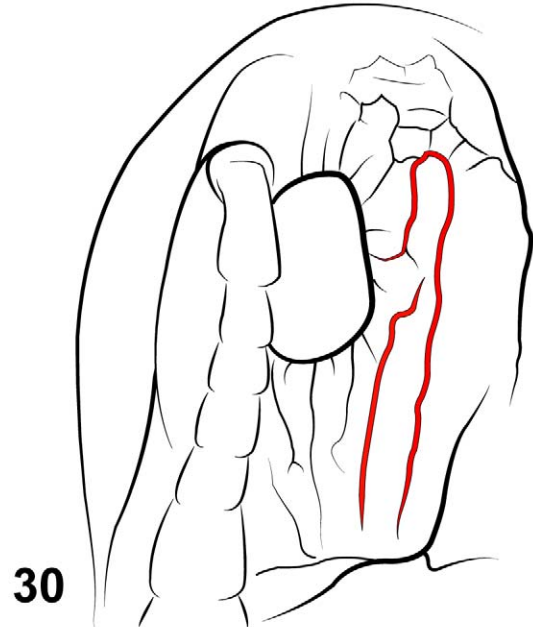
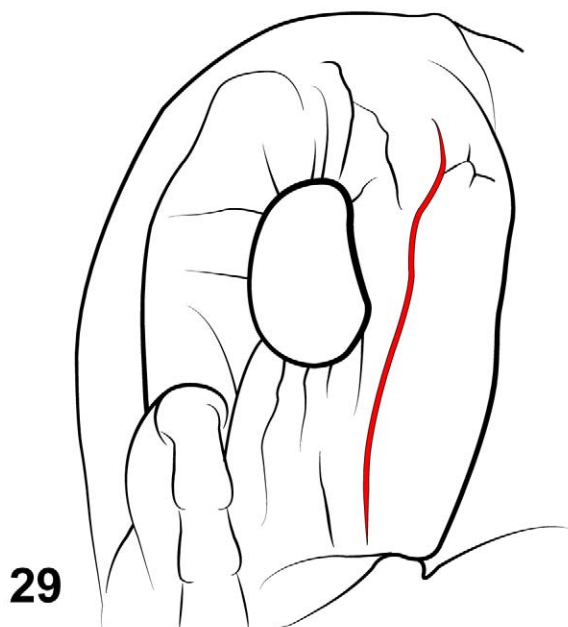
FIGURES 25–26. Fourth abdominal terga of *Meranoplus* gynes in dorsal view. **25.** *Meranoplus mayri*: densepunctate sculpture around setiferous punctures (CASENT0164932). **26.** *Meranoplus cryptomys*: stellate setiferous punctures (CASENT0132374).

- 2 Bicolored: head through postpetiole orange, abdominal segments IV–VII light-to-dark brown. Propodeal spines short and triangular (fig. 27; SLI < 14). Scapes short (SI < 63) *M. cryptomys*
- Concolorous dark or light brown to orange-brown. Propodeal spines longer and thorn-like (fig. 28; SLI > 15). Scapes long (SI > 65) 3



FIGURES 27–28. Propodea of *Meranoplus* gynes in lateral view. **27.** *Meranoplus cryptomys*: short, triangular propodeal spines (CASENT0132374). **28.** *Meranoplus sylvarius*: long, thornlike propodeal spines (CASENT0317567; E. Ortega 2012).

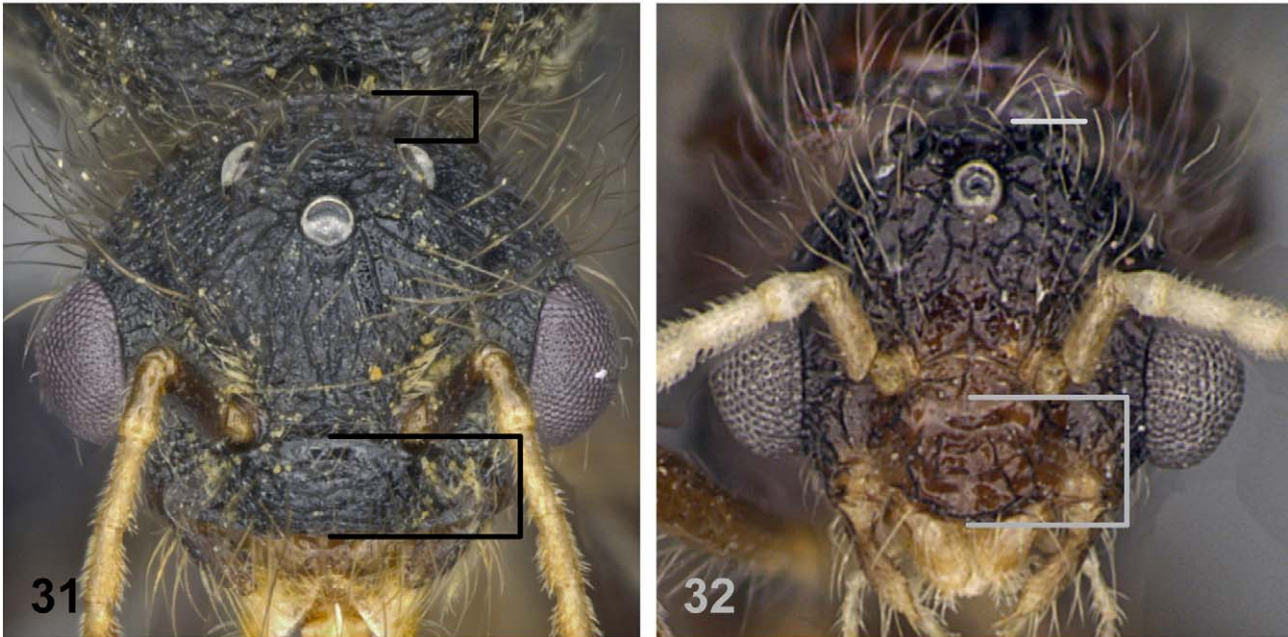
- 3 Chocolate brown to black. Tibial spurs absent, excepting the protibial calcar. In lateral view, area ventrad eye with a single longitudinal costa (fig. 29); without additional carination or rugosity between the carina and the posterolateral margin of the head *M. sylvarius*
- Orange through light brown, never dark brown. Tibial spurs present. In lateral view, area ventrad eye with two or more longitudinal rugae (fig. 30); often with additional rugosity between the rugae and the posterolateral margin of the head *M. radamae*



FIGURES 29–30. Illustrations of *Meranoplus* gyne heads in oblique posterolateral view. **29.** *Meranoplus sylvarius*: single subocular carina indicated in red (CASENT0132374). **30.** *Meranoplus radamae*: two subocular rugae indicated in red (CASENT0317524).

Key to males

- 1 Nuchal carina visible in full-face view (fig. 31). Clypeus greater than four times as broad as long (fig. 31). Maximum diameter of eye three to four times as long as malar area (OMI < 250) *M. mayri*
- Nuchal carina not visible in full-face view (fig. 32). Clypeus about three times as broad as long (fig. 32). Maximum diameter of eye less than two times as long as malar area (OMI > 280) *M. radamae*



FIGURES 31–32. Heads of *Meranoplus* males in full-face view; note that the lateral bar of the clypeus indicator delimits the lateral margin of the clypeus. **31.** Nuchal region of *M. mayri* visible above ocelli (CASENT0317521). **32.** Nuchal region of *M. radamae* hidden by ocellar bulge (CASENT0317525).

SPECIES ACCOUNTS

Meranoplus cryptomys Boudinot & Fisher sp. n.

(Figs. 21, 26, 27, 33–38, 63)

Holotype worker, MADAGASCAR: Toliara, P.N. Tsimanampetsotsa, Bemanateza 23.0 km 131° SE Behaloka, 23°00' S, 43°53' E, 90 m, malaise, spiny forest/thicket, collection code BLF6257, 22–26Mar2002 (*B.L. Fisher et al.*) (CASC: CASENT0440939).

Paratype worker: with same data as holotype, except collected via pitfall (CASC: CASENT0077998).

Paratype gyne, MADAGASCAR: Tuléar, P.N. Andohehala, 24°49.85' S, 46°32.17' E, 60 m, spiny forest, collection code Mg-21-35, 15–26Oct2003 (*Rin'Ha, M.E. Irwin*) (CASC: CASENT0132374).

Description

Worker (types). HL 0.95–0.99, HW 0.91, HLA 0.30–0.31, CW 0.35–0.37, CDD 0.13, SL 0.61–0.65, EL 0.22–0.23, EW 0.15–0.16, PML 0.71–0.73, PWA 0.91–0.96, PWP 0.64–0.67, SPL 0.12–0.17, WL 0.98–1.01, PTL 0.22, PTH 0.46–0.50, PPL 0.21–0.24, PPH 0.40–0.41, ATW 1.32–1.39, ATL 1.36–1.41, CI 92.2–95.0, SI 67.8–70.9, OMI 74.1–76.2, CDI 35.0–37.9, SEI 275–276, PMI 128.2–130.8, PWI 70.3–70.2, CS 0.9–1.0, EYE 40.8–41.2 (2 measured).

Bicolored; head, mesosoma, petiole and postpetiole orange; abdominal segments IV–VII dark brown.

Head longer than broad (CI 92–95). Basal area of mandibles smooth, grading into striations apically. Face rugose to areolate; anterior region of the nuchal carina areolate. Sculpture above and behind eyes areolate; sculpture beneath the eyes rugose. Scrobal carina well-developed, strong. Anterior margin of clypeus with bilobed lamina; lobes relatively wideset (CDI 35–38). Middle portion of clypeus costate laterally. Eyes large (EYE > 40). Maximum eye length about $\frac{3}{4}$ the length of the malar area (OMI 74–76). Face with dense suberect to erect short setae and somewhat more dilute erect long setae.

Promesonotal shield broader than long (PMI 128–131); pronotal shield wider anteriorly than posteriorly (PWI 70). Dorsum of promesonotum with areolate sculpture which weakens in posterior half. Setae on promesonotal shield erect to subdecumbent, of various lengths. Lateral face of pronotum with a few haphazardly oriented fine costae. Lateral face of mesonotum (beneath overhanging shield) with weak foveate sculpture. Incomplete costae present on meso- and metapleurae. Metapleural lobes well-developed. Propodeal spines narrow and curved upwards. Dorsomedian carina of propodeal spine curves medially across the posterior face of the propodeum. Posterior face of propodeum with costae crossing over the strongly arched promesonotal-propodeal suture.

Petiole cuneate in lateral view; without pedicel. Anteroventral process of petiole fingerlike, separated from the sternite and projecting anteroventrally. Postpetiole subrectangular in lateral view, taller than broad (PPI 52–57). Sub-postpetiolar process well-developed, sloping evenly towards posterior margin of post-petiolar sternum. Dorsal face of postpetiole rugose; lateral face weakly costate; posterior face weakly rugose. Fourth abdominal tergum (ATIV) large (ATW/WL > 1.34; ATL/WL > 1.38). ATIV shining; weakly areolate between strong stellate setiferous punctures. ATIV setae of mixed lengths; short setae suberect; long setae erect; relatively long setae decreasing in length from base of abdominal tergum IV.

Queen (paratype in parentheses). HL 1.01–1.12 (1.01), HW 1.00–1.07 (1.00), HLA 0.31–0.32 (0.31), CW 0.38–0.41 (0.38), CDD 0.10–0.13 (0.11), SL 0.70–0.74 (0.74), EL 0.26–0.29 (0.26), EW 0.21 (0.21), SPL 0.19–0.23 (0.23), WL 1.39–1.49 (1.43), PTL 0.27–0.31 (0.30), PTH 0.47–0.49 (0.47), PPL 0.24–0.30 (0.25), PPH 0.47–0.52 (0.49), ATW 1.47–1.58 (1.47), ATL 1.68–1.92 (1.77), CI 92.1–97.6 (96.1), SI 66.5–70.3 (70.3), OMI 72.6–78.5 (73.1), CDI 25.9–32.8 (29.4), SEI 253–283 (283), CS 1.1 (1.1), EYE 43.3–45.3 (43.9) (6 measured).

Bicolored; head, mesosoma, petiole, and postpetiole orange; abdominal segments IV–VII burnt orange laterally and ventrally; dark brown dorsally.

Head longer than broad (CI 94–99). Mandibles striate. Face with rugose sculpture grading into areolate sculpture posterior to the ocelli. Sculpture above eyes areolate; behind and beneath rugose. Scrobal carina well-developed; broadest at about ¼ along its length. Anterior margin of clypeus with frontal lamina produced into two wideset lobes (CDI 40–43). Middle portion of clypeus costate; costae in lateral thirds of this area strong; costae in middle third of this area weak. Eyes large (EYE 44–46). Maximum eye length greater than 4/5 the length of the malar area (OMI 82–92). Scapes short (SI 62–60). Face with erect setae; shorter setae more numerous than longer setae.

Mesosoma longer than tall. Anterolateral corners of pronotum produced into well-developed denticles; dorsolateral margin of pronotum somewhat indistinct. Mesosomal dorsum areolate to rugose. Dorsum of mesosoma with setae of various lengths; longest setae on mesoscutellum. Lateral face of pronotum areolate in ventral half grading into rugosity. Katepisternum costate with smooth areas in the dorsal half. Anterior portion of anepisternum shining; posterior portion rugose. Metapleuron and lateral face of propodeum costate, in addition to the usual costae across the metapleural gland bulla. Propodeal spines small and triangular (SPL 0.12–0.15). Procoxae without distinct anterolateral shoulders; weakly striate. Wings as in male diagnosis.

Petiole cuneate; anterior face longer than posterior face. Postpetiole nodiform, rounded posterodorsally. Sternal process of postpetiole well-developed. Dorsal face of postpetiole areolate to rugose; lateral faces strongly rugose-costate; posterior face weakly rugose-costate. Fourth abdominal tergum (ATIV) with sides in dorsal view parallel to sub-parallel. ATIV long (ATL/WL 1.21–1.38). The sculpture of ATIV is rough around the base of the tergum, with somewhat areolate sculpture in this area; posterior to this area, the sculpture is smooth and shining with weak-to-fine areolation between the stellate setiferous punctures. The setae of ATIV are very short: short setae are most numerous, and shorter than the propodeal spines.

Male. unknown.

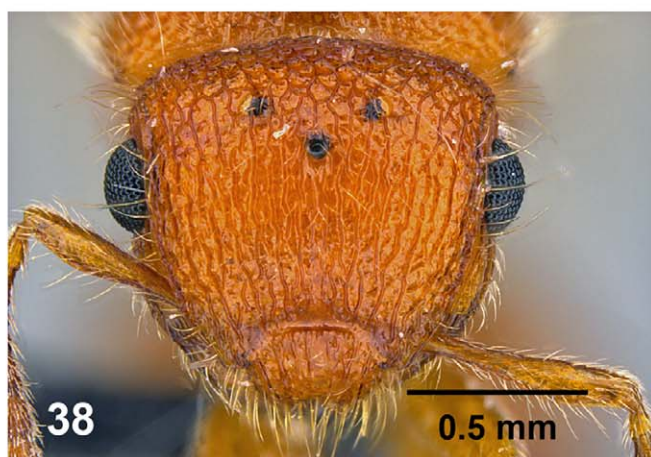
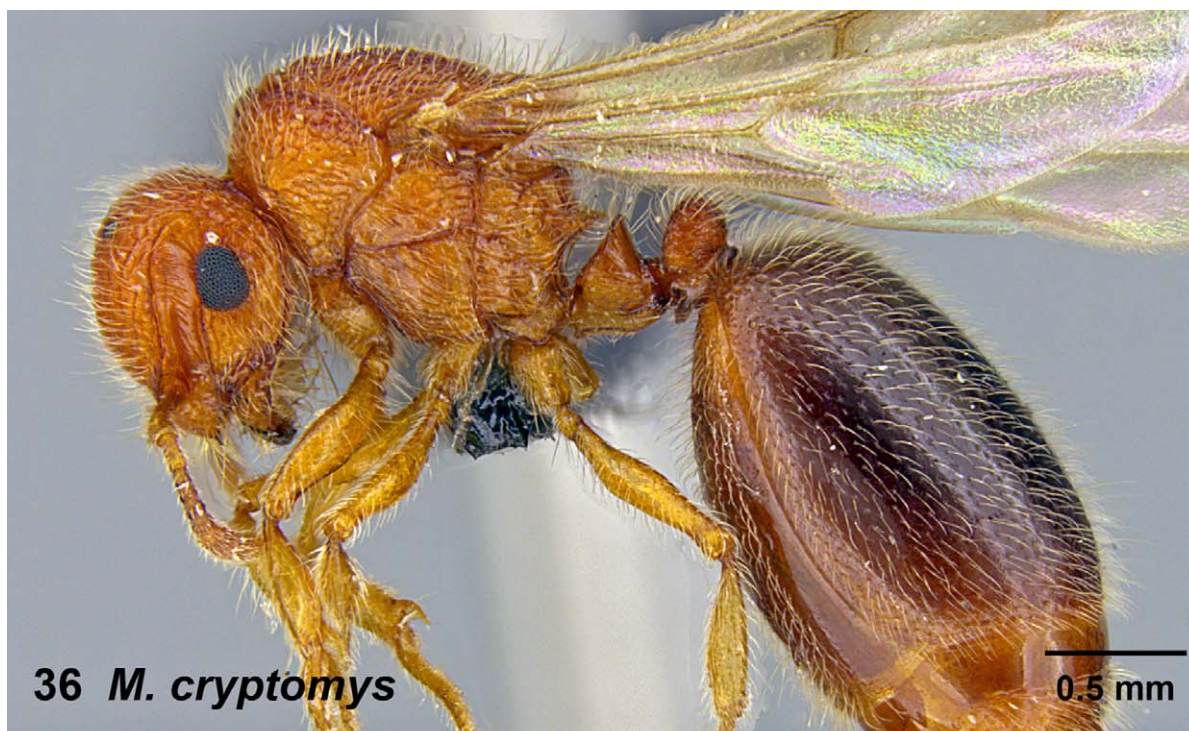
Diagnosis

Worker. The fingerlike subpetiolar process uniquely identifies this species in the Malagasy fauna. Additional characters include: head almost as broad as long (CI 92–95); eyes large (OMI > 65, EYE mean 41); scapes less than three times as long as eyes (SEI < 280); posterolateral denticles of promesonotal shield set wide (PWI > 68); ATIV large (ATW/HW > 1.40, ATL/HL > 1.40).

Gyne. The long malar area (OMI 82–92) and short scapes (SI 60–62) uniquely identify this species in the Malagasy fauna. Supporting diagnostic characters include: bicolored orange and brown; strong scrobal carinae; comparatively small (WL 1.4–1.6); wideset clypeal denticles (CDI 41–43); short, triangular propodeal spines (SPL 0.12–0.15); relatively few (< 30) long suberect setae on fourth abdominal tergum.



FIGURES 33–35. *M. cryptomys* sp. n., holotype worker (CASENT0440939). **33.** Body in lateral view. **34.** Body in dorsal view. **35.** Head in full-face view.



FIGURES 36–38. *M. cryptomys* sp. n., paratype gyne (CASENT0132374). 36. Body in lateral view. 37. Body in dorsal view. 38. Head in full-face view.

Comments

Despite the infrequent collection of this presumably rare species, *M. cryptomys* has a relatively broad range within the spiny forest/thickets and savanna woodland habitats of Madagascar. Workers of *Meranoplus cryptomys* are only known from two individuals collected at Tsimanampetsotsa, while gynes have been collected at the Isalo and Andohahela National Parks and the Beza Mahafaly Reserve. Neither hand-collected workers nor nests have been collected; all known individuals are from Malaise or pitfall traps. Although two female castes have not been collected together, they share characteristics unique to the Malagasy *Meranoplus* and indicate they belong to the same specie: comparatively short scapes, widely set clypeal denticles, high oculomandibular indices (OMI), characters of sculpturation, and the striking orange and black bicolored coloration. The strong orange and black bicolored coloration of *M. cryptomys* is notable for its similarity to that of *M. mayri*. These two species overlap in range across the south and southeast of Madagascar, from Andohahela to Isalo.

Etymology

The relatively widespread range and infrequent collection of this new species, coupled with its large eyes and relatively short pilosity, suggests the image of a mouse hiding from cats or collectors. The specific epithet is a noun in apposition and thus invariant.

Additional material examined

MADAGASCAR: Tuléar, Beza Mahafaly Reserve, Parcelle I, 23°41.19' S, 44°35.46' E, 165 m, malaise, tropical dry forest, coll'n code Ma-14A-01, 15Oct–10Nov2001 (*M.E. Irwin et al.*); Tuléar, P.N. Andohahela, 24°49.85' S, 46°32.17' E, 60 m, spiny forest, coll'n code Mg-21-23, 22-29Jun2003 (*Rin'Ha, M.E. Irwin*); Fianarantsoa, Ampotoampoto, P.N. Isalo, 22.62944° S, 45.18900° E, 91 m, savanna woodland, coll'n code ARA0120-18, 27–28Feb2010 (*A. Ravelomanana*).

Meranoplus mayri Forel, 1910

(Figs. 8, 11–13, 15, 19, 25, 31, 39–47, 65)

Meranoplus mayri Forel, 1910a: 19. Lectotype worker, here designated, MADAGASCAR: Toliara, Fort Dauphin, (*Sikora*) (MHNG: CASENT0101230) [examined].

Description

Worker. HL 0.93–1.27, HW 0.98–1.41, HLA 0.34–0.54, CW 0.37–0.49, CDD 0.17–0.25, SL 0.74–1.04, EL 0.18–0.26, EW 0.15–0.19, PML 1.06–1.53, PWA 0.90–1.45, PWP 0.53–0.99, SPL 0.27–0.47, WL 1.04–1.58, PTL 0.18–0.35, PTH 0.43–0.61, PPL 0.24–0.40, PPH 0.39–0.58, ATW 1.03–1.77, ATL 1.09–1.82, CI 100.4–111.8, SI 69.0–84.9, OMI 43.6–60.5, CDI 42.7–58.8, SEI 379–454, PMI 88.1–97.5, PWI 51.2–73.9, CS 0.9–1.3, EYE 30.0–35.3 (50 measured).

Bicolored; head, mesosoma, petiole and postpetiole orange, metasoma piceous to black.

Head as broad as or broader than long (CI > 100). Mandibles striate. Face with numerous (> 20) parallel costae which extend from the posterior margin of the clypeus to the posterior margin of the head; a few lateral costae curve posteriorly to the eye and either end at the eye or the base of the mandibles. Frontal carinae produced over the antennal scrobe as flanges, and with rugose sculpture on the dorsal surface. Scrobal carina dwarfed by the frontal carina flange, sometimes reduced to near absence. Anterior margin of clypeus without lamina; lateral corners of middle portion of clypeus produced into two stout, widely set denticles (CDI > 40). Middle portion of clypeus shining, with strong costae. Eyes small (EYE < 36). Maximum eye length less than $\frac{3}{4}$ length of malar area (OMI < 62). Face covered with numerous erect setae of various lengths; longest setae about 2.5 times as long as eye, and somewhat more frequent; shortest setae about equal in length to the eye.

Promesonotal shield longer than broad, including the posterolateral spines (PMI < 99). Lateral margins of promesonotal shield produced into translucent flanges. Anterolateral corners acute to subacute. Lateral flanges produced into flat denticles past midlength; these medial denticles are set off from rest of margin by anterior and posterior emarginations. Posterolateral spines dorsoventrally flattened; always longer than their base; sometimes depressed below the plane of the promesonotal dorsum; often parallel, sometimes curved medially. Promesonotal shield with arcing costae: the costae begin on the posterolateral spines or lateral flanges and curve anteriorly, with their

vertices anterior to the medial denticles. Promesonotal shield with rugose sculpture on the lateral and posterior flanges as well as on the spines. Setae on promesonotal dorsum of similar composition to those of the face. Mesosomal pleurae without visible sutures. Lateral faces of mesosoma covered with numerous (> 15) longitudinal costae. Metapleural lobes weakly projecting posteriorly. Propodeal spines long (SPL mean 0.38); mediolaterally flattened; translucent. Posterior face of propodeum with strong to weak punctuation; with or without longitudinal costae.

Petiole without pedicel or lobe-like ventral process, but otherwise variable: with strong to weak anterolateral bulges; dorsal margin with well- to poorly-developed lamina; dorsolateral margins swept backward and produced into lobe-like laminae which may be long or short, rounded acute to obtuse, directed posterolaterally or dorsolaterally, with dense or dilute ventral pubescence. Postpetiole nodiform (PPI > 60). Dorsal face of postpetiole with strong rugose-areolate sculpture; lateral face strongly costate and rugose; posterior face rugose to areolate. Fourth abdominal tergum (ATIV) small (ATW/WL 1.20; ATL/WL < 1.23). ATIV with dense-punctate sculpture always in posterior half; anterior half grading from dense-punctate with radiating costae to smooth and shining with very weak costae. Setiferous punctures of ATIV surrounded by a circular area of shining, weak punctae. The majority of setae on ATIV longer than the maximum width of the metafemora; longest setae present around the base of abdominal tergum IV; setae decrease in length posteriorly.

Queen. HL 1.35–1.44, HW 1.48–1.58, HLA 0.48–0.54, CW 0.50–0.55, CDD 0.21–0.25, SL 0.96–1.07, EL 0.28–0.31, EW 0.23–0.24, SPL 0.19–0.25, WL 1.95–2.12, PTL 0.33–0.38, PTH 0.51–0.65, PPL 0.38–0.47, PPH 0.62–0.69, ATW 1.95–2.26, ATL 2.17–2.35, CI 105.8–113.3, SI 64.7–67.8, OMI 54.4–60.9, CDI 39.1–49.1, SEI 333–367, CS 1.4–1.5, EYE 34.6–37.1 (8 measured).

Bicolored; head, mesosoma, petiole and postpetiole orange, metasoma piceous to black.

Head broader than long (CI > 105). Mandibles striate. Face with numerous parallel costae, varying in rugosity, which extend from posterior margin of clypeus to posterior margin of head; lateralmost costae curving over eyes and extending to base of mandibles. Sculpture above the eyes costate to weakly rugose. Scrobal carina variable, never strong or bulging. Anterior margin of clypeus without lamina, rather with two strong, widely set, cone-shaped denticles (CDI > 38). Middle portion of clypeus entirely costate; costae of varying rugosity. Eyes comparatively small (EYE < 38). Maximum length of eye less than $\frac{3}{4}$ as long as malar area (OMI 54–61). Scapes not notably short (SI 64–68). Setae on face erect and of various lengths.

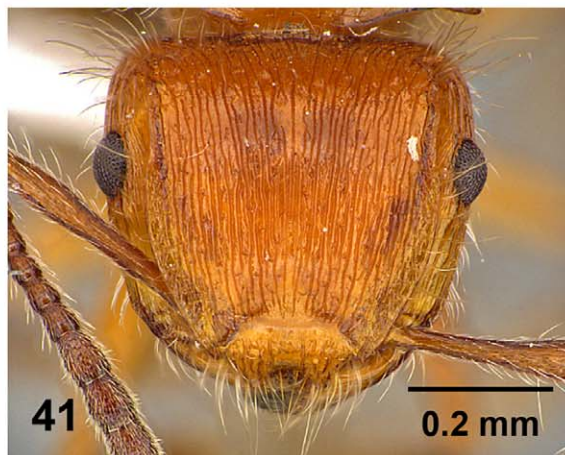
Mesosoma longer than tall. Anterolateral corners of pronotum produced into well-developed denticles; dorsolateral margin produced into a distinct carina. Mesosomal dorsum porcate; ridges of varying rugosity sometimes anastomosing. Setae on dorsum of mesosoma of various lengths; longest on the pronotum and mesoscutellum. Lateral face of pronotum costate, with costae in dorsal third curving upward to join dorsolateral carina. Katepisternum costate, occasionally with a smooth patch in anterior portion. Anepisternum with strong costae which are widely set relative to katepisternal costae. Mesopleuron and lateral face of propodeum costate. Propodeal spines variably short to long (SPL 0.14–0.25). Procoxae with distinct anterolateral basal shoulder. Procoxae with raised sculpture. Wings as in *Meranoplus* male diagnosis. Forewing discal cell 1 (*dl*) with marked intrapopulation variation: *dl* longer than broad, or as long as broad; *dl* posterodistal corner may be acute or sub-perpendicular.

Petiole cuneate in profile; with anterior bulge in ventral half; without pedicel. Anterolateral corners swept back, with laminar lobe variably developed. Postpetiole generally longer than tall, although exceptions may occur (PPI 64–69 [49]). Sternal process of postpetiole well-developed. Dorsal face of postpetiole strongly areolate-rugose; lateral face rugose-costate; posterior face rugose. Fourth abdominal tergum (ATIV) with sides convex in dorsal view. ATIV short (ATL/WL 1.16–1.09). Base of ATIV with weak to very strong dense-punctate sculpture; subparallel costae radiating from helcium strong to weak. Middle portion to posterior portion of ATIV always with dense-punctate sculpture; smooth around setiferous punctures. Majority of ATIV setae shorter than metafemora; setae longest at base of tergum.

Male. HL 0.75–0.92, HW 0.79–0.99, HLA 0.11–0.15, SL 0.23–0.30, EL 0.23–0.35, EW 0.23–0.28, WL 1.47–1.87, PTL 0.29–0.39, PTH 0.28–0.36, PPL 0.27–0.34, PPH 0.32–0.39, ATW 1.16–1.66, ATL 1.03–1.43, CI 105.3–112.6, SI 26.7–30.7, OMI 212–249, SEI 81–88, CS 0.8–1.0, EYE 61.6–65.5 (8 measured).

Body black, abdominal segments IV–VII brown to black above, appendages light to dark brown.

Large (WL 1.5–1.9, CS 0.8–1.0). Head broader than long (CI 105–113). Mandibles short and spatulate, otherwise variable: masticatory margin edentate, with one basal or apical tooth, or with two teeth; dentition sometimes variable between left and right mandibles of same specimen. Frontal carinae indistinct to obsolescent. In full face view, posterior margin of head raised above ocelli greater than distance between lateral ocelli. Head



FIGURES 39–41. *M. mayri*, worker (CASENT0430421). **39.** Body in lateral view (anon.). **40.** Body in dorsal view (anon.). **41.** Head in full-face view (BEB 2012).



FIGURES 42–44. *M. mayri*, gyne (CASENT0115084; E. Ortega 2012). **42.** Body in lateral view. **43.** Body in dorsal view. **44.** Head in full-face view.

with fine areolate sculpture and variable costae: costae posterior to ocelli may be longitudinal or transverse. Scapes short (SI 27–31). Eyes comparatively small (EYE 62–66); about two-and-a-half to about two times as long as malar area (OMI 212–243). Ocelli about the size of antennal sockets. Setae of head set in umbilicate punctures. Majority of setae on body longer than eye-length, suberect to erect, sinuate.

Notauli distinct and set with foveae; may continue to posterior margin of scutum after converging. Parapsidal lines distinct, faintly impressed. All dorsal surfaces of mesosoma coarsely rugose, with umbilicate setiferous punctures which are especially strong anterolaterally on the scutum. Rugae on scutellum may be transverse or longitudinal. Mesopleuron roughened by evanescent longitudinal costae; anepisternum may be somewhat smooth and shining. Metapleuron and lateral face of propodeum costate. Posterior face of propodeum with curving costae. Wing venation as in *Meranoplus* male diagnosis.

Petiole and postpetiole shape variable (PTI 92–123, PPI 83–95). Petiole and postpetiole sessile; apex of petiolar node rounded; postpetiole subglobose. Petiolar sternum occasionally with setae. Post-petiolar sternum setose. Fourth abdominal tergum shining; generally with weak, fine areolate sculpture but occasionally smooth; setae set on nodules or in punctures. Petiole and post-petiolar sculpture variable, with or without costae or rugae; foveate. Fourth abdominal sternum subopaque, with fine areolation. Setae of fourth abdominal tergum set in simple punctures, which may be somewhat raised.

Foramen genitale constricted, diameter about ½ height of basal ring; basal ring broadening posteriorly; basimere about 1.33 times longer than tall in profile; weakly pigmented dorsally in posterior half; medioventral margin of basimere produced medially as a lamina; telomere base less than 0.5 times basimere height; volsella with an apicoventral denticle; setae of cuspis short, no longer than telomere setae; digitus broad, ribbonlike; apical third of digitus sharply bent ventrally at an angle somewhat greater than 90°. Ventral half of penisvalva apex produced posteriorly beyond apicodorsal margin lateral view; lateral apicodorsal margin somewhat angulate in dorsal view; valvura short, stout: broad at base with apex sub-rectangular. Ventral margin of penisvalva sinuate: convex in basal half to concave in distal half. Penisvalva ventral margin with long, recurved teeth; width and distance between the penisvalvar teeth varies basally to apically, with broadest, shortest teeth basally, increasing in size and spacing toward apex; spaces between teeth bases about half height of each tooth in apical third.

Diagnosis

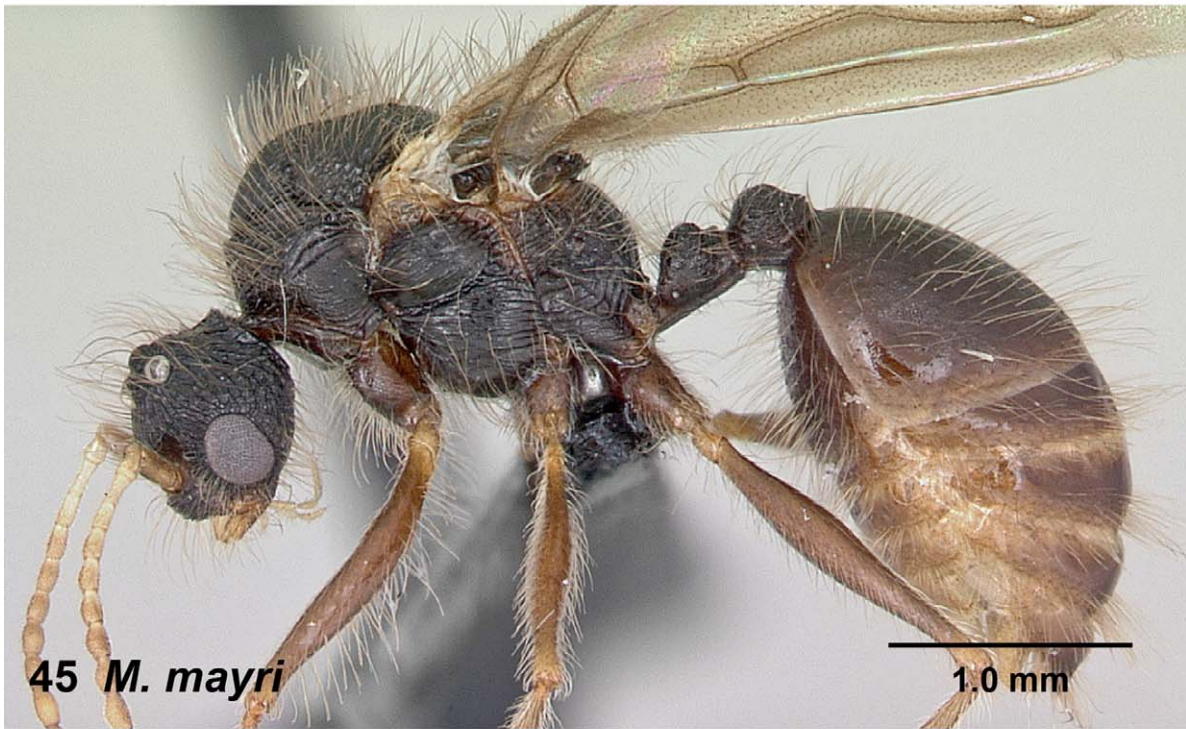
Worker. Each of the following characters is sufficient to uniquely identify this species in the Malagasy fauna: long posterolateral promesonotal spines; conelike clypeal denticles; longitudinally costate face and pleurae; concentric arcing costae on promesonotal shield; fourth abdominal tergum dense-punctate; head broader than long (CI > 100); malar space about twice as long as eye (OMI 44–61); clypeal denticles widely set (CDI > 40). The labrum of *M. mayri* is distinct from the labra of *M. radamae* and *sylvarius* (figs. 8–11). The labral lobes in *M. mayri* are evenly rounded distally, whereas those of *M. radamae* and *sylvarius* are evenly rounded apicolaterally and taper linearly to the midline.

Gyne. Each of the following characters is sufficient to uniquely identify this species in the Malagasy fauna: large (WL > 1.90); face longitudinally costate; head broader than long (CI > 102); eyes small (EYE < 39); eye length distinctly less than ¾ malar area length (OMI < 61).

Male. The large size (WL 1.6–1.9) and raised posterior margin of the head uniquely identify this species in the Malagasy fauna. Diagnosis is supported by the following characters: umbilicate setiferous punctures present on head and mesosomal dorsum; eyes comparatively small (EYE 62–66); eyes less than 2.5 times as long as the malar area (OMI 212–243); posteroventral apex of penisvalva produced beyond posterodorsal margin; penisvalva without apical lobe.

Comments

Meranoplus mayri is distributed throughout the drier regions of Madagascar from the Southwestern region near P.N. Andohahela all the way north into the Mahajanga province. The elevational range of *M. mayri* is 20–1345 m. This species displays subtle variation in morphometric and most sculptural characters across its range except for the sculpture of the base of abdominal tergum IV. This character varies from extremely smooth and shining in the southwest to strongly, dense-punctate and costate along the western edge of the High Plateau. Intergrades are common, however, occurring all along the western coast and into the High Plateau. Both smooth and punctate specimens may be found at the same locales, including Ampotoampoto, Ejada, Tsihombe and Ambinanitelo. The



FIGURES 45–47. *M. mayri*, male (CASENT0062813; A. Nobile 2008). **45.** Body in lateral view. **46.** Body in dorsal view. **47.** Head in full-face view.

variation of this character indicates that although the two extremes are reproductively isolated by distance and geography, but are otherwise linked across their range by intermediate populations.

Unfortunately, as with most of the diversity of *Meranoplus*, nothing is known about the behavior or ecology of *M. mayri* except that its ground nests may be found in urban gardens, grasslands, and deciduous and spiny forests. This is the most frequently collected Malagasy *Meranoplus*, with numerous specimens captured in pitfalls, malaise traps, and hand collections. Although few collections have been made of this species in the High Plateau region, it is predicted that they may be found there as well.

Material examined

MADAGASCAR: Antananarivo, Kaloy, 18°35.47' S, 47°39.19' E, 1338 m, grassland, 27Apr2007 (*B.L. Fisher et al.*); Antananarivo, Tan Morafeno, 15Dec1991 (*A. Pauly*); Fianarantsoa, P.N. Isalo, Ampotoampoto, 22.62803° S, 45.18843° E, 919 m, savanna woodland, coll'n code ARA0125, 24–28Feb2010 (*A. Ravelomanana*); Fianarantsoa, P.N. Isalo, Ampotoampoto, 22.62935° S, 45.19120° E, 923 m, savanna woodland, coll'n code ARA400, 27–28Feb2010 (*A. Ravelomanana*); Tuléar, Andohehala N.P., Ihazofotsy, 24°49.85' S, 46°32.17' E, 60 m, transition between spiny and dry forests, coll'n code MA-02-21-06, 5Jan2003 (*Irwin et al.*); Fianarantsoa, P.N. Isalo, Isalo, 22.61476° S, 45.31304° E, 867 m, *Bismarckia* woodland, coll'n code ARA314, 25Feb2010 (*A. Ravelomanana*); Fianarantsoa, P.N. Isalo, Isalo, 22.61594° S, 45.31084° E, 870 m, *Bismarckia* woodland, coll'n code ARA305, 24–25Feb2010 (*A. Ravelomanana*); Fianarantsoa, Itremo, Ampangabe, 20.61372° S, 46.60799° E, 1449 m, savanna grassland, coll'n code ARA877, 22–24Mar2010 (*A. Ravelomanana*); Mahajanga, P.N. Ampijoroa, 46°19.16' S, 46°48.80' E, 6 m, coll'n code MG-25-49, 16–27Apr2005 (*Rin'Ha, Irwin*); Toliara, Amboasary, 25°02.33' S, 46°23.01' E, 25 m, urban garden, coll'n codes BLF15906, BLF15915 and BLF15918, 9Dec2006 (*B.L. Fisher et al.*); Toliara, Andohehala NP, 24°56.21' S, 46°37.60' E, 174 m, transition forest, coll'n codes MG.20.56, MG.20.27, 31May–10Jun2003, 6–18Mar2004 (*Rin'Ha, Irwin*); Toliara, P.N. Andohehala, Manantalinho 7.6 km 99° E Hazofotsy, 24°49' S, 46°37' E, 150 m, under stone in spiny forest/thicket, coll'n codes BLF4863 and BLF41884, 12–16Jan2002 (*B.L. Fisher et al.*); ground nest in spiny forest/thicket, coll'n code BLF5303, 28Jan–1Feb2002 (*B.L. Fisher et al.*); Toliara, P.N. Andohehala, Manatalinho, 7.6 km 99° E Hazofotsy, 24°49' S, 46°37' E, 160 m, ground nest in spiny forest/thicket, coll'n codes BLF4811, BLF4884, 12–16Jan2002 (*B.L. Fisher et al.*); Toliara, Behara, 24°52.42' S, 46°23.86' E, 85 m, spiny forest/thicket, coll'n codes BLF15886 and BLF15895, 9Jul2006 (*B.L. Fisher et al.*); Toliara, Berenty Special Reserve, 25°01.26' S, 46°18.33' E, 36 m, spiny forest, coll'n code MG-22A, 15–29Apr2004 (*Rin'Ha, Irwin*); Toliara, Rés. Berenty, Forêt Anjapolo, 21.4 km 325° NW Amboasary, 24°56' S, 46°13' E, 65 m, ground nest in spiny forest/thicket, coll'n codes BLF5460 and BLF5490, 7Feb2002 (*B.L. Fisher et al.*); Toliara, Rés. Berenty, Forêt Bealoka, 14.6 km 329° NNW Amboasary, 24°57' S, 46°16' E, 35 m, ground nest “gallery forest”, coll'n code BLF5382, 3–8Feb2002 (*B.L. Fisher et al.*); Toliara, Ampanihy, 24°41.62' S, 44°44.82' E, 250 m, urban/garden, coll'n codes BLF15975, BLF15982, BLF15991, 10Dec2006 (*B.L. Fisher et al.*); Toliara, Rés. Berenty, Forêt Malaza, 8.6 km 314° NW Amboasary, 25°00' S, 46°18' E, 40 m, “gallery forest”, coll'n code BLF5419, 6Feb2002 (*B.L. Fisher et al.*); Toliara, Betsioky, 23°43.27' S, 44°22.81' E, 270 m, urban/garden, coll'n code BLF16035, 11Dec2006 (*B.L. Fisher et al.*); Toliara, Rés. Cap Sainte Marie, 14.9 km 261° W Marovato, 25°36' S, 45°09' E, 160 m, ground nest in spiny forest/thicket, coll'n codes BLF5695 and BLF5748, 13–19Feb2002, (*B.L. Fisher et al.*); Toliara, Col du Manangotry, 24°45' S, 16°48' E, 600 m, coll'n code BLF601, 6Jul1992 (*B.L. Fisher*); Toliara, Ehazoara Conyon, 26 km E Betsioky, 23°41' S, 44°38' E, 175 m, ground forager in tropical dry forest, coll'n code BLF1510-1, 27Apr1997 (*B.L. Fisher*); Toliara, Ejada, 24°21.03' S, 44°30.96' E, 250 m, urban/garden, coll'n codes BLF15999, BLF16009, BLF16011, BLF16018, BLF16025, 10Dec2006 (*B.L. Fisher et al.*); Toliara, P.N. Kirindy Mite, 16.3 km 127° SE Belo sur Mer, 20°48' S, 44°09' E, 80 m, ground nest tropical dry forest, coll'n codes BLF4744, BLF 4727, BLF4753, 6–10Dec2001 (*B.L. Fisher et al.*); Toliara, Kirindy, 15.5 km 64° ENE Marofandilia, 20°03' S, 44°40' E, 100 m, ground nest tropical dry forest, coll'n codes BLF4607 and BLF4613, 28Nov–3Dec2001 (*B.L. Fisher et al.*); Toliara, 4 km N Isaka-Ivondro, 24°46' S, 46°52' E, 180 m, ground foragers roadside, coll'n code PSW11804-1, 3Feb1993 (*P.S. Ward*); Toliara, S.F. Mandena, 8.4 km NNE 30° Tolagnaro, 24°57.1' S, 47°00.1' E, 20 m, ground forest “littoral rainforest”, coll'n code BLF2050, 20Nov1998 (*B.L. Fisher et al.*); Toliara, Mahafaly Plateau, 6.2 km 74° ENE Itampolo, 24°19' S, 43°69' E, 80 m, ground nest in spiny forest/thicket, coll'n code BLF5845, 21–25Feb2002 (*B.L. Fisher et al.*); Toliara, Forêt Mahavelo, Isantoria Riv., 5.2 km 44° NE Ifotaka, 24°46' S, 46°09' E, 110 m, ground nest in spiny forest/thicket, 28Jan–1Feb2002 (*B.L. Fisher et al.*); Toliara, Forêt Mandena,

24°57.16'S, 47°00.15'E, 20 m, littoral rainforest, coll'n code BLF15666, 5Dec2006 (*B.L. Fisher et al.*); Toliara, 48 km ENE Morondava, 20°04'S, 44°39'E, 30 m, tropical dry forest, 4–6Jan1991 (*D.M. Olsen*); Toliara, Tsihombe, 25°19.10'S, 45°29.02'E, 30 m, coll'n codes BLF15951, BLF15959, 10Dec2006 (*B.L. Fisher et al.*); Toliara, P.N. Tsimanampetsotsa, Bemananateza 23.0 km 131°SE Behaloka, 24°00'S, 43°53' E, 90 m, ground nest spiny forest/thicket, coll'n codes BLF6265, BLF6268, BLF6280, 22–26Mar2006 (*B.L. Fisher et al.*); Toliara, Forêt Vohidava, 24°14.446 S, 46°17.27' E, 500 m, dry forest, coll'n code BLF15851, 6–8Dec2006 (*B.L. Fisher et al.*); Tuléar, P.N. Andohehala, Tsimela, 24°56.21' S, 46°37.60' E, 177 m, transition forest, coll'n code MG-20-52, 15-28Jan2004 (*Rin'Ha, Irwin*); Tuléar, Andohehala, N.P., Tsimelaha, 24°56.21' S, 46°37.60' E, 180 m, coll'n code MA-02-20-16, 15–26Feb2001 (*M. Irwin et al.*); Tuléar, Berenty Special Reserve, 25°00.40' S, 46°18.20' E, “gallery forest”, 27Dec2007, 7–17Jan2003, 24Mar–3Apr2003 (*Rin'Ha, Irwin*); Tuléar, Reserve Berenty, 25°01' S, 46°18' E, 25 m, ground foragers in tropical dry forest, coll'n code BLF603-1, 10Dec1992 (*B.L. Fisher*).

***Meranoplus radamae* Forel, 1891**

(Figs. 9, 14, 16–18, 20, 22, 24, 30, 32, 48–56, 65)

Meranoplus radamae Forel, 1891: 148, pl. 4, fig. 10. Lectotype worker, here designated, MADAGASCAR: Imerina (Central Madagascar) (*M. Hildebrandt*) (MHNG: CASENT0101239) [examined].

Description

Worker. HL 0.86–1.04, HW 0.79–0.92, HLA 0.32–0.38, CW 0.29–0.36, CDD 0.08–0.10, SL 0.60–0.72, EL 0.18–0.22, EW 0.13–0.16, PML 0.58–0.76, PWA 0.73–0.92, PWP 0.43–0.55, SPL 0.16–0.22, WL 0.86–1.1.05, PTL 0.18–0.25, PTH 0.38–0.46, PPL 0.19–0.26, PPH 0.32–0.42, ATW 1.01–1.24, ATL 1.09–1.40, CI 88.7–93.8, SI 70.5–79.4, OMI 55.9–62.7, CDI 22.4–34.2, SEI 290–350, PMI 121.3–134.3, PWI 54.0–62.5, CS 0.8–1.0, EYE 36.2–40.5 (19 measured).

Coloration variable: dark orange, orange brown or yellowish brown with yellow abdominal segments IV–VII. Head longer than broad (CI 92–95). Mandibles striate. Face longitudinally rugose to dilutely costate; area anterior to nuchal carina areolate to rugose. Area around eyes areolate to rugose or costate beneath and behind. Frontal carinae concealing dorsal margin of eyes in full face view. Scrobal carina weak to nearly absent. Anterior margin of clypeus with weakly bilobed lamina; lobes relatively close set (CDI 22–36). Middle portion of clypeus costate to rugose laterally; smooth and shining medially. Setae on face subdecumbent to erect; of mixed lengths; longest setae about twice as long as shortest.

Promesonotal shield longer than broad (PMI 120–134). Lateral margins of promesonotum tapering to midline posteriorly; posterolateral denticles comparatively close-set (PWI 54–63). Dorsum of promesonotum areolate to dilutely rugose. Setae on promesonotal shield subdecumbent to erect; of mixed lengths; longest setae about 1.25 as long as shortest. Lateral face of pronotum rugose anteriorly; posterior portion shining, variably smooth to weakly areolate; setiferous nodules mostly hidden by sculpture. Lateral face of mesonotum smooth and shining to somewhat roughened. Anapleural and mesometapleural sutures present. Mesopleuron shining; with or without weak areolate sculpture or costae on katapisternum. Metapleuron shining with or without weak areolation; smooth anterodorsal metapleural bulla. Lateral face of propodeum shining, roughened with rugae dorsal to spiracle. Propodeal spines long, thorn-shaped (0.16–0.22), with both dorsolateral and dorsomedian costae reaching notopropodeal suture. Posterior face of propodeum with costae in dorsal region.

Petiole cuneate in profile although sometimes with bulge posteriorly near apex; without pedicel. Subpetiolar process dentiform. Anterior and posterior faces of petiole smooth and shining. Postpetiole nodiform; without distinct posterodorsal angle. Dorsal face of postpetiole areolate to rugose; lateral face rugose; posterior face areolate to rugose. Fourth abdominal tergite (ATIV) can be small (ATW/WL 1.13–1.33, ATL/WL 1.15–1.48). ATIV base variably rugose and rough to shining between setiferous punctures. ATIV with fine areolate sculpture, which may be weak, between stellate setiferous punctures. ATIV setae of mixed lengths; short setae subdecumbent; long setae suberect; longest setae 1.25–1.5 times as long as shortest setae.

Queen. HL 1.09–1.15, HW 1.05–1.10, HLA 0.35–0.38, CW 0.37–0.41, CDD 0.10–0.13, SL 0.70–0.74, EL 0.26–0.29, EW 0.21, SPL 0.19–0.23, WL 1.39–1.49, PTL 0.27–0.31, PTH 0.47–0.49, PPL 0.24–0.30, PPH 0.47–0.52, ATW 1.47–1.58, ATL 1.68–1.92, CI 92.1–96.1, SI 68.0–70.3, OMI 72.6–78.5, CDI 25.9–32.8, SEI 253–283, CS 1.1, EYE 43.3–44.8 (6 measured).

Light brown to pale yellowish orange.

Small (WL 1.4–1.5). Head longer than broad (CI 92–97). Mandibles striate; ridges may be evenly curved or wavy. Face areolate to longitudinally rugose; area posterior to ocelli areolate to transversely rugose. Area above and below eyes areolate; areolate to rugose behind eyes. Scrobal carina distinct to indistinct; broadest in anterior half. Anterior margin of clypeus with bilobed lamina; lobes relatively close-set (CDI 26–33). Middle portion of clypeus rugose to costate laterally, smooth medially; lateral ridges may meet anteriorly. Eyes large (EYE 43–53). Maximum eye length $\frac{3}{4}$ length of malar area (OMI 73–79). Scapes long (SI 67–70). Face with setae of mixed lengths; longest setae 1.25–2 times as long as shortest setae.

Pronotum with anterolateral angles; dorsolaterally ecarinate. Pronotal dorsum variably areolate to rugose. Scutum smooth to rugose on anterior half; always with some rugae on posterior half. Scutellum areolate to longitudinally rugose. Lateral face of pronotum areolate to sub-areolate on anterior portion; shining, roughened, sometimes with rugae on posterior portion. Katepisternum smooth and shining, with longitudinal costae often extending from anapleural suture to mesometapleural suture. Anepisternum shining ventrally; rugose dorsally. Metapleuron and lateral face of propodeum rugose, with variable shining area anterodorsal to metapleural bulla. Propodeal spines long, thorn-like (SPL 0.19–0.23). Wings as in *Meranoplus* male diagnosis.

Petiole cuneate in profile, without pedicel. Postpetiole nodiform, without distinct posterodorsal angle. Subpostpetiolar process well-developed; robust to thin. Dorsal face of postpetiole areolate to rugose; lateral face rugose-costate; posterior face areolate with interstices punctate to longitudinally rugose. Fourth abdominal tergum (ATIV) with sides convex in dorsal view; long (ATL/WL 1.20–1.29). Base of ATIV rough to smooth, with variably developed rugae; setiferous punctures strong near base, increasing in stellation posteriorly; ATIV with weak fine areolation between setiferous punctures. ATIV setae of mixed lengths: short setae subdecumbent, shortest setae about $\frac{1}{2}$ length of longest setae; long setae erect, varying in density.

Male. HL 0.52–0.63, HW 0.55–0.60, HLA 0.06–0.09, SL 0.15–0.18, EL 0.24–0.26, EW 0.19–0.23, WL 0.70–1.20, PTL 0.19–0.25, PTH 0.20–0.22, PPL 0.15–0.19, PPH 0.19–0.22, ATW 0.79–1.01, ATL 0.83–0.96, CI 96.3–106.4, SI 27.0–29.7, OMI 301–428, SEI 61–69, CS 0.5–0.6, EYE 75.9–80.5 (3 measured).

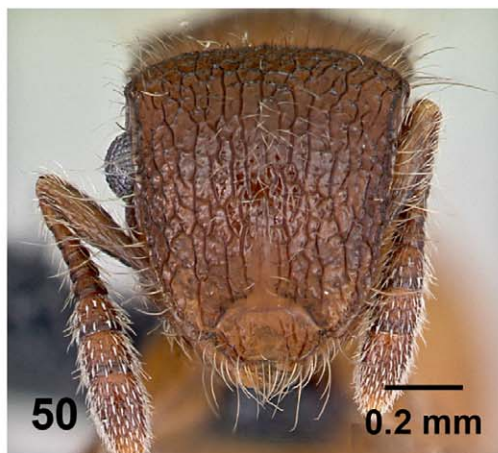
Body piceous brown, appendages light brown.

Small (WL 0.7–1.2, CS 0.5–0.6). Head longer than broad or broader than long (CI 96–106). Mandibles variably developed: short and spatulate with edentate masticatory margin to longer, bladelike, with apical tooth. Frontal carinae distinct to indistinct. In full-face view, posterior margin of head not raised above ocelli greater than distance between lateral ocelli. Head variably rugose with foveate sculpture. Scapes short (SI 27–30). Eyes large (EYE 76–81), greater than three times as long as malar area (OMI 300–430). Ocelli about the size of the antennal socket. Majority of setae on body shorter than eye length, subdecumbent to erect, uniformly straight to evenly curved.

Notauli distinct; may continue to posterior margin of scutum after converging. Parapsidal lines distinct, impressed or not. Scutum smooth and shining, albeit undulating with coarse setiferous punctures. Scutellum shining at least medially; roughened laterally. Katepisternum smooth and shining. Anepisternum smooth and shining; posterior half variably rough and rugose to smooth and shining. Lower half of metapleuron with a shining patch of variable size; dorsal half rugose. Posterior face of propodeum with longitudinal costae laterally; variably foveate to smooth.

Petiole and postpetiole shape variable (PTI 87–114, PPI 72–95). Petiole and postpetiole sessile; apex of petiolar node acute to rounded; postpetiole subglobose. Petiolar sternum occasionally with setae. Postpetiolar sternum setose. Fourth abdominal tergum shining, with weak, fine areolate sculpture and with stellate setiferous punctures. Fourth abdominal sternum shining.

Foramen genitale constricted; basal ring broadening posteriorly; basimere longer than tall; basimere dorsomedian margin folded ventrally; basimere ventromedian margin dorsally curved, cupping the volsella; telomere arrowhead-shaped with a ventral membrane basally; setae of cuspis numerous, subequal in length to the apex of the telomere in ventral view; basal setose region of cuspis triangular; ventral margin of cuspis edentate, evenly curved; digitus long, thin, narrowing to apex which is evenly ventrally curved; valviceps of penisvalva strongly rounded with an apicoventral lobe; valvura apex subrectangular, narrow; ventral margin of penisvalva slightly concave to straight in basal half, otherwise straight and serrate, with teeth short and pointed anteriorly.



FIGURES 48–50. *M. radamae*, worker (CASENT0486686; A. Nobile 2007). **48.** Body in lateral view. **49.** Body in dorsal view. **50.** Head in full-face view.



FIGURES 51–53. *M. radamae*, gyne (CASENT0317524; E. Ortega 2012). **51.** Body in lateral view. **52.** Body in dorsal view. **53.** Head in full-face view.

Diagnosis

Worker. Workers of this species are immediately differentiable from *M. mayri* by the absence of promesonotal spines. The following characters diagnose this species within the *M. nanus* group: posterolateral denticles close-set (PWI < 64); meso- and metatibial spurs present; dorsomedian costa of propodeal spine present, extending to promesonotum; postpetiole posterior face never smooth and shining.

Gyne. Within the Malagasy *Meranoplus* fauna, gynes of *M. radamae* may be identified by the following characters: stellate setiferous punctures present on fourth abdominal tergum; propodeal spines thorn-like; smooth area behind eyes interrupted by rugae, or ruga behind eye terminates at ventrolateral mandibular condyle; eye length about ¾ length of malar area (OMI mean 75); never bicolored nor dark brown.

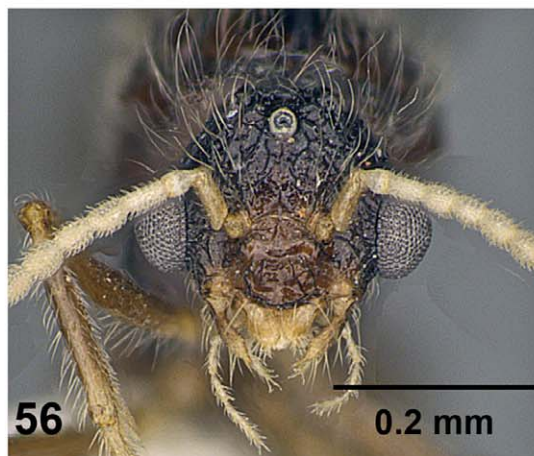
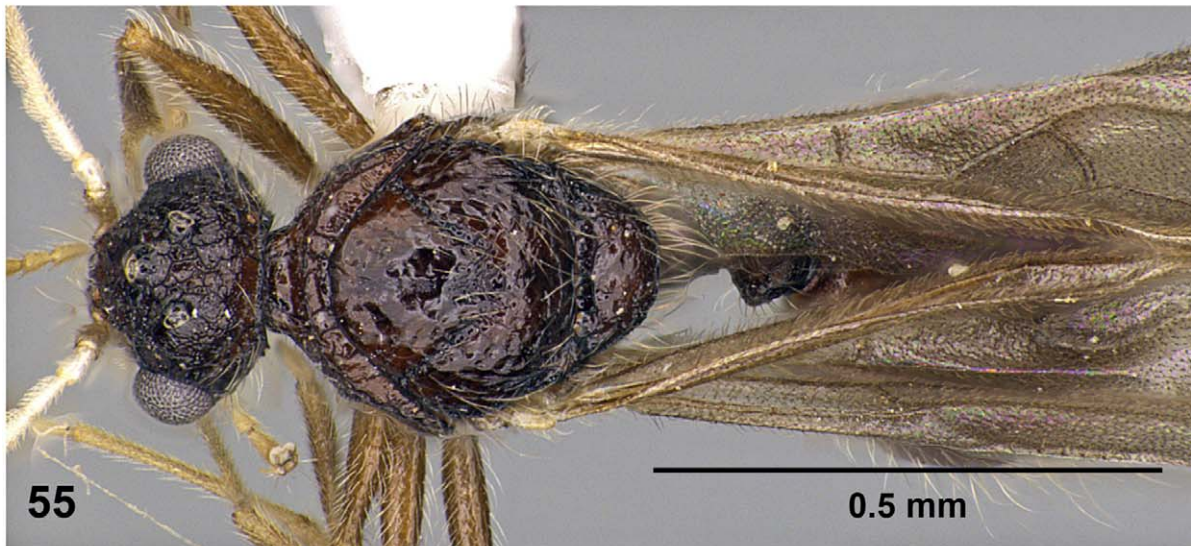
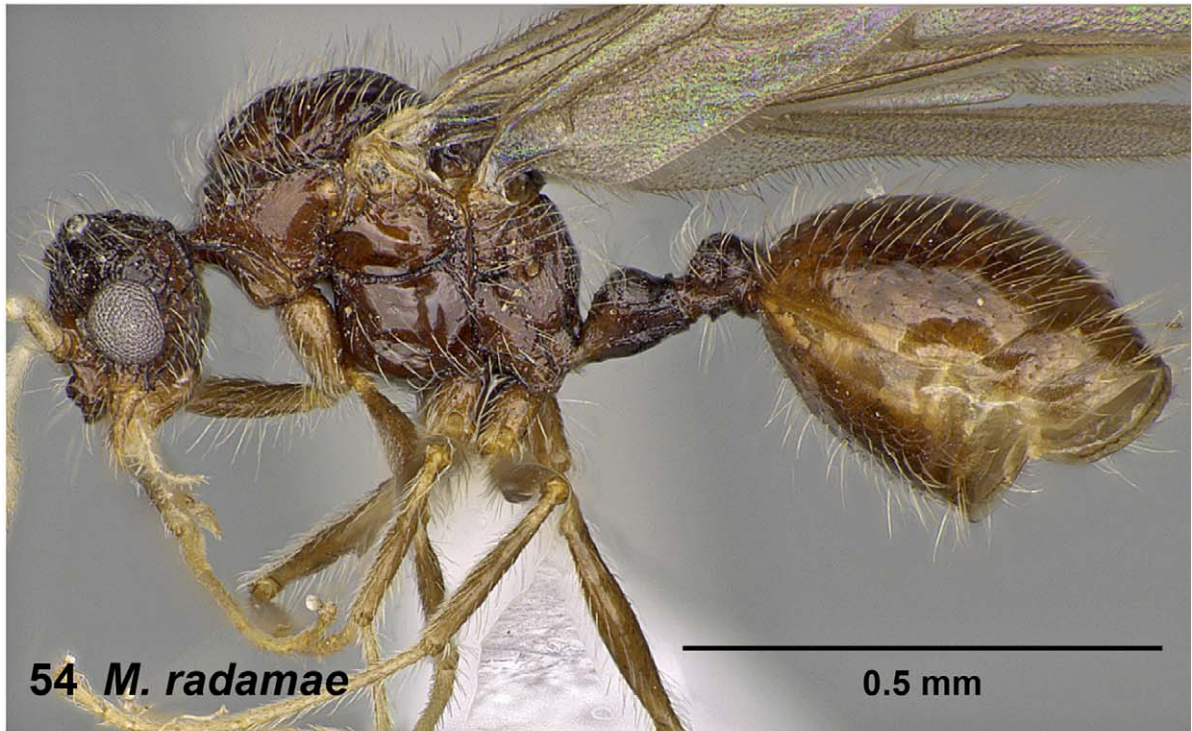
Male. Males of *M. radamae* may be separated from those of *M. mayri* by the presence of the following characters: posterior margin of head not visible in full face view; small (WL 0.70–1.20); eyes large (EYE 76–81); maximum eye length greater than or equal to three times length of malar area (OMI 301–428); head comparatively small (CS 0.5–0.6); apex of penisvalva evenly rounded; penisvalva with apicoventral lobe; ventral margin of penisvalva serrate, without long spine-like teeth.

Comments

Meranoplus radamae is restricted to the grasslands and woodlands of the High Plateau, and the spiny forests of southern Madagascar. Specimens are known from 370–1550 m above sea level, and nests have been collected under stones in grassland and from ground nests. A few collections have been made in southern rainforest sites, but these may represent local adaptation to disturbed habitats. It is interesting to note that the southern rainforest collections of *M. radamae*, at R.S. Kalambatitra and Mount Vasiha, have reduced sculpturation on the face and promesonotal shield; these characters are represented in extreme form by the distinct *M. sylvarius* described here.

Material examined

MADAGASCAR: Antananarivo, Ambatolaona, 18°55.68' S, 47.52.97° E, 1382 m, urban/garden, coll'n codes BLF16883, BLF16899, 19Feb2007 (*B.L. Fisher et al.*); Antananarivo, Angavokely, 18°56' S, 47°45' E, 10Feb1992 (*B. Pettersson*); 29.5 km WNW Tolanaro, Vasiha Mt., 24°55'37" S, 46°44'49" E, 300 m, sifted leaf litter in rainforest, 6–7Feb1995 (*K.C. Emberton et al.*); Antananarivo, Ankalalahana, 19.00659° S, 47.11220° E, 1375 m, *Uapaca* woodland, coll'n codes BLF26350, BLF26357, BLF26360, BLF26366, BLF2637, BLF26391, 29–31Mar2010 (*B.L. Fisher et al.*); Antananarivo, Antsahadinta, 19°00.76' S, 47°27.40' E, 1403 m, urban garden, coll'n codes BLF17519, BLF17522, 8May2007 (*B.L. Fisher et al.*); Antananarivo, Arivonimamo, Navoatra, 18.97799° S, 47.11929° E, 1373 m, *Uapaca* woodland, coll'n code ARA915, 6–8May2010 (*A. Ravelomanana*); Antananarivo, Manalalondo, Antaponimanadala, 19.25531° S, 47.17710° E, 1984 m, savanna grassland, coll'n code ARA1053, 13–16May2010 (*A. Ravelomanana*); Fianarantsoa, Ambositra, Antapia, 20.71971° S, 47.08685° E, 1495 m, *Uapaca* woodland, coll'n code ARA600, 3–5Feb2010 (*A. Ravelomanana*); Fianarantsoa, Ambositra, Mampiarika, 20.73456° S, 47.08355° E, 1480 m, *Uapaca* woodland, coll'n code ARA468, Feb2010 (*A. Ravelomanana*); Fianarantsoa, Ambositra, Mampiarika, 20.73568° S, 47.08384° E, 1464 m, *Uapaca* woodland, coll'n code ARA469, 1–3Feb2010 (*A. Ravelomanana*); Fianarantsoa, Forêt Atsirakambiaty 7.6 km 285° WNW Itremo, 20°35.6' S, 46°33.8' E, 1550 m, under stone in grassland, coll'n codes BLF7206, BLF7226, 22–26Jan2003 (*B.L. Fisher et al.*); Fianarantsoa, Itremo, Ampangabe, 20.6119° S, 46.60688° E, 1414 m, savanna woodland, coll'n code ARA791, 21–23Mar2010 (*A. Ravelomanana*); Fianarantsoa, Itremo, Antohatsahomby, 20.55436° S, 46.58438° E, 1640 m, *Uapaca* woodland, coll'n code ARA611, 18Mar2010 (*A. Ravelomanana*); Mahajanga, Ambohimanga, 18°45.67' S, 47.33.86' E, 1361 m, disturbed montane rainforest, coll'n code BLF17326, 26Apr2007 (*B.L. Fisher et al.*); Toliara, R.S. Kalambatitra, 23.4185° S, 46.4583° E, 1365 m, grassland, coll'n codes BLF21500, BLF21538, BLF21535, 8Feb2009 (*B.L. Fisher et al.*); Toliara, Forêt Vohidava 88.9 km N Amboasary, 24°14'26" S, 46°17'16" E, 500 m, coll'n codes BLF15846, BLF15847, BLF15849, BLF15850, BLF15692, BLF15738, 9Dec2006 (*B.L. Fisher et al.*); Toliara, Vohibasias Forest, 59 km E Sakaraha, 22°28' S, 44°51' E, 750 m, sifted litter in tropical dry forest, coll'n code BLF1310, 13Jan1996 (*B.L. Fisher et al.*).



FIGURES 54–56. *M. radamae*, male (CASENT0317525). **54.** Body in lateral view. **55.** Body in dorsal view. **56.** Head in full-face view.

***Meranoplus sylvarius* Boudinot & Fisher sp. n.**

(Figs. 10, 23, 28, 29, 57–62, 66)

Holotype worker, MADAGASCAR: Fianarantsoa, Vevembe, 22°47.46' S, 47°10.91' E, 600 m, rainforest transition to montane forest, collection code BLF14131, 23–24Apr2006 (*B.L. Fisher et al.*) (CASC: CASENT017529). Paratype gyne with same data as holotype worker (CASC: CASENT0317567).

Paratype workers with same data as holotype worker (BMNH: CASENT0317527; CASC: CASENT0317536, CASENT0317566, CASENT0070611, CASENT0317528, CASENT0317540–CASENT0317542, CASENT0317557–CASENT0317559, CASENT0317544, CASENT0317547, CASENT0317548, CASENT0317548–CASENT0317552, CASENT0317554–CASENT0317556; MHNG: CASENT0317538; MCZ: CASENT0317543; USNM: CASENT0317549; NHMB: CASENT0317553).

Description

Worker (holotype in parentheses). HL 1.03–1.13 (1.06), HW 0.90–1.02 (0.96), HLA 0.37–0.41 (0.39), CW 0.36–0.38 (0.38), CDD 0.09–0.11 (0.11), SL 0.73–0.80 (0.78), EL 0.22–0.23 (0.23), EW 0.15–0.16 (0.16), PML 0.72–0.80 (0.76), PWA 0.88–0.98 (0.94), PWP 0.47–0.53 (0.48), SPL 0.19–0.22 (0.21), WL 1.04–1.17 (1.12), PTL 0.23–0.25 (0.25), PTH 0.43–0.49 (0.46), PPL 0.23–0.24 (0.24), PPH 0.40–0.45 (0.42), ATW 1.23–1.34 (1.32), ATL 1.27–1.48 (1.42), CI 87.4–90.6 (90.1), SI 77.7–81.3 (81.1), OMI 58.3–59.6 (59.4), CDI 23.9–31.2 (27.3), SEI 324–355 (336), PMI 122.7–124.4 (122.8), PWI 51.5–55.3 (51.5), CS 1.0–1.1 (1.0), EYE 37.7–40.4 (38.5) (7 measured).

Chocolate brown to almost black.

Head longer than broad (CI 77–82). Mandibles with nearly parallel striation. Face with dilute costae which veer away from posterior margin of head; area anterior to nuchal carina without rugae or areolation. Area around eyes costate; costae in malar area somewhat rugose. Frontal carinae comparatively narrow, not concealing margin of eyes in full-face view. Scrobal carina weakly developed; anterior half bulging. Anterior margin of clypeus with weakly bilobed lamina; lobes close-set (CDI 24–31). Middle portion of clypeus shining and weakly costate; lateral thirds of middle portion with about two costae; middle third without costae. Eyes large (EYE 35–41). Maximum length of eye distinctly less than $\frac{3}{4}$ length of malar area (OMI 55–60). Face with erect to subdecumbent setae of various lengths. Setae ventrally and anterior to the eye mostly subdecumbent.

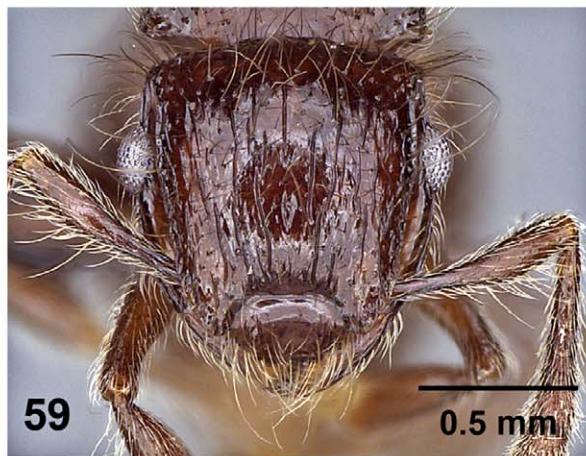
Promesonotal shield longer than broad (PMI 122–125); posterolateral corners close-set (PWI 51–55). Dorsum of promesonotum with dilute costae, mostly concentrated in anterior half; interstices with setae raised on tiny nodules. Promesonotal shield setae decumbent to suberect, of mixed lengths. Lateral face of pronotum with weak rugae; setae raised on nodules. Lateral face of mesonotum smooth and shining. Katepi-anepisternal suture present; mesopleural-mesonotal suture present; mesopleural-metapleural suture absent to present. Mesopleuron smooth and strongly shining, with very dilute (1 to 4), very weak indications of raised sculpture other than in posteroventral area. Metapleural lobes well-developed. Propodeal spines thornlike; dorsomedian carina absent; dorsolateral carina extends dorsolaterally to promesonotum. Posterior face of propodeum smooth and shining; very weak costae may be present in top third, which otherwise has setae raised on nodules.

Petiole cuneate in profile, without pedicel. Anteroventral process of petiole a simple denticle. Postpetiole nodiform, about as tall as long (PTI 50–55). Sub-post-petiole process well-developed, with a strong inflection between posterior half of sternum. Dorsal face of postpetiole with weak to indistinct rugae; lateral face with weak to indistinct rugae; posterior face smooth and shining except for nodulose setae and transverse costae near extreme base. Fourth abdominal tergum (ATIV) comparatively small (ATW/WL 1.15–1.23, ATL/HL 1.20–1.33). ATIV shining, with fine areolate sculpture between stellate setiferous punctures; smooth near base of tergum. Setae of ATIV of mixed lengths; shortest subdecumbent and longer than width of metafemora; longest setae about twice as long as shortest.

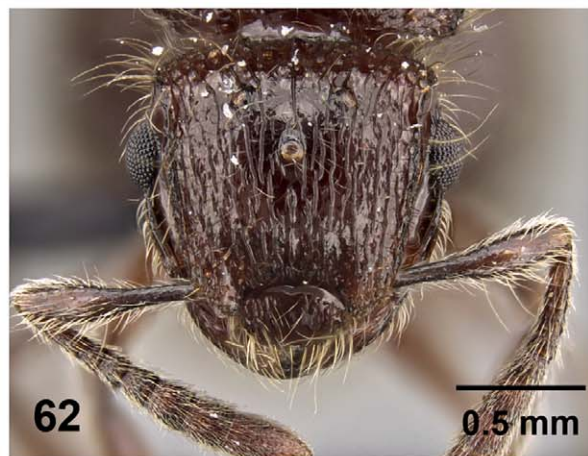
Queen (paratype). HL 1.22, HW 1.17, HLA 0.41, CW 0.44, CDD 0.13, SL 0.82, EL 0.29, EW 0.22, SPL 0.20, WL 1.61, PTL 0.31, PTH 0.56, PPL 0.29, PPH 0.56, ATW 1.82, ATL 1.89, CI 95.2, SI 70.6, OMI 71.4, CDI 29.1, SEI 285, CS 1.2, EYE 42.4.

Color: chocolate brown.

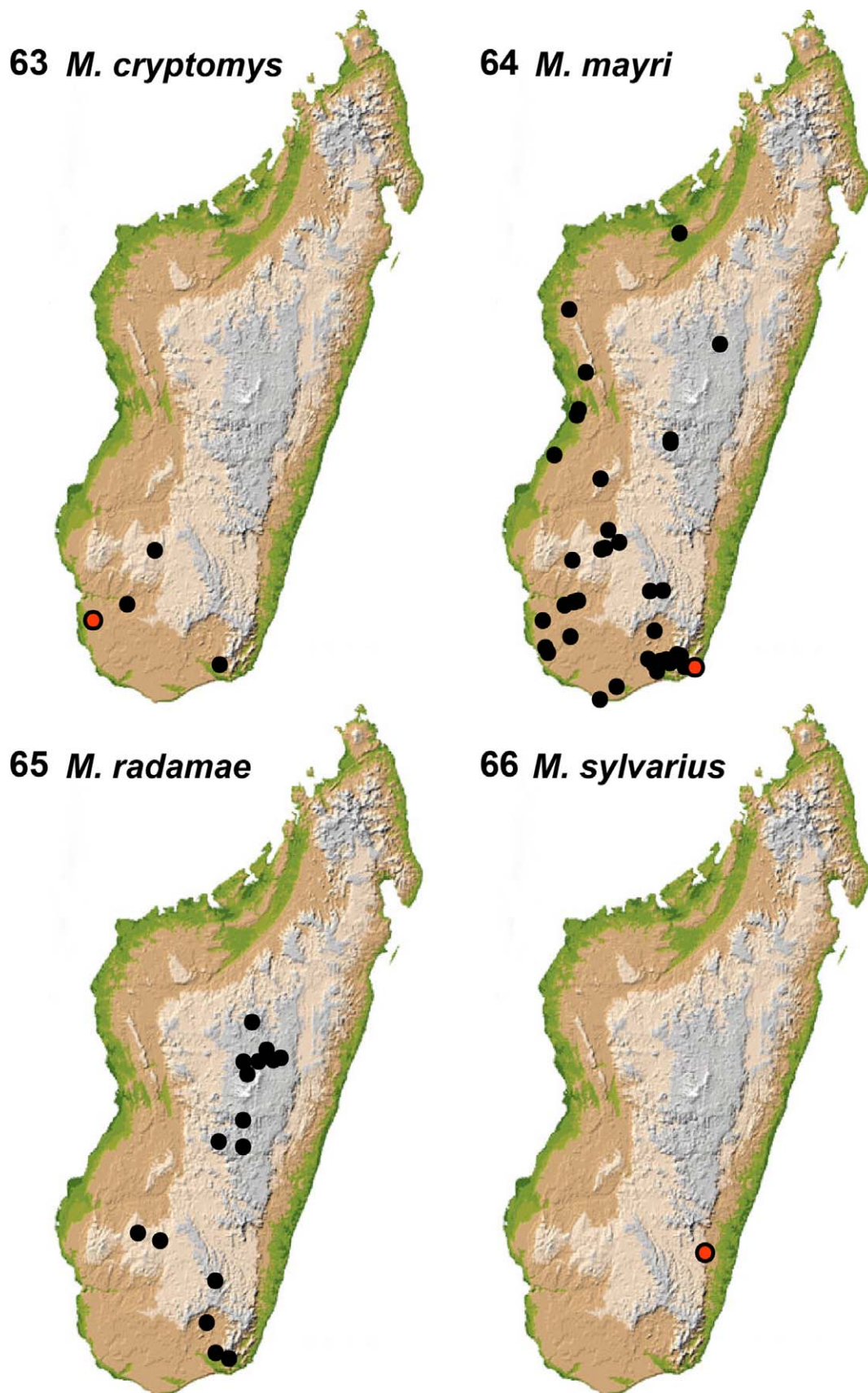
Large (WL 1.61). Head longer than broad (CI 95). Mandibles with more-or-less parallel striae. Face with weakly rugose costae which continue to the posterior margin of the head. Area above eye areolate; behind and beneath eye costate. Scrobal carina weakly bulging in anterior half. Anterior margin of clypeus with two well-



FIGURES 57–59. *M. sylvarius* sp. n., holotype worker (CASENT0317539). **57.** Body in lateral view. **58.** Body in dorsal view. **59.** Head in full-face view.



FIGURES 60–62. *M. sylvarius* sp. n., paratype gyne (CASENT0317567; S. Hartman 2012). **60.** Body in lateral view. **61.** Body in dorsal view. **62.** Head in full-face view.



FIGURES 63–66. Distribution maps of Malagasy *Meranoplus* species; type localities are indicated by red markers. Elevation is indicated by color: green 0–100 m, peach 101–500 m, pink 501–1000 m, grey 1001–2000+ m (map provided by NASA). **63.** *M. cryptomys* sp. n. **64.** *M. mayri*. **65.** *M. radamae*; the exact type locality is unknown, but is in “Central Madagascar”. **66.** *M. sylvarius* sp. n.

developed, close-set laminar lobes (CDI 29). Middle portion of clypeus with strong costae in lateral thirds; middle third without sculpture. Eyes large (EYE 42). Maximum eye length about $\frac{3}{4}$ length of malar area (OMI 71). Scapes long (SI 71). Face with erect to subdecumbent setae; longest setae about 1.5 length of shortest setae.

Mesosoma longer than tall. Anterolateral corners of pronotum angled; dorsolateral margin of pronotum ecarinate. Mesosomal dorsum with little sculpture: pronotum smooth medially, rugose laterally; scutum smooth and shining in anterior half, with dilute rugae in posterior half; scutellum with transverse rugae branching more frequently in lateral portions. Mesosomal dorsum with subdecumbent to erect setae of mixed lengths. Lateral face of pronotum rugose anteriorly; with setae raised on strong nodules. Katepisternum mostly smooth and shining; without costae extending longitudinally margin to margin. Anteroventral portion of anepisternum smooth and shining; dorsal portion with longitudinal rugae, interstices roughened. Metapleuron roughened with rugae; area anteroventral to propodeal spiracle smooth and shining. Propodeal spines thorn-like, long (SPL 0.20). Meso and metatibial spurs absent. Wings unknown.

Petiole cuneate in profile; subpetiolar process dentiform. Postpetiole nodiform; sternal process large. Dorsal and lateral faces of postpetiole rugose; posterior face roughened near base and with dilute longitudinal costae. Fourth abdominal tergum (ATIV) with sides convex; nearly as broad as long (ATW/GL 0.96). ATIV with fine, weak areolate sculpture between stellate setiferous punctures; weak, dilute costae present in basal region. ATIV with subdecumbent short setae; suberect setae about 1.5-2 times as long as shorter setae.

Diagnosis

Worker. The absence of meso- and metatibial spurs is unique in the Malagasy fauna. This new species may be separated from *M. radamae* by the absence of a dorsomedial costa extending from the base of the propodeal spine to the promesonotum.

Gyne. The combination of stellate setiferous punctures, comparatively large size (WL 1.61), dark chocolate-brown color, malar area about $\frac{3}{4}$ the length of the eye (OMI 71.4), long scapes (SI 70.6), uniquely identify gynes of this species in the Malagasy fauna.

Comments

The type series of *M. sylvarius* is designated from a large nest collection from the rainforest/montane forest of Vevembe, the only known locale of this species. Restriction to moist forest habitat is unique for Malagasy *Meranoplus*.

Although not collected in sympatry with *M. radamae*, *M. sylvarius* is morphologically distinct enough to support the hypothesis of reproductive isolation. The lack of meso- and metatibial spurs is unique in the Malagasy *Meranoplus* fauna. Although *M. radamae* shows much geographic variation in its sculpturation, the trends of sculpture reduction across body parts never move in synchrony to such extremes, suggesting that the almost complete reduction of sculpture on specimens of *M. sylvarius* would be highly unlikely under circumstances of gene flow.

Etymology

The new species name is Latin for “forester”, as this species is unique in the Malagasy *Meranoplus* fauna for its restriction to rainforest habitat. The specific epithet is a noun in apposition and thus invariant.

Additional material examined

MADAGASCAR: Fianarantsoa, Vevembe, 22°47.46' S, 47°10.91' E, 600 m, montane forest, collection code BLF14314, 23–24Apr2006 (*B.L. Fisher et al.*).

ACKNOWLEDGMENTS

We would like to express our gratitude to Prof. John Longino (University of Utah, Salt Lake City, U.S.A), Mr. Barry Bolton (BMNH), Mr. Zachary Lieberman (CASC) and especially an anonymous reviewer for critical review of the manuscript. Discussions with Drs. Francisco Hita Garcia, Georg Fischer, and Masashi Yoshimura (all CASC) improved the manuscript. We also would like to thank Ms. Michele Esposito (CASC) for her meticulous

support with databasing, imaging processing, proofreading, and her overall support in the lab. We are very thankful to our current and past AntWeb imagers Ms. April Nobile, Ms. Estella Ortega, and Ms. Shannon Hartman. We appreciate the support from Dr. Bernhard Merz (MHNG) who loaned important type material and welcomed us to image type material. We also want to thank Prof. Phil S. Ward (University of California, Davis, U.S.A.) for providing material collected in Madagascar. Moreover, the fieldwork on which this study is based could not have been completed without the gracious support of the Malagasy people and the Arthropod Inventory Team (Balsama Rajemison, Jean-Claude Rakotonirina, Jean-Jacques Rafanomezantsoa, Chrislain Ranaivo, Hanitriniana Rasoazanamavo, Nicole Rasoamanana, Clavier Randrianandrasana, Dimby Raharinjanahary, Njaka Ravelomanana, Manoa Ramamonjisoa, and Mihary Razafimamonjy). Research, collecting and export permits were obtained through collaboration with the “Ministère de l' Environnement et des Forêts” and the Madagascar National Parks. This study was supported by the National Science Foundation under Grant No. DEB-0072713, DEB-0344731, and DEB-0842395.

REFERENCES

- Anderson, A.N., Azcárate, F.M. & Cowie, I.D. (2000) Seed selection by an exceptionally rich community of harvester ants in the Australian seasonal tropics. *Journal of Animal Ecology*, 69, 975–984.
<http://dx.doi.org/10.1046/j.1365-2656.2000.00452.x>
- Anderson, A.N. (2006) A systematic overview of Australian species of the myrmicine ant genus *Meranoplus* F. Smith, 1853 (Hymenoptera: Formicidae). *Myrmecologische Nachrichten*, 8, 157–170.
- André, E. (1892) Matériaux myrmécologiques. *Revue d'Entomologie (Caen)*, 11, 45–56.
- Bernard, F. (1953) La réserve naturelle intégrale du Mt Nimba. XI. Hyménoptères Formicidae. *Mémoires de l'Institut Français d'Afrique Noire*, 19, 165–270.
- Billen, J. & Taylor W. (1993) Notes on the aberrant venom gland morphology of some Australian dolichoderine and myrmicine ants (Hymenoptera, Formicidae). *Belgian Journal of Zoology*, 123, 159–163.
- Billen, J., Morgan, E.D., Drijfhout, F. & Farmier, K. (2009) Unusual structural and chemical characteristics of the Dufour gland in the ant *Meranoplus diversus*. *Physiological Entomology*, 34, 93–97.
<http://dx.doi.org/10.1111/j.1365-3032.2008.00659.x>
- Bolton, B. (1981) A revision of the ant genera *Meranoplus* F. Smith, *Dicroaspis* Emery and *Calyptomymex* Emery (Hymenoptera: Formicidae) in the Ethiopian zoogeographical region. *Bulletin of the British Museum of Natural History*, 42, 43–81.
- Bolton, B. (2003) Synopsis and Classification of Formicidae. *Memoirs of the American Entomological Institute*, 71, 1–370.
- Bolton, B. (2012) *An online catalog of the ants of the world*. Available from: <http://antcat.org/> (15 August 2012).
- Brady, S.G., Schultz, T.R., Fisher, B.L. & Ward, P.S. (2006) Evaluating alternative hypotheses for the early evolution and diversification of ants. *Proceedings of the National Academy of Sciences*, 103, 18172–18177.
<http://dx.doi.org/10.1073/pnas.0605858103>
- Brady, S.G. & Ward, P.S. (2005) Morphological phylogeny of army ants and other dorylomorphs (Hymenoptera: Formicidae). *Systematic Entomology*, 30, 593–618.
<http://dx.doi.org/10.1111/j.1365-3113.2005.00290.x>
- Boudinot, B.E. (in press) The male genitalia of ants: musculature, homology, and functional morphology (Hymenoptera, Aculeata, Formicidae). *Journal of Hymenoptera Research*, 30, 29–49.
<http://dx.doi.org/10.3897/jhr.30.3535>
- Donisthorpe, H. (1942) Ants from the Colombo Museum Expedition to Southern India, September–October 1938. *Annals and Magazine of Natural History*, 9, 449–461.
<http://dx.doi.org/10.1080/03745481.1942.9755496>
- Donisthorpe, H. (1949) A fifth installment of the Ross collection of ants from New Guinea. *Annals and Magazine of Natural History*, 12, 487–506.
<http://dx.doi.org/10.1080/00222934808653927>
- Dornhaus, A. & Powell, S. (2010) Foraging and defense strategies. In: Lach, L., Parr, C.L. & Abbot, K.L. (Eds.), *Ant Ecology*. Oxford University Press, Oxford, pp. 402.
- Emery, C. (1895) Voyage de M. E. Simon dans l'Afrique australe (Janvier–Avril 1893). 3e mémoire. Formicides. *Annales de la Société Entomologique de France*, 64, 15–56.
- Engel, M.S. (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bulletin of the American Museum of Natural History*, 259, 1–192.
[http://dx.doi.org/10.1206/0003-0090\(2001\)259%3C0001:AMOTBA%3E2.0.CO;2](http://dx.doi.org/10.1206/0003-0090(2001)259%3C0001:AMOTBA%3E2.0.CO;2)
- Fisher, B.L. (2003) Ants (Formicidae: Hymenoptera). In: S.M. Goodman & J.P. Benstead (Eds). *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 811–819.
- Fisher, B.L. (2005) A model for a global inventory of ants: a case study in Madagascar. *Proceedings of the California Academy of Sciences*, 56, 86–97.
- Fisher, B.L. (2010) Biogeography. In: Lach, L., Parr, C.L. & Abbot, K.L. (Eds), *Ant Ecology*. Oxford University Press, Oxford, pp. 402.
- Forel, A. (1891) Les Formicides. [part]. In: Grandidier, A. (Ed) *Histoire physique, naturelle, et politique de Madagascar. Volume XX. Histoire naturelle des Hyménoptères. Deuxième partie (28e fascicule)*. Hachette et Cie, Paris, pp. 1–280.
- Forel, A. (1910) Glanures myrmécologiques. *Annales de la Société Entomologique de Belgique*, 54, 6–32.

- Forel, A. (1915) Results of Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. 2. Ameisen. *Arkiv för Zoologi*, 9, 1–119.
- Goodman, S.M. and Benstead, J.P. (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39, 73–77.
<http://dx.doi.org/10.1017/S0030605305000128>
- Gotwald, W.H. (1969) Comparative morphological studies of the ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). *Cornell University Agricultural Experiment Station Memoir*, 408, 1–150.
- Gross, C.L., Whalen, M.A. & Andrew, M.H. (1991) Seed selection and removal by ants in a tropical savanna woodland in northern Australia. *Journal of Tropical Ecology*, 7, 99–122.
<http://dx.doi.org/10.1017/S0266467400005150>
- Harris, R.A. (1979) A glossary of surface sculpturing. *California Department of Food and Agriculture, Bureau of Entomology*, 28, 1–31.
- Hita Garcia, F. & Fisher, B.L. (2012) The ant genus *Tetramorium* Mayr (Hymenoptera: Formicidae) in the Malagasy region—taxonomy of the *T. bessonii*, *T. bonibony*, *T. dysalum*, *T. marginatum*, *T. tsingy*, and *T. weitzckeri* species groups. *Zootaxa*, 3365, 1–123.
- Hölldobler, B. (1988) Chemical communication in *Meranoplus* (Hymenoptera: Formicidae). *Psyche*, 95, 139–151.
<http://dx.doi.org/10.1155/1988/74829>
- Kaspari, M., Longino, J., Pickering, J. & Windsor, D. (2001) The phenology of a Neotropical ant assemblage – evidence for continuous and overlapping reproduction. *Behavioral Ecology and Sociobiology*, 50, 382–390.
<http://dx.doi.org/10.1007/s002650100378>
- Keller, R. (2011) A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the Poneromorph subfamilies. *Bulletin of the American Museum of Natural History*, 335, 1–90.
<http://dx.doi.org/10.1206/355.1>
- Kugler, C. (1979) Evolution of the sting apparatus in the myrmicine ants. *Evolution*, 33, 117–130.
<http://dx.doi.org/10.2307/2407370>
- LaPolla, J.S. (2004) *Acropyga* (Hymenoptera: Formicidae) of the world. *Contributions of the American Entomological Institute*, 33, 1–130.
- Longino, J.T. (2003) The *Crematogaster* (Hymenoptera, Formicidae, Myrmicinae) of Costa Rica. *Zootaxa*, 151, 1–150.
- Maschwitz, U., Fiala, B. & Dolling, W.R. (1987) New trophobiotic symbioses of ants with South East Asian bugs. *Journal of Natural History*, 21, 1097–1107.
<http://dx.doi.org/10.1080/00222938700770681>
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B. & Pierce, N. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science*, 312, 101–104.
<http://dx.doi.org/10.1126/science.1124891>
- Robertson and Villet (1989) Mating behavior in three species of myrmicine ants (Hymenoptera; Formicidae). *Journal of Natural History*, 23, 767–773.
<http://dx.doi.org/10.1080/00222938900770401>
- Schödl, S. (1998) Taxonomic revision of Oriental *Meranoplus* F. Smith, 1853 (Insecta: Hymenoptera: Formicidae: Myrmicinae). *Annalen des Naturhistorischen Museums in Wien*, 100, 361–394.
- Schödl, S. (1999) Description of *Meranoplus birmanus* sp. nov. from Myanmar, and the first record of *M. bicolor* from Laos (Hymenoptera: Formicidae). *Entomological Problems*, 30, 61–65.
- Schödl, S. (2004) On the taxonomy of *Meranoplus puryi* Forel, 1902 and *Meranoplus puryi curvispina* Forel, 1910 (Insecta: Hymenoptera: Formicidae). *Annalen des Naturhistorischen Museums in Wien*, 105, 349–360.
- Schödl, S. (2007) Revision of Australian *Meranoplus*: the *Meranoplus diversus* group. In: Snelling, R., Fisher, B. & Ward, P. (Eds), *Advances in Ant Systematics: Homage to E.O. Wilson*. The American Entomological Institute, Gainesville, Florida, pp. 370–424.
- Smith, F. (1876) Descriptions of new species of Cryptoceridae, belonging to the genera *Cryptocerus*, *Meranoplus*, and *Catalaucus*. *Transactions of the Royal Entomological Society of London*, 24, 603–612.
<http://dx.doi.org/10.1111/j.1365-2311.1876.tb01932.x>
- Song, H. & Bucheli, S.R. (2010) Comparison of phylogenetic signal between male genitalia and non-genital characters in insect systematics. *Cladistics*, 26, 23–35.
<http://dx.doi.org/10.1111/j.1096-0031.2009.00273.x>
- Taylor, R.W. (1990) The nomenclature and distribution of some Australian and New Caledonian ants of the genus *Meranoplus* Fr. Smith (Hymenoptera: Formicidae: Myrmicinae). *General and Applied Entomology*, 22, 31–40.
- Taylor, R.W. (2006) Ants of the genus *Meranoplus* F. Smith, 1853 (Hymenoptera: Formicidae): three new species and others from northeastern Australian rainforests. *Myrmecologische Nachrichten*, 8, 21–29.
- Wheeler, W.M. (1915) The ants of the Baltic amber. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg*, 55, 1–142.
- Wheeler, W.M. (1935) Check list of the ants of Oceania. *Bernice P. Bishop Museum Occasional Papers*, 11, 2–56.
- Wilson, E.O. (1955) A monographic revision of the ant genus *Lasius*. *Bulletin of the Museum of Comparative Zoology*, 113, 1–201.
<http://dx.doi.org/10.1086/401086>
- Yoshimura, M. & Fisher, B.L. (2009) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): Key to genera of the subfamily Proceratiinae. *Zootaxa*, 22, 1–21.
- Yoshimura, M. & Fisher, B.L. (2011) A revision of male ants of the Malagasy region (Hymenoptera: Formicidae): key to genera of the subfamily Dolichoderinae. *Zootaxa*, 2794, 1–34.
- Yoshimura, M. & Fisher, B.L. (2012a) A revision of male ants of the Malagasy Amblyoponinae (Hymenoptera: Formicidae) with resurrections of the genera *Stigmatomma* and *Xymmer*. *PLoS ONE*, 7.
<http://dx.doi.org/10.1371/journal.pone.0033325>
- Yoshimura, M. & Fisher, B.L. (2012) A revision of the Malagasy endemic genus *Adetomyrma* (Hymenoptera: Formicidae: Amblyoponinae). *Zootaxa*, 3341, 1–31.