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## Monograph

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# Taxonomy of the *Crematogaster degeeri*-species-assemblage in the Malagasy region (Hymenoptera: Formicidae)

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**Abstract.** We revise the species-level taxonomy of the *Crematogaster* (*Crematogaster*) *degeeri*-species-assemblage, a group of related ants occurring in Madagascar and the wider Malagasy region, and further provide an identification key to all species-groups of the genus *Crematogaster* in this region. Within the *C. degeeri*-assemblage, we recognize twelve species based upon morphological data from worker, queen and male ants, as well as genetic data from the barcode region of cytochrome oxidase I. Seven new species are described: *Crematogaster alafara* Blaimer sp. nov., *C. bara* Blaimer sp. nov., *C. mafybe* Blaimer sp. nov., *C. maina* Blaimer sp. nov., *C. malahelo* Blaimer sp. nov., *C. masokely* Blaimer sp. nov., *C. ramamy* Blaimer sp. nov. *Crematogaster tricolor* Gerstäcker, 1859 (stat. rev.) and *C. dentata* Dalla Torre, 1893 (stat. nov.) are raised to species level, and the following new synonymies are proposed: *Crematogaster degeeri lunaris* Santschi, 1928 as a synonym of *C. degeeri* Forel, 1886; *Crematogaster sewelli improba* Forel, 1907 and *C. sewelli mauritiana* Forel, 1907 as synonyms of *C. dentata* Dalla Torre, 1893, and *C. pacifica* Santschi, 1919 as a synonym of *C. lobata* Emery, 1895. Species descriptions, images, and distribution maps and identification keys based on worker ants, as well as on queen ants where available, are presented for all twelve species. In addition, we present a molecular gene tree for cytochrome oxidase I and summarize levels of sequence divergence within and between species of the *C. degeeri*-species-assemblage. Our findings are discussed in the light of previous work on Malagasy *Crematogaster* ants.

**Keywords.** *Crematogaster*, Malagasy region, ants, species-groups, barcoding.

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## Introduction

*Crematogaster* Lund, 1831 ants are a species-rich clade commonly known as “acrobat ants”. This group currently includes more than 460 existing nominal species names (Blaimer 2012d; Bolton 2012) and is distributed worldwide. High intraspecific morphological variation renders the species-level taxonomy of acrobat ants challenging (Blaimer 2010, 2012a, Blaimer & Fisher 2013). The situation

is further complicated by many synonyms and intraspecific names (Brown 1973). On the one hand, many widespread species are clearly in need of taxonomic revision (Longino 2003; Ward 2007, 2010), while on the other hand, a large portion of the more locally endemic species remain to be discovered or described in this genus (e.g. Blaimer 2010, 2012c; Hosoiishi & Ogata 2009, 2012; Longino 2003, Blaimer & Fisher 2013). Nomenclatural problems make identification of the Afrotropical *Crematogaster* fauna particularly unmanageable, and much of the diversity of these ants in this region probably has not yet been revealed.

Within the Afrotropics, Madagascar has become a flagship for progress in ant taxonomy (e.g. Hita-Garcia & Fisher 2011, 2012; LaPolla *et al.* 2010; Yoshimura & Fisher 2012), since recent comprehensive inventories have created a solid basis for revisionary work (Fisher 2003, 2005, 2008). Based on the large quantity of specimens and data collected in these surveys, the *Crematogaster* of Madagascar have been undergoing revision in a series of taxonomic treatments (Blaimer 2010; Blaimer 2012a, 2012c, Blaimer & Fisher 2013). Moreover, the evolution of these ants has recently been investigated via molecular phylogenetics. The findings reveal that Madagascar was colonized by *Crematogaster* most likely from Africa in at least eight to nine (Blaimer 2012b, 2012c) independent dispersal events. These events gave rise to six species-groups and assemblages and three phylogenetically more isolated species: the *Crematogaster* (*Crematogaster*) *hova*-group (7 species), the *C.* (*Crematogaster*) *ranavalonae*-group (3 species), the *C.* (*Crematogaster*) *kelleri*-group (6 species), the *C.* (*Orthocrema*) *madecassa*-group (2 species), the *C.* (*Orthocrema*) *volamena*-group (2 species), the *C.* (*Crematogaster*) *degeeri* species-assemblage (12 species, including the more distantly related *C. tricolor* Gerstäcker, 1859 stat. rev.), *C. rasoherinae* Forel, 1891 and *C. tsisitsilo* Blaimer, 2013. Together, these comprise 34 described and yet undescribed species of *Crematogaster* in Madagascar.

The present study focuses on the *C. degeeri*-species-assemblage, a group that we choose here to call an “assemblage” rather than a species-group since no morphological characters that unite these ants have been discovered to date. This group was referred to in Blaimer (2012b) as the “*Crematogaster degeeri-sewellii* group”; after subsequent broadening by Blaimer (2012d) to include a few African species, it was hence dubbed the “*C. castanea*-group”. This grouping likely does not form a clade, but rather represents a group of loosely related species that may have closer affinities with African species (but see phylogeny in Blaimer 2012b). We choose here to revert to a description of the Malagasy species in this group only, since our taxonomic insight into the related African species is not yet sufficient. Most species in the *C. degeeri*-assemblage occur in Madagascar only, but three species are also found in the wider Malagasy region, including the Indian Ocean Islands of Comoros, Mayotte and Mauritius. The group is not present in the Seychelles.

The natural history and ecology of species within this group do not follow a common theme but are highly diverse. The *C. degeeri*-assemblage includes arboreal species nesting in dead twigs or branches, as well as ground-dwelling species found in nests under stones or in the soil. Ground-nesting is rather atypical for *Crematogaster* ants, which often dominate the canopy. All major macrohabitats are occupied by one or the other representative of the *C. degeeri*-assemblage in Madagascar: dry and spiny forests, littoral forest, rainforest, montane forest, savannah and grasslands, as well as coastal and mangrove habitat. A few species further appear to adapt quite well to urban or disturbed areas.

In the following, we present a comprehensive taxonomic revision of the *C. degeeri*-species-assemblage, depending both upon morphological and on mitochondrial genetic data. In summary and addendum to prior work, we further provide an identification key to all of the aforementioned species-groups and species of *Crematogaster* in Madagascar, and hereby conclude the series of taxonomic work on this genus in Madagascar.

## Material and methods

### Morphological study

Morphological observations were made on worker ants, as well as queen and male ants where available, with a Leica MZ9.5, MZ12.5 and MZ Apo stereomicroscope. Standard measurements (in mm) were taken at 16-50 $\times$  with a Leica MZ Apo stereomicroscope and a dual-axis Acu-Rite Quikcount micrometer wired to a digital readout. Measurements are given to the second decimal place, indices are presented as decimal fractions (also to the second decimal) and ranges express minimum – maximum values. Measured specimens were chosen to represent the entire respective species distribution range and morphological variation. The abbreviations used for measurements and indices are explained below; illustrations can be found in Blaimer (2010; 2012a, 2012c).

- CI = Cephalic index: HW/HL.  
 EL = Eye length; measured along the maximum diameter.  
 HL = Head length; perpendicular distance from line tangent to rearmost points of vertex margin to line tangent to anterior most projections of clypeus, in full face view.  
 HW = Maximum head width including eyes, in full face view.  
 LBI = Leg-body index: WL/LHT.  
 LHT = Length of metatibia, excluding the proximomedial condyle.  
 OI = Ocular index: EL/HL.  
 PPL = Postpetiole length; measured in dorsal view at an angle that maximizes length.  
 PPI = Postpetiole width index: PPW/PPL.  
 PPW = Postpetiole width; measured in same view as and perpendicular to postpetiole length.  
 PTH = Petiole height; measured in lateral profile as vertical distance from ventral margin to highest point of dorsoposterior margin.  
 PTHI = Petiole height index: PTH/PTL.  
 PTL = Petiole length; measured in lateral profile as the distance from dorsoposterior margin of segment to anterior inflection point where petiole curves up to condyle.  
 PTW = Petiole width; maximum width of petiole in dorsal view.  
 PTWI = Petiole width index: PTW/PTL.  
 SI = Scape index: SL/HW.  
 SL = Scape length; length of scape shaft from apex to basal flange, not including basal condyle and neck. If scape is strongly arched, this measurement is taken as the chord length from the basal flange to the apex.  
 SPI = Propodeal spine index: SPL/WL.  
 SPL = Propodeal spine length; measured from tip of propodeal spine to closest point on outer rim of propodeal spiracle, maximizing spine length in lateral view.  
 WL = Weber's length; measured in lateral profile of mesosoma, distance from approximate inflection point, where downward sloping pronotum curves into anteriorly projecting neck, to posteroventral propodeal lobes.

Queen and male specific measurements:

- MSNI = Mesonotal index: MSNW/MSNL.  
 MSNL = Mesonotal length; maximum length of mesonotum, measured in dorsal view.  
 MSNW = Mesonotal width; maximum width of mesonotum, measured in dorsal view.

Color images were created with a JVC KY-F75U digital camera, a Leica MZ16A stereomicroscope, Syncrosopy Auto-Montage (v5.0) and ZERENE STACKER (v1.04) software. All ant images presented here are also publicly available on AntWeb ([www.antweb.org](http://www.antweb.org)). All distribution maps presented here

were plotted with the packages “maps” and “mapdata” within the software R (R Development Core Team 2008), based on collection coordinates (latitude and longitude) of all material examined. Due to the extent of material examined we decided to provide a full list of collection data for all species in the supplementary material only (see Supplementary Material 1). For material lacking primary collection information, i.e. syntype specimens and older material, the following sources were used to georeference collection sites: the GEOnet Names Server (National Geospatial-Intelligence Agency) and the Gazetteer to Malagasy Botanical Collecting Localities (Schatz & Lescot 2012). Classification of major geographic regions in Madagascar throughout species descriptions follows Gautier & Goodman (2003).

### **Nomenclatural Acts**

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999), and hence the new names contained herein are available under that Code. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication is: [urn:lsid:zoobank.org:pub:D20CE35E-08CF-41EE-9700-ABDEA6F4413E](http://urn:lsid:zoobank.org:pub:D20CE35E-08CF-41EE-9700-ABDEA6F4413E). The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repository: LOCKSS.

The International Commission on Zoological Nomenclature requires lectotypes designated after 1999 to “contain an express statement of deliberate designation” (amended Article 74.7.3). We use the statement “lectotype by present designation” to fulfill this requirement. Lectotypes have been designated where a name lacks a holotype or lectotype and unambiguous syntypes have been identified. The purpose is to provide stability of nomenclature, and designation is done in a revisionary context in agreement with the amended Recommendation 74G of Article 74.7.3.

### **Specimens were examined and/or deposited in the following collections:**

- BBBC = B.B. Blaimer Coll., National Museum of Natural History, Washington, DC, USA
- CASC = California Academy of Sciences, San Francisco, CA, USA
- MCZC = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA
- MHNG = Muséum d’Histoire Naturelle, Genève, Switzerland
- MSNG = Museo Civico di Storia Naturale, Genova, Italy
- NHMB = Naturhistorisches Museum, Basel, Switzerland
- PSWC = P.S. Ward Collection, University of California, Davis, CA, USA
- SAMC = South African Museum, Cape Town, South Africa
- ZMHB = Museum für Naturkunde der Humboldt Universität, Berlin, Germany

### **Molecular data collection and analyses**

For mitochondrial genetic analysis DNA was extracted destructively from the legs of worker ants at the Biodiversity Institute of Ontario, University of Guelph under the Barcode of Life Initiative, using extraction protocols as outlined in Smith & Fisher (2009). One to 33 specimens for the twelve species treated here were used for extractions. In general, the number of specimens per species submitted to the Barcode of Life Initiative was much larger, but success rates were poor overall due to the advanced age of specimens. Sequence data were collected for cytochrome oxidase I (COI, 592 bp used for inference) at the Biodiversity Institute of Ontario, with amplification and sequencing protocols as detailed in Smith & Fisher (2009). Three Malagasy *Crematogaster* species from different species-groups were chosen as outgroups, *C. madecassa* Emery, 1895, *C. ranavalonae* Forel, 1887 and the *C. hova*-complex. These range from moderately to distantly related to the focal group (Blaimer 2012b). For the geographic distribution of the sampled taxa refer to Supplementary Material 2.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assembly**Table 1.** GenBank accession numbers and voucher specimens.

<i>Crematogaster</i>	voucher specimen	accession	<i>Crematogaster</i>	voucher specimen	accession	<i>Crematogaster</i>	voucher specimen	accession
<i>alafara</i>	CASENT0492838	HM418787	<i>maina</i>	CASENT0107367	HM418731	<i>sewellii</i>	CASENT0206185	KC501961
<i>bara</i>	CASENT0208888	KC501979	<i>maina</i>	CASENT0107707	DQ176072	<i>sewellii</i>	CASENT0209236	KC501962
<i>bara</i>	CASENT0209137	KC501980	<i>maina</i>	CASENT0120361	KC501988	<i>sewellii</i>	CASENT0209261	KC501957
<i>bara</i>	CASENT0491170	HM418784	<i>maina</i>	CASENT0138039	HQ925455	<i>sewellii</i>	CASENT0210000	KC501958
<i>degeeri</i>	CASENT0071423	KC501978	<i>maina</i>	CASENT0146407	GU710979	<i>sewellii</i>	CASENT0496779	HM418789
<i>degeeri</i>	CASENT0107466	HM880704	<i>maina</i>	CASENT0146414	GU710978	<i>tricolor</i>	CASENT0076476	HM418730
<i>degeeri</i>	CASENT0120677	HM418734	<i>maina</i>	CASENT0155973	JN283111	<i>tricolor</i>	CASENT0114405	KC501972
<i>degeeri</i>	CASENT0122383	HM418745	<i>maina</i>	CASENT0156620	JN283133	<i>tricolor</i>	CASENT0120922	HM418736
<i>degeeri</i>	CASENT0125324	HM418750	<i>maina</i>	CASENT0156888	JN283148	<i>tricolor</i>	CASENT0120949	HM418737
<i>degeeri</i>	CASENT0128356	HM418752	<i>maina</i>	CASENT0193387	HQ547858	<i>tricolor</i>	CASENT0121060	HM418738
<i>degeeri</i>	CASENT0128363	HM418745	<i>maina</i>	CASENT0193388	HQ547859	<i>tricolor</i>	CASENT0122066	HM418742
<i>degeeri</i>	CASENT0218965	HQ925353	<i>maina</i>	CASENT0193398	HQ547860	<i>tricolor</i>	CASENT0122269	KC501973
<i>dentata</i>	CASENT0003915	HM418715	<i>maina</i>	CASENT0193399	HQ547861	<i>tricolor</i>	CASENT0122274	HM418743
<i>dentata</i>	CASENT0059574	EF609793	<i>maina</i>	CASENT0204443	KC501975	<i>tricolor</i>	CASENT0123050	HM418748
<i>dentata</i>	CASENT0059579	EF609796	<i>maina</i>	CASENT0204445	KC501976	<i>tricolor</i>	CASENT0132240	KC501981
<i>dentata</i>	CASENT0059761	EF609804	<i>maina</i>	CASENT0209210	KC501977	<i>tricolor</i>	CASENT0132258	KC501984
<i>dentata</i>	CASENT0059870	EF609811	<i>maina</i>	CASENT0209221	KC501974	<i>tricolor</i>	CASENT0132767	KC501987
<i>dentata</i>	CASENT0059871	EF609814	<i>maina</i>	CASENT0436047	HM418775	<i>tricolor</i>	CASENT0132771	KC501985
<i>dentata</i>	CASENT0070942	KC501964	<i>maina</i>	CASENT0484986	HM418778	<i>tricolor</i>	CASENT0134116	HM418756
<i>dentata</i>	CASENT0071738	KC501967	<i>maina</i>	CASENT0485307	HM418780	<i>tricolor</i>	CASENT0134341	GU709621
<i>dentata</i>	CASENT0107098	KC501965	<i>maina</i>	CASENT0490152	HM418782	<i>tricolor</i>	CASENT0134342	GU709620
<i>dentata</i>	CASENT0120373	HM418733	<i>maina</i>	CASENT0496596	HM418788	<i>tricolor</i>	CASENT0134346	GU709623
<i>dentata</i>	CASENT0137569	HQ925454	<i>malahelo</i>	CASENT0125705	HM879914	<i>tricolor</i>	CASENT0134362	GU709624
<i>dentata</i>	CASENT0138306	HQ925456	<i>malahelo</i>	CASENT0141211	HQ925457	<i>tricolor</i>	CASENT0134838	KC501982
<i>dentata</i>	CASENT0208601	KC501970	<i>malahelo</i>	CASENT0141212	HQ925458	<i>tricolor</i>	CASENT0134950	KC501986
<i>dentata</i>	CASENT0208678	KC501966	<i>masokely</i>	CASENT0004906	GU710477	<i>tricolor</i>	CASENT0134964	KC501983
<i>dentata</i>	CASENT0209207	KC501968	<i>masokely</i>	CASENT0068954	HM879913	<i>tricolor</i>	CASENT0136333	HM418757
<i>dentata</i>	CASENT0209223	KC501969	<i>ramamy</i>	CASENT0021958	HM418720	<i>tricolor</i>	CASENT0136515	GU709628
<i>dentata</i>	CASENT0484998	HM418779	<i>ramamy</i>	CASENT0049627	HM418725	<i>tricolor</i>	CASENT0136639	GU709629
<i>dentata</i>	CASENT0490355	HM418783	<i>ramamy</i>	CASENT0137653	HM418763	<i>tricolor</i>	CASENT0136684	GU709630
<i>lobata</i>	CASENT0040949	HM418721	<i>ramamy</i>	CASENT0137876	HM418766	<i>tricolor</i>	CASENT0137360	GU709637
<i>lobata</i>	CASENT0041264	HM418722	<i>ramamy</i>	CASENT0147704	GU714795	<i>tricolor</i>	CASENT0137615	HM418759
<i>lobata</i>	CASENT0073517	HM418729	<i>ramamy</i>	CASENT0156746	JN283139	<i>tricolor</i>	CASENT0137623	HM418760
<i>lobata</i>	CASENT0156861	JN283145	<i>ramamy</i>	CASENT0157292	JN283185	<i>tricolor</i>	CASENT0137632	GU710479
<i>lobata</i>	CASENT0193036	HM418773	<i>sewellii</i>	CASENT0121076	HM418739	<i>tricolor</i>	CASENT0137650	HM418762
<i>lobata</i>	CASENT0484854	HM418777	<i>sewellii</i>	CASENT0121077	HM418740	<i>tricolor</i>	CASENT0137830	HM418764
<i>mafye</i>	CASENT0107856	HQ925451	<i>sewellii</i>	CASENT0125862	HM418751	<i>tricolor</i>	CASENT0138272	HM418768
<i>mafye</i>	CASENT0122362	HM418744	<i>sewellii</i>	CASENT0128361	HM418753	<i>tricolor</i>	CASENT0191124	HM418771
<i>mafye</i>	CASENT0193017	HQ925460	<i>sewellii</i>	CASENT0128802	HM418755	<i>tricolor</i>	CASENT0209220	KC501971
<i>mafye</i>	CASENT0409618	HQ925462	<i>sewellii</i>	CASENT0203837	KC501963	<i>hova-complex</i>	CASENT0193380	HQ547857
<i>maina</i>	CASENT0003222	HM418714	<i>sewellii</i>	CASENT0204541	KC501959	<i>madecassa</i>	CASENT0068164	KC501955
<i>maina</i>	CASENT0052467	HM418726	<i>sewellii</i>	CASENT0206148	KC501960	<i>ranavalonae</i>	CASENT0193531	HQ547877

**Table 2.** Data partitions and selected substitution models. Data subsets used in phylogenetic analyses and their characteristics. VC = variable characters; PIC = parsimony informative characters; [ ] = ingroup only. The partitioning scheme and the respective substitution models were chosen under the AIC with the software PartitionFinder (Lanfear *et al.* 2012).

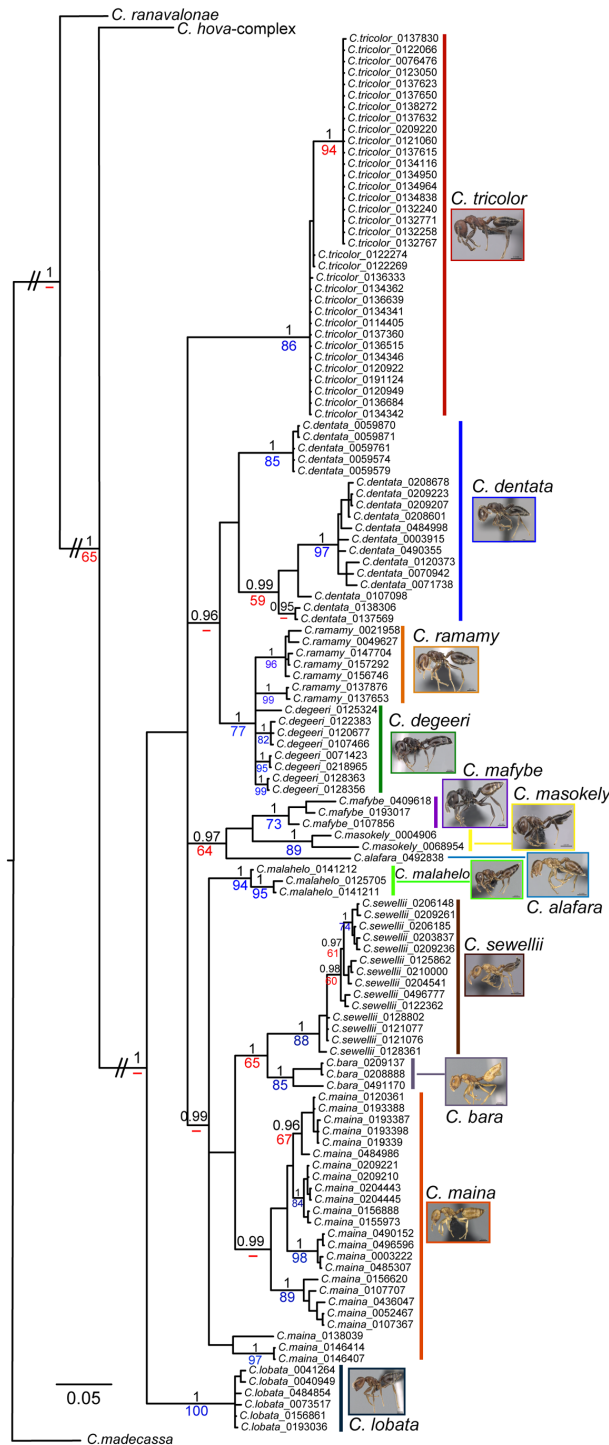
Data partition	No. bases	No. VC	No. PIC	Substitution model
COI positions 1+2	395	14 [3]	44 [38]	HKY+I+G
COI positions 3	197	17 [10]	171 [163]	GTR+G
<b>Total</b>	<b>592</b>	<b>31 [13]</b>	<b>215 [201]</b>	

All newly generated sequences have been deposited in GenBank, and accession numbers are listed in Table 1; the data matrix and trees used to create Figs 1 and 2 have further been deposited in TreeBase under the accession <http://purl.org/phylo/treebase/phylows/study/TB2:S14163>. Sequence data were aligned with MUSCLE (Edgar 2004), accessed through the CIPRES science gateway (Miller *et al.* 2010). The dataset was subdivided into three data subsets according to codon positions. We then used PartitionFinder (Lanfear *et al.* 2012) to simultaneously choose the best-scoring partition scheme and to select best-fitting models of nucleotide sequence evolution for each data subset (under the AIC, Akaike Information Criterion). The selected models for the chosen partition scheme can be found in Table 2.

Phylogenetic analyses were performed within a Bayesian framework using MRBAYES v3.2 (Ronquist *et al.* 2012), accessed through the CIPRES science gateway (Miller *et al.* 2010), and within a maximum likelihood framework using GARLI v2.0 (Zwickl 2006), accessed through the GARLI Web Service (<http://molecularevolution.org>). Bayesian analyses each employed two runs of Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) consisting of four chains (temp = 0.05) and sampling every 1000 generations. The model parameters transition-transversion ratio, gamma shape, proportion of invariable sites, rate matrix and state frequencies were unlinked across partitions. A dirichlet rate prior (1,5) was used and the branch length prior settings were modified (*unconstrained:exponential (100)*) to obtain realistic values for rate multipliers and tree length. In MrBayes output files, we confirmed that the ASDSF (Average Standard Deviation of Split Frequencies) had reached values well below 0.01 and PSRF (Potential Scale Reduction Factor) values had approached 1.0 for all parameters. In TRACER v1.5 (Rambaut & Drummond 2007), convergence was confirmed visually and mixing of chains was evaluated with effective sample size (ESS) values. To assess whether tree topologies were sampled in proportion to their true posterior distribution, we further used the compare, slide and cumulative plotting functions on the AWTY-online server (Nylander *et al.* 2008). All the above indicators returned good values after MCMCMC-sampling for 10 million generations; consensus trees were summarized in MrBayes after discarding 25 % of samples as burnin. A maximum likelihood bootstrap search with 100 replicates was performed in GARLI, with the resulting trees summarized as a majority-rule consensus tree. All trees were rooted with the outgroup method using a more distantly related taxon, *Crematogaster madecassa* (see Blaimer 2012b). We used FigTree 1.3.1 (Rambaut 2006-2009) for tree visualization and then exported these into AdobeIllustrator CS5 to create our figures as displayed here.

Mean, minimum and maximum sequence divergences of COI within and between species were calculated under the Tamura-Nei model (Tamura & Nei 1993) with the software MEGA5 (Tamura *et al.* 2011).

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**Fig. 1.** Mitochondrial phylogeny of species in the *Crematogaster degeeri*-assemblage. Results of Bayesian inference based on 592 bp of COI, summarized as a consensus tree in MrBayes. Support values in black represent posterior probabilities (pp), those in blue ML (Maximum Likelihood) bootstrap values > 70, and those in red ML bootstrap values < 70. Values pp < 0.96 are not shown; nodes not present in the ML analysis are represented by a dash instead of a bootstrap value. The scale bar shows nucleotide changes per base pair. Long branches subtending the outgroup taxa *C. madecassa* Emery, 1895, *C. ranavalonae* Forel, 1887 and *C. hova-complex* have been shortened. Appended numbers on taxon labels represent CASENT#’s of respective voucher specimens.

## Results

### Molecular taxonomy

In this study, we used 592 bp of the barcoding region of cytochrome oxidase I to corroborate our hypotheses on species boundaries in the *C. degeeri*-species-assemblage formed from morphological observations. We present the results of this molecular analysis 1) in the form of a phylogenetic tree (Fig. 1), and 2) as a distance matrix of sequence divergences within and between species (Table 3). We further illustrate the relationships of populations between Madagascar and the wider Malagasy region where applicable (Fig. 2). The phylogenies shown here are results from Bayesian inference, with bootstrap values from maximum likelihood analyses mapped on the relevant nodes. These trees represent a single mitochondrial gene tree and should not be mistaken as species-level phylogenies depicting relationships between these ants.

Except for four cases (*C. dentata* Dalla Torre, 1893 stat. nov., *C. maina* sp. nov., *C. degeeri* Forel, 1886, *C. ramamy* sp. nov.), we found good evidence for our putative species, and phylogenetic support values ranged from posterior probabilities (pp) = 1 and bootstraps between 73-100 (Fig. 1). Excluding the unsupported species, mean within-species sequence divergence was <6.1 %, and mean between-species sequence divergence ranged between 7.9-22.2 %.

Our analysis recovered *Crematogaster degeeri* and *C. ramamy* sp. nov. as not reciprocally monophyletic, but forming a grade (Fig. 1). Mean sequence divergence between the two species was 4.7 % (Table 3), and thus lower than the maximum within-species divergence in *C. ramamy* sp. nov. (6.6 %). However, our morphological and ecological observations here outweigh these results and we did not alter our decision to separate these into two distinct species.

In the case of *Crematogaster maina* sp. nov. we found weak support that sequenced individuals of this species from Madagascar form a genetic clade, which did, however, not cluster with the Comoros population (Fig. 1 and Fig. 2A). The two individuals sequenced from the Comoros cluster (albeit without much support) along with an individual from a small island off the northern Madagascar coast, Nosy Faly (Fig. 2A), show 9.8-13.3 % sequence divergence with the Madagascar mainland population (Table 3; only maximum value shown). We could not find correlated morphological differences between these two genetic clusters, and were reluctant to distinguish separate species on the basis of only two to three mitochondrial sequences that could potentially be compromised in quality (see discussion). Our new species *Crematogaster maina* sp. nov. as described below thus includes both the Madagascar and Comoros populations.

A similar case is seen in *C. dentata* stat. nov. Virtually no support is recovered for a cluster of sequences that includes both individuals from Madagascar and Mauritius (Fig. 2B), and the sequence divergence between the two clusters was found to be 8.8-11.2 %. We again choose to include the Mauritius population in the species definition of *C. dentata* stat. nov. and discuss this decision below in the context of species descriptions and the general discussion.

However, a very different picture is seen in *Crematogaster tricolor* stat. rev., the other species in the *C. degeeri*-assemblage distributed beyond Madagascar in the wider Malagasy region (Fig. 2C). Here we find an astonishingly level of low genetic divergence within the species as a whole (Table 3; mean 1.8 %, max. 3.9%). Furthermore, an interesting genetic structure emerges from the sequence data: one cluster contains individuals from northern and western Madagascar and all individuals sampled from Mayotte (Fig. 2C). This cluster diverges from a grade of sequences containing all individuals sampled from Comoros and from eastern Madagascar. These results suggest interesting phylogeographic relationships in *C. tricolor* stat. rev., and may be evidence of multiple recent dispersal events between Madagascar and the Indian Ocean Islands.



BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assembly**Table 3.** Summary of Tamura-Nei distance matrix. Divergences of cytochrome oxidase I sequences, as estimated under the Tamura-Nei Model (Tamura & Nei 1993) within the software MEGA5 (Tamura *et al.* 2011). Bold font emphasizes highest levels of divergence within and between species.

	Within species			Between species (mean)											
	mean	min.	max.	<i>C. alafara</i>	<i>C. bara</i>	<i>C. degeeri</i>	<i>C. dentata</i>	<i>C. lobata</i>	<i>C. mafybe</i>	<i>C. maina</i>	<i>C. malahelo</i>	<i>C. masokely</i>	<i>C. ramamy</i>	<i>C. sewellii</i>	<i>C. tricolor</i>
<i>C. alafara</i>	n/a	n/a	n/a	\											
<i>C. bara</i>	0.028	0.000	0.042	0.184	\										
<i>C. degeeri</i>	0.030	0.000	0.048	0.177	0.132	\									
<i>C. dentata</i>	0.066	0.000	0.112	0.200	0.160	0.135	\								
<i>C. lobata</i>	0.009	0.002	0.015	0.193	0.143	0.155	0.191	\							
<i>C. mafybe</i>	0.043	0.031	0.061	0.157	0.139	0.165	0.160	0.185	\						
<i>C. maina</i>	0.062	0.000	<b>0.133</b>	0.184	0.113	0.165	0.176	0.172	0.169	\					
<i>C. malahelo</i>	0.019	0.007	0.028	0.196	0.109	0.146	0.158	0.157	0.148	0.115	\				
<i>C. masokely</i>	0.059	n/a	n/a	0.165	0.139	0.167	0.189	0.183	0.128	0.178	0.163	\			
<i>C. ramamy</i>	0.033	0.002	0.066	0.178	0.140	<b>0.047</b>	0.127	0.162	0.163	0.178	0.156	0.165	\		
<i>C. sewellii</i>	0.018	0.000	0.037	<b>0.222</b>	0.079	0.140	0.147	0.172	0.156	0.130	0.129	0.175	0.159	\	
<i>C. tricolor</i>	0.018	0.000	0.039	0.215	0.180	0.166	0.213	0.199	0.202	<b>0.222</b>	0.184	0.218	0.187	0.206	\
outgroup: <i>C. hova</i> -complex				0.324	0.279	0.289	0.275	0.267	0.285	0.288	0.275	0.266	0.289	0.281	0.326

**Checklist of species treated in this revision**

Based on both molecular and morphological taxonomic observations we therefore recognize twelve species in the *C. degeeri*-assembly, including seven new species. Proposed synonymies are based on comparison of type specimens with morphological data.

*Crematogaster alafara* Blaimer sp. nov.

*Crematogaster bara* Blaimer sp. nov.

*Crematogaster degeeri* Forel, 1886

= *Crematogaster degeeri* var. *lunaris* Santschi, 1928 syn. nov.

*Crematogaster dentata* Dalla Torre, 1893 stat. nov.

= *Crematogaster sewellii* var. *improba* Forel, 1907 syn. nov.

= *Crematogaster sewellii* subsp. *mauritiana* Forel, 1907 syn. nov.

*Crematogaster lobata* Emery, 1895

= *Crematogaster pacifica* Santschi, 1919 syn. nov.

*Crematogaster mafybe* Blaimer sp. nov.

*Crematogaster maina* Blaimer sp. nov.

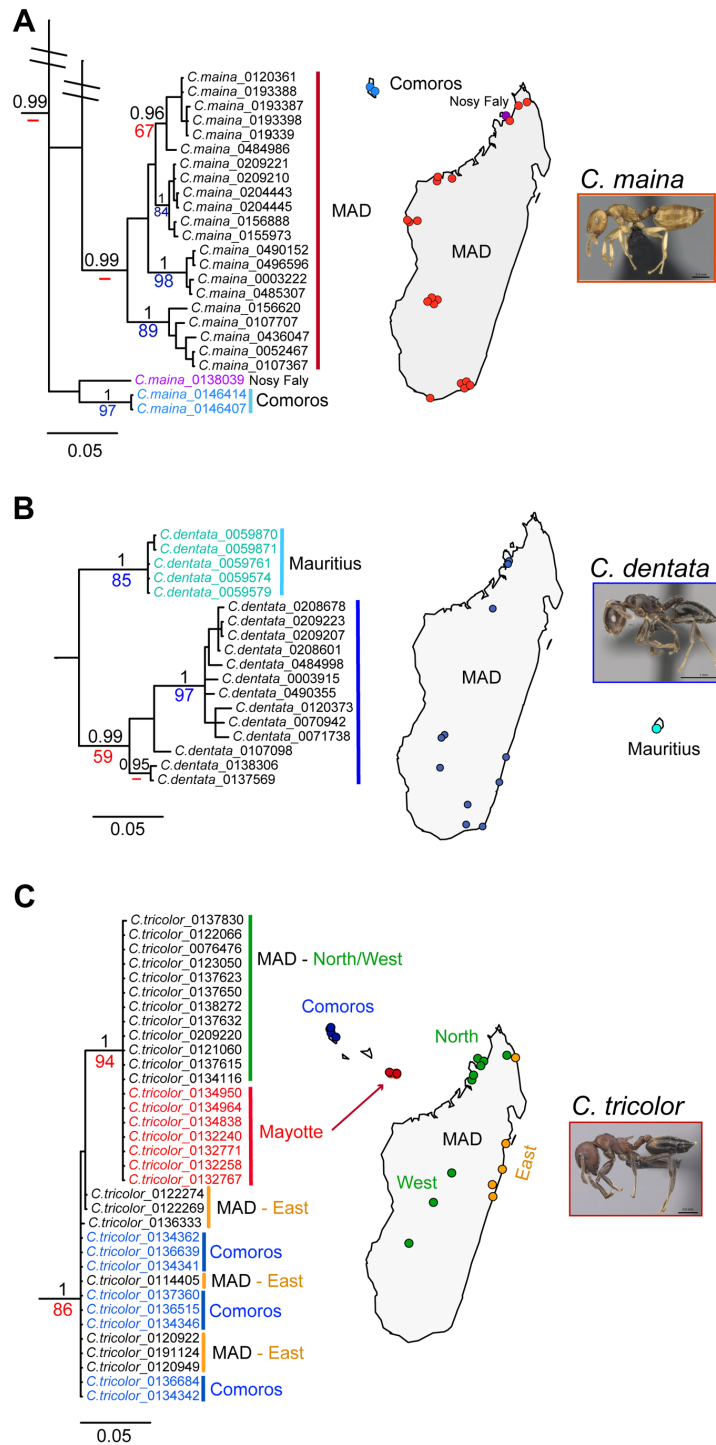
*Crematogaster malahelo* Blaimer sp. nov.

*Crematogaster masokely* Blaimer sp. nov.

*Crematogaster ramamy* Blaimer sp. nov.

*Crematogaster sewellii* Forel, 1891

*Crematogaster tricolor* Gerstäcker, 1859 stat. rev.



**Fig. 2.** Relatedness of populations between Madagascar and the wider Malagasy region. Subsets of the same phylogeny as shown in Fig. 1, with broad geographical origin of sequenced individuals mapped onto the tree for: **A.** *Crematogaster maina* sp. nov. **B.** *Crematogaster dentata* stat. nov. **C.** *Crematogaster tricolor* stat. rev. Support values in black represent posterior probabilities (pp), those in blue ML bootstrap values > 70 and those in red ML bootstrap values < 70. Values pp < 0.96 are not shown; nodes not present in the ML analysis are represented by a dash instead of a bootstrap value. The scale bar shows nucleotide changes per base pair. Distance between Madagascar and Islands is not drawn to scale. Appended numbers on taxon labels represent CASENT#'s of respective voucher specimens.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assembly**Key to subgenera and species-groups of *Crematogaster* in the Malagasy region**

1. Antennae with 11 segments (including scape).....2
  - Antennae with 10 segments (including scape).....
    - ..... ***Crematogaster hova*-group** (former subgenus *Decacrema* Forel, 1910; refer to Blaimer 2010)
2. Petiole ovo-rectangular (Fig. 3A), or rectangular (Fig. 3B), with postero-lateral denticles bearing long erect setae; antennae with a 2-segmented club (Fig. 3E).....
  - ..... subgenus ***Orthocrema*** Santschi, 1918 (refer to Blaimer 2012b)
  - Petiole of different shape, but never rectangular or ovo-rectangular (as e.g. in Fig. 3C, D); antennae with a 3-segmented club (as e.g. in Fig. 18A), or antennal club indistinct (as in Fig. 3F)..... 3
3. Median portion of clypeus with a flange (cf) projecting somewhat over mandibles (Fig. 3G); promesonotal suture (pms) present and mesonotum (m) in dorsal view longer than pronotum (p) (Fig. 3H); head round (Fig. 3F); eyes situated distinctly above midline of head in full-face view (Fig. 3F).....
  - ..... ***Crematogaster ranavalonae*-group** (former subgenus *Oxygyne* Forel, 1901; refer to Blaimer 2012a)
  - Median portion of clypeus not protruding as a flange over mandibles (Fig. 4A); promesonotal suture often absent (e.g. as in Figs 7C; 12D; 15C; 18D), if present then mesonotum in dorsal view shorter than pronotum; head shape variable, rounded or quadrate (as e.g. in Figs 6A; 7A; 10A, D; 12A; 13A); position of eyes variable, situated at or above midline of head in full-face view ..... 4
4. Propodeal spines entirely absent (SPI 0.00), at most obtuse tubercles present (as e.g. in Figs 4B; 12C; 13B).....5
  - Propodeal spines present (SPI > 0.01), from minute dents to distinct spines (as e.g. in Figs 6B; 7B; 8B; 10E; 15B; 17C; 18C; 19C; 20B; 22B)..... 6
5. Mesonotum (m) greatly raised with respect to pronotum and propodeum (Fig. 4B); eyes larger (OI > 0.21); medium to small size (HW 0.66-1.03, WL 0.62-0.98); color orange or brown.....
  - ..... ***C. tsitsitilo*** Blaimer, 2013 (refer to Blaimer & Fisher 2013)
  - Promesonotum not much raised with respect to propodeum (as e.g. in Figs 12C, 13B); eyes small (OI < 0.21) (as e.g. Figs 12A, 13A); medium to very large size (HW 0.80-1.43, WL 0.86-1.48); color brown or black ..... ***C. degeeri*-species-assembly** (refer to species key in this study)
6. In lateral view promesonotum forming a straight (or at most slightly rounded) plane (Fig. 4D); posterior face of mesonotum (pfm) long, distinctly set off from dorsal face (Fig. 4C), abruptly and steeply sloping into metanotal groove (Fig. 4D); propodeal spines always spiniform, very short to medium-sized (SPI 0.07-0.24), situated high on propodeum (pd) (Fig. 4D)..... ***C. kelleri*-group** (refer to Blaimer & Fisher 2013)
  - Promesonotum variable, but never fitting above description; propodeal spines variable, minute denticles to distinct spines (SPI 0.01-0.26), usually situated lower on propodeum (as in Figs 6B; 7B; 8B; 10B, E; 15B; 17C; 18C; 19C) ..... ***C. degeeri*-species-assembly** (refer to species key in this study)

**Key to the workers of the *C. degeeri*-species-assembly in the Malagasy region**

1. Propodeal spines absent, reduced to small tubercles or denticles (as in Figs 10E; 12C; 13B; 18C; 20B), or short triangular spines (as in Fig. 17C) with SPI < 0.07; if very rarely propodeal spines spiniform and longer (SPI 0.08-0.10) (as in Fig. 6B), then small species (HW 0.72-0.88, WL 0.79-0.91), color dirty-yellow, montane rainforest habitats..... 2
  - Propodeal spines longer, distinctly spiniform (as in Figs 7B; 8B; 10B; 15B; 22B) and SPI > 0.07; size and color variable; all habitats..... 9
2. Eyes small (OI < 0.21) and largely confluent with lateral head margin (as in Fig. 12A; 13A; 18A).... 3
  - Eyes larger (OI > 0.20) and distinctly protruding from lateral head margin (as in Figs 6A; 17A; 20A).....6

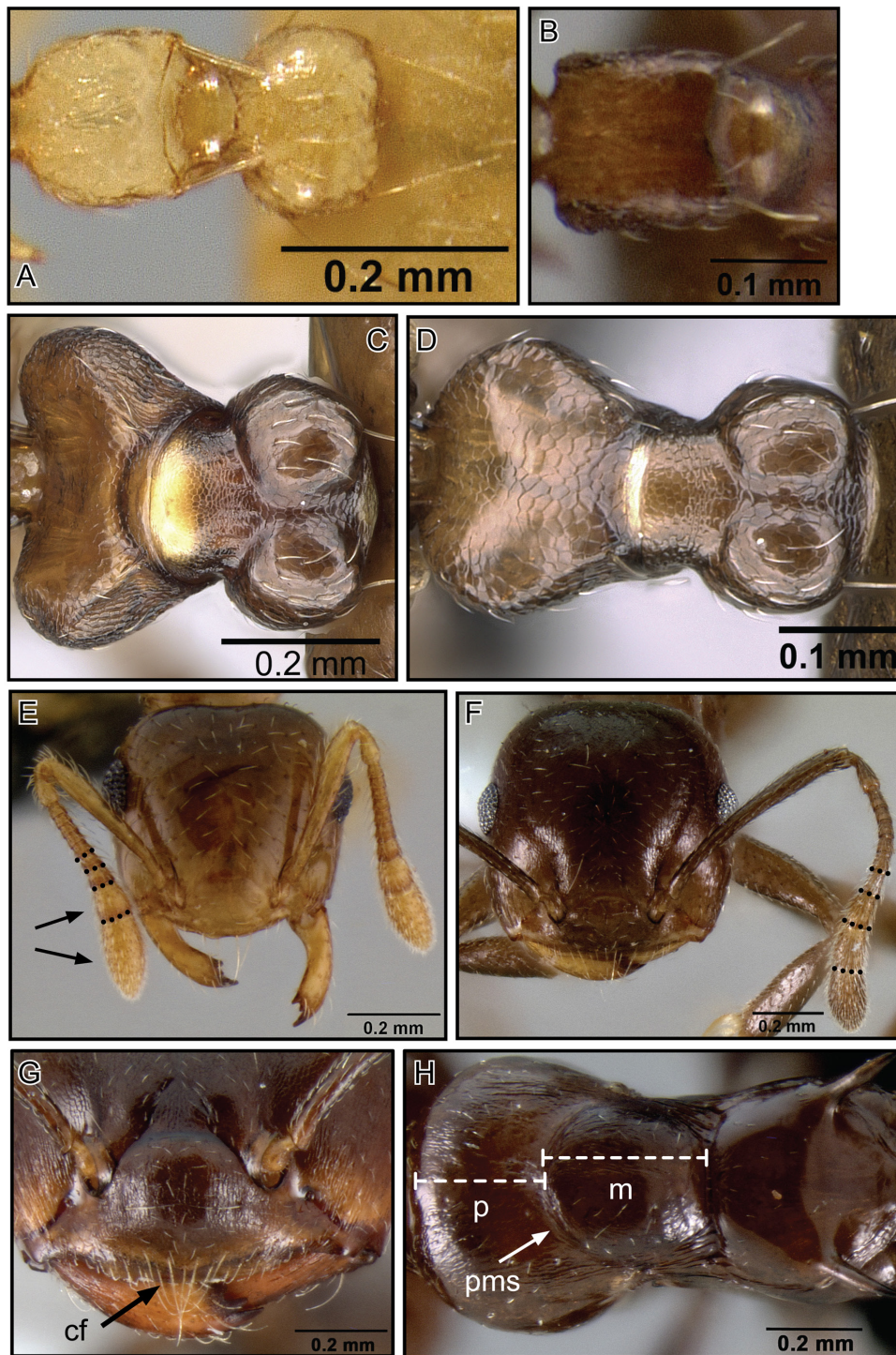
3. Pronotum dorsally with a distinct median longitudinal groove (Fig. 4E), medium to large species (HW 0.98-1.43, WL 0.98-1.48) ..... *C. mafybe* sp. nov.  
 – Pronotum dorsally without median longitudinal groove (as e.g. Figs 4F; 18D), size variable ..... 4
4. Propodeum with spines absent or at most small tubercles (SPI 0.00) ..... *C. lobata* Emery, 1895  
 – Propodeum with short triangular spines or sharp minute denticles ..... 5
5. Antennal scapes very short (SI 0.67-0.75), not reaching head margin (as in Fig. 18A); mesonotum usually with posterolateral denticles (as in Fig. 18C) ..... *C. masokely* sp. nov.  
 – Antennal scapes variable, but usually longer (SI 0.69-0.82) and about reaching head margin (as in Fig. 10A, D); mesonotum usually without posterolateral denticles (as in Fig. 10B, E) .....  
 ..... *C. dentata* Dalla Torre, 1893 stat. nov. [part]
6. Eyes very large (OI 0.24-0.29), situated above midline of head in full-face view (as in Fig. 20A); antennal scapes mostly longer (SI 0.77-0.87), reaching or surpassing head margin; bicolored: head and thorax yellowish to dark orange, metasoma with A4-7 brown or black (as in Fig. 20B, C) ..... *C. sewellii* Forel, 1891  
 – Eyes mostly smaller (OI 0.20-0.26), usually situated at midline of head in full-face view (as e.g. Figs 6A; 10A, D; 17A); antennal scapes variable, but often shorter (SI 0.69-0.83), just about or not reaching head margin (as e.g. Figs 6A; 10A, D; 17A); color variable ..... 7
7. Propodeum usually distinctly set off from promesonotum in lateral view (Figs 6B; 17C) and often with posterolateral denticles; promesonotum with sparse erect pilosity (<8 setae); petiole often much wider than long (PTWI 1.18-1.52), and strongly flared (as in e.g. Fig. 3C) ..... 8  
 – Propodeum not distinctly set off from promesonotum (in lateral view) (Fig. 10B, E), never with distinct posterolateral denticles; promesonotum usually with abundant erect pilosity (>8 setae); petiole not much wider than long (PTWI 0.95-1.31), moderately flared (Fig. 3D) .....  
 ..... *C. dentata* Dalla Torre, 1893 stat. nov. [part]
8. Medium-sized species (HW 0.86-1.03, WL 0.92-1.08); propodeal spines short and triangular (SPI 0.03-0.07); pronotum with sharp lateral margins (Fig. 5A) ..... *C. malahelo* sp. nov.  
 – Small species (HW 0.72-0.88, WL 0.79-0.91); propodeal spines longer (SPI 0.06-0.10); pronotum lacking sharp lateral margins (Fig. 5B) ..... *C. alafara* sp. nov.
9. Body color dirty to bright yellow (as in Fig. 7B, 15B) ..... 10  
 – Predominant color either orange (as in Fig. 20B), brown (e.g. as in Fig. 19C) or black (e.g. as in Fig. 8B) ..... 11
10. Medium to large species (HW 0.87-1.03, WL 0.98-1.22); antennal scapes very long (SI 0.91-1.01), easily surpassing head margin (as in Fig. 7A) ..... *C. bara* sp. nov.  
 – Small species (HW 0.60-0.86, WL 0.66-0.93); antennal scapes short (SI 0.71-0.83), not or about reaching head margin (as in Fig. 15A) ..... *C. maina* sp. nov.
11. Head distinctly broader than long (CI 1.10-1.19) (as in Fig. 22A); propodeal spines longer (SPI 0.10-0.26); tricolored: orange-red, yellow and black (as in Fig. 22C) *C. tricolor* Gerstäcker, 1859 stat. rev.  
 – Head not much broader than long (CI 1.01-1.13); propodeal spines shorter (SPI < 0.16); (as e.g. Figs 8A; 10A, D; 19A); uniformly colored or bicolored ..... 12
12. Mesonotum often with posterolateral denticles (Fig. 5C); in lateral view distinctly set off from propodeum (Fig. 5C); eyes large (OI 0.22-0.26); propodeal spines longer (SPI 0.10-0.16); erect pilosity on promesonotum often sparse (<8 long erect setae) (as e.g. Figs 5C; 8B) ..... *C. degeeri* Forel, 1886

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

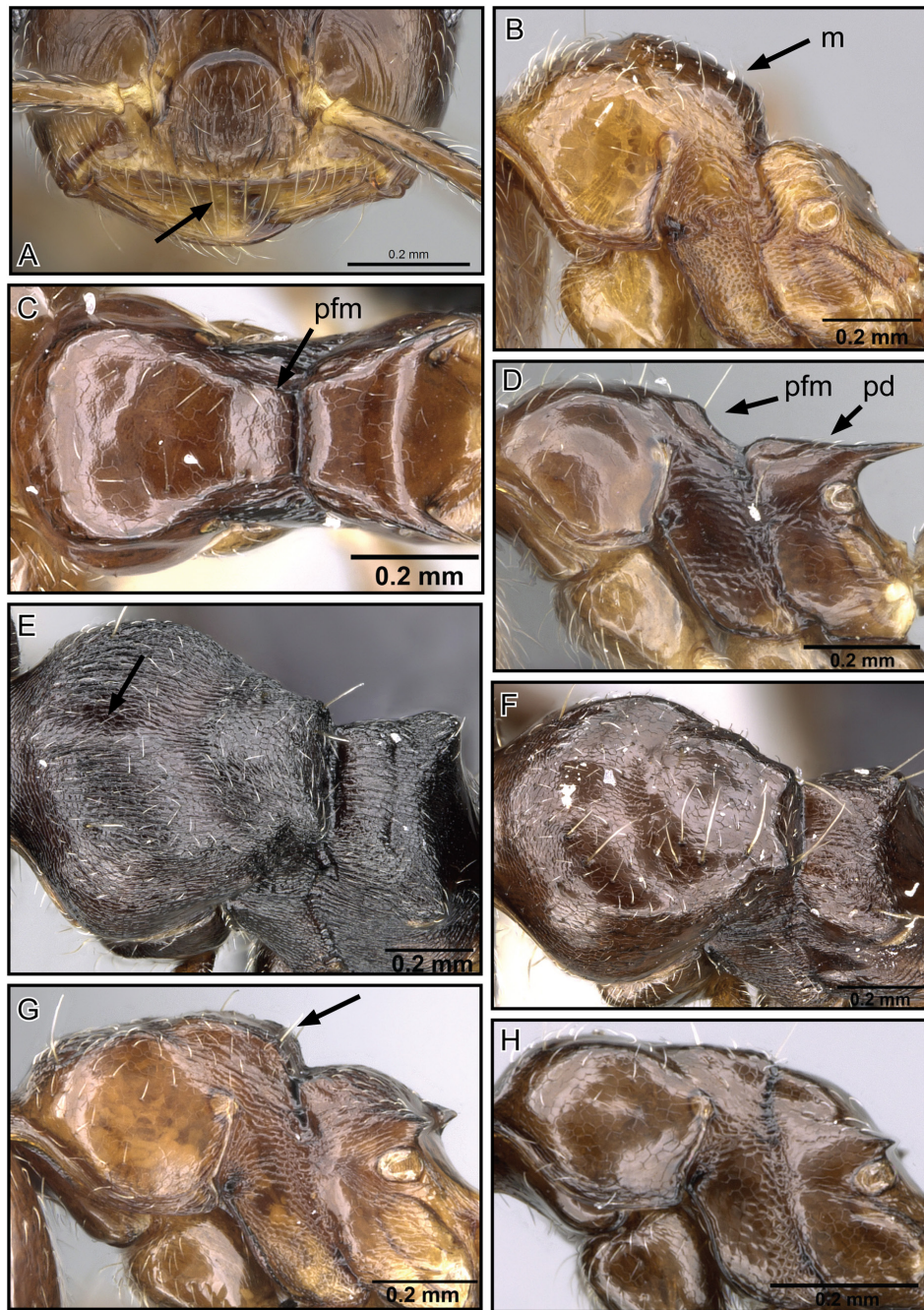
- Mesonotum variable, but more often without posterolateral denticles, and thus in lateral view not as distinctly set off from promesonotum (Fig. 5D); erect pilosity usually more abundant ( $> 8$  long erect setae) (as in Fig. 5D, E); propodeal spines shorter (SPI  $< 0.12$ ) ..... 13
- 13. Propodeum with a distinct short dorsal face, and with a transverse impression (Fig. 5E); sculpture on pronotum carinate or reticulate (Fig. 5E); petiole oval, fairly slender; (PTWI 0.95-1.14); propodeal spines longer (SPI 0.07-0.12) ..... *C. ramamy* sp. nov.
- Propodeum usually without a distinct dorsal face, never with transverse impression (Fig. 5F); sculpture on propodeum rugulose or aciculate (Fig. 5F); petiole variable, but often wider (PTWI 0.95-1.31); propodeal spines usually shorter (SPI 0.01-0.10) ..... *C. dentata* Dalla Torre, 1893 stat. nov. [part]

**Key to the queens of the *C. degeeri*-species-assemblage in the Malagasy region**

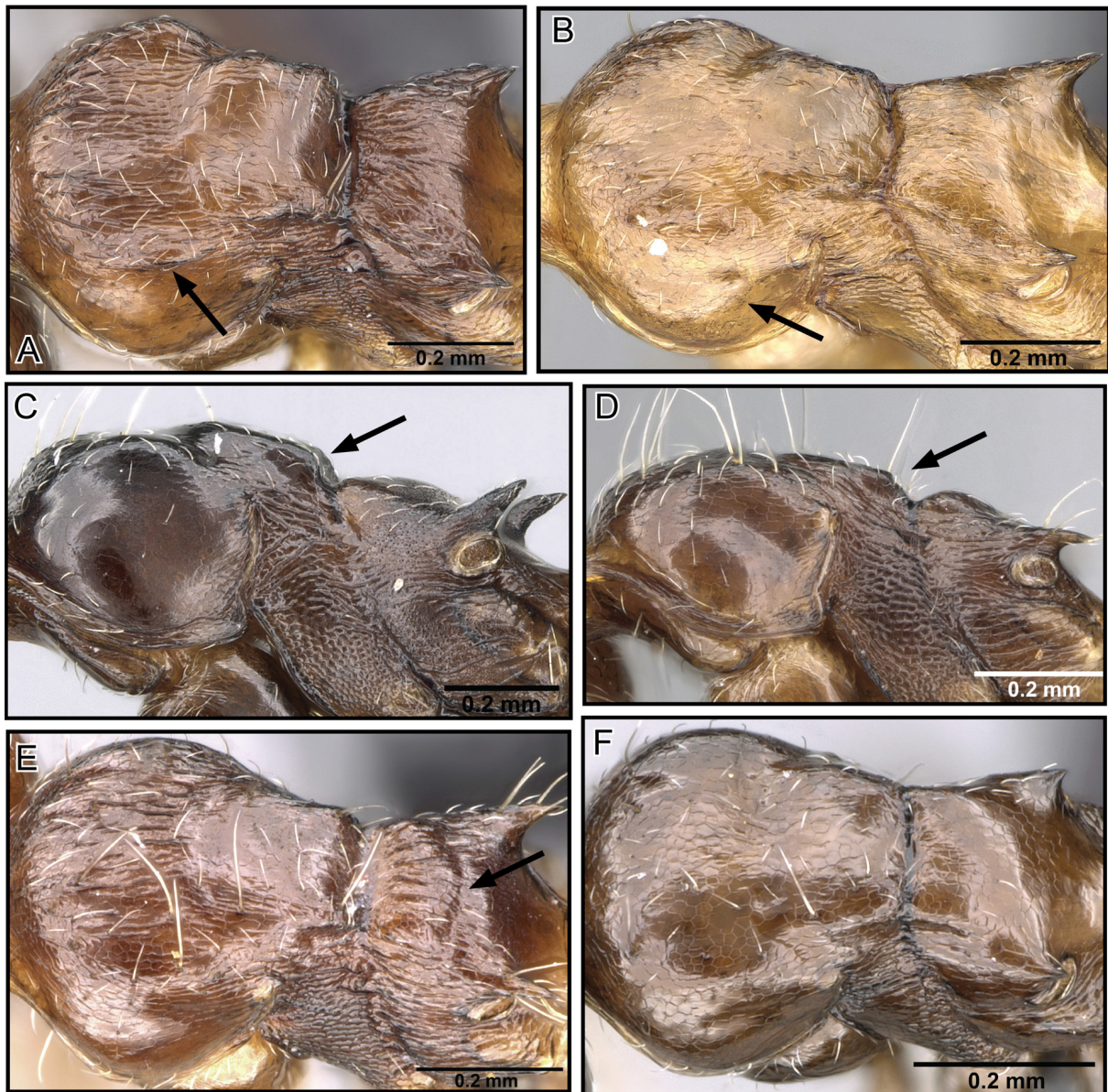
1. Small queens (HW  $< 1.30$ , WL  $< 2.20$ ) ..... 2
  - Large queens (HW  $> 1.30$ , WL  $> 2.20$ ) ..... 5
2. Head shape variable, but usually elongate, appearing longer than wide (CI 0.94-1.03) (as in Figs 6F; 11A; 16A); eyes smaller (OI  $< 0.32$ ), situated below midline of head in full-face view (as in Figs 6F; 11A; 16A); antennal scapes shorter, often not surpassing level of lateral ocelli (SI  $< 0.67$ )..... 3
  - Head shape square, appearing as wide as long (CI 1.06); eyes larger (OI  $> 0.33$ ), situated at midline of head in full-face view (as in Fig. 20D); antennal scapes longer, surpassing level of lateral ocelli (SI  $> 0.68$ ) (as in Fig. 20D); ..... *C. sewellii* Forel, 1891
3. Body color brown ..... 4
  - Body color yellow..... *C. maina* sp. nov.
4. Very small species (HW 1.01, WL 1.68); head sculpture finely reticulate; ocelli small and protruding very little from head surface (as in Fig. 6F) ..... *C. alafara* sp. nov.
  - Larger species (HW 1.13-1.41, WL 1.73-2.43); head sculpture aciculate-shiny; ocelli distinctly protruding from head surface (as in Fig. 11A) ..... *C. dentata* Dalla Torre, 1893 stat. nov. [part]
5. Antennal scapes long, surpassing lateral ocelli easily and almost reaching head margin (SI  $> 0.76$ ) (as in Fig. 7F); body color yellow ..... *C. bara* sp. nov.
  - Antennal scapes shorter (SI  $< 0.74$ ) (as in Figs 8D; 13D; 22D); body color other than yellow ..... 6
6. Eyes small (OI 0.23-0.26); antennal scapes very short (SI 0.57-0.59) (as in Fig. 13D); large queens (HW 1.70-2.18, WL 2.56-3.44); color black ..... *C. mafybe* sp. nov.
  - Eyes usually larger (OI 0.25-0.33) (as in Figs 8D; 22D); antennal scapes mostly longer (SI 0.57-0.74) (as in Figs 8D, 22D); usually smaller queens (HW 1.30-1.77, WL 2.20-2.69); color variable, usually not black ..... 7
7. Head distinctly wider than long (CI 1.14-1.21) (as in Fig. 22D); tricolored: reddish-orange, yellow and black (as worker in Fig. 22C); or at least abdominal segment 4 dorsally with a yellowish patch (as in Fig. 22F)..... *C. tricolor* Gerstäcker, 1859 stat. rev.
  - Head shape variable, but usually not much wider than long (CI  $< 1.10$ ) (as in Fig. 8D); uniformly colored ..... 8
8. Eyes situated at about midline of head in full-face view (as in Fig. 8D); antennal scapes longer (SI 0.68-0.72), surpassing level of lateral ocelli..... *C. degeeri* Forel, 1886
  - Eyes situated below midline of head in full-face view (as in Fig. 11A); antennal scapes shorter (SI 0.57-0.67), not surpassing level of lateral ocelli..... *C. dentata* Dalla Torre, 1893 [part]



**Fig. 3.** Key to subgenera & species-groups of Malagasy *Crematogaster* (part I). **A.** Petiole ovo-rectangular [*C. telolafy* Blaimer, 2012, CASENT0419808]. **B.** Petiole rectangular [*C. rasoherinae* Forel, 1891, CASENT0070841]. **C.** Petiole broadly flared [*C. malahelo* sp. nov., CASENT0317768]. **D.** Petiole oval [*C. dentata* sp. nov., CASENT0138289]. **E.** Antennal club two-segmented [*C. razana* Blaimer, 2012, CASENT0149655]. **F.** Antenna lacking distinct club [*C. ranavalonae* Forel, 1887, CASENT0423149]; **G.** Median portion of clypeus with flange (cf) [*C. ranavalonae*, CASENT0433703]. **H.** Promesonotal suture (pms) present, mesonotum (m) in dorsal view longer than pronotum (p) [*C. agnetis* Forel, 1892, CASENT0107473].

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

**Fig. 4.** Key to subgenera & species-groups of Malagasy *Crematogaster* (part II); key to the species of the *C. degeeri*-assemblage (part I). **A.** Median portion of clypeus lacking flange [*C. kelleri* Forel, 1891, CASENT0466090]. **B.** Propodeal spines absent; mesonotum (m) greatly raised with respect to pronotum and propodeum [*C. tsisisilo* Blaimer, 2013, CASENT0120279]. **C.** Posterior face of mesonotum (pfm) long; promesonotal suture absent [*C. kelleri*, CASENT0466090]. **D.** Promesonotum forming a straight plane, posterior face of mesonotum (pfm) abruptly sloping into metanotal groove, propodeal spines situated high on propodeum (pd) [*C. kelleri*, CASENT0466090]. **E.** Pronotum dorsally with distinct median longitudinal groove [*C. mafybe* sp. nov., CASENT0317762]. **F.** Pronotum dorsally without median longitudinal groove [*C. lobata* Emery, 1895, CASENT0125498]. **G.** Propodeum distinctly set off from promesonotum in lateral view [*C. malahelo* sp. nov., CASENT0317768]. **H.** Propodeum not distinctly set off from promesonotum in lateral view [*C. dentata* Dalla Torre, 1893 stat. nov., CASENT0138289].



**Fig. 5.** Key to the species of the *C. degeeri*-assemblage (part II). **A.** Pronotum with sharp lateral margins [*C. malahelo* sp. nov., CASENT0317768]. **B.** Pronotum lacking sharp lateral margin [*C. alafara* sp. nov., CASENT0492837]. **C.** Mesonotum with posterolateral denticles [*C. degeeri* Forel, 1886, CASENT0071423]. **D.** Mesonotum without distinct posterolateral denticles [*C. ramamy* sp. nov., CASENT0317764]. **E.** Propodeum with distinct short dorsal face and transverse impression, sculpture carinulate [*C. ramamy* sp. nov., CASENT0317764]. **F.** Propodeum lacking distinct dorsal face and transverse impression, sculpture rugulose [*C. dentata* Dalla Torre, 1893 stat. nov., CASENT0138289].



## Morphological taxonomy

Class Insecta Linnaeus, 1758  
Order Hymenoptera Linnaeus, 1758  
Suborder Apocrita Gerstäcker, 1867  
Superfamily Vespoidea Latreille, 1802  
Family Formicidae Latreille, 1809  
Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835  
Genus *Crematogaster* Lund, 1831

*Crematogaster alafara* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:957DBC9B-0B2D-4ABF-B179-E18F67603927](https://doi.org/10.21203/rs.3.rs-1000000)

Fig. 6

## Diagnosis

Workers of *Crematogaster alafara* sp. nov. are fairly small (HW 0.72-0.88, WL 0.79-0.91) and have short to medium-sized propodeal spines (SPI 0.06-0.10). The characteristic promesonotal characters, with the propodeum usually distinctly set off from the promesonotum in lateral view (as Fig. 6B), render this species moderately easy to recognize from other species in the *C. degeeri*-assembly. Possibly this species could be confused with *C. malahelo* sp. nov.; the latter, however, bears sharp lateral margins on the pronotum (absent in *C. alafara* sp. nov.) and has shorter, more triangular spines (SPI 0.03-0.07) than *C. alafara* sp. nov.. Mean genetic distance in the barcode region of *C. alafara* sp. nov. to other species within the *C. degeeri*-assembly is 15.7-22.2 % (Table 3).

## Etymology

The Malagasy word *alafara* means “last forest”, alluding to the restricted distribution of this species as a reminder of forest conservation concerns in Madagascar. This name is treated as a noun in apposition.

## Type specimens

### Holotype

Worker: pinned, CASENT0492837, BLF08619, ex rotten log [imaged on AntWeb]; original locality label: MADG'R: P.N. Ranomafana, Sahamaloatra, 6.6 km 310° NW Ranomafana, 31 Mar. 2003, 21°14.2'S, 47°23.8'E, 1150 m, Fisher *et al.*, BLF# (Brian L. Fisher); deposited at CASC.

### Paratypes

4 workers, pinned, #1 and #2 same collection and locality data as holotype. #1: CASENT0317785, deposited at SAMC. #2: CASENT0317786, deposited at MHNG. #3 and #4: BLF08628, ex dead twig above ground, remaining data same as holotype. #3: CASENT0317787, deposited at MCZC. #4: CASENT0317788, deposited at UCDC.

## Type locality

MADAGASCAR: Fianarantsoa: P.N. Ranomafana, Sahamaloatra River: -21.23667, 47.39667, 1150 m, montane rainforest.

## Other material examined

(CASC, PSWC): refer to Supplementary Material 1.

## Worker

### Measurements

(n = 12) [holotype] HW 0.72-0.88 [0.83]; HL 0.69-0.80 [0.78]; EL 0.15-0.19 [0.17]; SL 0.54-0.64 [0.61]; WL 0.79-0.91 [0.90]; SPL 0.05-0.08 [0.06]; PTH 0.17-0.20 [0.20]; PTL 0.22-0.26 [0.26]; PTW 0.29-0.35 [0.35]; PPL 0.13-0.18 [0.16]; PPW 0.23-0.28 [0.25]; LHT 0.56-0.67 [0.66]; CI 1.02-1.11 [1.06]; OI 0.20-0.25 [0.21]; SI 0.73-0.83 [0.77]; SPI 0.06-0.10 [0.07]; PTHI 0.71-0.81 [0.79]; PTWI 1.18-1.47 [1.36]; PPI 1.56-1.97 [1.59]; LBI 1.30-1.47 [1.38].

### Description

(Fig. 6A-C) Small size (HW 0.72-0.88, WL 0.79-0.91).

Masticatory margin of mandibles with four teeth; head shape quadrate, as long, or slightly longer than wide (CI 1.02-1.11); posterior margin of head in full-face view laterally rounded; occipital carinae distinct; antennal scapes reaching or slightly surpassing head margin; midline of eyes situated slightly above midline of head in full-face view; eyes moderately large (OI 0.20-0.25) and protruding.

Pronotum laterally angular; promesonotal suture indistinct, promesonotum forming one plane; mesonotum usually without posterior face; laterally mesonotum carinate, sometimes ending in small denticles, but not greatly set off from propodeum; metanotal groove shallow, laterally constricted and bordered by carinae; propodeal spines short, spiniform (SPI 0.06-0.10) and straight; dorsal face of propodeum distinct; posterior face of propodeum gently sloping; petiole in dorsal view greatly flared and convex, dorsolaterally rounded to carinate, without posterolateral tubercles or denticles; subpetiolar process usually a small, angular dent; postpetiole distinctly bilobed, with a narrow median impression; subpostpetiolar process absent.

Head sculpture aciculate to faintly reticulate; sculpture otherwise mostly reticulate; face usually with < six erect, longer setae, and regular appressed to decumbent pubescence; erect pilosity on promesonotum usually sparse, < six long setae; otherwise promesonotum dorsally with sparse appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short, erect setae posterolaterally, and sparse suberect, decumbent or appressed pubescence; abdominal tergites and sternites four to seven usually with moderately abundant, short, erect pilosity, and regular appressed to decumbent pubescence throughout. Color yellow-brown to brown.

## Queen

### Measurements

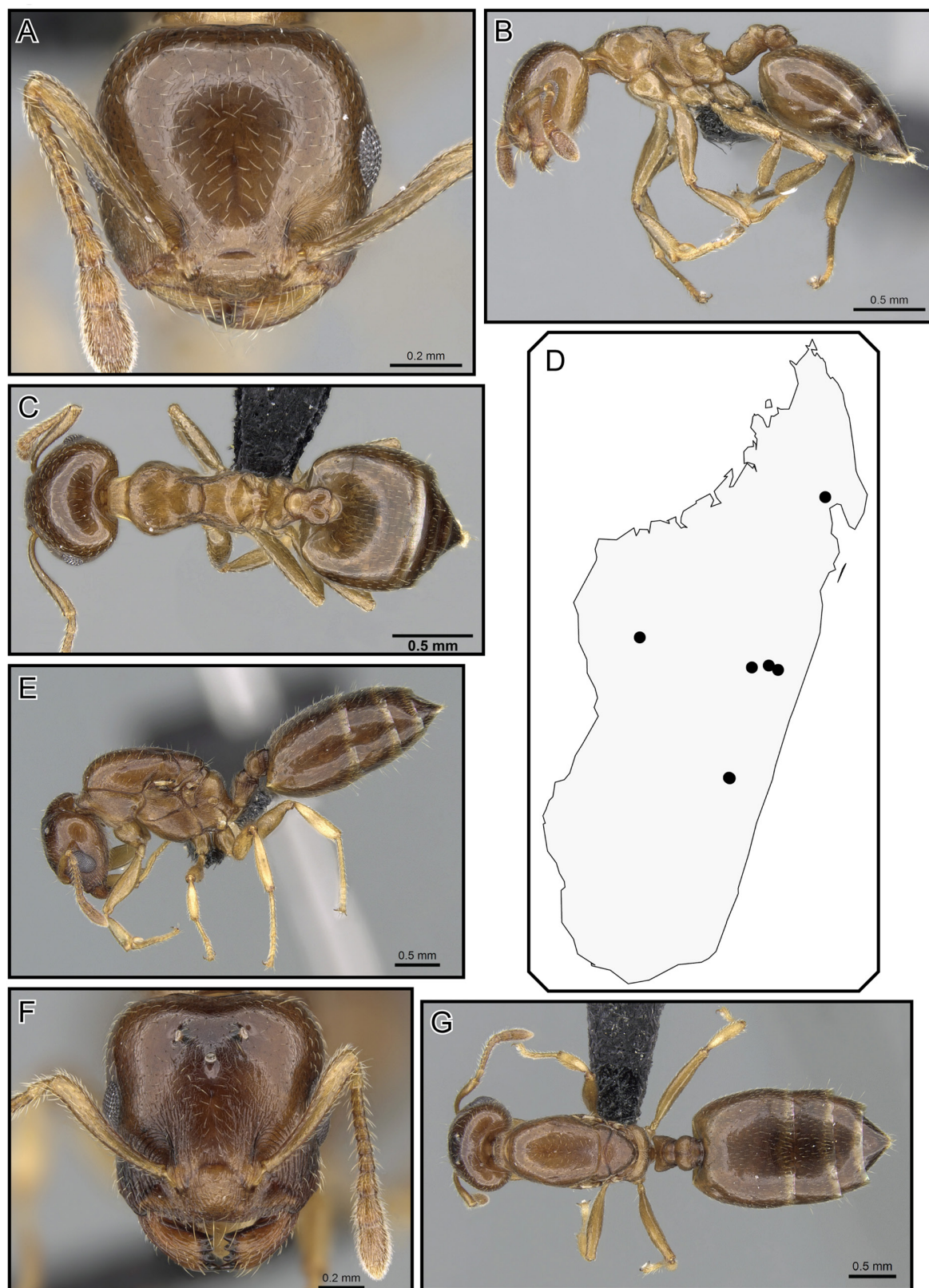
(n = 1) HW 1.01, HL 1.01, EL 0.33, SL 0.64, MSNW 0.76, MSNL 0.87, WL 1.68, SPL 0.00, PTH 0.29, PTL 0.33, PTW 0.39, PPL 0.23, PPW 0.39, LHT 0.75, CI 0.99, OI 0.32, SI 0.63, MSNI 0.87, SPI 0.00, PTHI 0.87, PTWI 1.18, PPI 1.68, LBI 2.24.

### Description

(Fig. 6E-G) Small queen (HW 1.01, WL 1.68). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth; antennal scapes reaching level of lateral ocelli; eyes large (OI 0.33), situated below midline of head in full-face view; head elongate-rectangular (CI 0.99), posterior margin straight.

Mesoscutum in dorsal view longer than wide (MSNI 0.87); dorsal face of propodeum short; propodeal tubercles or denticles absent; petiole moderately flared, postpetiole with complete impression; subpetiolar process present as minute tooth.



**Fig. 6.** *Crematogaster alafara* sp. nov., worker, queen and distribution. A-C. Worker (CASENT0492837). A. Full-face. B. Profile. C. Dorsal. D. Species distribution. E-G. Queen (CASENT0050441). E. Profile. F. Full-face. G. Dorsal.

Sculpture aciculate to reticulate throughout; face with six longer erect setae (but  $n = 1$ ) and regular short suberect to decumbent pubescence; mesonotum with regular short, erect to suberect pubescence, interspersed with abundant, longer, erect setae; petiole and postpetiole with fairly dense, short, suberect to decumbent pilosity, and postpetiole with additional longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant, short, erect pilosity and dense appressed to decumbent pubescence. Color yellowish brown.

### Male

Males of this species are unknown.

### Distribution and biology

MADAGASCAR. *Crematogaster alafara* sp. nov. has only been collected at a few rainforest localities in central, northern and western Madagascar (Fig. 6D) ranging from 600 m to 1350 m in elevation. The species is known to co-occur with *C. sewellii*, *C. dentata* stat. nov. and *C. mafybe* sp. nov.. The few collections have been made from dead twigs above ground at the lower elevation range, and from rotten logs at higher altitudes. Otherwise nothing is known of the biology of this species.

### *Crematogaster bara* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:CD497C84-8C12-4005-9817-5236FA0AC4C2](http://urn:lsid:zoobank.org:act:CD497C84-8C12-4005-9817-5236FA0AC4C2)

Fig. 7

### Diagnosis

*Crematogaster bara* sp. nov. is easily distinguished from all other species of the *C. degeeri*-assemblage by a combination of the following characters: yellow body color, medium to large size (HW 0.87-1.03, WL 0.98-1.22) and very long antennal scapes (SI 0.91-1.01). Mean barcode divergence between *C. bara* sp. nov. and the remaining species is 7.9-18.0% (Table 3).

### Etymology

*Crematogaster bara* sp. nov. is named after the Malagasy “Bara” tribe that inhabits the countryside within the distribution range of this species. The name is treated as noun in apposition.

### Type specimens

#### Holotype

Worker: pinned, CASENT0491123, BLF07783, under stone [imaged on AntWeb]; original locality label: MADG’R: Fianarantsoa: P.N. Isalo, Ambovo Springs, 29.3 km 4° N Ranohira 990 m, 22°19.9’S, 45°21.1’E, 14 Feb. 2003, Fisher *et al.*, BLF#; deposited at CASC.

#### Paratypes

4 workers, pinned, same collection and locality data as holotype. #1: CASENT0317776, deposited at SAMC. #2: CASENT0317777, deposited at MHNG. #3: CASENT0317778, deposited at MCZC. #4: CASENT0317779, deposited at UCDC.

### Type locality

MADAGASCAR: Fianarantsoa: P.N. Isalo, Ambovo Springs, 29.3 km 4° N Ranohira, -22.29833, 45.35167, 990 m, *Uapaca* woodland.

### Other material examined

(CASC): refer to Supplementary Material 1.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assembly**Worker****Measurements**

(n = 16) [holotype] HW 0.87-1.03 [0.96]; HL 0.78-0.95 [0.89]; EL 0.18-0.23 [0.20]; SL 0.77-0.87 [0.83]; WL 0.98-1.22 [1.07]; SPL 0.10-0.18 [0.12]; PTH 0.18-0.24 [0.20]; PTL 0.27-0.34 [0.30]; PTW 0.28-0.36 [0.31]; PPL 0.15-0.19 [0.16]; PPW 0.28-0.35 [0.29]; LHT 0.77-0.93 [0.82]; CI 1.04-1.14 [1.08]; OI 0.21-0.25 [0.22]; SI 0.91-1.01 [0.93]; SPI 0.09-0.17 [0.12]; PTHI 0.62-0.75 [0.68]; PTWI 0.97-1.17 [1.02]; PPI 1.65-2.00 [1.86]; LBI 1.20-1.32 [1.29].

**Description**

(Fig. 7A-C) Medium to large size (HW 0.87-1.03, WL 0.98-1.22).

Masticatory margin of mandibles with four teeth; head shape quadrate, or longer than wide (CI 1.04-1.14); posterior margin of head in full-face view laterally rounded or subangular; occipital carinae usually distinct; antennal scapes always easily surpassing head margin; midline of eyes situated at midline of head in full-face view; eyes moderately large (OI 0.21-0.25) and protruding.

Pronotum laterally subangular to rounded; promesonotal suture indistinct; promesonotum more or less forming one rounded plane, mesonotum usually with a short posterior face; laterally mesonotum angular, ending in minuscule posterolateral denticles that set off the promesonotum from propodeum; metanotal groove shallow, laterally constricted; propodeal spines short, spiniform (SPI 0.09-0.17); propodeal spiracles large, situated directly at base of spines; dorsal face of propodeum convex, almost as long as posterior face; posterior face of propodeum gently sloping; petiole in dorsal view broadly oval or moderately flared, usually concave, without posterolateral tubercles or denticles; subpetiolar process usually present as angular dent; postpetiole very distinctly bilobed, with broad median impression; subpostpetiolar process absent.

Head sculpture reticulate; pronotum dorsally rugulose-reticulate; mesonotum reticulate, mesopleuron areolate, dorsal face of propodeum reticulate-carinulate; otherwise sculpture mostly reticulate; face usually with < six erect, longer setae, and regular, shorter, appressed to decumbent pubescence; erect pilosity on promesonotum usually < eight long setae; otherwise promesonotum dorsally with regular appressed pubescence; petiole and postpetiole usually with a pair of longer erect setae posterolaterally, and shorter decumbent or appressed pubescence; abdominal tergites four to seven with fairly regular, short, erect pilosity, more abundant and longer on sternites four to seven, and abundant appressed pubescence throughout. Color bright to reddish yellow.

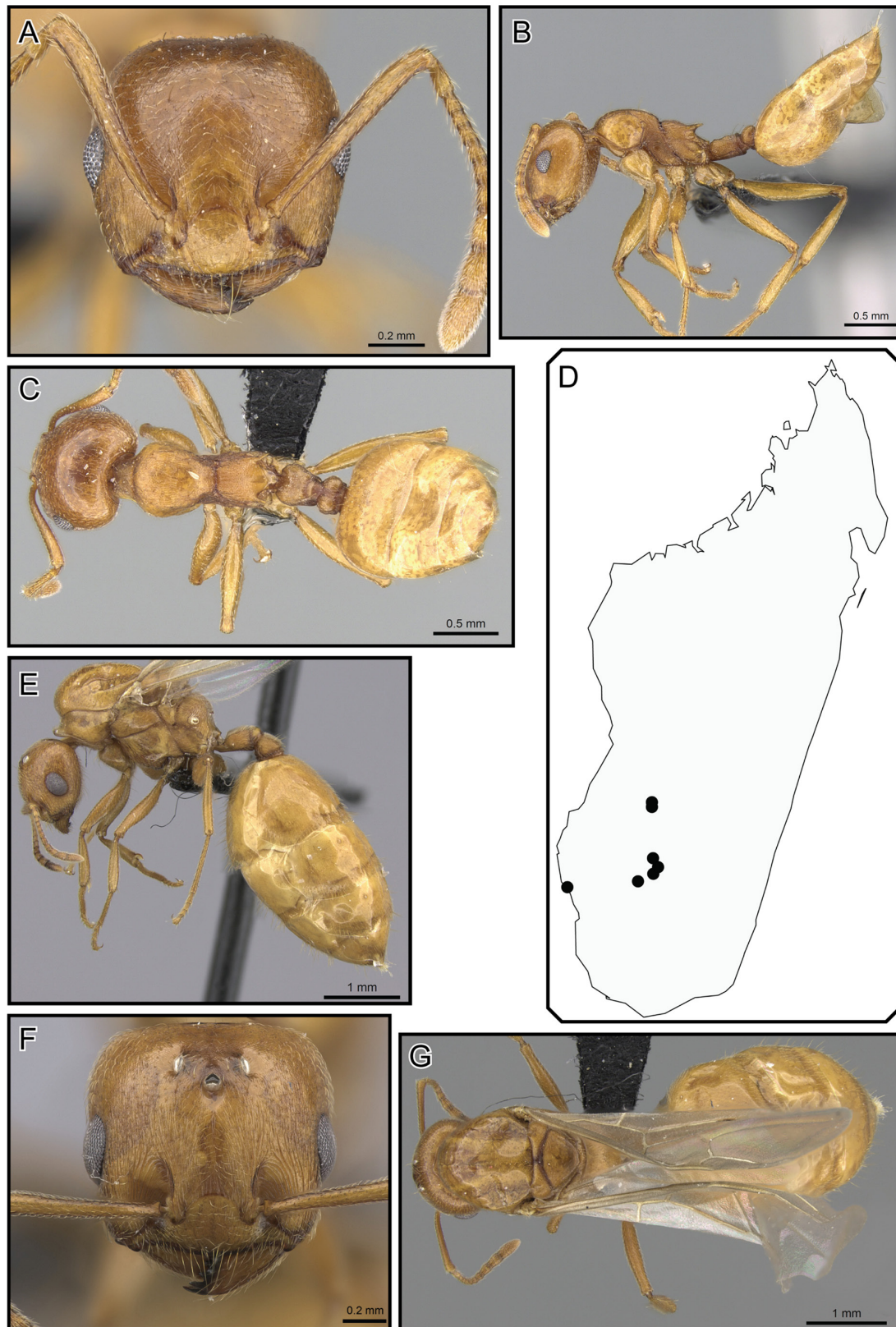
**Queen****Measurements**

(n = 3) HW 1.42-1.45; HL 1.32-1.37; EL 0.39-0.40; SL 1.03-1.12; MSNW 1.22-1.48; MSNL 1.37-1.44; WL 2.46-2.75; SPL 0.00; PTH 0.37-0.40; PTL 0.44-0.47; PTW 0.55-0.61; PPL 0.37-0.38; PPW 0.59-0.61; LHT 1.22-1.25; CI 1.06-1.08; OI 0.28-0.31; SI 0.76-0.82; MSNI 0.89-1.07; SPI 0.00; PTHI 0.84-0.87; PTWI 1.23-1.31; PPI 1.61; LBI 2.12-2.20.

**Description**

(Fig. 7E-G) Medium size (HW 1.42-1.45, WL 2.46-2.75). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth; antennal scapes easily surpassing level of lateral ocelli; eyes fairly large (OI 0.28-0.31), situated at midline of head in full-face view; head shape more or less quadrate (CI 1.06-1.08), posterior margin straight.



**Fig. 7.** *Crematogaster bara* sp. nov., worker, queen and distribution. **A-C.** Worker (CASENT0491123). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D.** Species distribution. **E-G.** Queen (CASENT0064664). **E.** Profile. **F.** Full-face. **G.** Dorsal.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

Mesoscutum in dorsal view variable (MSNI 0.89-1.07); dorsal face of propodeum short; propodeal tubercles or denticles may be present; petiole moderately flared, postpetiole merely impressed posteriorly; subpetiolar process absent.

Head sculpture reticulate; dorsal face of propodeum carinulate; petiole and postpetiole reticulate; otherwise sculpture reticulate throughout; face usually with < ten longer, erect setae and dense, short, erect to decumbent pubescence; mesonotum with regular, short, suberect pubescence, interspersed with longer, erect setae; petiole and postpetiole with dense, short, suberect to decumbent pilosity, and postpetiole with additional, longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant, short, erect pilosity and dense appressed to decumbent pubescence. Colored yellow as in workers; wings clear.

### Male

Males of this species are unknown.

### Distribution and biology

MADAGASCAR. *Crematogaster bara* sp. nov. has a very narrow distribution range in gallery forest, savannah, *Uapaca* woodland and spiny forest habitat in southwestern Madagascar (Fig. 7D). It has been collected at elevations from 30 m to 1100 m, and occurs in sympatry with *C. sewellii*, *C. dentata* stat. nov. and *C. maina* sp. nov. Not much is known about the biology of this species. One collection has been made of a colony nesting under a stone, indicating that this species may be ground-nesting.

### *Crematogaster degeeri* Forel, 1886

Figs 8-9

*Crematogaster degeeri* Forel, 1886: cvii.

*Crematogaster (Acrocoelia) degeeri* var. *lunaris* Santschi, 1928: 64. Worker from MADAGASCAR: Mont. Voiposa, Ambohimahosoa (Descarpentries, leg.) [NHMB, examined]. Lectotype worker by present designation [CASENT0101174, image on AntWeb]. syn. nov.

*Crematogaster degeeri* – Forel 1891: 190 (queen and male described).

*Crematogaster geeri* – Schulz 1906: 155; unjustified subsequent emendation.

*Crematogaster (Crematogaster) degeeri* – Wheeler 1922b: 1022. — Bolton 1995: 166.

*Crematogaster (Acrocoelia) degeeri* – Emery 1922: 146.

### Diagnosis

Within the *C. degeeri*-assemblage, this species is most easily recognized by its large eyes (OI 0.22-0.26), fairly long propodeal spines (SPI 0.10-0.16), and a promesonotum that usually bears angular posterolateral denticles (Fig. 5C) and is distinctly set off from propodeum in lateral view. *Crematogaster degeeri* could be confused with *C. ramamy* sp. nov. and *C. dentata* stat. nov., but in both of the latter the promesonotum is not distinctly set off from the propodeum. Furthermore, the latter two species have generally shorter propodeal spines (*C. dentata* stat. nov. SPI 0.01-0.10; *C. ramamy* sp. nov. SPI 0.07-0.12).

Mean barcode divergences between *C. degeeri* and species within the *C. degeeri*-assemblage are 13.2-18.0%, except with regard to *C. ramamy*, where this level is only 4.7% (Table 3). In our analysis, *C. degeeri* is paraphyletic with respect to *C. ramamy* (see comments below).

### **Type material examined**

(MHNG) MADAGASCAR (M. Grandidier), 2 worker syntypes. Lectotype worker by present designation: top worker of these two specimens on one pin [CASENT0101690; imaged on AntWeb].

### **Other material examined**

(CASC, MCZC, MHNG, NMBH, PSWC): refer to Supplementary Material 1.

### **Worker**

#### **Measurements**

(n = 15) HW 0.81-1.05; HL 0.76-0.97; EL 0.18-0.24; SL 0.63-0.78; WL 0.81-1.09; SPL 0.08-0.16; PTH 0.17-0.22; PTL 0.25-0.33; PTW 0.28-0.41; PPL 0.14-0.20; PPW 0.24-0.33; LHT 0.60-0.81; CI 1.06-1.11; OI 0.22-0.26; SI 0.77-0.86; SPI 0.10-0.16; PTHI 0.56-0.77; PTWI 1.01-1.39; PPI 1.52-1.95; LBI 1.29-1.44.

#### **Description**

(Fig. 8A-C) Small to medium size (HW 0.81-1.05, WL 0.81-1.09).

Masticatory margin of mandibles with four teeth; head shape quadrate, mostly as long as wide (CI 1.06-1.11); posterior margin of head in full-face view laterally rounded or subangular; occipital carinae usually distinct; antennal scapes reaching or surpassing head margin; midline of eyes situated slightly above midline of head in full-face view; eyes fairly large (OI 0.22-0.26) and moderately protruding.

Pronotum laterally angular; promesonotal suture indistinct; mesonotum more or less forming one plane with pronotum, but often the two separated by distinct variation in sculpture (see below); mesonotum usually with a short posterior face; laterally mesonotum angular to carinate, and often with posterolateral denticles, which set off the promesonotum distinctly from propodeum; posterior face of mesonotum longitudinally depressed with respect to lateral carinae, slopes gently into metanotal groove; metanotal groove fairly shallow, laterally constricted; propodeal spines short, spiniform (SPI 0.10-0.16), usually straight and moderately diverging; propodeal spiracles large, situated directly at base of spines; dorsal face of propodeum convex, almost as long as posterior face; posterior face of propodeum gently sloping; petiole in dorsal view from moderately to strongly flared and usually strongly concave, dorsolaterally carinate but without posterolateral tubercles or denticles; subpetiolar process variable; postpetiole wider than long, very distinctly bilobed by a sharp median impression; subpostpetiolar process absent.

Head sculpture shiny to aciculate; pronotum usually dorsally costulate and contrasting abruptly with a shiny to aciculate mesonotum; propleuron aciculate or reticulate, mesopleuron areolate, metapleuron mostly carinate; dorsal face of propodeum carinate or reticulate, posterior face shiny; dorsal face of petiole reticulate; helcium reticulate; postpetiole dorsally aciculate-reticulate; lateral and ventral face of petiole and postpetiole reticulate; face usually with four to eight erect, longer setae, and regular shorter appressed to suberect pubescence; erect pilosity on promesonotum variable, usually < eight long setae; otherwise promesonotum dorsally with regular appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short erect setae posterolaterally, and shorter suberect, decumbent or appressed pubescence; abdominal tergites four to seven with very sparse, short, erect pilosity, more abundant and longer on sternites four to seven, and abundant appressed to decumbent pubescence throughout. Color reddish brown to dark brown or black.

### **Queen**

#### **Measurements**

(n = 3) HW 1.44-1.56; HL 1.32-1.42; EL 0.40-0.45; SL 0.95-0.99; MSNW 1.20-1.46; MSNL 1.42-1.50; WL 2.49-2.68; SPL 0.00; PTH 0.38-0.41; PTL 0.43-0.53; PTW 0.51-0.59; PPL 0.35-0.38; PPW 0.56-



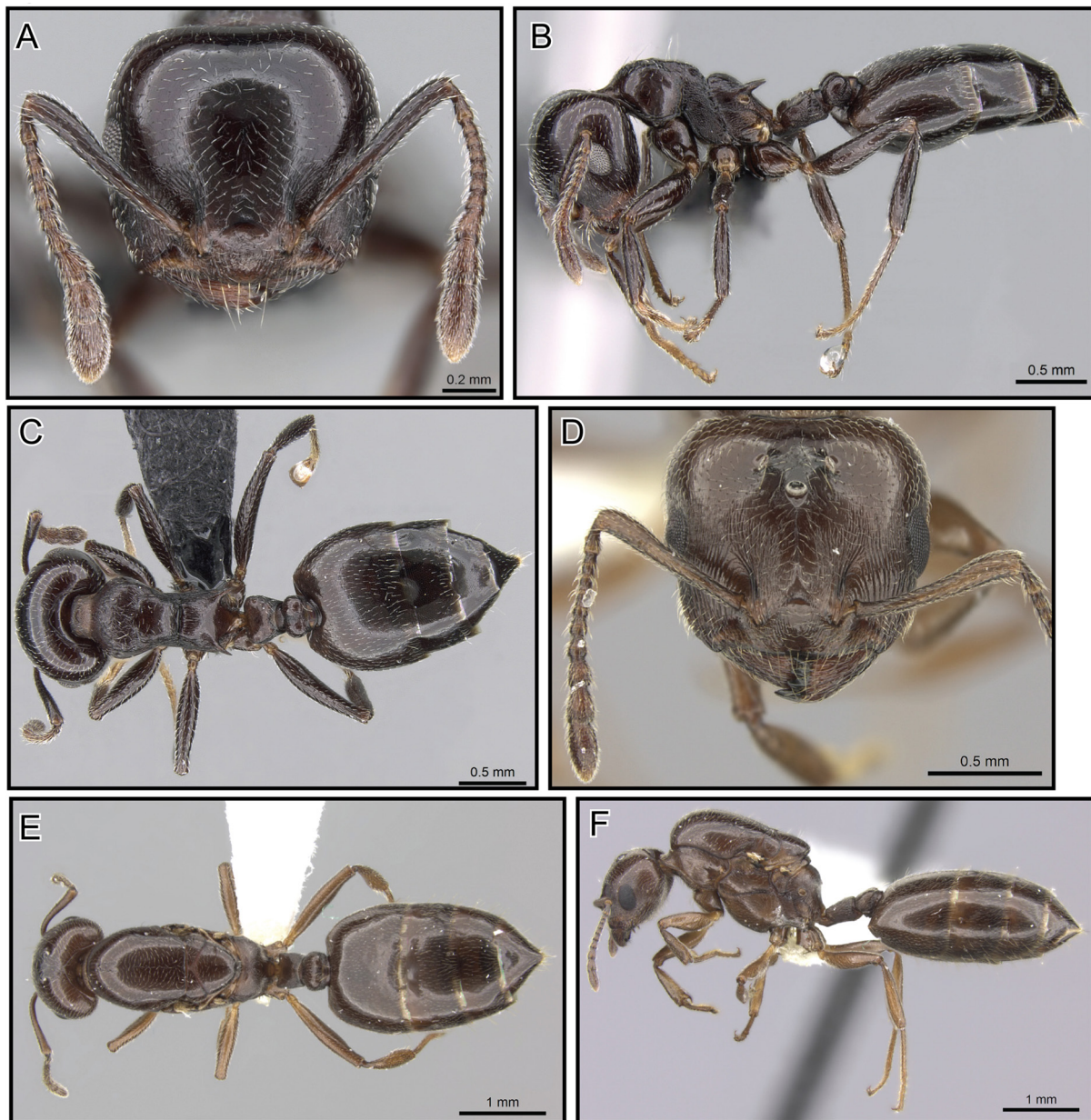
BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

0.60; LHT 1.12-1.14; CI 1.09-1.10; OI 0.28-0.32; SI 0.68-0.72; MSNI 0.83-0.97; SPI 0.00; PTHI 0.72-0.95; PTWI 1.06-1.27; PPI 1.53-1.60; LBI 2.23-2.37.

**Description**

(Fig. 8D-F) Medium size (HW 1.44-1.56, WL 2.49-2.68). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth. Antennal scapes not reaching posterior margin of head, but surpassing level of lateral ocelli; eyes large (OI 0.28-0.32), situated at midline of head in full-face view; head shape fairly quadrate (CI 1.09-1.10), moderately tapering from posterior to anterior margin; posterior margin straight.



**Fig. 8.** *Crematogaster degeeri* Forel, 1886, worker and queen. **A-C.** Worker (CASENT0118982). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Queen (CASENT0012763). **D.** Full-face. **E.** Dorsal **F.** Profile.

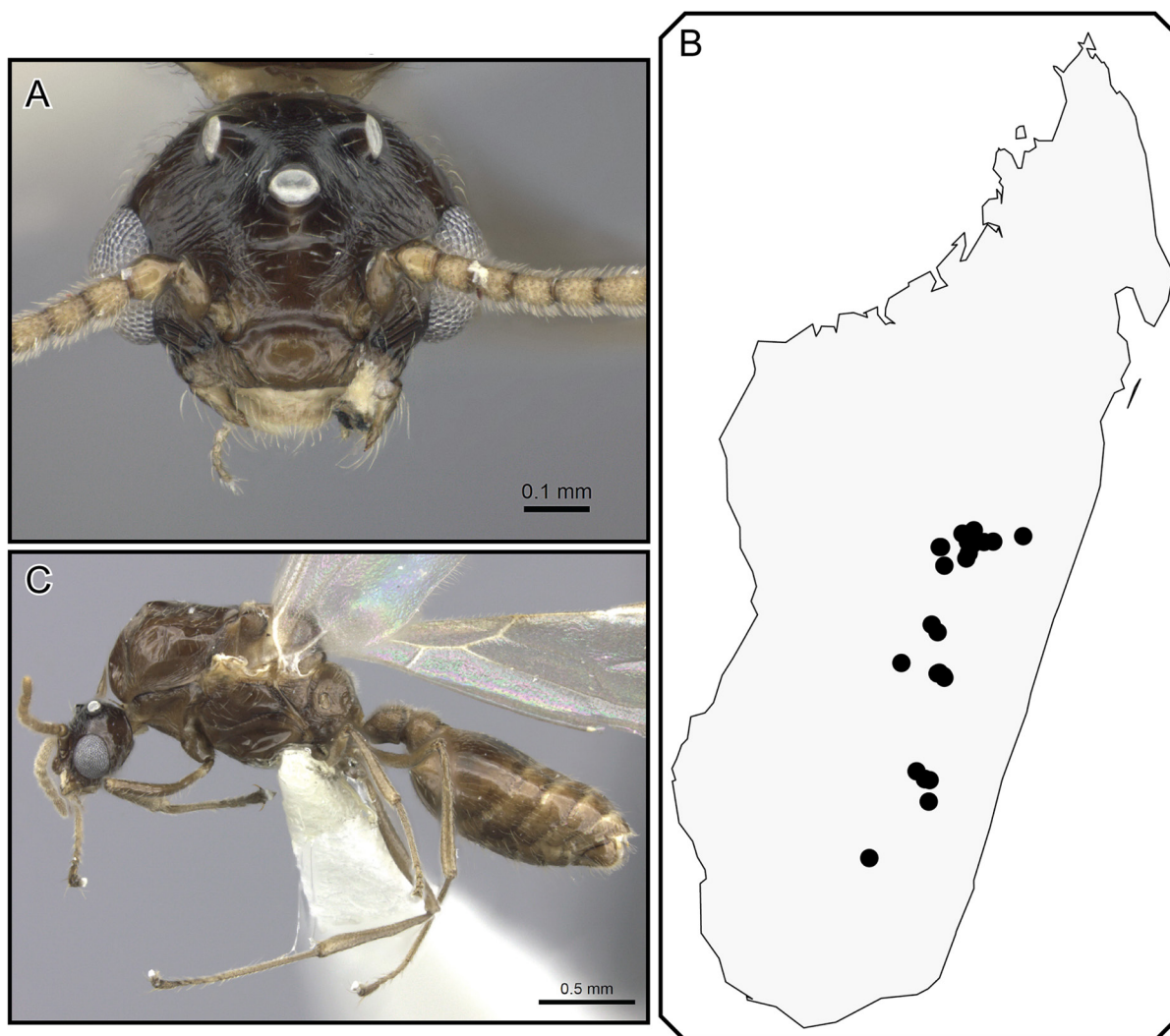
Mesosoma fairly compact (MSNI 0.83-0.97, WL 2.49-2.68); mesoscutum in dorsal view about as wide as long; dorsal face of propodeum distinct but short; propodeum tuberculate but distinct spines absent; petiole moderately flared, postpetiole merely impressed behind; subpetiolar process variable.

Sculpture shiny to aciculate throughout; face with four to six longer erect setae and abundant shorter erect to suberect pilosity; mesonotum with abundant, short, and scattered longer erect setae; petiole and postpetiole with very dense short suberect pilosity, and postpetiole often with additional longer dorso-posterior setae; abdominal tergites and four to seven with abundant appressed pilosity and regular, short, erect pilosity. Color similar to respective workers; wings clear.

### Male

#### Measurements

(n = 1) HW 0.74; HL 0.51; EL 0.29; SL 0.12; MSNW 0.91; MSNL 0.82; WL 1.53; SPL 0.00; PTH 0.24; PTL 0.26; PTW 0.30; PPL 0.19; PPW 0.35; LHT 0.86; CI 1.46; OI 0.57; SI 0.24; MSNI 1.12; SPI 0.00; PTHI 0.91; PTWI 1.16; PPI 1.82; LBI 1.78.



**Fig. 9.** *Crematogaster degeeri* Forel, 1886, male and distribution. A, C. (CASENT0127520). A. Full-face. C. Profile. B. Species distribution.

### Description

(Fig. 9A, C) Small (HW 0.74, WL 1.53).

Mandibles very short and reduced, masticatory margin with two teeth, one large apical and a minute second; clypeus moderately protruding; eyes large (OI 0.57) and protruding, midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head much wider than long (CI 1.46); in full-face view ocellar triangle situated at posterior head margin and elevated with respect to rest of face; occipital carinae distinct.

Mesoscutum in dorsal view as wide as long (MSNI 1.12); scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposteriorly rounded; metanotum protruding from below scutellum; dorsal face of propodeum almost as long as posterior face; propodeal spines absent; petiole in dorsal view oval, laterally rounded, in lateral view anteriorly greatly tapering; subpetiolar process absent; postpetiole round, lacking median impression.

Head sculpture shiny to rugulose, clypeus shiny; mesoscutum with very fine longitudinal carinulae; otherwise sculpture more or less shiny to aciculate; scattered, short, erect pilosity and a few longer setae on face, mesoscutum, and scutellum; remaining pilosity as in queens. Color brown.

### Distribution and biology

MADAGASCAR. *Crematogaster degeeri* occurs in montane rainforest, savannah, woodland and grassland habitats in central and south-central Madagascar at altitudes from 800 to 2650 m (Fig. 9B). This species occurs often in sympatry with *C. mafybe* sp. nov., and at some locations with *C. sewelli*. These ants are often found nesting on the ground under stones or in the soil, although a few records of arboreal twig collections also exist.

### Comments

In the molecular analysis, *Crematogaster degeeri* was found to be not reciprocally monophyletic with respect to *C. ramamy* (see above and Fig. 1). Refer to comments under *C. ramamy* for further discussion.

### *Crematogaster dentata* Dalla Torre, 1893 stat. nov.

Figs 10-11

*Crematogaster sewellei* var. *dentata* Dalla Torre, 1893: 86.

*Crematogaster sewelli* var. *improba* Forel, 1907: 80 (footnote). Worker syntypes from MADAGASCAR: Morondava (collector unknown) [MHNG, examined]. Lectotype worker by present designation: CASENT0101677, image on AntWeb, middle w of 3w specimens on one pin. syn. nov.

*Crematogaster sewelli mauritiana* Forel, 1907: 79; worker syntypes from MAURITIUS (Voeltzkow) [MHNG, examined]. Lectotype worker by present designation: CASENT0101752, image on AntWeb. syn. nov.

*Crematogaster inermis* r. *sewellii* var. *dentatus* – Forel 1891: 196; unavailable name.

*Crematogaster sewellei dentata* – Forel 1907: 79. — Donisthorpe 1946: 30.

*C. (Acrocoelia) sewellei* var. *dentata* – Emery 1922: 148.

*C. (Acrocoelia) sewelli* var. *improba* – Emery 1922: 148.

*C. (Acrocoelia) sewelli mauritiana* – Emery 1922: 148.

### Diagnosis

*Crematogaster dentata* stat. nov. is a highly variable, widespread species and thus very difficult to diagnose based upon a single or even a few characters. Workers can be very small to medium size (HW

0.72-1.10, WL 0.74-1.11), but usually have very abundant pilosity on the promesonotum (> eight setae) and sculpture is mostly aciculate to reticulate throughout. This species is most likely to be confused with *C. degeeri* and *C. ramamy* sp. nov.. *Crematogaster degeeri*, however, has a promesonotum very distinctly set off from the propodeum and bears posterolateral denticles on the mesonotum, whereas typically in *C. dentata* stat. nov. the transition between mesonotum and propodeum is fluent and the metanotal groove shallow. *Crematogaster ramamy* sp. nov. always shows costulate sculpture on the pronotum, whereas in *C. dentata* the sculpture on the pronotum is reduced-aciculate or reticulate. Genetic divergence in the barcode region of this species with respect to other taxa within the *C. degeeri*-assemblage ranges from 12.7-21.3% in our analysis (Table 3).

### Type material examined

(MHNG): MADAGASCAR (M. Grandidier), 1 worker, holotype by monotypy [CASENT0101683; imaged on AntWeb].

### Other material examined

(BBBC, CASC, MHNG, NHMB, PSWC, ZMHB): refer to Supplementary Material 1.

### Worker

#### Measurements

(n = 31) HW 0.72-1.10; HL 0.70-1.03; EL 0.13-0.24; SL 0.52-0.78; WL 0.74-1.11; SPL 0.01-0.10; PTH 0.12-0.24; PTL 0.23-0.35; PTW 0.24-0.41; PPL 0.11-0.21; PPW 0.21-0.38; LHT 0.55-0.84; CI 1.01-1.11; OI 0.17-0.26; SI 0.69-0.82; SPI 0.01-0.10; PTHI 0.52-0.77; PTWI 0.95-1.31; PPI 1.51-2.02; LBI 1.26-1.46.

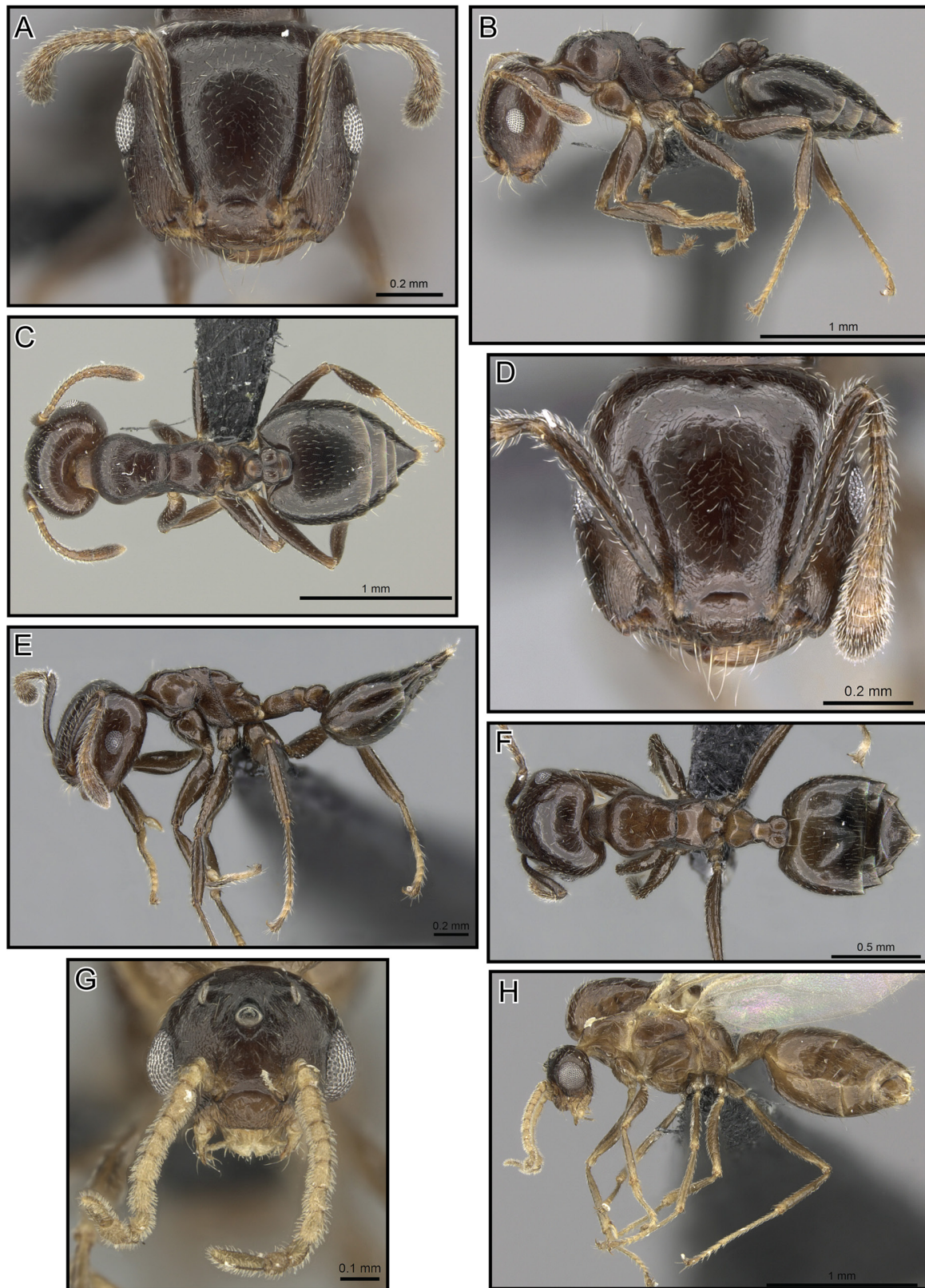
#### Description

(Fig. 10A-F) Very small to medium-sized (HW 0.72-1.10, WL 0.74-1.11).

Masticatory margin of mandibles with four teeth; head shape quadrate, mostly as long as wide (CI 1.01-1.11); posterior margin of head in full-face view laterally rounded or subangular; occipital carinae usually distinct; antennal scapes variable, but often not reaching head margin; midline of eyes situated at midline of head in full-face view; eye size fairly variable (OI 0.17-0.26), usually only slightly protruding.

Pronotum laterally subangular; promesonotal suture indistinct, mesonotum more or less forming one plane with pronotum; mesonotum usually without a distinct posterior face; laterally mesonotum angular and often with posterolateral tubercles or denticles; mesonotum longitudinally depressed with respect to lateral borders, sloping gently into metanotal groove; metanotal groove more or less absent; propodeal spines highly variable, from reduced minute denticles to short and spiniform (SPI 0.01-0.10), if spiniform then often downcurved; propodeal spiracles large, situated directly at base of spines; dorsal face of propodeum variable, from almost as long as posterior face to nearly absent; posterior face of propodeum from gently to steeply sloping; petiole in dorsal view oval, or moderately to strongly flared, moderately to strongly concave, usually not dorsolaterally carinate and without posterolateral tubercles or denticles; subpetiolar process variable; postpetiole wider than long, distinctly bilobed with a broad median impression; subpostpetiolar process absent.

Head sculpture aciculate; promesonotum usually dorsally reticulate or aciculate, rarely pronotum carinate; propleuron aciculate, mesopleuron areolate, metapleuron mostly reticulate; dorsal face of propodeum reticulate or aciculate, posterior face shiny; dorsal face of petiole reticulate to shiny; helcium reticulate; postpetiole dorsally aciculate; lateral and ventral face of petiole and postpetiole reticulate; face usually with four to eight erect, longer setae, and regular, shorter, appressed to suberect pubescence; erect pilosity on promesonotum variable, but usually very abundant > eight long setae; otherwise promesonotum



**Fig. 10.** *Crematogaster dentata* Dalla Torre, 1893 stat. nov., workers and male. **A-C.** Worker (CASENT0456641). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Worker (CASENT0138289). **D.** Full-face **E.** Profile **F.** Dorsal. **G-H.** Male (CASENT0456644). **G.** Full-face. **H.** Profile.

dorsally with regular to sparse appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of longer erect setae posterolaterally, and shorter suberect, decumbent or appressed pubescence; abdominal tergites four to seven with moderately abundant, short, erect pilosity, and regular appressed to decumbent pubescence throughout. Color light brown to dark brown, black, orange-red with black abdominal segment four to seven (western and southern dry and spiny forest localities).

## Queen

### Measurements

(n = 5) HW 1.13-1.41; HL 1.17-1.46; EL 0.30-0.42; SL 0.67-0.88; MSNW 0.92-1.19; MSNL 1.00-1.30; WL 1.73-2.43; SPL 0.00; PTH 0.30-0.38; PTL 0.35-0.43; PTW 0.41-0.52; PPL 0.26-0.39; PPW 0.40-0.55; LHT 0.80-1.05; CI 0.95-1.03; OI 0.25-0.31; SI 0.57-0.67; MSNI 0.86-0.92; SPI 0.00; PTHI 0.76-0.90; PTWI 1.10-1.21; PPI 1.39-1.68; LBI 2.17-2.32.

### Description

(Fig. 11A-C) Small to medium size (HW 1.13-1.41, WL 1.73-2.43). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth. Antennal scapes very short, often not reaching level of lateral ocelli; eyes fairly large (OI 0.25-0.31), situated distinctly below midline of head in full-face view; head shape usually rectangular, elongate, longer than wide (CI 0.95-1.03); posterior margin straight.

Mesoscutum in dorsal view longer than wide (MSNI 0.86-0.92); dorsal face of propodeum distinct but short; propodeal spines or tubercles absent; petiole moderately flared, postpetiole merely impressed behind; subpetiolar process variable.

Sculpture shiny to aciculate throughout; face usually with > six longer erect setae and abundant, shorter, erect to suberect pilosity; mesonotum with abundant short, and scattered longer, erect setae; petiole and postpetiole with dense short suberect pilosity, and postpetiole often with additional longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant appressed pilosity and sparse, short, erect pilosity. Color similar to respective workers; wings clear.

## Male

### Measurements

(n = 3) HW 0.56-0.64; HL 0.42-0.48; EL 0.21-0.23; SL 0.10-0.13; MSNW 0.65-0.74; MSNL 0.50-0.69; WL 1.09-1.40; SPL 0.00; PTH 0.16-0.17; PTL 0.20-0.24; PTW 0.22-0.27; PPL 0.12-0.14; PPW 0.24-0.27; LHT 0.54-0.62; CI 1.32-1.35; OI 0.47-0.53; SI 0.23-0.27; MSNI 1.08-1.45; SPI 0.00; PTHI 0.71-0.83; PTWI 0.97-1.24; PPI 1.74-2.16; LBI 2.01-2.25.

### Description

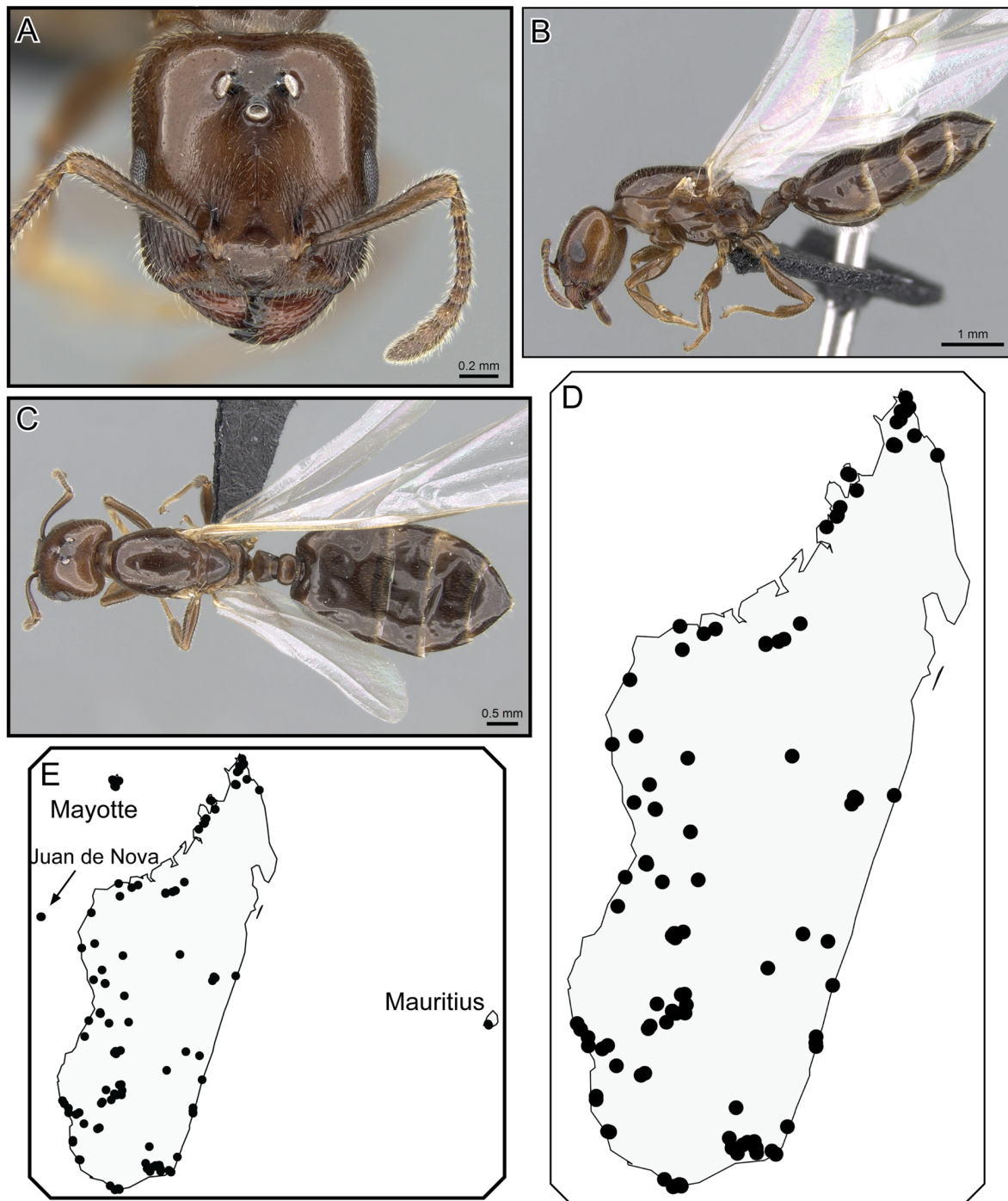
(Fig. 10G-H) Small (HW 0.56-0.64, WL 1.09-1.40).

Mandibles short and reduced, blunt and edentate; clypeus moderately protruding; eyes moderately sized (OI 0.47-0.53) and protruding, midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head wider than long (CI 1.32-1.35); in full-face view ocellar triangle situated at posterior head margin, but not much elevated with respect to rest of face; occipital carinae distinct.

Mesoscutum in dorsal view as wide as long or wider than long (MSNI 1.08-1.45); scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposterior part rounded; metanotum protruding from below scutellum; dorsal face of propodeum almost as long as posterior face; propodeal

spines absent; petiole in dorsal view oval, laterally rounded, in lateral view greatly tapering anteriorly; subpetiolar process absent; postpetiole fairly flat, lacking median impression.

Head sculpture, including clypeus, shiny to rugulose; mesoscutum with very fine longitudinal carinulae; otherwise sculpture more or less shiny to aciculate; scattered short, erect pilosity and a few longer setae on face, mesoscutum, and scutellum; remaining pilosity as in queens. Color brown.



**Fig. 11.** *Crematogaster dentata* Dalla Torre, 1893 stat. nov., queen and distribution. A-C. Queen (CASENT0484998). A. Full-face. B. Profile. C. Dorsal. D-E. Species distribution.

### Distribution and biology

MADAGASCAR, MAURITIUS, MAYOTTE and JUAN DE NOVA. *Crematogaster dentata* stat. nov. is the most widespread species within the *C. degeeri*-assemblage in the Malagasy region (Fig. 11D-E). The species occurs in dry deciduous and littoral forests of western, southwestern and northern Madagascar, in the spiny forest of southern Madagascar and in coastal shrub and mangrove habitats. A few records exist from rainforest sites, but the species is clearly adapted to more mesic habitats. *Crematogaster dentata* stat. nov. is thus most common at low elevations, but its elevational distribution range seems to be quite broad, with a maximum record of 1410 m in transition forest in Ambohitantely Reserve. On Mayotte and Juan de Nova it has been found to occupy coastal shrub habitats, whereas on Mauritius it is known to occur in rainforest habitat. Given its broad distribution range, this species co-occurs with most other species in the *C. degeeri*-assemblage, with the exception of the species generally adapted to higher elevations (*C. alafara* sp. nov., *C. degeeri*, *C. malahelo* sp. nov.). *Crematogaster dentata* stat. nov. is most often found nesting arboreally in dead twigs and branches, and also in live plant parts. In baiting surveys in western Madagascar this species was active and attracted to fish baits during both day and night.

### Comments

*Crematogaster dentata* stat. nov. is morphologically the most variable species within the *C. degeeri*-assemblage. Workers show a wide range of gradual variation in size and mesosomal structure. The variation in mesosomal characters in particular can lead to confusion with other species, making *C. dentata* stat. nov. difficult to diagnose. A general trend seems to be that workers from populations of the southern and western spiny forests are on average larger than on the rest of the island. Dry and spiny forest populations are reddish to orange in color, whereas rainforest populations are brown.

The allopatric population of *Crematogaster dentata* stat. nov. on Mauritius shows 8.8-11.2% divergence with respect to Madagascar. The decision of whether or not to give species status to this population is arbitrary, since it is unknown if reproductive isolation exists with the mainland. A species name would already be available (with *C. sewellii mauritiana*). We decided against describing a separate species for Mauritius, since we were not able to find any distinct diagnostic morphological characters for this population.

### *Crematogaster lobata* Emery, 1895

Fig. 12

*Crematogaster sevellei* var. *lobata* Emery, 1895: 342.

*Crematogaster pacifica* Santschi, 1919: 236. Worker holotype (by monotypy) from MADAGASCAR (Leg. J. de Gaulle) [NHMB, examined]. Lectotype worker by present designation: CASENT0101160, image on AntWeb. syn. nov.

*Crematogaster sevellei lobata* – Forel 1907: 80 (footnote).

*Crematogaster sewellii lobata* var. *gigantea* – Forel 1907: 80 (footnote) (w.) MADAGASCAR. Unavailable name (Bolton 1995: 153).

*Crematogaster (Acrocoelia) sevellei* var. *lobata* – Emery 1922: 148.

*Crematogaster (Crematogaster) pacifica* – Wheeler 1922b: 1023.

*Crematogaster lobata* – Santschi 1930: 63.

*Crematogaster lobata pacifica* – Santschi 1930: 63.

*Crematogaster (Crematogaster) sevellei* var. *lobata* – Bolton 1995: 166.



## Diagnosis

*Crematogaster lobata* is easily recognizable by its small eyes (OI < 0.21) and lack of pronotal spines. These characters are otherwise only shared with *C. mafybe* sp. nov.; from the latter *C. lobata* can be distinguished by the absence of a distinct median longitudinal groove on the pronotum. In our molecular analysis, *C. lobata* is shown to have 14.3-19.9% mean sequence divergence in COI with regard to the rest of species in the *C. degeeri*-assembly.

## Type material examined

(MSNG): MADAGASCAR (Ch. Alluaud), 1 worker, lectotype worker by present designation [CASENT0102055; imaged on Antweb].

## Other material examined

(BBBC, CASC, MCZC, MSNG, NHMB, PSWC): refer to supplementary Supplementary Material 1.

## Worker

### Measurements

(n = 20) HW 0.80-1.38; HL 0.78-1.33; EL 0.15-0.23; SL 0.57-0.90; WL 0.86-1.42; SPL 0.00; PTH 0.15-0.24; PTL 0.26-0.38; PTW 0.25-0.46; PPL 0.15-0.25; PPW 0.24-0.39; LHT 0.63-1.00; CI 1.00-1.09; OI 0.16-0.21; SI 0.66-0.80; SPI 0.00; PTHI 0.50-0.68; PTWI 0.95-1.27; PPI 1.41-1.74; LBI 1.29-1.44.

### Description

(Fig. 12A, C, D) Small to very large size (HW 0.80-1.38, WL 0.86-1.42); this species seems to have a polymorphic worker caste reminiscent of majors and minors.

Masticatory margin of mandibles with four teeth; head shape quadrate, mostly as long as wide (CI 1.00-1.09); posterior margin of head in full-face view laterally angular; occipital carinae usually distinct; antennal scapes short, not reaching head margin; midline of eyes situated slightly above midline of head in full-face view; eyes very small (OI 0.16-0.21), and confluent with lateral head margin in full-face view.

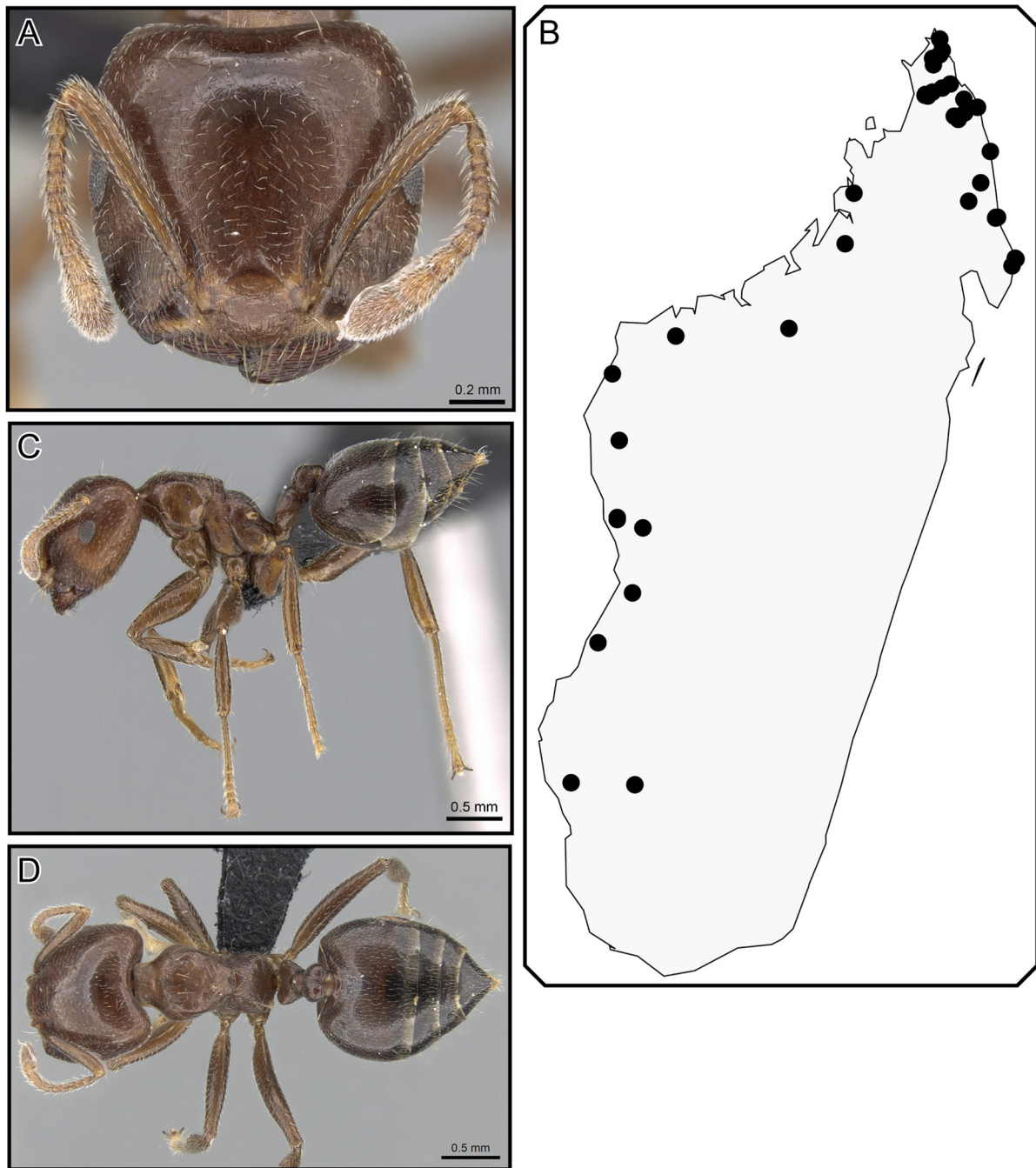
Pronotum laterally subangular; promesonotal suture usually indistinct in small workers and mesonotum more or less forming one plane with pronotum; in large workers, mesonotum often slightly raised with respect to pronotum and a median tubercle is present; mesonotum usually with a short, distinct posterior face; mesonotum angular laterally, ending in posterolateral tubercles; metanotal groove fairly shallow; propodeal spines absent, propodeum tuberculate directly above spiracles; dorsal face of propodeum short, posterior face of propodeum gently sloping; petiole in dorsal view broadly oval and moderately concave, without dorsolateral carinate margins and posterolateral tubercles or denticles; subpetiolar process variable, but often entirely absent; postpetiole wider than long, distinctly bilobed with a narrow median impression; subpostpetiolar process absent.

Head sculpture aciculate; promesonotum usually dorsally reticulate; propleuron aciculate, mesopleuron areolate, metapleuron reticulate-carinate; dorsal face of propodeum carinate, posterior face reticulate; dorsal face of petiole reticulate, helcium reticulate; postpetiole dorsally reticulate; lateral and ventral face of petiole and postpetiole reticulate; face usually with sparse (two to eight) erect, longer setae, and abundant, short, appressed to suberect pubescence; erect pilosity on promesonotum highly variable, often very abundant, usually including at least eight long setae; otherwise promesonotum dorsally with regular to sparse, appressed to subdecumbent pubescence; propodeum usually laterally with long, erect setae (> six); petiole and postpetiole usually with a pair of short erect setae posterolaterally, and shorter

appressed pubescence; abdominal tergites four to seven with sparse, short, erect pilosity more abundant ventrally, and regular appressed to decumbent pubescence throughout. Color light brown to dark brown, with abdominal segments four to seven usually black.

**Queen and male**

Unknown.



**Fig. 12.** *Crematogaster lobata* Emery, 1895, worker and distribution. **A, C-D.** Worker (CASENT0439060). **A.** Full-face. **C.** Profile. **D.** Dorsal. **B.** Species distribution.

### Distribution and biology

MADAGASCAR. *Crematogaster lobata* is found throughout the dry and littoral forests of western and northern Madagascar (Fig. 12B), mostly at low elevations ranging from 0 m to 400 m. The species seems to occur in fairly low abundance. Some isolated records exist from rainforest and gallery forest up to 770 m altitude. *Crematogaster lobata* co-occurs often with *C. dentata* stat. nov., *C. maina* sp. nov., *C. ramamy* sp. nov. and *C. tricolor* stat. rev., as well as with *C. sewellii* at RS Beanka. The few colony collections available indicate that this species nests arboreally in dead branches and twigs. *Crematogaster lobata* is attracted to fish baits during both day and night baiting studies.

*Crematogaster mafybe* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:66E18466-A2C6-4EA5-A92D-1D74D7A74CC5](https://zoobank.org/act:66E18466-A2C6-4EA5-A92D-1D74D7A74CC5)

Figs 13-14

### Diagnosis

*Crematogaster mafybe* sp. nov. can be readily distinguished by its small eyes (OI 0.18-0.21) and lack of pronotal spines. These characters are otherwise only shared with *C. lobata*; from the latter *C. mafybe* sp. nov. can be distinguished by the presence of a distinct median longitudinal groove on the pronotum. Our data shows a mean sequence divergence between *C. mafybe* sp. nov. and the other species in the *C. degeeri*-assembly of 12.7-21.3% (Table 3).

### Etymology

The Malagasy word *mafybe* means “very strong”, as this species is one of the largest and most robust *Crematogaster* species in Madagascar. The name is treated as a noun in apposition.

### Type specimens

#### Holotype

Worker: pinned, CASENT0317762, BBB224, ex dead tree [imaged on AntWeb]; original locality label: Madagascar: Fianarantsoa: P.N. Andringitra, 15.5 km S Ambalamanenjana, 1730 m, 22°12.453'S, 46°58.314'E, 4 Mar. 2010, montane rainforest, B.B. Blaimer, BBB224; deposited at CASC.

#### Paratypes

4 workers, pinned, same collection and locality data as holotype. #1: CASENT0317793, deposited at SAMC; #2: CASENT0317794, deposited at MHNG. #3: CASENT0317795, deposited at MCZC. #4: CASENT0317796, deposited at UCDC.

### Type locality

MADAGASCAR: Fianarantsoa: P.N. Andringitra: -22.2076, 46.9719, 1730 m, montane rainforest.

### Other material examined

(BBBC, CASC, MCZC, PSWC): refer to Supplementary Material 1.

### Worker

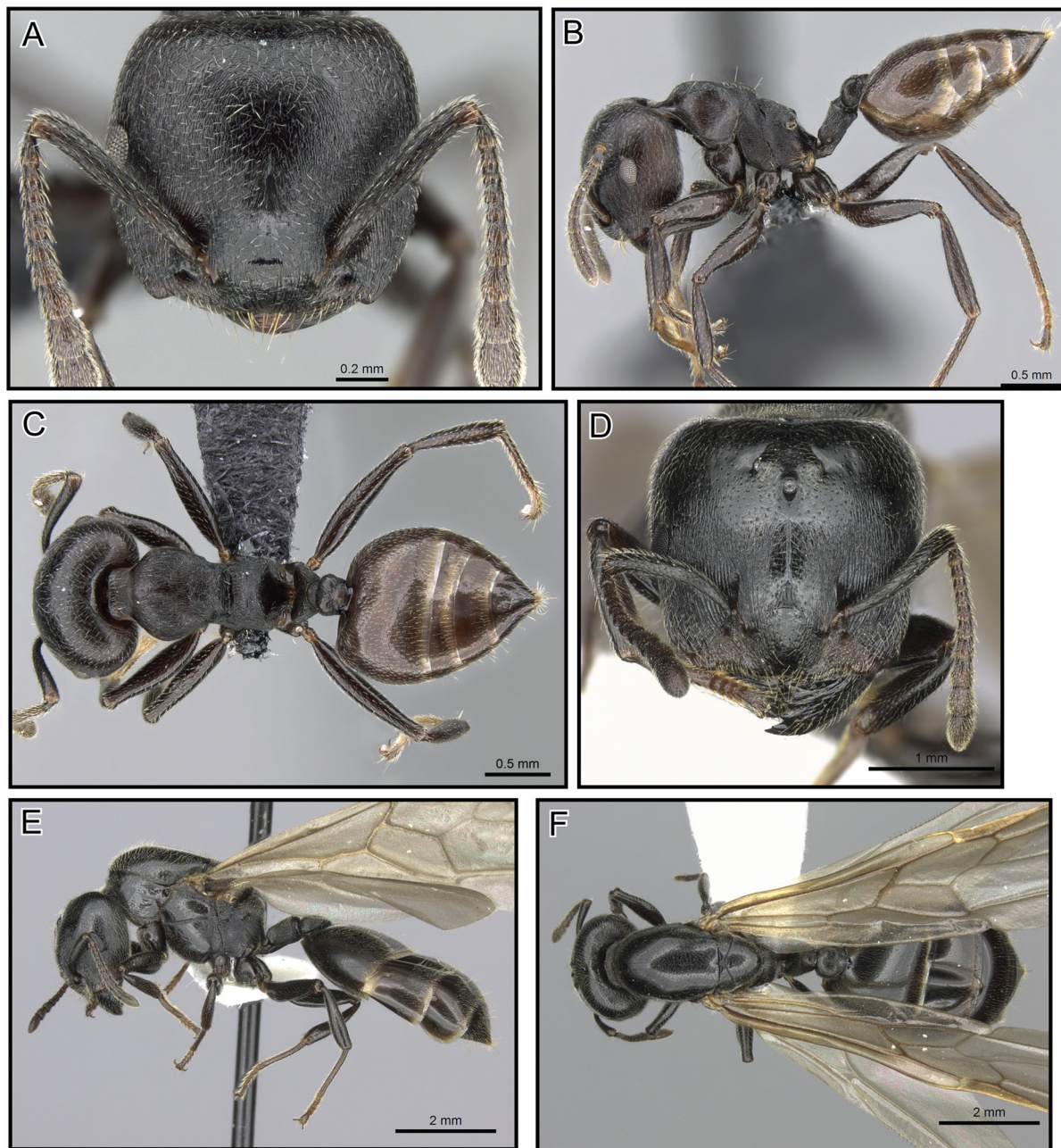
#### Measurements

(n = 21) [holotype] HW 0.98-1.43 [1.24]; HL 0.89-1.30 [1.16]; EL 0.18-0.27 [0.21]; SL 0.63-0.94 [0.83]; WL 0.98-1.48 [1.26]; SPL 0.00-0.03 [0.02]; PTH 0.19-0.27 [0.22]; PTL 0.27-0.44 [0.35]; PTW 0.34-0.52 [0.45]; PPL 0.16-0.25 [0.23]; PPW 0.26-0.40 [0.33]; LHT 0.76-1.23 [0.98]; CI 1.04-1.11 [1.07]; OI 0.18-0.21 [0.18]; SI 0.60-0.79 [0.72]; SPI 0.00-0.03 [0.01]; PTHI 0.59-0.84 [0.62]; PTWI 1.06-1.41 [1.27]; PPI 1.39-1.79 [1.45]; LBI 1.15-1.42 [1.29].

**Description**

(Fig. 13A-C) Medium to very large size (HW 0.98-1.43, WL 0.98-1.48).

Masticatory margin of mandibles with four teeth; head shape quadrate, more or less as long as wide (CI 1.04-1.11); posterior margin of head in full-face view laterally angular or subangular, sometimes medially depressed; occipital carinae usually distinct; antennal scapes of variable length, not reaching or surpassing head margin; midline of eyes situated at midline of head in full-face view; eyes small (OI 0.18-0.21), and confluent with lateral head margin in full-face view.



**Fig. 13.** *Crematogaster mafybe* sp. nov., worker and queen. **A-C.** Worker (CASENT0317762). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Queen (CASENT0193464). **D.** Full-face. **E.** Profile **F.** Dorsal.

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Pronotum laterally angular; promesonotal suture usually indistinct, the mesonotum more or less forming one plane with pronotum; pronotum with a longitudinal groove; mesonotum usually without distinct posterior face; mesonotum laterally angular, ending in small posterolateral tubercles; metanotal groove fairly shallow; propodeal spines absent, or propodeum with small denticles or tubercles; dorsal face of propodeum very short to absent, posterior face of propodeum sloping fairly steeply, often with sharp transverse groove; petiole in dorsal view broadly oval to moderately flared, concave, without dorsolateral carinate margins and posterolateral tubercles or denticles; subpetiolar process variable, but often entirely absent; postpetiole bilobed with a narrow to broad median impression; subpostpetiolar process absent.

Head sculpture carinulate to reticulate; promesonotum carinulate to reticulate; propleuron reticulate, mesopleuron areolate, metapleuron reticulate-carinulate; dorsal face of propodeum carinulate to reticulate, posterior face reticulate; petiole and postpetiole dorsally and ventrally reticulate; erect pilosity on face sparse, < eight longer setae, and abundant, short, appressed to suberect pubescence; erect pilosity on promesonotum variable, usually < 12 long setae; otherwise promesonotum dorsally with very sparse appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short erect setae posterolaterally, and shorter appressed pubescence; abdominal tergites four to seven with very sparse short erect pilosity, ventrally more abundant, and regular appressed to decumbent pubescence throughout. Color black or brown, abdominal segments four to seven yellowish.

**Queen****Measurements**

(n = 5) HW 1.70-2.18; HL 1.58-2.06; EL 0.40-0.48; SL 0.93-1.18; MSNW 1.35-1.54; MSNL 1.40-1.95; WL 2.56-3.34; SPL 0.00; PTH 0.38-0.53; PTL 0.51-0.65; PTW 0.64-0.79; PPL 0.38-0.50; PPW 0.56-0.71; LHT 1.08-1.42; CI 0.99-1.08; OI 0.23-0.26; SI 0.57-0.59; MSNI 0.79-1.02; SPI 0.00; PTHI 0.73-0.90; PTWI 1.21-1.26; PPI 1.28-1.74; LBI 2.22-2.36.

**Description**

(Fig. 13D-F) Large to very large size (HW 1.70-2.18, WL 2.56-3.34). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth; antennal scapes short, usually not surpassing level of lateral ocelli; eyes small (OI 0.23-0.26), situated at or slightly below midline of head in full-face view; head shape more or less quadrate (CI 0.99-1.08), posterior margin straight.

Mesoscutum in dorsal view usually longer than wide (MSNI 0.79-1.02); dorsal face of propodeum short, meeting posterior face at a right angle; propodeal spines or tubercles absent; petiole broadly flared, postpetiole merely impressed posteriorly; subpetiolar process absent.

Head sculpture aciculate to carinulate; otherwise aciculate to reticulate throughout; face usually with abundant, longer, erect setae and dense, short, erect to decumbent pubescence; mesonotum with dense, short, suberect pubescence, and interspersed longer, erect setae; petiole and postpetiole with dense short suberect to decumbent pilosity, and postpetiole with additional longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant erect pilosity and dense appressed pubescence. Colored black; wings with a brown hue.

**Male****Measurements**

(n = 3) HW 0.84-0.88; HL 0.68-0.71; EL 0.27-0.31; SL 0.17-0.18; MSNW 1.07-1.13; MSNL 0.96-1.09; WL 1.82-2.10; SPL 0.00; PTH 0.24-0.30; PTL 0.26-0.36; PTW 0.33-0.41; PPL 0.18-0.22; PPW 0.37-

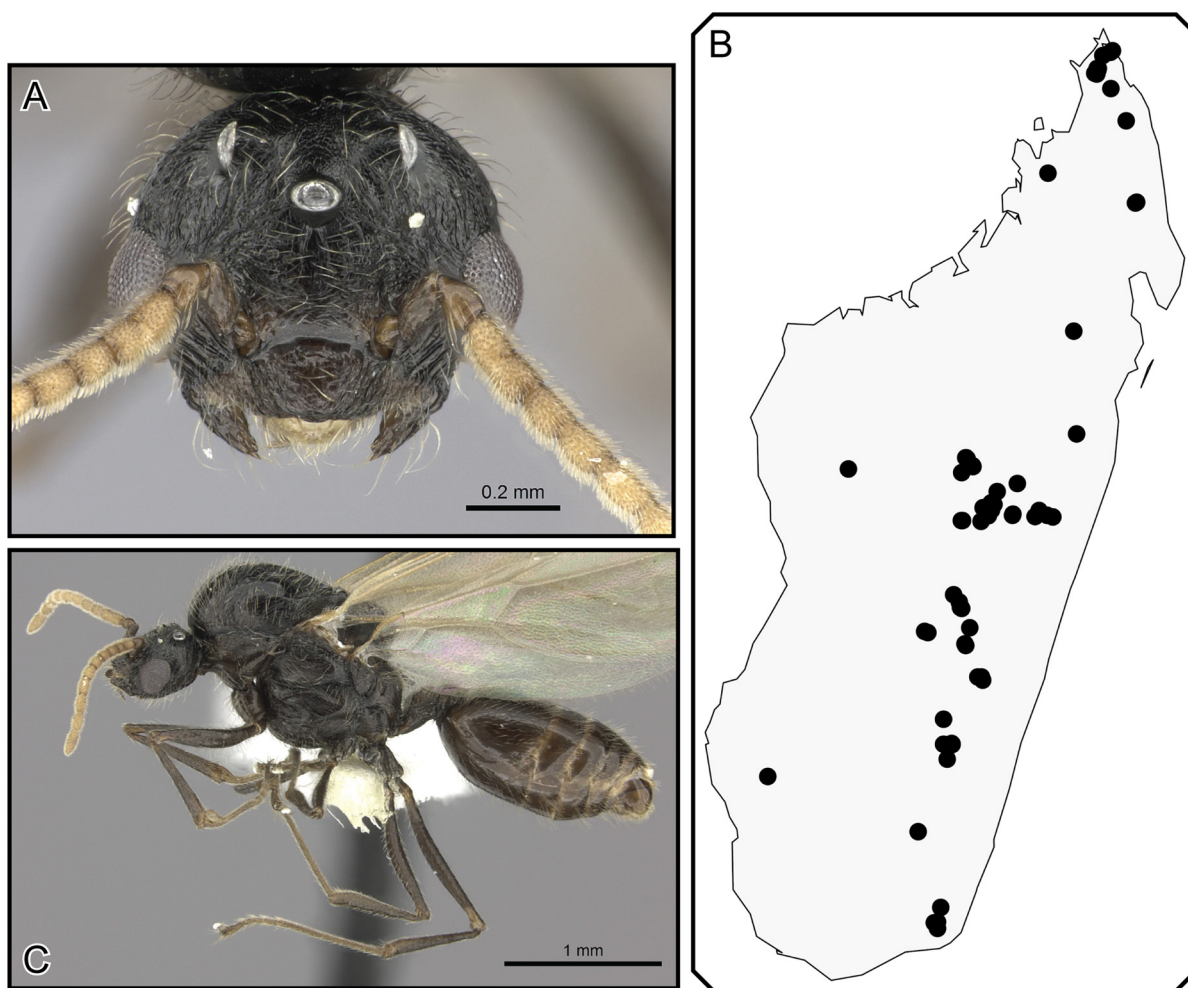
0.43; LHT 0.97-1.01; CI 1.22-1.24; OI 0.40-0.44; SI 0.25-0.27; MSNI 1.03-1.12; SPI 0.00; PTHI 0.82-0.94; PTWI 1.13-1.26; PPI 1.91-2.09; LBI 1.84-2.07.

**Description**

(Fig. 14A, C) Large males (HW 0.84-0.88, WL 1.82-2.10).

Mandibles short and reduced, one minute apical tooth present; clypeus not much protruding; eyes fairly small (OI 0.40-0.44); midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head wider than long (CI 1.22-1.24); in full-face view ocellar triangle situated below posterior head margin, elevated with respect to rest of face; occipital carinae very distinct, with a thin flange projecting backwards.

Mesoscutum in dorsal view as wide as or slightly wider than long (MSNI 1.03-1.12); scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposterior part rounded; metanotum protruding only slightly from below scutellum; dorsal face of propodeum short; propodeal spines absent; petiole in dorsal view oval, laterally rounded, in lateral view anteriorly greatly tapering; subpetiolar process absent; postpetiole fairly flat and short, lacking median impression.



**Fig. 14.** *Crematogaster mafybe* sp. nov., male and distribution. **A, C.** Male (CASENT0193465). **A.** Full-face. **C.** Profile. **B.** Species distribution.

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Head sculpture rugulose-reticulate; mesosoma dorsally with very fine longitudinal carinulae; otherwise sculpture more or less reticulate to aciculate; dense, short, erect to decumbent pubescence covering head, meso- and metasoma, interspersed with a few longer, erect setae. Color black.

### Distribution and biology

MADAGASCAR. *Crematogaster mafybe* sp. nov. is a high-elevation specialist mostly found throughout the rainforest and montane forests of the central and south-central highland region and northern Madagascar from 700 m to 2150 m in elevation (Fig. 14B). Interesting disjunct populations exist in western Madagascar in the isolated montane forests of Analavelona and RS Ambohijanahary. There are some records of this species from coastal littoral and dry forest in northern Madagascar (see Supplementary Material 1) at low elevations, but we suspect that this habitat is suboptimal for this species. *Crematogaster mafybe* sp. nov. co-occurs mostly with *C. degeeri*, *C. alafara* sp. nov. and *C. malahelo* sp. nov. in montane habitats, but is also found in sympatry with *C. tricolor* stat. rev., *C. dentata* stat. nov., *C. maina* sp. nov., *C. ramamy* sp. nov., *C. lobata* and *C. sewellii* at several locations. This species has been collected mostly from nests in dead branches and twigs above ground, and we thus assume that its preferred nesting sites are arboreal. In montane habitats, however, this species also nests in rotten logs on the ground and under stones.

*Crematogaster maina* Blaimer sp. nov.

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Figs 15-16

### Diagnosis

*Crematogaster maina* sp. nov. is easily distinguished from other species in the *C. degeeri*-assemblage by its yellow body coloration. It is considerably smaller than *C. bara* sp. nov., which shares its yellow color (HW 0.60-0.86, WL 0.66-0.93 vs *C. bara* sp. nov. HW 0.87-1.03, WL 0.98-1.22) and shorter antennal scapes (SI 0.71-0.83 vs *C. bara* sp. nov. SI 0.91-1.01). Molecular sequence divergence to the remaining species ranges from 11.3-20.2%.

### Etymology

This species is named after its predominant distribution in the dry forests of Madagascar: *maina* is the Malagasy word for “dry.” The name is treated as a noun in apposition.

### Type specimens

#### Holotype

Worker: pinned, CASENT0317758, BBB246, ex dead twig above ground [imaged on AntWeb]; original locality label: Madagascar: Toliara: PN Andohahela, p3: Ankasofotsy, 4.5 km W Ranopiso, S 25°00.820', E 46°38.790', 160 m, 21 Mar. 2010, transition forest, B.B. Blaimer, BBB#246; deposited at CASC.

#### Paratypes

4 workers, pinned, same collection and locality data as holotype. #1: CASENT0317789, deposited at SAMC. #2: CASENT0317790, deposited at MHNG. #3: CASENT0317791, deposited at MCZC. #4: CASENT0317792, deposited at UCDC.

### Type locality

MADAGASCAR: Toliara: P.N. Andohahela (parcel 3): -25.0137, 46.6465, 160 m, dry forest/transition forest.

### **Other material examined**

(BBBC, CASC, MCZC, PSWC): refer to Supplementary Material 1.

### **Worker**

#### **Measurements**

(n = 21) [holotype] HW 0.60-0.86 [0.77]; HL 0.56-0.80 [0.74]; EL 0.13-0.20 [0.18]; SL 0.43-0.64 [0.59]; WL 0.66-0.93 [0.87]; SPL 0.05-0.12 [0.10]; PTH 0.12-0.21 [0.18]; PTL 0.19-0.27 [0.26]; PTW 0.26-0.36 [0.30]; PPL 0.10-0.19 [0.15]; PPW 0.21-0.34 [0.28]; LHT 0.44-0.64 [0.60]; CI 1.02-1.12 [1.04]; OI 0.20-0.26 [0.24]; SI 0.71-0.83 [0.80]; SPI 0.07-0.14 [0.11]; PTHI 0.63-0.81 [0.69]; PTWI 1.13-1.44 [1.13]; PPI 1.61-2.02 [1.84]; LBI 1.10-1.69 [1.45].

#### **Description**

(Fig. 15A-F) Very small to small size (HW 0.60-0.86, WL 0.66-0.93).

Masticatory margin of mandibles with four teeth; head shape fairly quadrate or slightly wider than long (CI 1.02-1.12); posterior margin of head in full-face view laterally subangular or rounded, sometimes slightly medially depressed; occipital carinae distinct; antennal scapes usually about reaching head margin; midline of eyes situated at or slightly above midline of head in full-face view; eyes moderately large (OI 0.20-0.26) and only slightly protruding from head margin.

Pronotum laterally subangular, often carinate; usually promesonotal suture indistinct, and mesonotum forming a flat plane with respect to pronotum; in larger workers (Fig. 15D-F) promesonotal suture present, and mesonotum raised and anteriorly projecting over pronotum; mesonotum usually without a posterior face; mesonotum posterolaterally with raised carinae or sometimes small denticles, but not distinctly set off from propodeum, forming one convex outline with the latter in lateral view; metanotal groove very shallow, laterally bordered by carinae but not constricted; propodeal spines short (SPI 0.07-0.14), straight and spiniform; dorsal face of propodeum very short or absent; posterior face of propodeum usually gently sloping; petiole in dorsal view broadly or sharply flared and convex, dorsolaterally rounded, without posterolateral tubercles; subpetiolar process mostly present as sharp acute tooth; postpetiole very distinctly bilobed, separated by a broad median impression; subpostpetiolar process absent.

Head sculpture aciculate; pronotum costulate, carinulate or reticulate, propodeum often carinulate; rest of mesosoma, petiole, postpetiole reticulate; face usually with < ten erect longer setae, and regular shorter appressed pubescence; erect pilosity on promesonotum usually restricted to lateral margins, usually < ten setae; otherwise promesonotum dorsally with sparse appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short erect setae posterolaterally, and shorter appressed pubescence; abdominal tergites and sternites four to seven with abundant, short, erect pilosity, and sparse appressed to decumbent pubescence throughout. Color uniformly yellow.

### **Queen**

#### **Measurements**

(n = 5) HW 0.98-1.13; HL 1.04-1.17; EL 0.29-0.34; SL 0.66-0.73; MSNW 0.86-1.02; MSNL 0.96-1.05; WL 1.65-1.82; SPL 0.00; PTH 0.31-0.34; PTL 0.36-0.41; PTW 0.45-0.50; PPL 0.22-0.30; PPW 0.40-0.47; LHT 0.72-0.87; CI 0.94-1.00; OI 0.27-0.31; SI 0.61-0.66; MSNI 0.85-0.99; SPI 0.00; PTHI 0.83-0.90; PTWI 1.18-1.28; PPI 1.50-1.79; LBI 2.14-2.38.

#### **Description**

(Fig. 16A-C) Very small to small size (HW 0.98-1.13, WL 1.65-1.82). With worker characters, except as follows.

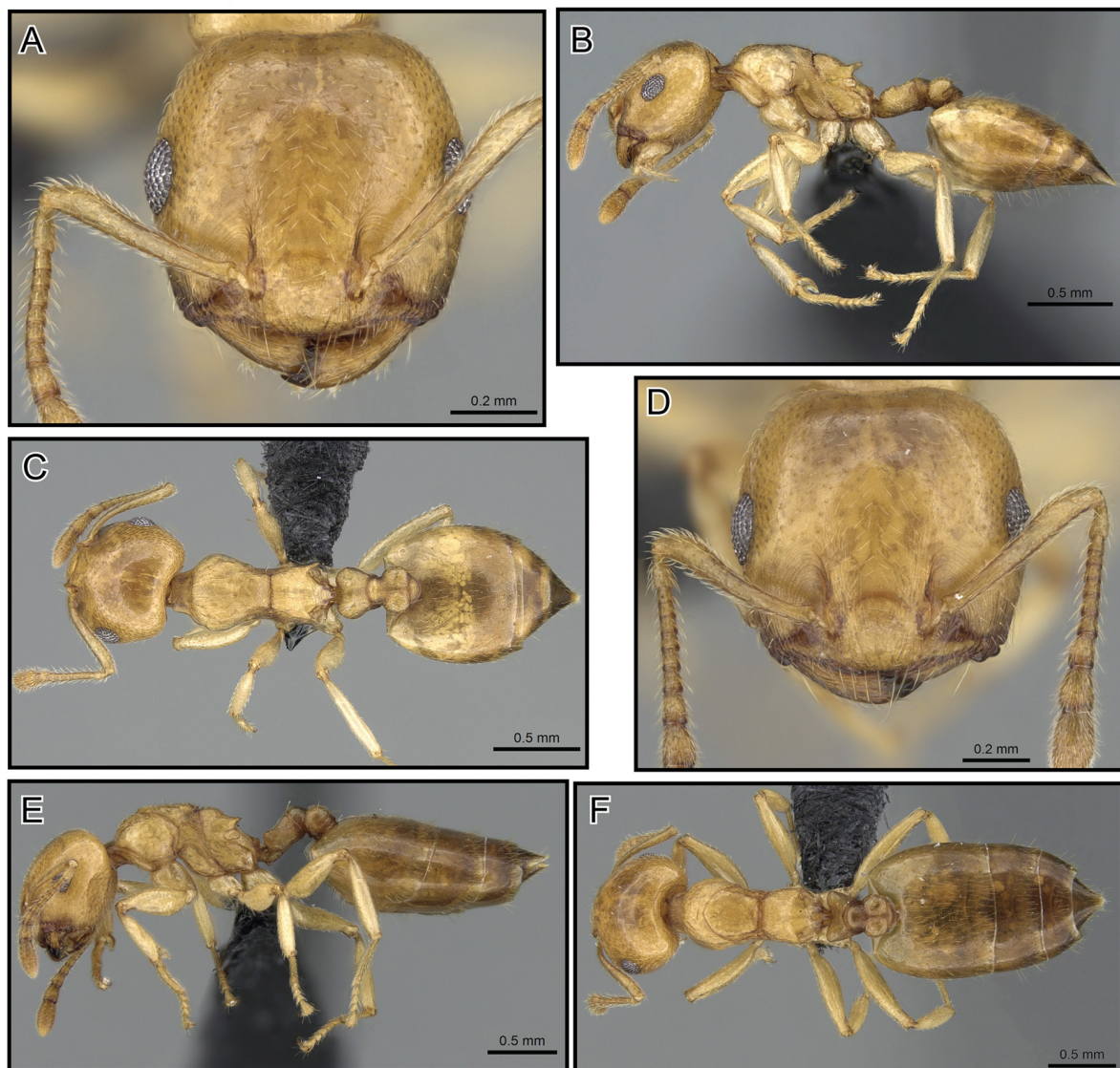


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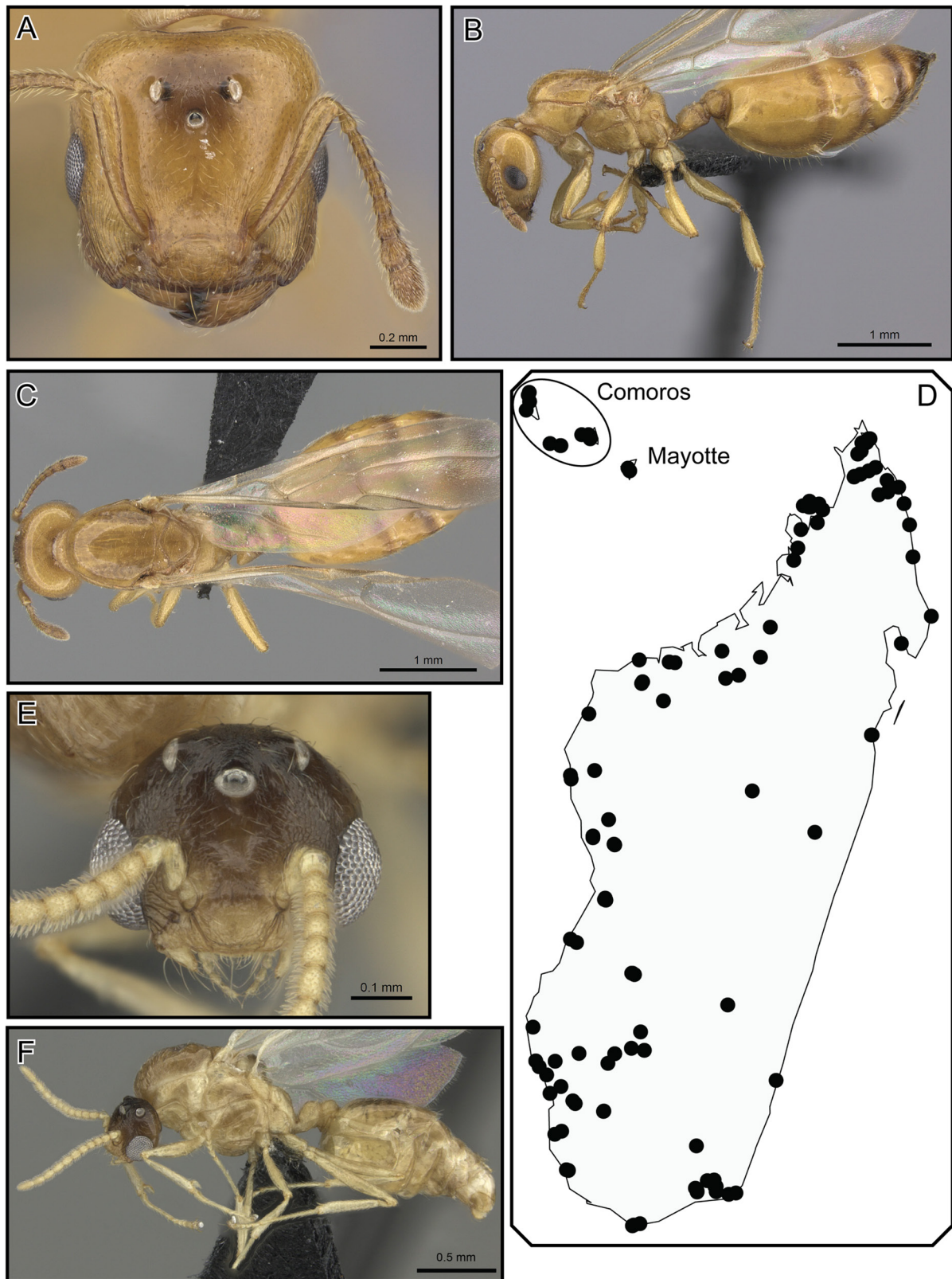
Masticatory margin of mandibles with five teeth; antennal scapes usually not surpassing level of lateral ocelli; eyes moderately large (OI 0.27-0.31), situated slightly below midline of head in full-face view; head shape square or rectangular-elongate (CI 0.94-1.00); posterior margin straight.

Mesoscutum in dorsal view usually longer than wide (MSNI 0.85-0.99); dorsal face of propodeum short; propodeal spines or tubercles absent; petiole moderately to greatly flared, postpetiole with a complete, but superficial impression; subpetiolar process variable, usually absent.

Sculpture aciculate throughout; face usually with < ten longer erect setae and abundant, shorter, erect to suberect pilosity; mesonotum with abundant short, and scattered longer, erect setae; petiole and postpetiole with dense short suberect to decumbent pilosity, and postpetiole with additional longer dorso-posterior setae; abdominal tergites and sternites four to seven with sparse, scattered erect pilosity and regular appressed pubescence. Color as in workers; wings clear.



**Fig. 15.** *Crematogaster maina* sp. nov., workers. **A-C.** Worker (CASENT0317758). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Worker (CASENT0317760). **D.** Full-face. **E.** Profile. **F.** Dorsal.



**Fig. 16.** *Crematogaster maina* sp. nov., queen, male and distribution. A-C. Queen (CASENT0485040). A. Full-face. B. Profile. C. Dorsal. D. Species distribution. E-F. Male (CASENT0455252). E. Full-face. F. Profile.

## Male

### Measurements

(n = 3) HW 0.57-0.59; HL 0.45-0.48; EL 0.22-0.23; SL 0.10-0.11; MSNW 0.67-0.74; MSNL 0.61-0.66; WL 1.19-1.24; SPL 0.00; PTH 0.17-0.20; PTL 0.22-0.24; PTW 0.22-0.25; PPL 0.12-0.15; PPW 0.25-0.27; LHT 0.60-0.64; CI 1.23-1.31; OI 0.48; SI 0.20-0.25; MSNI 1.02-1.18; SPI 0.00; PTHI 0.81-0.84; PTWI 0.93-1.17; PPI 1.74-2.02; LBI 1.94-2.03.

### Description

(Fig. 16E-F) Very small (HW 0.57-0.59, WL 1.19-1.24).

Mandibles very short and reduced, with one singular apical tooth; clypeus not much protruding; eyes fairly large (OI 0.48) and protruding, midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head wider than long (CI 1.23-1.31); in full-face view ocellar triangle situated below posterior head margin, elevated with respect to rest of face; occipital carinae distinct.

Mesoscutum in dorsal view as wide as to a little wider than long (MSNI 1.02-1.18); scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposterior part rounded; metanotum protruding from below scutellum; dorsal face of propodeum short; propodeal spines absent; petiole in dorsal view oval, laterally rounded, in lateral view anteriorly greatly tapering; subpetiolar process absent; postpetiole fairly flat and short, lacking median impression.

Head sculpture reticulate; mesoscutum with very fine longitudinal carinulae; otherwise sculpture more or less shiny to aciculate; sparse appressed to decumbent pubescence on head and mesosoma, a few short erect setae on face may be present; rest of pilosity similar to queens. Color pale to light brown.

### Distribution and biology

MADAGASCAR, COMOROS, MAYOTTE. *Crematogaster maina* sp. nov. is a very abundant species at low elevations throughout the dry forests, littoral forests and spiny forests of Madagascar, the Comoros Islands and Mayotte (Fig. 16D). It has also been collected at higher elevations in more humid habitats (up to 1410 m), but we suspect that some of these occurrences could represent tramp-like introductions to suboptimal habitats. *Crematogaster maina* sp. nov. is commonly found in sympatry with *C. dentata* stat. nov., *C. ramamy* sp. nov., *C. tricolor* stat. rev. and *C. lobata*, and at some locations is also known to co-occur with *C. mafybe* sp. nov., *C. sewellii*, *C. bara* sp. nov. and *C. masokely* sp. nov. The species is most often encountered nesting arboreally in dead twigs or branches. This species has only been found at baits during the night and has never been observed foraging during the day. We conclude that it is nocturnal, which would explain its pale coloration.

### Comments

As discussed above, the two individuals of *C. maina* sp. nov. sampled for the genetic analysis are highly divergent from all but one of the rest of the Madagascar samples (13.3% maximal distance; Table 3), and further do not group as closest relatives to these in our analysis (Figs 1 and 2A). However, since we cannot find conclusive morphological evidence to distinguish the island population from the one on Madagascar, we refrain from splitting the two. With only three individuals sampled, spurious sequences (discussed below) are a possibility.

*Crematogaster malahelo* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:E66A64F7-7DBF-4580-8217-9E31A16A50D6](http://urn:lsid:zoobank.org:act:E66A64F7-7DBF-4580-8217-9E31A16A50D6)

Fig. 17

**Diagnosis**

Workers of *Crematogaster malahelo* sp. nov. can usually be distinguished from other species in the *C. degeeri*-assemblage given the characteristic promesonotal structure with a propodeum usually distinctly set off from the promesonotum in lateral view (as in Fig. 17C). *C. alafara* sp. nov. could cause possible confusion with this species, but *C. malahelo* sp. nov. bears sharp lateral margins on the pronotum (absent in *C. alafara* sp. nov.) and has shorter, triangular spines (SPI 0.03-0.07).

Mean genetic distance for *C. malahelo* sp. nov. to other species within the *C. degeeri*-assemblage in the barcode region is 10.9-19.6% (Table 3).

**Etymology**

The Malagasy word *malahelo* means “sad.” This name alludes to the rather sad fact that all three of the montane rainforest locations where this species is known to occur is heavily disturbed. The name is treated as noun in apposition.

**Type specimens**

**Holotype**

Worker: pinned, CASENT0317768, BLF17431, ex dead twig above ground [imaged on AntWeb]; original locality label: MADG'R: Kaloy, 1423 m, 18°35.39'S, 47°39.06'E, 27 Apr. 2007, disturbed montane rainforest, Fisher *et al.*, BLF#; deposited at CASC.

**Paratypes**

4 workers, pinned. #1: CASENT0317767, deposited at SAMC. #2: CASENT0317769, deposited at MHNG. #3: CASENT0317770, deposited at MCZC. #4: CASENT0317771, deposited at UCDC. #1 and #2 same collection and locality data as holotype. #3 and #4: BBB004, on tree trunk, Station Forestière Manjakatampo, -19.37083, 47.33900, 1575 m, disturbed montane rainforest, 31 Mar. 2007, B.B.Blaimer.

**Type locality**

MADAGASCAR: Antananarivo: Kaloy: -18.58998, 47.65102, 1423 m, disturbed montane rainforest.

**Other material examined**

(BBBC, CASC): refer to Supplementary Material 1.

**Worker**

**Measurements**

(n = 10) [holotype] HW 0.86-1.03 [0.93]; HL 0.80-0.94 [0.80]; EL 0.18-0.24 [0.20]; SL 0.63-0.71 [0.63]; WL 0.92-1.08 [0.94]; SPL 0.03-0.07 [0.05]; PTH 0.19-0.25 [0.21]; PTL 0.25-0.31 [0.29]; PTW 0.33-0.43 [0.43]; PPL 0.15-0.20 [0.17]; PPW 0.28-0.37 [0.34]; LHT 0.64-0.77 [0.67]; CI 1.03-1.16 [1.16]; OI 0.22-0.26 [0.25]; SI 0.74-0.80 [0.79]; SPI 0.03-0.07 [0.06]; PTHI 0.66-0.82 [0.72]; PTWI 1.24-1.52 [1.52]; PPI 1.71-2.04 [2.04]; LBI 1.36-1.53 [1.40].

**Description**

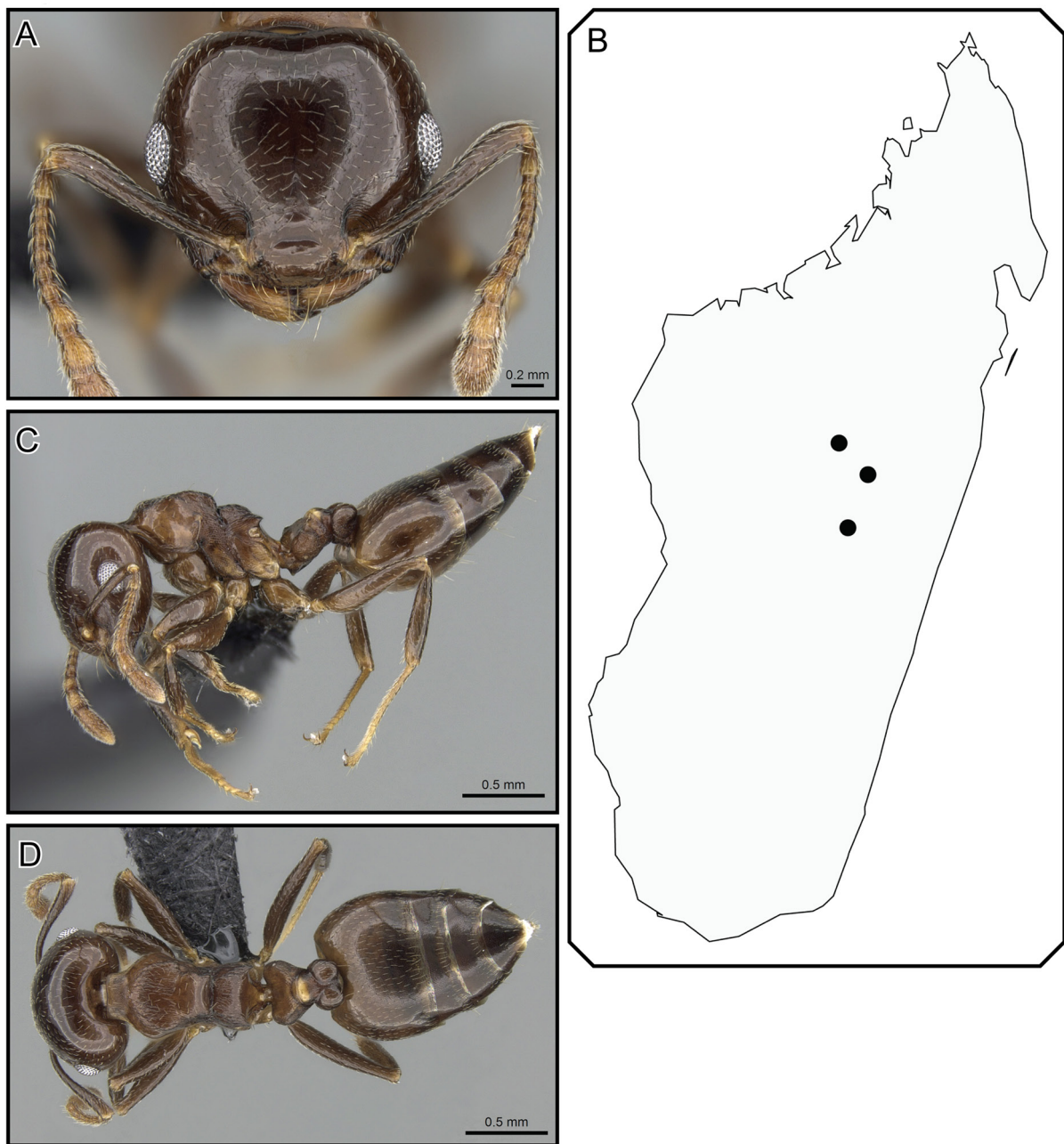
(Fig. 17A, C-D) Small to medium size (HW 0.86-1.03, WL 0.92-1.08).

Masticatory margin of mandibles with four teeth; head shape fairly quadrate or slightly wider than long (CI 1.03-1.16); posterior margin of head in full-face view laterally subangular or rounded, sometimes

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slightly medially depressed; occipital carinae distinct; antennal scapes usually about reaching or surpassing head margin; midline of eyes situated at or slightly above midline of head in full-face view; eyes moderately large (OI 0.22-0.26), slightly protruding.

Pronotum laterally angular, with sharp, raised margins; promesonotal suture indistinct, mesonotum more or less forming one plane with pronotum, but often the two separated by distinct variation in sculpture (see below); mesonotum usually without a distinct posterior face; laterally mesonotum angular to carinate, often with posterolateral denticles setting off the promesonotum distinctly from propodeum; metanotal groove fairly shallow, laterally constricted; propodeal spines very short (SPI 0.03-0.07),



**Fig. 17.** *Crematogaster malahelo* sp. nov., worker and distribution. **A, C-D.** Worker (CASENT0317768). **A.** Full-face. **C.** Profile. **D.** Dorsal. **B.** Species distribution.

triangular dents or spines; dorsal face of propodeum distinct, convex; posterior face of propodeum steeply sloping; petiole in dorsal view from broadly to strongly flared and usually strongly concave, dorsolaterally carinate but without posterolateral tubercles or denticles; subpetiolar process usually present as small rounded tooth; postpetiole wider than long, very distinctly bilobed, with broad median impression; subpostpetiolar process absent.

Head sculpture shiny to aciculate; pronotum dorsally costulate and contrasting abruptly with a shiny to aciculate mesonotum; dorsal face of propodeum carinate or reticulate; rest of mesosoma, petiole and postpetiole aciculate to reticulate; face usually with < four erect, longer setae, and regular, shorter, appressed to suberect pubescence; promesonotum usually with < eight erect, long setae; otherwise promesonotum dorsally with sparse appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short, erect setae posterolaterally, and shorter suberect, decumbent or appressed pubescence; abdominal tergites four to seven with sparse, short, erect pilosity, more abundant and longer on sternites four to seven, and regular appressed to decumbent pubescence throughout. Color reddish brown to dark brown.

### Queen and male

Queens and males remain unknown for this species.

### Distribution and biology

MADAGASCAR. *Crematogaster malahelo* sp. nov. is a rare species endemic to montane forest of the central highlands in Madagascar (Fig. 17B). It has been collected from only three locations, all of which harbor unprotected, rather disturbed forest fragments (SF Manjakatempo, Andranorovitra, Kaloy). Given this restricted distribution the species is exclusively sympatric with *C. mafybe* sp. nov. and allopatric with the rest of the *C. degeeri*-assemblage. The few collections have been made from dead twigs above the ground, indicating arboreal nesting preferences.

*Crematogaster masokely* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:44FEB42B-C008-4831-BA5B-47AFF14CC7D9](http://urn:lsid:zoobank.org:act:44FEB42B-C008-4831-BA5B-47AFF14CC7D9)

Fig. 18

### Diagnosis

*Crematogaster masokely* sp. nov. can be distinguished from the rest of the *C. degeeri*-assemblage by a combination of the following characters: small eyes (OI 0.17-0.20), short antennal scapes (SI 0.67-0.75) and a tuberculate or denticulate mesonotum.

### Etymology

*Crematogaster masokely* sp. nov. is named after the species' small eyes: *maso* is Malagasy for "eye" and *kely* means "small." The name is treated as a noun in apposition.

### Type specimens

#### Holotype

Worker: pinned, CASENT0068954, BLF12840(9), ex sifted litter [imaged on Antweb]; original locality label: MADG'R: Toamasina: Ambohidena, 20 m, 24 Nov. 2005, 16°49.46'S, 49°57.85'E, littoral forest, Fisher *et al.*, BLF12840; deposited at CASC.

#### Paratypes

Workers not designated, due to the small number of existing specimens.

**Type locality**

MADAGASCAR: Toamasina: Ile St. Marie, Forêt Ambohidena: -16.82433, 49.96417, 20 m, littoral forest.

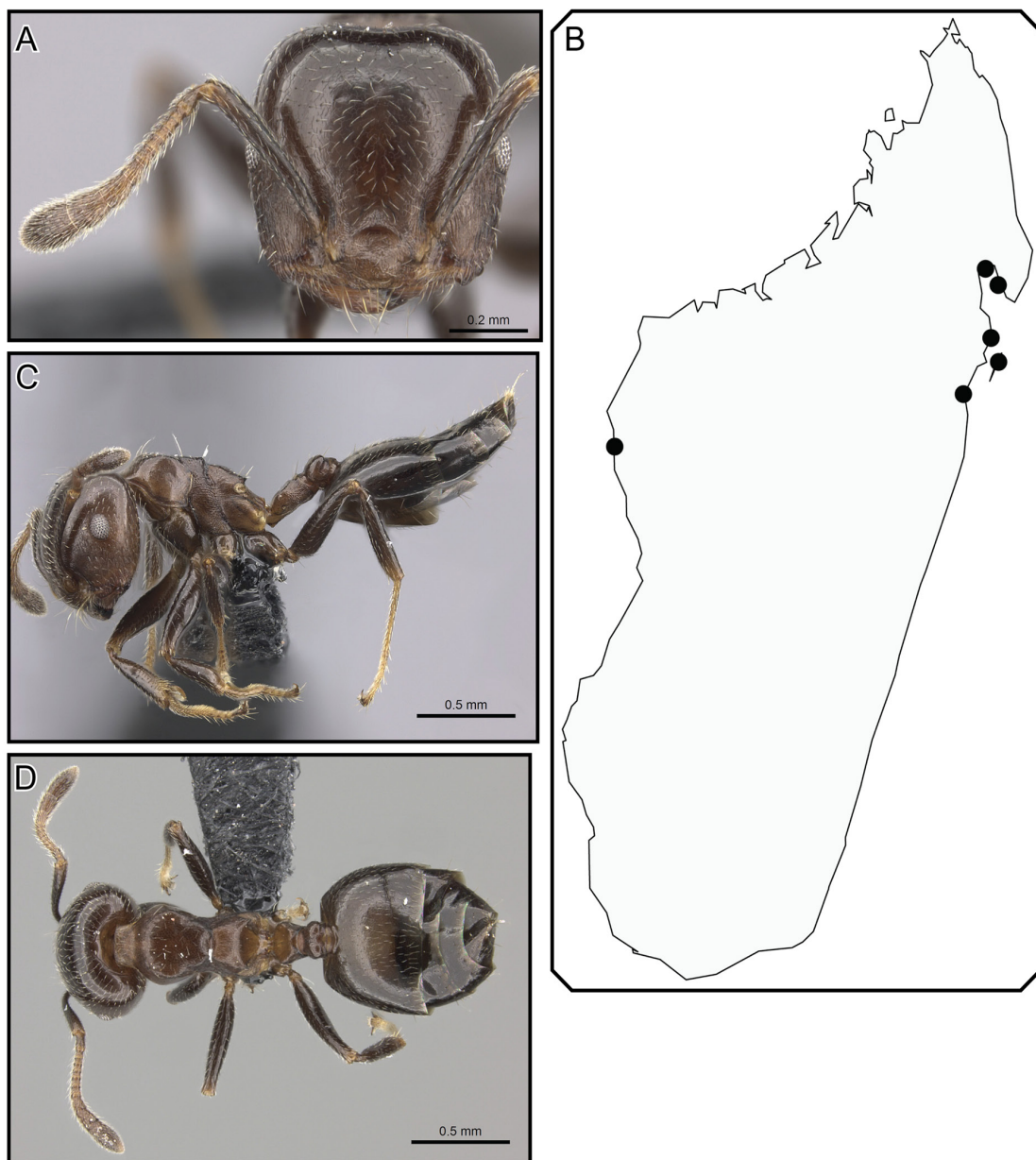
**Other material examined**

(CASC, PSWC): refer to Supplementary Material 1.

**Worker**

**Measurements**

(n = 11) [holotype] HW 0.72-0.91 [0.85]; HL 0.66-0.91 [0.83]; EL 0.13-0.18 [0.14]; SL 0.48-0.62 [0.60]; WL 0.74-0.95 [0.88]; SPL 0.01-0.06 [0.03]; PTH 0.15-0.19 [0.15]; PTL 0.21-0.29 [0.27]; PTW 0.23-



**Fig. 18.** *Crematogaster masokely* **sp. nov.**, worker and distribution. **A, C-D.** Worker (CASENT0068954). **A.** Full-face. **C.** Profile. **D.** Dorsal. **B.** Species distribution.

0.34[0.27]; PPL 0.12-0.19 [0.15]; PPW 0.19-0.28[0.24]; LHT 0.49-0.67 [0.63]; CI 0.99-1.09 [1.02]; OI 0.17-0.20 [0.17]; SI 0.67-0.75 [0.72]; SPI 0.01-0.06 [0.04]; PTHI 0.57-0.74 [0.57]; PTWI 1.01-1.23 [1.01]; PPI 1.39-1.75 [1.59]; LBI 1.33-1.68 [1.39].

### **Description**

(Fig. 18A, C-D) Small (HW 0.72-0.91, WL 0.74-0.95).

Masticatory margin of mandibles with four teeth; head shape more or less quadrate (CI 0.99-1.09); posterior margin of head in full-face view laterally angular or subangular, sometimes medially depressed; occipital carinae usually distinct; antennal scapes usually short, not reaching or surpassing head margin; midline of eyes situated at midline of head in full-face view; eyes small (OI 0.17-0.20), and confluent with lateral head margin in full-face view.

Pronotum laterally angular; promesonotal suture usually indistinct, mesonotum more or less forming one plane with pronotum; mesonotum usually without distinct posterior face; laterally mesonotum angular, ending in small posterolateral denticles or tubercles, that set mesonotum off from propodeum; metanotal groove fairly shallow, laterally constricted; propodeum with small denticles or tubercles (SPI 0.01-0.06); dorsal face of propodeum short to indistinct, posterior face of propodeum gently sloping; petiole in dorsal view broadly oval, concave, without dorsolateral carinate margins and posterolateral tubercles or denticles; subpetiolar process variable, usually small angular dent; postpetiole bilobed with a narrow median impression; subpostpetiolar process absent.

Head sculpture aciculate; promesonotum reticulate to aciculate; mesopleuron areolate, dorsal face of propodeum carinulate to reticulate; otherwise sculpture reticulate to aciculate; erect pilosity on face sparse, usually < four longer setae, and regular, short, appressed to suberect pubescence; promesonotum usually with < ten long erect setae, and very sparse, appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short erect setae posterolaterally, and sparse appressed pubescence; abdominal tergites four to seven with scattered short erect pilosity, ventrally more abundant, and regular appressed to decumbent pubescence throughout. Color medium to dark brown.

### **Queen and male**

Queens and males of this species are unknown.

### **Distribution and biology**

MADAGASCAR. *Crematogaster masokely* sp. nov. is highly endemic to the littoral forests of eastern Madagascar, with the exception of one peculiar disjunct distribution in the tsingy of the SF Beanka on the west coast (Fig. 18B). The species co-occurs with *C. tricolor* stat. rev., *C. maina* sp. nov., *C. dentata* stat. nov. and *C. ramamy* sp. nov. No colony collections of this species have been made, therefore nothing is known of its biology.

*Crematogaster ramamy* Blaimer sp. nov.

[urn:lsid:zoobank.org:act:5CE5408D-724C-4F67-819C-CB22D69360EB](http://urn:lsid:zoobank.org:act:5CE5408D-724C-4F67-819C-CB22D69360EB)

Fig. 19

### **Diagnosis**

Within the *C. degeeri*-assemblage, this species is uniquely recognized by a transverse impression (Fig. 5E) across the propodeum, although this character can be faint and difficult to see. Additional useful distinguishing characters are abundant erect pilosity on the promesonotum (> eight setae) and carinulate or costulate sculpture on the pronotum. In its distribution range *C. ramamy* sp. nov. can only be confused with *C. dentata* stat. nov., however, the species has longer propodeal spines than the latter



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(*C. dentata* stat. nov.: SPI 0.01-0.10; *C. ramamy* sp. nov.: SPI 0.07-0.12), and costulate sculpture on the pronotum (aciculate - reticulate in *C. dentata* stat. nov.). Mean barcode divergences between *C. ramamy* sp. nov. and other species within the *C. degeeri*-assembly are 12.7-18.7%, except with regard to *C. degeeri*, where this is only 4.7% (Table 3). In our analyses, *C. ramamy* sp. nov. renders *C. degeeri* paraphyletic (see comments in description of *C. degeeri*).

### Etymology

*Crematogaster ramamy* sp. nov. is named after a Malagasy friend and research assistant, Maminiaina “Mamy” Rajaonarivo, in appreciation of support over several years. The name is treated as a noun in apposition.

### Type specimens

#### Holotype

Worker: pinned, CASENT0317780, BLF20074, on low vegetation [imaged on AntWeb]; original locality label: MADG’R: Mahajanga: Antanambezo, 20 m -14.87893° S, 47.97712° E, 20 Apr. 2008, mangrove, Fisher *et al.*, BLF#; deposited at CASC.

#### Paratypes

4 workers, pinned, same collection and locality data as holotype. #1: CASENT0317781, deposited at SAMC. #2: CASENT0317782, deposited at MHNG. #3: CASENT0317783, deposited at MCZC. #4: CASENT0317784, deposited at UCDC.

### Type locality

MADAGASCAR: Mahajanga: Antanambezo: -14.87893, 47.97712, 20 m, mangrove.

### Other material examined

(BBBC, CASC, PSWC): refer to Supplementary Material 1.

### Worker

#### Measurements

(n = 16) [holotype] HW 0.75-1.04 [0.95]; HL 0.71-0.94 [0.90]; EL 0.16-0.22 [0.17]; SL 0.62-0.82 [0.72]; WL 0.86-1.12 [1.03]; SPL 0.06-0.12 [0.09]; PTH 0.12-0.22 [0.18]; PTL 0.22-0.31 [0.27]; PTW 0.22-0.33 [0.28]; PPL 0.13-0.19 [0.17]; PPW 0.20-0.33 [0.27]; LHT 0.65-0.82 [0.73]; CI 1.05-1.13 [1.05]; OI 0.19-0.24 [0.19]; SI 0.75-0.87 [0.80]; SPI 0.07-0.12 [0.09]; PTHI 0.55-0.76 [0.66]; PTWI 0.95-1.14 [1.04]; PPI 1.36-1.80 [1.58]; LBI 1.27-1.41 [1.40].

#### Description

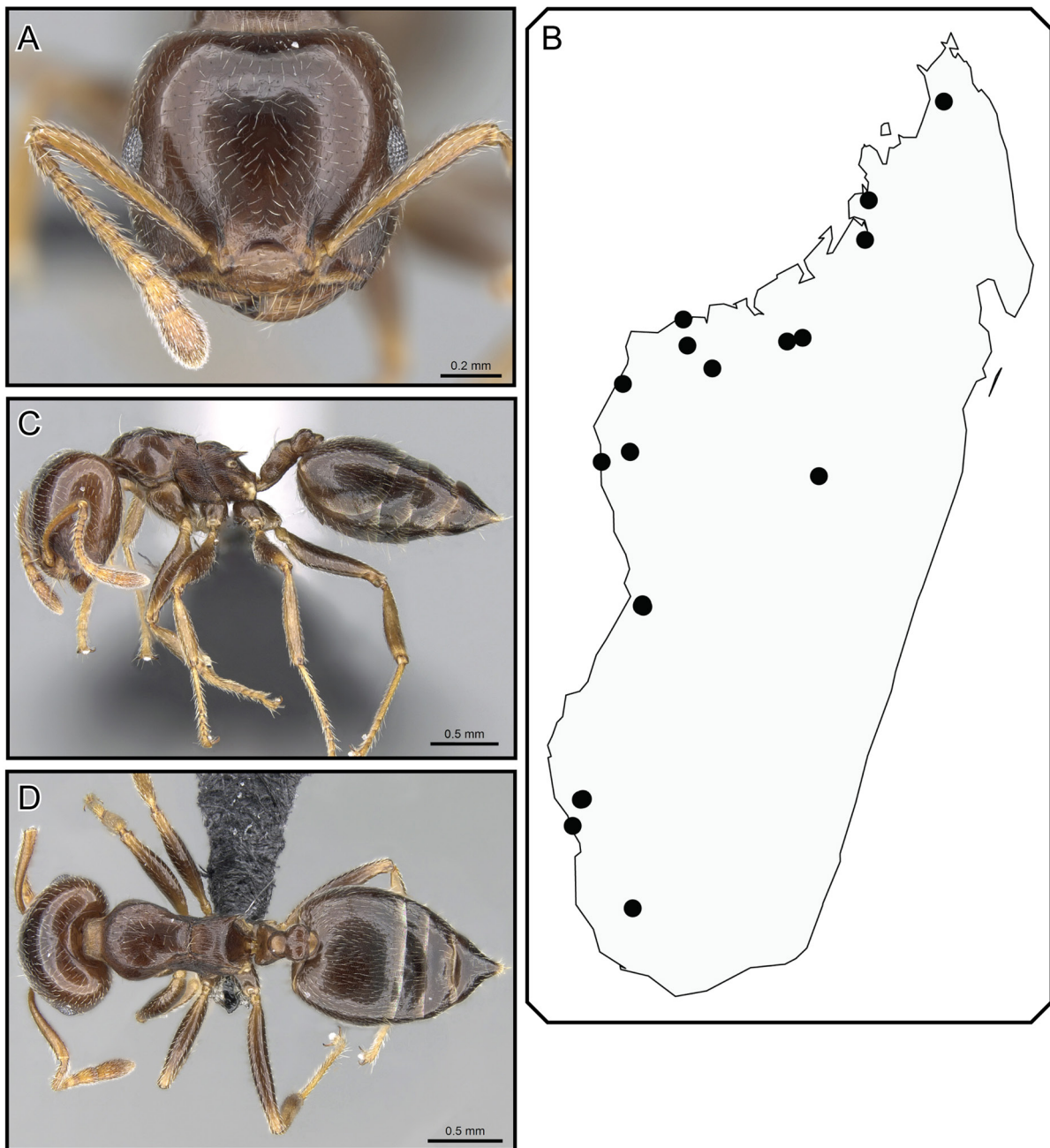
(Fig. 19A, C-D) Small to medium size (HW 0.75-1.04, WL 0.86-1.12).

Masticatory margin of mandibles with four teeth; head shape quadrate, as long or slightly longer than wide (CI 1.05-1.13); posterior margin of head in full-face view laterally rounded or subangular; occipital carinae usually distinct; antennal scapes reaching or surpassing head margin; midline of eyes situated slightly above midline of head in full-face view; eyes moderately large (OI 0.19-0.24) and protruding.

Pronotum laterally angular; promesonotal suture indistinct; mesonotum more or less forming one plane with pronotum, but often the two separated by distinct variation in sculpture (see below); mesonotum usually without posterior face; laterally mesonotum angular to carinate, not distinctly set off from propodeum; metanotal groove shallow, laterally constricted; propodeal spines short, spiniform (SPI 0.07-0.12), usually curved downwards; dorsal face of propodeum short but distinct; posterior face of

propodeum gently sloping, often with a transverse groove; petiole in dorsal view oval and fairly slender, dorsolaterally rounded, without posterolateral tubercles or denticles; subpetiolar process variable, usually a small dent; postpetiole distinctly bilobed, with a narrow median impression; subpostpetiolar process absent.

Head sculpture aciculate to reticulate; pronotum usually dorsally carinulate and contrasting abruptly with a shiny to aciculate mesonotum; mesopleuron areolate, metapleuron mostly carinulate; dorsal face of propodeum carinulate or reticulate; otherwise sculpture reticulate; face usually with six to ten



**Fig. 19.** *Crematogaster ramamy* sp. nov., worker and distribution. **A, C-D.** Worker (CASENT0317780). **A.** Full-face. **C.** Profile. **D.** Dorsal. **B.** Species distribution.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

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erect, longer setae, and regular appressed to decumbent pubescence; erect pilosity on promesonotum usually abundant, with > eight long setae; otherwise promesonotum dorsally with regular appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short erect, setae posterolaterally, and shorter suberect, decumbent or appressed pubescence; abdominal tergites and sternites four to seven usually with abundant, short, erect pilosity, and abundant appressed to decumbent pubescence throughout. Color reddish brown to dark brown.

### Queen and male

Queens and males of this species are unknown.

### Distribution and biology

MADAGASCAR. *Crematogaster ramamy* sp. nov. is a species found at low elevations in dry forest, savannah and sometimes mangrove habitats in western and northwestern Madagascar (Fig. 19B). The species further has a disjunct, isolated population at higher altitude in the transitional dry forest of RS Ambohitantely (1410 m). *Crematogaster ramamy* sp. nov. usually co-occurs with *C. dentata* stat. nov., *C. maina* sp. nov. and *C. lobata*, and at some locations also with *C. tricolor* stat. rev., *C. mafybe* sp. nov. and *C. sewellii*. Generally it has been collected nesting arboreally in dead twigs above the ground, and is attracted to arboreal fish baits as strongly during the day as at night.

### Comments

This species has close affinities with *C. degeeri*, and does not appear to be reciprocally monophyletic according to our analysis (Fig. 1). *Crematogaster ramamy* sp. nov. is however sufficiently distinguishable morphologically from *C. degeeri*, and more importantly seems quite distinct in its distribution and ecological adaptation (dry forest in contrast to montane grassland and woodland for *C. degeeri*).

### *Crematogaster sewellii* Forel, 1891

Figs 20-21

*Crematogaster inermis* r. *sewellii* Forel, 1891: 196, pl. 6, fig. 9.

*Crematogaster sewellii* – Dalla Torre 1893: 86. — Mayr 1895: 138. — Emery 1895: 342.

*Crematogaster* (*Crematogaster*) *inermis* r. *sewellii* – Wheeler 1922a: 844. — Bolton 1995: 166.

*Crematogaster* (*Acrocoelia*) *inermis* r. *sewellii* – Emery 1922: 148.

### Diagnosis

*Crematogaster sewellii* can be identified with the following unique combination of characters: very large eyes (OI 0.24-0.29), antennal scapes usually long (SI 0.77-0.87) and surpassing head margin, propodeal spines reduced to small denticles, and distinct bicoloration with head and thorax yellowish to dark orange and metasoma with abdominal segments four to seven black. Sequence divergence between *C. sewellii* and the rest of the *C. degeeri*-assemblage ranges between 12.9% and 22.2% (Table 3).

### Type material examined

(MHNG): MADAGASCAR: Fianarantsoa (Dr. Besson), six workers. Lectotype worker by present designation: CASENT0101599, lower worker of three workers on one pin, image on AntWeb.

### Other material examined

(BBBC, CASC, MHNG): refer to Supplementary Material 1.

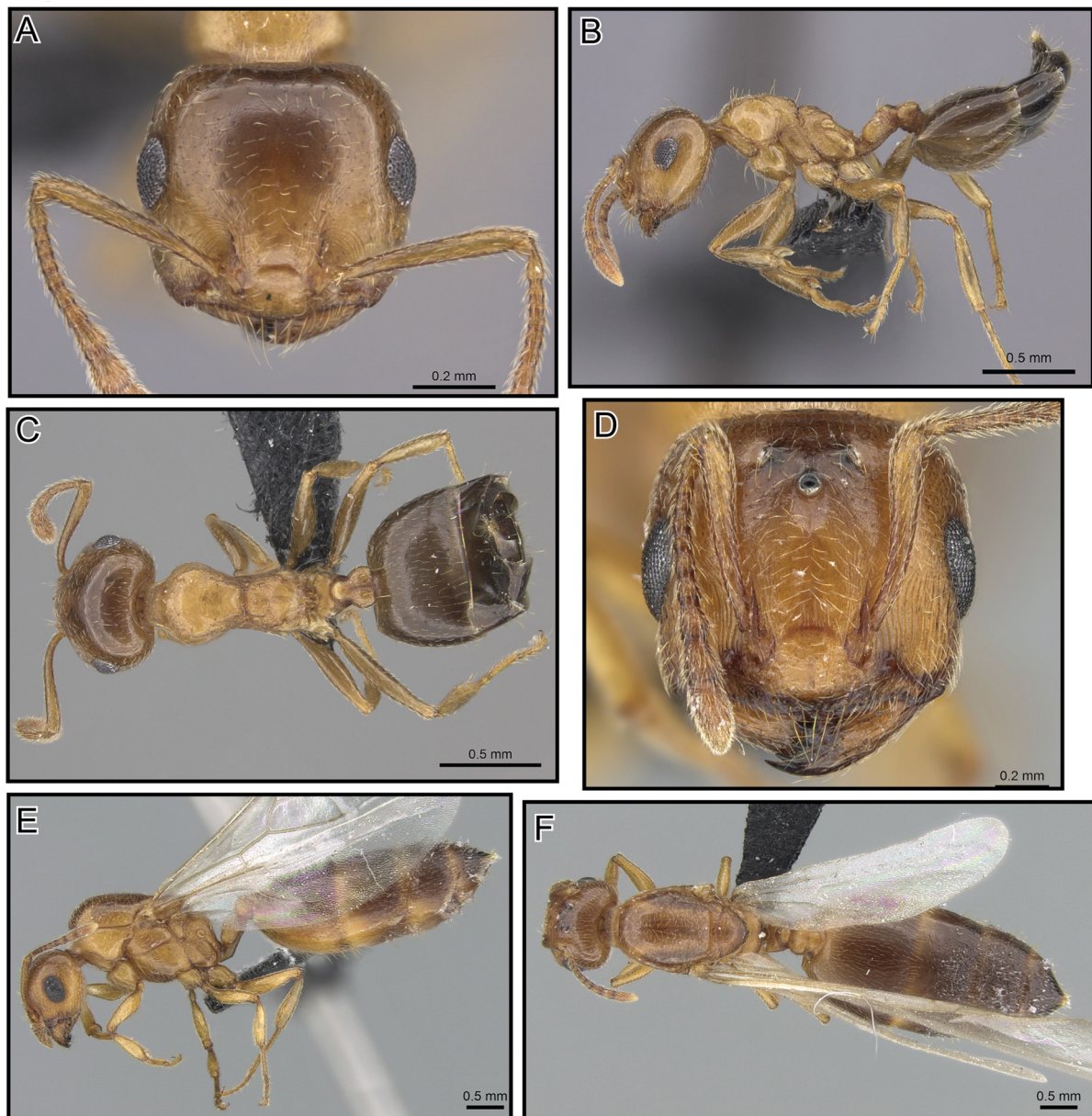
## Worker

### Measurements

(n = 20) HW 0.72-0.99; HL 0.66-0.89; EL 0.18-0.23; SL 0.56-0.70; WL 0.75-1.01; SPL 0.01-0.04; PTH 0.15-0.21; PTL 0.20-0.28; PTW 0.24-0.33; PPL 0.12-0.19; PPW 0.22-0.29; LHT 0.54-0.73; CI 1.08-1.13; OI 0.24-0.29; SI 0.77-0.87; SPI 0.01-0.05; PTHI 0.68-0.87; PTWI 1.07-1.32; PPI 1.54-1.92; LBI 1.30-1.45.

### Description

(Fig. 20A-C) Small to medium size (HW 0.72-0.99, WL 0.75-1.01).



**Fig. 20.** *Crematogaster sewellii* Forel, 1891, worker and queen. **A-C.** Worker (CASENT0120975). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Queen (CASENT0496779). **D.** Full-face. **E.** Profile. **F.** Dorsal.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

Masticatory margin of mandibles with four teeth; head shape fairly quadrate or slightly wider than long (CI 1.08-1.13); posterior margin of head in full-face view laterally subangular or rounded, often slightly medially depressed; occipital carinae distinct; antennal scapes usually reaching or surpassing head margin; midline of eyes situated distinctly above midline of head in full-face view; eyes large (OI 0.24-0.29) and strongly protruding.

Pronotum laterally angular; promesonotal suture indistinct; mesonotum usually forming a flat plane with respect to pronotum; mesonotum usually with a short posterior face; mesonotum angular laterally, posterior face carinate, distinctly set off from propodeum; posterior face of mesonotum sloping steeply into metanotal groove; metanotal groove fairly shallow, laterally constricted and bordered by carinae; propodeal spines reduced to small denticles (SPI 0.01-0.05); dorsal face of propodeum short, but distinct; posterior face of propodeum gently sloping; petiole in dorsal view broadly oval, dorsolaterally rounded, without posterolateral tubercles or denticles; subpetiolar process variable; postpetiole bilobed with a broad median impression; subpostpetiolar process absent.

Head sculpture aciculate; mesosoma, petiole, helcium and postpetiole reticulate; face usually with six to eight erect longer setae, and regular shorter, appressed pubescence; erect pilosity on promesonotum abundant, usually > ten setae; otherwise promesonotum dorsally with regular appressed to subdecumbent pubescence; propodeum laterally with two to four erect setae; petiole and postpetiole usually with a pair of long, erect setae posterolaterally, and shorter appressed pubescence; abdominal tergites and sternites four to seven with abundant short erect pilosity, and regular appressed to decumbent pubescence throughout. More or less bicolored: head, mesosoma, petiole and postpetiole reddish-orange to yellow, rest of metasoma black.

## Queen

### Measurements

(n = 1) HW 1.25; HL 1.18; EL 0.40; SL 0.80; MSNW 1.13; MSNL 1.08; WL 1.97; SPL 0.00; PTH 0.33; PTL 0.42; PTW 0.47; PPL 0.30; PPW 0.47; LHT 0.93; CI 1.06; OI 0.34; SI 0.68; MSNI 1.04; SPI 0.00; PTHI 0.79; PTWI 1.14; PPI 1.59; LBI 2.12.

### Description

(Fig. 20D-F) Small size (HW 1.25, WL 1.97). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth; antennal scapes surpassing level of lateral ocelli; eyes large (OI 0.34), situated at midline of head in full-face view; head shape square (CI 1.06); posterior margin straight.

Mesoscutum in dorsal view as wide as long (MSNI 1.04); dorsal face of propodeum long and set off at right angle to posterior face; propodeal spines or tubercles absent; petiole moderately flared, postpetiole merely impressed behind; subpetiolar process variable.

Sculpture aciculate throughout; face with eight longer erect setae (n = 1!) and abundant shorter erect to suberect pilosity; mesonotum with abundant short and scattered longer erect setae; petiole and postpetiole with dense short suberect pilosity, and postpetiole with additional longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant erect pilosity and appressed pubescence. Color as in workers; wings clear.

## Male

### Measurements

(n = 1) HW 0.57; HL 0.46; EL 0.22; SL 0.11; MSNW 0.69; MSNL 0.61; WL 1.24; SPL 0.00; PTH 0.17; PTL 0.22; PTW 0.22; PPL 0.14; PPW 0.24; LHT 0.60; CI 1.23; OI 0.47; SI 0.24; MSNI 1.14; SPI 0.00; PTHI 0.77; PTWI 0.99; PPI 1.64; LBI 2.07.

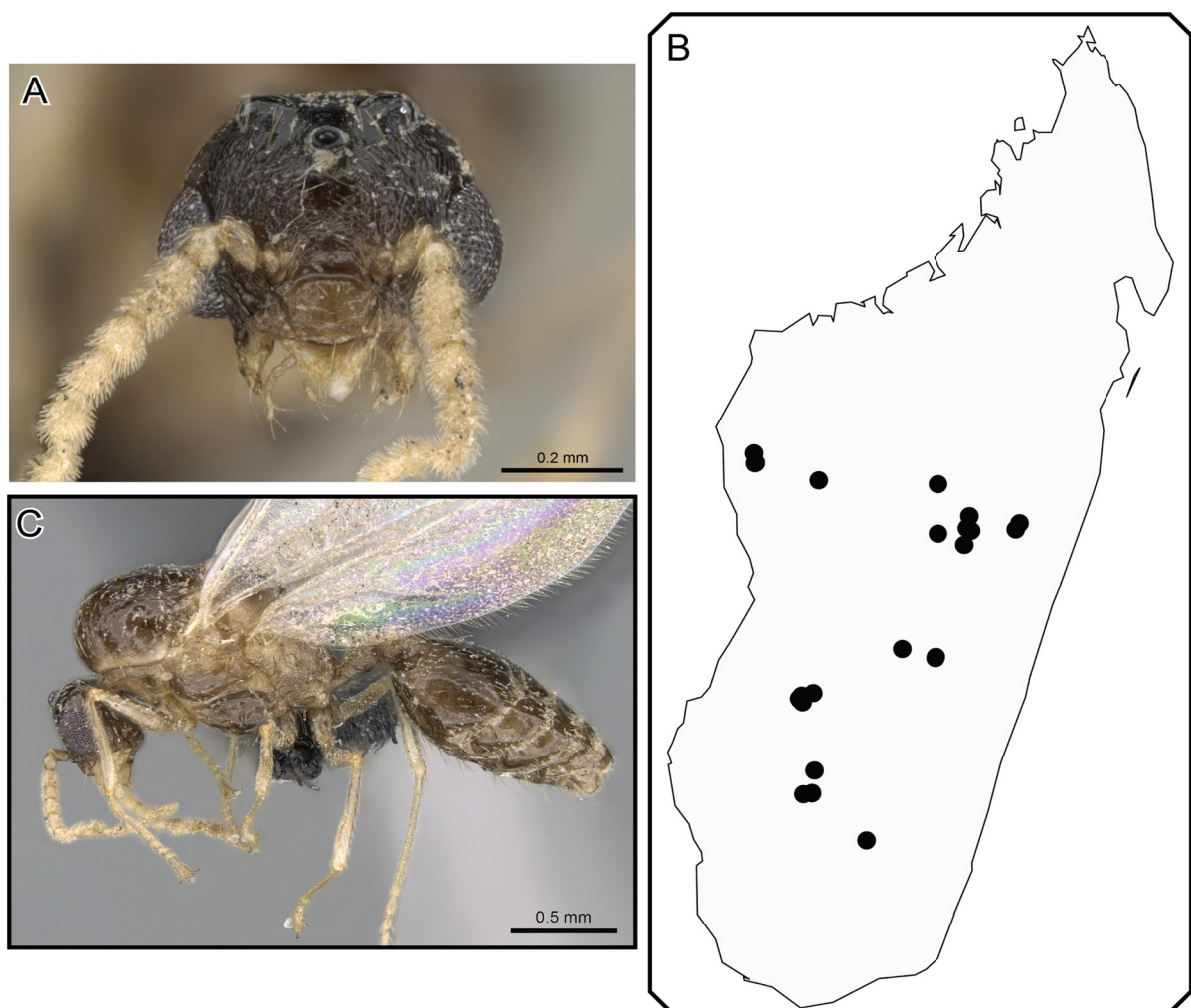
**Description**

(Fig. 21A, C) Small (HW 0.57, WL 1.24).

Mandibles very short and reduced, blunt and edentate; clypeus fairly flat; eyes fairly large (OI 0.47) and protruding, midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head wider than long (CI 1.23); in full-face view ocellar triangle situated at posterior head margin and elevated with respect to rest of face; occipital carinae distinct.

Mesoscutum in dorsal view as wide as long (MSNI 1.14), scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposterior part rounded; metanotum not protruding from below scutellum; dorsal face of propodeum almost as long as posterior face; propodeal spines absent; petiole in dorsal view oval, laterally rounded, in lateral view anteriorly greatly tapering; subpetiolar process absent; postpetiole fairly flat and short, lacking median impression.

Head sculpture reticulate; mesoscutum with very fine longitudinal carinulae; otherwise sculpture more or less shiny to aciculate; regular appressed to decumbent pubescence, and a few longer setae on face, mesoscutum, and scutellum; remaining pilosity as in queen. Color brown.



**Fig. 21.** *Crematogaster sewellii* Forel, 1891, male and distribution. **A, C.** Male (CASENT0317761). **A.** Full-face. **C.** Profile. **B.** Species distribution.

### Distribution and biology

MADAGASCAR. *Crematogaster sewellii* is commonly found in high-altitude grassland, savannah and woodland habitat in the central and south-central highland region (800-1500 m), and at lower elevations (160-600 m) in the Makay massif and the RF Beanka in western Madagascar (Fig. 21B). The species often co-occurs with *C. mafybe* sp. nov. and *C. degeeri*, and otherwise with all other species of the *C. degeeri*-assembly except *C. malahelo* sp. nov. This species appears to nest exclusively on the ground, either in the soil or under stones.

*Crematogaster tricolor* Gerstäcker, 1859 stat. rev.  
Figs 22-23

*Crematogaster tricolor* Gerstäcker, 1859: 263 (w.) [also described as new by Gerstäcker 1862: 515].

*Crematogaster tricolor* – Forel 1887: 388 (q.m.).

*Crematogaster tricolor*, junior synonym of *Crematogaster castanea* – Mayr 1907: 16. — Emery 1915: 12. — Wheeler 1922a: 830.

*Crematogaster castanea tricolor* – Arnold 1920: 489. — Emery 1922: 145. — Santschi 1926: 213.

*C. (Acrocoelia) tricolor* – Emery 1922: 145.

### Diagnosis

The tricoloration of this species (see Fig. 22B, C) serves to uniquely identify this species from all other *Crematogaster* species in the *C. degeeri*-assembly. Beyond the color, the mostly very long propodeal spines (SPI 0.10-0.26) are also useful diagnostic characters. Sequence divergence between *C. tricolor* stat. rev. and the remaining species ranges from 16.6-22.2% (Table 3).

### Type material examined

(ZMHB): MOZAMBIQUE: Tete (S. Peters), one worker; lectotype worker by present designation: CASENT0104590, image on AntWeb.

### Other material examined

(BBBC, CASC, MCZC, PSWC, ZMHB): refer to Supplementary Material 1.

### Worker

#### Measurements

(n = 20) HW 0.71-1.27; HL 0.65-1.14; EL 0.16-0.26; SL 0.54-0.88; WL 0.73-1.37; SPL 0.08-0.30; PTH 0.16-0.30; PTL 0.20-0.37; PTW 0.23-0.47; PPL 0.11-0.25; PPW 0.18-0.39; LHT 0.54-0.96; CI 1.10-1.19; OI 0.21-0.25; SI 0.77-0.83; SPI 0.10-0.26; PTHI 0.60-0.80; PTWI 1.07-1.26; PPI 1.46-1.85; LBI 1.30-1.45.

#### Description

(Fig. 22A-C) Small to large size (0.71-1.27, WL 0.73-1.37), usually large.

Masticatory margin of mandibles with four teeth; head shape usually wider than long (CI 1.10-1.19); posterior margin of head in full-face view laterally subangular, medially depressed; occipital carinae distinct; antennal scapes reaching or surpassing head margin; midline of eyes situated above midline of head in full-face view; eyes fairly large (OI 0.21-0.25) and strongly protruding.

Pronotum laterally angular; promesonotal suture indistinct; mesonotum often slightly raised with respect to pronotum, and with a median tubercle or carinae; mesonotum usually with a short posterior face; laterally mesonotum angular, posterior face carinate, distinctly set off from propodeum; posterior

face of mesonotum sloping steeply into metanotal groove; metanotal groove fairly shallow, laterally constricted and bordered by carinae; propodeal spines short to medium-sized (SPI 0.10-0.26), straight and moderately diverging; dorsal face of propodeum as long as posterior face; posterior face of propodeum gently sloping; petiole in dorsal view moderately flared and concave, dorsolaterally rounded, without posterolateral tubercles or denticles; subpetiolar process variable; postpetiole narrowly bilobed with a sharp median impression; subpostpetiolar process absent.

Head and mesosomal sculpture areolate; petiole, helcium and postpetiole dorsally and ventrally reticulate; erect pilosity on face scarce, usually less than four erect longer setae, and regular, shorter, appressed pubescence; erect pilosity on promesonotum scarce, usually only two to four humeral setae; otherwise promesonotum dorsally with regular appressed to subdecumbent pubescence; petiole and postpetiole usually with a pair of short, erect setae posterolaterally, and shorter appressed pubescence; abdominal tergites four to seven with sparse, short, erect pilosity, more abundant and longer on sternites four to seven, and abundant appressed to decumbent pubescence throughout. Distinctly tricolored: Head and mesosoma reddish-orange, first half of abdominal segment four yellow, rest black.

## Queen

### Measurements

(n = 8) HW 1.61-1.77; HL 1.38-1.49; EL 0.44-0.49; SL 0.98-1.10; MSNW 1.20-1.45; MSNL 1.32-1.46; WL 2.43-2.69; SPL 0.00-0.04; PTH 0.38-0.44; PTL 0.42-0.57; PTW 0.57-0.67; PPL 0.36-0.40; PPW 0.57-0.64; LHT 1.13-1.30; CI 1.14-1.21; OI 0.31-0.33; SI 0.69-0.74; MSNI 0.85-1.04; SPI 0.00-0.02; PTHI 0.72-1.05; PTWI 1.18-1.53; PPI 1.41-1.69; LBI 1.98-2.30.

### Description

(Figs 22D-F) Medium size (HW 1.61-1.77, WL 2.43-2.69). With worker characters, except as follows.

Masticatory margin of mandibles with five teeth; antennal scapes reaching or surpassing level of lateral ocelli; eyes fairly large (OI 0.31-0.33), situated at midline of head in full-face view; head distinctly wider than long (CI 1.14-1.21), tapering from anterior to posterior margin; posterior margin straight.

Mesoscutum in dorsal view longer than wide, or as wide as long (MSNI 0.85-1.04); dorsal face of propodeum short; propodeal tubercles present; petiole moderately flared, postpetiole merely impressed behind; subpetiolar process variable.

Sculpture carinulate on face and propodeum, otherwise aciculate throughout; face usually with > six longer erect setae and abundant shorter erect to suberect pilosity; mesonotum with abundant short and scattered longer erect setae; petiole and postpetiole with dense, short, suberect pilosity, and postpetiole often with additional, longer dorso-posterior setae; abdominal tergites and sternites four to seven with abundant appressed pilosity and sparse, short, erect pilosity. Tricoloration is similar to workers, but less distinct; wings clear.

## Male

### Measurements

(n = 3) HW 0.73-0.82; HL 0.54-0.60; EL 0.27-0.31; SL 0.10-0.15; MSNW 0.80-0.95; MSNL 0.77-0.91; WL 1.40-1.78; SPL 0.00; PTH 0.21-0.24; PTL 0.25-0.29; PTW 0.27-0.31; PPL 0.18; PPW 0.28-0.35; LHT 0.73-0.91; CI 1.32-1.36; OI 0.50-0.53; SI 0.19-0.26; MSNI 1.01-1.04; SPI 0.00; PTHI 0.80-0.83; PTWI 1.05-1.10; PPI 1.59-1.91; LBI 1.92-2.00.

### Description

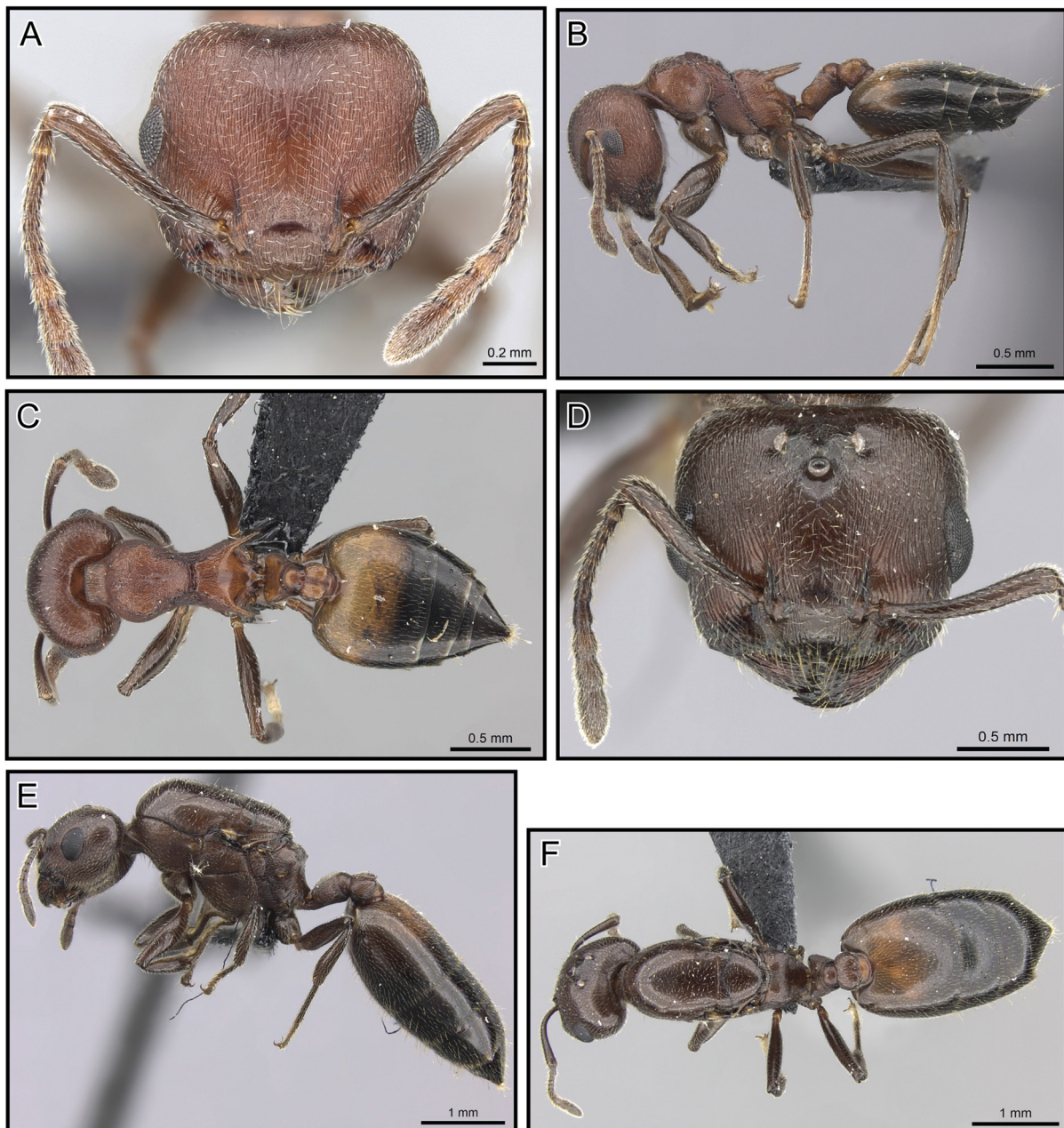
(Fig. 23A, C) Small (HW 0.73-0.82, WL 1.40-1.78).



BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

Mandibles short (not touching when closed) with two regular-sized teeth; clypeus fairly flat; eyes large (OI 0.50-0.53) and protruding, midline of eyes situated well below midline of head, almost extending to clypeal margin; antennae 12-segmented; head wider than long (CI 1.32-1.36); in full-face view ocellar triangle situated at posterior head margin and elevated with respect to rest of face; occipital carinae distinct.

Mesoscutum in dorsal view as wide as long (MSNI 1.01-1.04); scutellum in dorsal view broadly tapering from anterior to posterior end, dorsoposterior part rounded; metanotum protruding from below



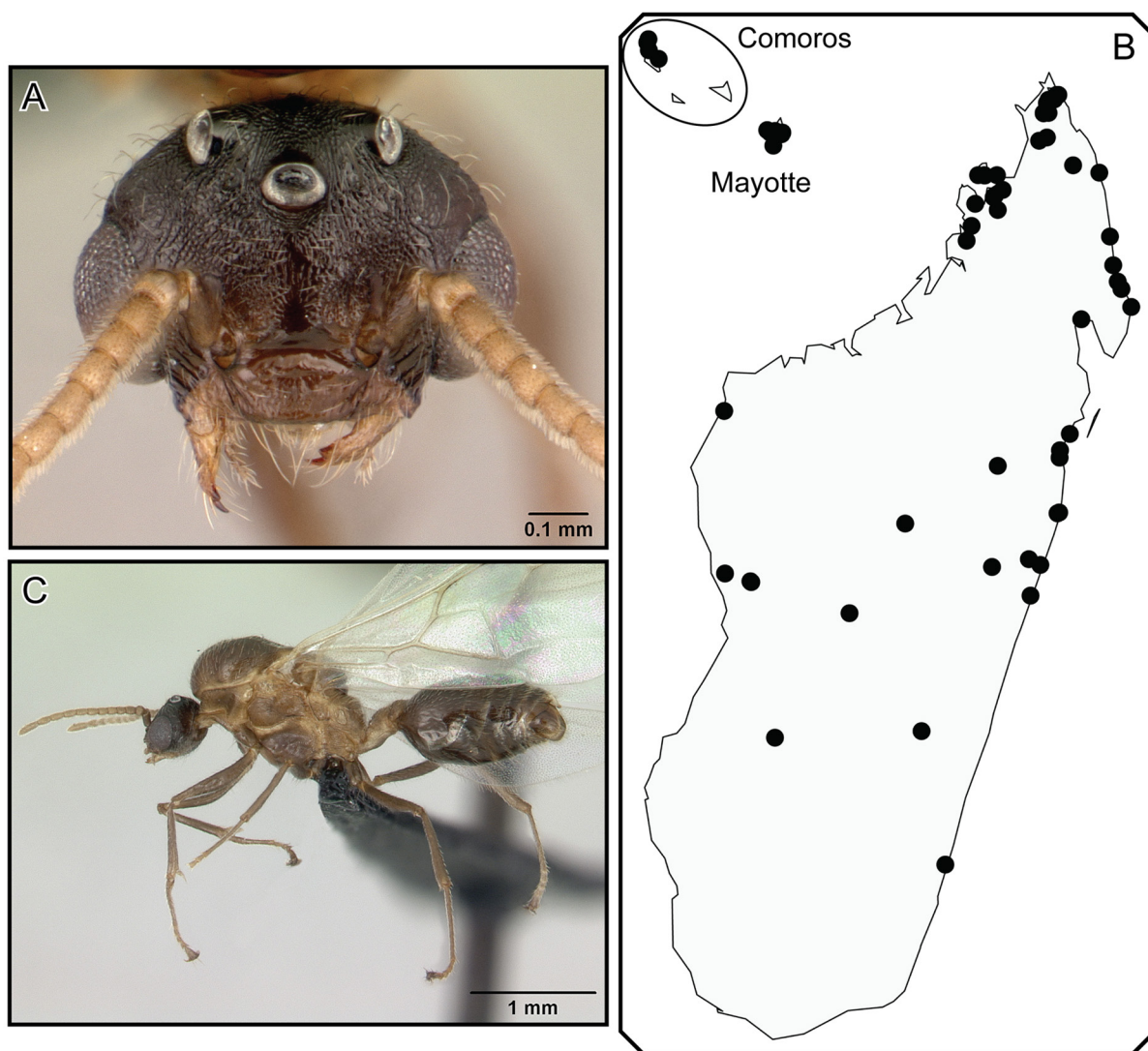
**Fig. 22.** *Crematogaster tricolor* Gerstäcker, 1859 stat. rev., worker and queen. **A-C.** Worker (CASENT0120944). **A.** Full-face. **B.** Profile. **C.** Dorsal. **D-F.** Queen (CASENT0120949). **D.** Full-face. **E.** Profile. **F.** Dorsal.

scutellum; dorsal face of propodeum almost as long as posterior face; propodeal spines absent; propodeal spiracle situated in a margined depression on propodeum; petiole in dorsal view oval, laterally rounded, in lateral view anteriorly greatly tapering; subpetiolar process absent; postpetiole fairly flat and short, lacking median impression.

Head sculpture reticulate to carinulate; mesoscutum with very fine longitudinal carinulae; otherwise sculpture more or less shiny to aciculate; abundant, short, erect pilosity, but very few longer setae on face, mesoscutum, and scutellum; remaining pilosity as in queens. Color brown.

### Distribution and biology

MADAGASCAR, COMOROS, MAYOTTE, MOZAMBIQUE [East Africa?]. *Crematogaster tricolor* stat. rev. was originally described from Mozambique (see comments), but we limit ourselves here to its description in the Malagasy region. The species has been recently collected in scrublands of coastal areas and urban and disturbed habitats in northern, eastern and central Madagascar, and in Comoros and



**Fig. 23.** *Crematogaster tricolor* Gerstäcker, 1859 stat. rev., male and distribution. A, C. Male (CASENT0136505). A. Full-face. C. Profile. B. Species distribution.

BLAIMER B. & FISHER B.L., The *Crematogaster degeeri*-species-assemblage

Mayotte, occurring at elevations from 0 m to 1240 m (Fig. 23B). Collections in native habitat have been made in dry forest and littoral forest in northern Madagascar. *Crematogaster tricolor* stat. rev. co-occurs usually with *C. dentata* stat. nov., *C. maina* sp. nov. and *C. lobata*, and at a few localities also with *C. sewellii*, *C. mafybe* sp. nov. and *C. masokely* sp. nov. Very few colonies have been collected from dead twigs above ground, indicating that this species has an arboreal nesting habit.

### Comments

We raised *Crematogaster tricolor* from subspecies to species status considering the following points.

1) We examined the syntype specimens of *C. castanea tricolor* in ZMHB and found them to be conspecific to our recent collections from the Malagasy region.

2) We examined images of syntype specimens of *C. castanea* Smith, which are available on AntWeb (CASENT0102953), and found them to be a good match for specimens one of us (B. Blaimer) had received from a colleague collected in Mozambique.

3) Both this *C. castanea* material and the *C. tricolor* material from Madagascar were included in a molecular biogeographic study on *Crematogaster* ants (Blaimer 2012b), where the sequences of these specimens proved to be divergent and clearly not conspecific.

In this study, we limit ourselves to describing the presence of *C. tricolor* stat. rev. in the Malagasy region, although the species should still occur on the African mainland. Recent ant collections from Mozambique are poor, and historic collections are in such disarray for this genus that they would be only manageable to cite in a large scale taxonomic project on African *Crematogaster*, which is not the focus of this project. Moreover, apart from *C. tricolor* stat. rev., there are 18 further subspecies currently listed by Bolton (2012) for *C. castanea*, described from all over East and Central Africa, that would need to be revised during such a comprehensive undertaking.

The predominant occurrence of this species in urban and disturbed habitats, and the two distinct clades in the mitochondrial data with different affinities to the Comoros and Mayotte populations (Fig. 2, see above) suggest that this species was only recently introduced to Madagascar.

### Discussion

In this study, we have presented a revision of the *C. degeeri*-species-assemblage based on morphological and molecular data, and describe and re-describe a total of 12 species, seven of which are new to science. In four cases (*C. degeeri*, *C. ramamy* sp. nov., *C. maina* sp. nov., *C. dentata* stat. nov.) the mitochondrial data has not lent unequivocal support for our preformed species hypotheses based on morphology. We have reported on this in the context of species descriptions, but it seems worthwhile to reiterate and elaborate briefly on the potential causes of these discrepancies.

In the case of *C. degeeri* and *C. ramamy* sp. nov. the data indicate that these species are not reciprocally monophyletic with respect to each other (Fig. 1). These two species are indeed morphologically very similar, with differences mainly in promesonotal structure and sculpture. They could represent the products of a very recent, or even ongoing speciation event, and given their diverging habitat preferences (mainly low elevation dry forest for *C. ramamy* sp. nov. and mainly montane habitats for *C. degeeri*), this process may well be environmentally driven. A different issue to consider is the possibility that pseudogene (Nuclear mitochondrial DNA [NUMTs], Buhay 2009; Song *et al.* 2008) sequences are responsible for this pattern. Although we found no evidence of NUMTs in the relevant sequences, such as heteroplasmy or stop codons, we are reluctant to give much credence to potentially questionable results. The same line of reasoning has led us to ignore the non-monophyly of the individuals sampled for *C. maina* sp. nov. (see Figs 1 and 2A). These results could either represent a highly divergent population on Comoros (and Nosy Faly), or be caused by spurious data. In any case, the 13.3% sequence divergence between Comoros and Madagascar in *C. maina* sp. nov. remains within the limits of sequence divergence found

for other widespread species of *Crematogaster* in Madagascar, for example in *C. kelleri* (Blaimer & Fisher 2013) or *C. ranavalonae* (Blaimer 2012a).

Similarly, our analyses have lent virtually no support to grouping the Mauritius and the Madagascar population of *C. dentata* stat. nov. (Fig. 1 and Fig. 2B). Here the sequence divergence is somewhat smaller (11.2%) than in *C. maina* sp. nov. Despite the fact that Mauritius is separated by almost 900 km of open ocean from Madagascar and gene flow between the two populations is probably non-existent, this result seems to indicate a low level of mitochondrial genetic divergence. Since reproductive isolation between these disjunct populations cannot be tested, the question of whether to separate the populations into two species or not is a rather philosophical one, and our decision must be somewhat arbitrary.

The limitations of our molecular data are obvious, as only a short stretch of the barcoding region was sampled, and we wish to avoid drawing poorly supported conclusions about phylogeographic relationships between regions. The pattern seen in *Crematogaster tricolor* stat. rev. (as discussed above, Fig. 2C) is nonetheless quite intriguing and could be evidence of more frequent dispersal events of this species between Madagascar and the Indian Ocean Islands. This may also indicate that this species could be a very recent addition to the Malagasy fauna, though this hypothesis currently lacks sufficient data for support. For the reasons already stated above, we had to further ignore the potential that any of the widespread species treated here could also occur on the African mainland. For *C. tricolor* stat. rev., *C. maina* sp. nov. and *C. dentata* stat. nov. this possibility should be considered in the future when more specimens and data on East African *Crematogaster* become available.

To conclude, this revision solves the last piece of the taxonomic puzzle of *Crematogaster* ants in the Malagasy region. Prior to the start of this revisionary work, there were 20 species and numerous subspecies described for this genus and region. With the publication of this study we have raised the total number of species for *Crematogaster* in Madagascar to 34, of which 19 were new to science (Blaimer 2010; Blaimer 2012c). With each of these taxonomic papers it has become clearer that even in such a seemingly conspicuous ant genus as *Crematogaster*, a large part of the species diversity actually consists of rare, endemic species with very restricted distributions. In other parts of the world much of this diversity surely remains hidden and undescribed, and we hope that the present study can help provide guidelines for future, much-needed taxonomic work on *Crematogaster* ants.

## Acknowledgements

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