Zoological Journal of the Linnean Society, 2022, **194**, 893–937. With 9 figures.

Taxonomy in the phylogenomic era: species boundaries and phylogenetic relationships among North American ants of the *Crematogaster scutellaris* group (Formicidae: Hymenoptera)

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Received 5 February 2021; revised 20 May 2021; accepted for publication 24 June 2021

We investigate the species-level taxonomy and evolutionary history of Nearctic ants in the *Crematogaster scutellaris* group (Hymenoptera: Formicidae), drawing on evidence from morphology and UCE (ultraconserved element) phylogenomics. The New World species in this group form a well-supported clade that originated in the Late Miocene (~7.3 Mya) and subsequently diverged into three major lineages: the *C. coarctata* clade (south-western Nearctic), the *C. opaca* clade (south-western Nearctic and northern Neotropics) and the *C. lineolata* clade (eastern Nearctic and Caribbean, with four isolated south-west endemics). We hypothesize trans-Beringian dispersal into the New World, west-to-east movement within North America and restriction of mesophilic species to the east with increasing aridification of the west. The ancestral nesting behaviour of these ants is inferred to be ground-dwelling, and this is still the predominant condition in the arid west, whereas most species in the eastern United States are arboreal. We resurrect from synonymy nine species and describe three new species: ***C. detecta* sp. nov.** (from Nevada**),** ***C. parapilosa* sp. nov.** (Florida) and ***C. vetusta* sp. nov.** (Arizona). We provide a worker-based key to the 34 species of *Crematogaster* occurring in America north of Mexico, but emphasize that there are still ongoing taxonomic issues that need to be resolved.

ADDITIONAL KEYWORDS: biogeography – morphology – Nearctic – Neotropical – systematics – ultraconserved elements.

INTRODUCTION

Knowledge of species-level diversity is incomplete for many insect groups (Cardoso *et al.*, 2011; Foottit & Adler, 2017). The situation is particularly acute for tropical insects, but there are also many species-rich taxa in temperate regions that pose taxonomic challenges (Danks & Smith, 2017). Here we consider one such example, the Nearctic ants in the *Crematogaster scutellaris* group (Hymenoptera: Formicidae). We employ a combination of morphological and phylogenomic data to make progress towards clarifying species boundaries and relationships among these species. While molecular (usually DNA sequence) data have been used for decades to assist in the resolution of taxonomic problems in insects, the deployment of genome-scale data, involving hundreds to thousands of orthologous loci, is a more recent development (Ješovnik *et al.*, 2017; Cong *et al.*, 2020; Huang *et al.*, 2020; Longino & Branstetter, 2020; Prebus, 2021). Our study adds to the growing body of evidence of the usefulness of this approach.

At present the ant genus *Crematogaster* Lund, 1831 is divided into two subgenera: *Crematogaster s.s.* and *Orthocrema* Santschi, 1918 (Blaimer, 2012b). A global phylogeny shows three distinct lineages within the genus, wherein the initial split occurs between *Orthocrema* and *Crematogaster s.s.*, and the latter is divided into a global clade and a distinct Australasian

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[Version of record, published online 8 March 2022; http://zoobank.org/ urn:lsid:zoobank.org:pub:6144DD31-0F7B-4589-86A3-F40994452C9]

endemic clade (Blaimer, 2012a). Within the global clade of the subgenus *Crematogaster*, the *C. scutellaris* group (*sensu* Blaimer, 2012b) forms a distinct group with a distribution encompassing the Palaearctic, Nearctic and northernmost Neotropical regions. The New World representatives of the *C. scutellaris* group form a subclade that is estimated to have originated in the Late Miocene (Blaimer, 2012a). In the current study we recognize 37 nominal species in this New World subgroup, 28 of which occur in the United States.

Ants in the genus *Crematogaster* have a number of intriguing biological features that have attracted the attention of myrmecologists, including, in at least some species, the use of carton in nest construction, extrusion of toxic repellents via the sting, and close associations with plants and honeydew-producing insects (Blaimer, 2021). However, the species-level taxonomy of the genus has generally proved to be challenging, and the Nearctic species are no exception. Descriptions of North American species, mostly belonging to what is now known as the *C. scutellaris* group, accumulated in a piecemeal fashion until Creighton (1950) attempted to provide a coherent treatment of all species. This was followed by two important contributions by Buren (1959, 1968), with his second paper providing the most recent usable key to Nearctic species of *Crematogaster* (*Crematogaster*). Other significant work since then has included a review of the species of the eastern United States (Johnson, 1988) and the description of a new, cryptic species from Florida (Deyrup & Cover, 2007).

Recently, a taxonomic treatise on the North American *Crematogaster* was published (Morgan & Mackay, 2017), under the imprint of a publishing company that accepts manuscripts 'as is', without editorial oversight (Fang, 2014). In this instance, the resulting product contains a number of serious taxonomic misjudgements. In particular, several well-known and distinctive *Crematogaster* species were synonymized under the names of other species, with inadequate justification. This synonymy has increased confusion because the affected species are now removed from online databases and catalogues (e.g., https://antmaps.org/, https://antweb.org), and information about the biology and distribution of these species has become conflated with that of other species.

The first objective of this paper is to address these problems by resurrecting and diagnosing nine of the recently synonymized species, and by highlighting ongoing taxonomic issues that need to be resolved. We use a phylogenomic approach – targeted enrichment of ultraconserved elements or UCEs (Faircloth *et al.*, 2012; Branstetter *et al.*, 2017) – to generate a well-supported phylogenetic tree, which provides a framework for more extensive morphological studies. The morphological work focuses largely on the western Nearctic fauna, where both species diversity and taxonomic difficulties are greatest. Although we employ traditional qualitative features, such as shape, integument sculpture and pilosity, we also attempt to provide more objective, quantitative measures of species differences. Our findings are summarized in a provisional worker-based key to the species of *Crematogaster* occurring in North America north of Mexico. Our second objective is to delineate the evolutionary history of the *C. scutellaris* group in North America. We use the newly reconstructed phylogeny and our phylogenomic data to infer divergence ages, reconstruct the biogeographic history of the group and estimate ancestral nesting preferences. We discuss these findings in the context of existing work on the dispersal history of insects to, and within, the Nearctic region.

MATERIAL AND METHODS

PHYLOGENOMICS

We selected 47 individuals representing 27 putative North American species of the *Crematogaster scutellaris* group; six additional samples from Mexico, Central America and the Caribbean; and two Old World members of the clade [*C. ionia* Forel, 1911 and *C. scutellaris* (Olivier, 1792)]. Two other species of *Crematogaster*, outside but near the *C. scutellaris* group, *C. lotti* Weber, 1943 and *C.* cf. *rogenhoferi*, were used as outgroups. Table S1 in the Supporting Information provides voucher information for all sequenced samples.

DNA was extracted from single ants, either adults or pupae, using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA) and quantified with a Qubit fluorometer (HS Assay Kit, Life Technologies Inc., Carlsbad, CA). We sheared 5–50 ng input DNA to a target size of ~600 bp using either a Diagenode BioRuptor (Diagenode Inc., Denville, NJ) or QSonica Q800R3-110 (Qsonica Inc., Newtown, CT). This product served as input for a modified genomic DNA library preparation protocol (Kapa Hyper Prep Library Kit, Kapa Biosystems) that included SPRI bead cleanup using a generic substitute (Rohland & Reich, 2012) and custom dual-indexing barcodes (Glenn *et al.*, 2019). For UCE enrichment, nine to ten libraries were combined at equimolar ratios and adjusted close to a final pool target concentration of 147 ng/mL. Each pool was enriched using a set of custom-designed probes, hym-v2-ants (MYcroarray, Inc., now ArborBiosciences, Ann Arbor, MI) targeting 2524 UCE loci in ants (Branstetter *et al.*, 2017), following a standardized in-solution protocol (Ward & Branstetter, 2017; Blaimer *et al.*, 2018). The DNA concentration of enriched pools was quantified with qPCR using a CFX96 Thermal Cycler (Bio-Rad, Hercules, CA), and these values were used to make an equimolar pool-of-pools, which was submitted for sequencing on an Illumina HiSeq 4000 at Novogene (Novogene Corporation, Sacramento, CA). For 22 of the samples, library preparation, enrichment and sequencing were carried out by RAPiD Genomics (Gainesville, FL), using similar protocols.

Initial bioinformatics steps, including read cleaning, assembly and alignment, were performed using the software package PHYLUCE v.1.6.7 (Faircloth, 2016). Demultiplexed FASTQ data were cleaned and trimmed using Illumiprocessor, a wrapper programme around Trimmomatic (Bolger *et al.*, 2014). Cleaned reads were assembled with SPAdes v.3.12.0 (Bankevich *et al.*, 2012). Sequence statistics are given in the Supporting Information, Table S2. Identification of UCE loci, alignment with Mafft and alignment trimming with GBlocks (Castresana, 2000) were carried out as described in Blaimer *et al.* (2015; 2016). We chose two subsets of trimmed UCE locus alignments, retaining 1869 and 2204 loci in which each locus was present in at least 90% and 80% of the taxa, respectively. These two subsets were then concatenated to a 90% and 80% matrix, and further inspected and trimmed for outliers and misaligned sequences using the programme spruceup (Borowiec, 2019) with *cut-off* initially set to 0.95, 0.97 and 0.98, and all other parameters at the default values. From the resulting spruceup-trimmed (90%-0.95-spruceup, 90%-0.97-spruceup, 90%-0.98-spruceup, 80%-0.95-spruceup, 80%-0.97-spruceup, 80%-0.98-spruceup), as well as the untrimmed 90% and 80% alignments, we then calculated alignment statistics, such as length, amount of missing data, number of parsimony-informative sites (PIC) and base composition using the programme AMAS v.1.0 (Borowiec, 2016) (Supporting Information, Table S3).

Concatenated phylogenetic analyses were performed on six untrimmed and spruceup-trimmed matrices, both with and without employing data partitioning prior to analyses. We did not proceed with the 0.95 cutoff as this amount of trimming proved too stringent. Our partitioning strategy aimed at modelling patterns of rate variation within and among UCE loci by dividing loci into core and flanking regions, using the Sliding-Window Site Characteristics (SWSC-EN) algorithm described in Tagliacollo & Lanfear (2018). The *r cluster* algorithm (Lanfear *et al.*, 2014) in PartitionFinder2 (Lanfear *et al.*, 2017) was then used to combine subsets with similar properties. We analysed the resulting concatenated data matrices with 934 (90%-untrimmed), 746 (90%-0.98-spruceup), 700 (90%-0.97-spruceup), 1065 (80%-untrimmed), 866 (80%-0.98-spruceup) and 768 (80%-0.97-spruceup) partitions, as well as their unpartitioned counterparts with maximum likelihood (ML) best-tree and ultrafast bootstrap searches (N = 1000) in IQ-TREE v.1.6.12 (Nguyen *et al.*, 2015; Chernomor *et al.*, 2016; Hoang *et al.*, 2018). For all partitioned analyses, we applied a GTR+G model to each data subset, while unpartitioned analyses used the ModelFinder option in IQ-TREE (Kalyaanamoorthy *et al.*, 2017) to select the best-fitting model of nucleotide evolution. Models selected and implemented in the latter analyses were TVM+F+R3 (90%-untrimmed, 90%-0.97-spruceup and 80%-untrimmed), TVM+F+R7 (90%-0.98-spruceup), TVM+F+R6 (80%-0.98-spruceup) and HKY+F+R7 (80%-0.97-spruceup). All analyses were rooted using the most distantly related outgroup taxon *C.* cf. *rogenhoferi*. To perform coalescent analysis, we also estimated gene trees for the 2204 UCE loci with ≥ 80% of taxa present using IQ-TREE, from which we then created a second subset of trees with a representation of ≥ 90% of taxa. These two sets of ML best trees were then used to perform coalescent species-tree analysis in ASTRAL-III v.5.6.3 (Zhang *et al.*, 2018).

DIVERGENCE DATING

We estimated time-calibrated phylogenies using approximate likelihood in mcmctree and codeml as included in PAMLv.4.9 (Yang, 2007). Approximate likelihood calculation in mcmctree consists first of branch length estimation by maximum likelihood and estimation of the gradient and Hessian of the likelihood function at the maximum likelihood estimates. Divergence times are then estimated in a second step using MCMC and the gradient and Hessian to construct an approximation to the likelihood function (Yang, 2007; dos Reis & Yang, 2011; dos Reis *et al.*, 2012). As input for these analyses, we used the 90% completeness matrix in combination with spruceup trimming with a cut-off of 0.98 (90%-0.98-spruceup) and the best maximum-likelihood tree resulting from SWSC-EN partitioning of this matrix. We pruned this matrix and tree to a reduced dataset of 34 taxa, excluding all but one representative per species and excluding the most distant outgroup *C.* cf. *rogenhoferi*. We implemented two secondary calibrations (employed as soft minimum and soft maximum age within a truncated Cauchy distribution with default parameters) in all analyses, by summarizing over 95% HPD divergence intervals estimated in Blaimer (2012a): (1) root—split between *C. lotti* and remaining taxa (13.4–20.0 Mya, node 145 in fig. 3 in Blaimer, 2012a; note that *C. lotti* is not represented in this dataset, but is closely related to *C. bequaerti* Forel, 1913 and *C. luctans* Forel, 1907); (2) crown node *C. scutellaris* group (4.9–9.6 Mya, node 144 in fig. 3 in Blaimer, 2012a). We set up four independent runs using the independent-rates models and standard parameters, achieving convergence using *nsamples* = 1 000 000 with *samplefreq* = 10 and *burnin* = 500 000. We visualized mcmc convergence and effective sample sizes using TRACER v.1.7.1 (Rambaut *et al.*, 2018) and summarized across all results. To assess the impact of our calibrations, we also performed analyses without sequence data using only the prior.

BIOGEOGRAPHY AND NESTING PREFERENCE

We explored the biogeographic range evolution of the North American *C. scutellaris* group using BioGeoBEARS v.1.1.2 (Matzke, 2013). We assembled a distribution matrix by coding species according to four geographic ranges: E = eastern US and north-east Mexico, W = western US and north-west Mexico, C = the Caribbean and M = southern Mexico to Honduras (see Supporting Information, Table S2). We pruned the remaining outgroup and the Palaearctic members of the *C. scutellaris* group from the chronogram and used this modified phylogeny as input for BioGeoBEARS analysis following the tutorial available on the BioGeoBEARS PhyloWiki (http://phylo.wikidot.com/biogeobears). We implemented the standard two-parameter dispersal and extinction cladogenesis (DEC) model (Ree & Smith, 2008), restricting max_range_size = 2, since none of the species in our analysis occur in more than two geographic ranges. We coded the nesting habit of each species as either ground-dwelling or arboreal, based on personal collecting experience, information gathered from the literature and specimen records on AntWeb. Twelve species were scored as being arboreal and 19 as ground-dwelling (Supporting Information, Table S2). Using the same chronogram as for biogeographical inference, we reconstructed ancestral states for these trait categories with the rayDISC function in the R package corHMM v.2.5 (https://www.R-project.org/). We performed these estimations under the 'equal rates' model (ER) and the 'all rates different' model (ARD), and chose the better-fitting model based on a likelihood ratio test performed on the resulting –lnL scores *[1-pchisq(Δ lnL, df)]*. We repeated both analyses twice, obtaining identical results each time.

DATA AVAILABILITY

Raw sequence reads have been deposited in the NCBI Sequence Read Archive repository under Bioproject accession PRJNA683817. Assembled contig files, data matrices and tree files, as well as input files and code for biogeographic and trait analyses, have been deposited in the Dryad repository under accession doi:10.5061/dryad.t1g1jwt29.

SPECIES-LEVEL TAXONOMY

Specimens for morphological study were examined in the following collections. CASC: California Academy of Sciences, San Francisco, CA, USA. CSCA: California State Collection of Arthropods, California Department of Food & Agriculture, Sacramento, CA, USA (= CDFA). JTLC: J. T. Longino Collection, University of Utah, Salt Lake City, UT, USA. LACM: Los Angeles County Museum of Natural History, Los Angeles, CA, USA. MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. MHNG: Muséum d'Histoire naturelle, Geneva, Switzerland. MSNG: Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy (= MCSN). NCSU: North Carolina State University Insect Museum, Raleigh, NC, USA. RAJC: Robert A. Johnson Collection, Tempe, AZ, USA. SBMN: Santa Barbara Museum of Natural History, Santa Barbara, CA, USA. UCDC: Bohart Museum of Entomology, University of California, Davis, CA, USA. USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. UTIC: University of Texas Insect Collection, Austin, TX, USA.

Other collection abbreviations used: BMNH: Natural History Museum, London, UK. FSCA: Florida State Collection of Arthropods, Gainesville, FL, USA. NHMW: Naturhistorisches Museum Wien, Vienna, Austria.

Measurements and indices follow Longino (2003) and Blaimer (2010), except that head width excludes the compound eyes. Three new measurements are introduced here: SPTD, MtFL and PP-SL. All measurements were taken at 50× magnification with a Wild M5A microscope and a dual-axis Nikon micrometre wired to a digital readout.

HW	Head width: maximum measurable head width, excluding the compound eyes.
HL	Head length: measured along the midline from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin of the head.
ED	Eye diameter: maximum diameter of the compound eye, measured in oblique lateral view.
SL	Scape length: chord length of the scape, excluding the basal condyle and neck.
WL	Weber's length: length of mesosoma, taken in lateral view from the anterior margin of the pronotum, excluding the pronotal collar, to the posteroventral extremity of the metapleuron.
SPL	Propodeal spine length: maximum measurable distance from the outer cuticular rim of the propodeal spiracle to the apex of the propodeal spine.
SPTD	Propodeal spine tip distance: distance between the apices of the propodeal spines, measured in dorsal view and taken at the posterior-most extremities of the spines.

MtFL	Metafemur length: length of the metafemur measured in dorsal or anterior view; the trochanter is not included in this measurement.
MtTL	Metatibia length: length of the metatibia, measured in dorsolateral view, from the articulation with the femur, excluding the medioproximal condyle, to the distal extremity of the tibia.
PTW	Petiolar width: maximum width of the petiole in dorsal view.
PPW	Postpetiolar width: maximum width of the postpetiole (third abdominal segment) in dorsal view.
PP-SL	Postpetiole setal length: length of longest seta on the postpetiole; this is usually one of a pair of setae that arise from the posterolateral extremities of the postpetiole.
CI	Cephalic index: HW/HL.
OI	Ocular index: ED/HW.
SI	Scape index: SL/HW.

Terms for inclination of pilosity follow Wilson (1955) and Hölldobler & Wilson (1990): erect hairs are those positioned at, or near, 90° to the cuticular surface; subdecumbent hairs incline at 45° and appressed hairs are nearly parallel to the surface. Suberect hairs are intermediate between erect and subdecumbent (i.e. about 70°) and decumbent signifies a condition between appressed and subdecumbent (i.e. about 25°). The term 'standing pilosity' refers to all hairs that lie at an angle of 45° or more from the surface, i.e. erect, suberect and subdecumbent hairs. The small appressed hairs that cover most of the body of *Crematogaster* workers are referred to as pubescence; in some species this pubescence has a tendency to become uplifted, so that the hairs become decumbent or suberect while remaining short in length.

The following setal counts were employed:

MSC	Mesosomal setal count: number of standing hairs greater than 0.04 mm in length, visible in profile on the mesosoma dorsum.
A4SC	Abdominal tergite 4 setal count: number of standing hairs greater than 0.04 mm in length on the dorsum of the fourth abdominal (first gastric) tergite, including the posterior margin of the tergite. This count is taken by observing the tergite in both dorsal and lateral views, and by arranging the light source and background to maximize the visibility of such hairs.

Altogether, we obtained linear measurements and setal counts for 361 workers belonging to 29 species in the *Crematogaster scutellaris* group. The full set of measurements is given in the Supporting Information, Table S4, which also includes the locality, collector, unique specimen code and repository for each measured specimen. The complete collection data of all measured specimens is accessible on AntWeb (www.antweb.org), by searching on the specimen codes cited in the Supporting Information, Table S4.

Sculpture was evaluated under a soft (fluorescent) light that reduced glare compared to fibre-optic light sources. Terminology for sculpture follows Harris (1979). The surface sculpture of some North American species of *Crematogaster* has been described in the literature as 'punctate' or 'punctulate', but we consider 'foveolate' to be a more accurate term. The small, shallow depressions are typically bounded by a network of fine ridges, and we refer to this sculpture as 'reticulate-foveolate'.

RESULTS

Phylogenetic inference

Sequence data characteristics are summarized in the Supporting Information, Table S2. In brief, we were able to obtain, on average, 3 208 038 (296 401–13 504 515) base pairs (bp) raw reads per sample, which were assembled by SPAdes to an average of 147 544 (2877–426 694) contigs per sample with an average length of 363 (205–548) bp. From the total assembled reads, we recovered an average of 2222 (1070–2372) UCE loci with an average length of 1200 (331–2542) bp. Alignment statistics were calculated for the eight concatenated matrices (90%-untrimmed, 90%-0.95-spruceup, 90%-0.97-spruceup, 90%-0.98-spruceup, 80%-untrimmed 80%-0.95-spruceup, 80%-0.97-spruceup, 80%-0.98-spruceup) and are detailed in the Supporting Information, Table S3. Trimming of potentially misaligned sites with spruceup proved to be a trade-off, since overly stringent cut-off values may trim genuine sequence variation and lead to an increase in missing data and a decrease in informative sites. We found this to be the case at a 0.95 cutoff value for our dataset and, therefore, did not implement this cutoff in phylogenetic analyses. For our dataset, a cutoff of 0.98 proved optimal to remove long branches without excessive trimming across clean and informative sequence data. The 90%-0.98-spruceup matrix has a total alignment length of 1 926 988 bp, 21.8% missing data and 3.4% parsimony informative characters (PIC) (Supporting Information, Table S3).

We performed analyses on the remaining six untrimmed and spruceup-trimmed matrices, both with and without employing data partitioning prior to analyses, for a total of 12 different ML analyses in IQ-TREE. These are summarized in Figure 1 (depicting partitioned analysis of the 90%-0.98-spruceup matrix) and in the Supporting Information (Figs S1–S5). Spruceup trimming mostly shortened the *C. lucayana*

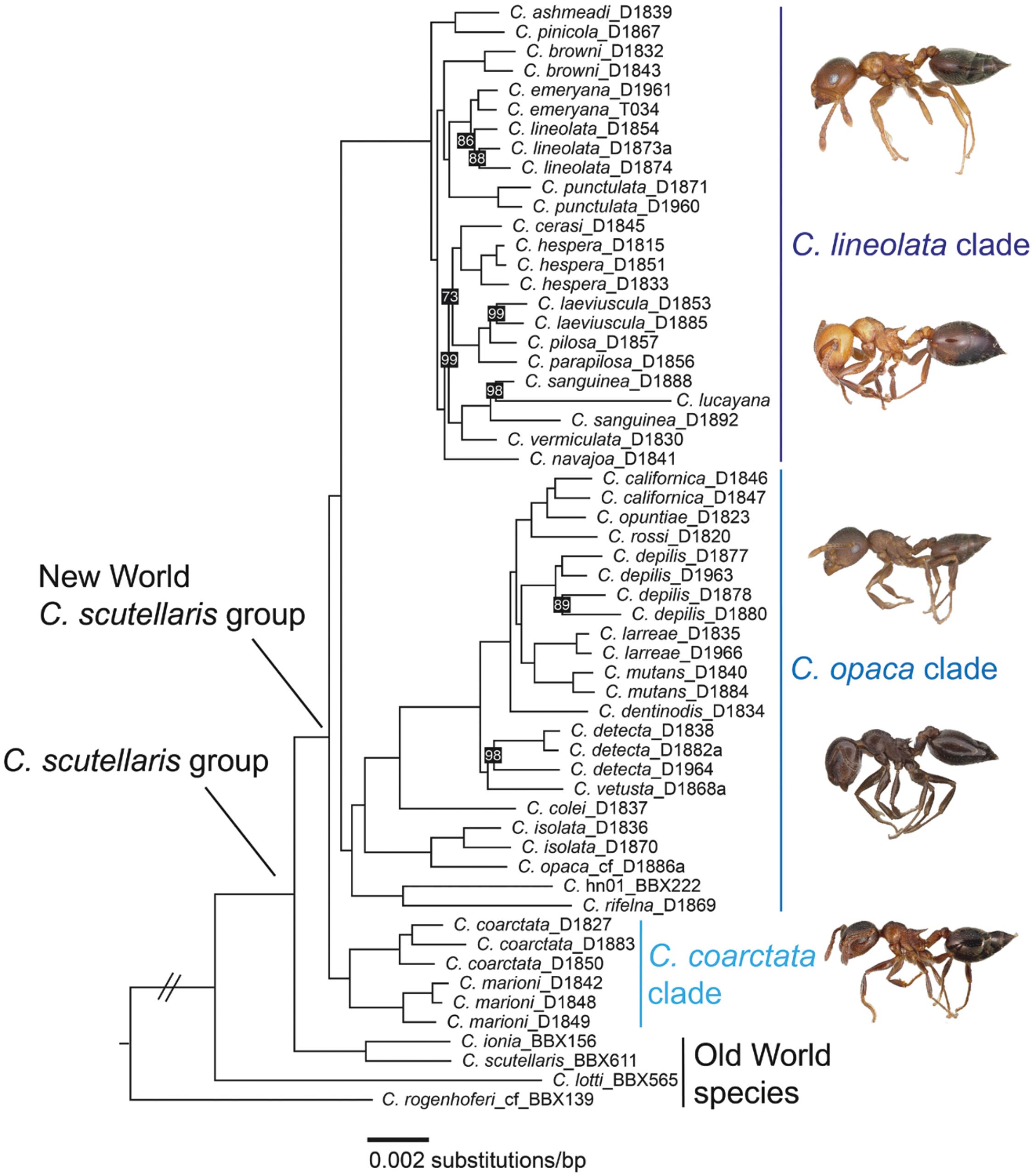


Figure 1. Phylogeny of the North American *Crematogaster scutellaris* group. Maximum likelihood phylogenetic tree estimated from the 90% taxon completeness matrix after application of spruceup trimming with a 0.98 cut-off (90%-0.98-spruceup), using a combined best tree and ultrafast bootstrap (N = 1000) search in IQ-TREE v.1.6.12 and implementing 746 partitions. The analysis was rooted using the most distantly related outgroup taxon *C.* cf. *rogenhoferi*; the long branch leading to this taxon has been shortened for space-saving purposes. All nodes have bootstrap support = 100% unless labelled otherwise. Species images courtesy of *AntWeb* (www.antweb.org).

Wheeler, 1905 branch (compare Fig. 1 with, for example, Supporting Information, Fig. S1), a taxon with a high proportion of missing data due to low locus capture and short contigs. All ML analyses generated highly supported and congruent results, with a few minor exceptions outlined below. Coalescent analyses (Supporting Information, Fig. S6) overall were less well-supported and showed some incongruence with ML results.

All results reveal three major clades in the Nearctic region (here named after the oldest valid name in each group) (Fig. 1). The *Crematogaster coarctata* subgroup comprises just two western United States species (*C. coarctata* Mayr, 1870 and *C. marioni* Buren, 1968), which are together sister to the other New World species. The *Crematogaster opaca* subgroup consists of (1) two isolated Mesoamerican species, that are sister to all others in the subgroup, (2) *C. isolata* Buren, 1968 and a *C. opaca*-like species and (3) a series of species occurring in the American South-West and adjacent Mexico, characterized by reticulate-foveolate sculpture on the promesonotum (including *C. colei* Buren, 1968, *C. californica* Wheeler, 1919, *C. dentinodis* Forel, 1901, *C. depilis* Wheeler, 1919, *C. larreae* Buren, 1968, *C. mutans* Buren, 1968, *C. opuntiae* Buren, 1968 and *C. rossi* Buren, 1968). The *Crematogaster lineolata* subgroup comprises a diverse array of species, occurring mostly in eastern United States and the Caribbean, but including four western endemics (*C. browni* Buren, 1968, *C. emeryana* Creighton, 1950, *C. hespera* Buren, 1968 and *C. navajoa* Buren, 1968).

Relationships within the *C. coarctata* and *C. opaca* subgroups are well supported and congruent across all ML analyses (Fig. 1; Supporting Information, Figs S1–S5). Coalescent analyses recover a different position for *C. depilis* in the *C. opaca* subgroup, but with little support [local posterior probabilities (pp) = 0.31–0.48; Supporting Information, Fig. S6]. Within the *C. lineolata* subgroup, we observe lower support and changes in the position of the clade containing *C. laeviuscula* Mayr, 1870, *C. pilosa* Emery, 1895 and the new species *C. parapilosa*. While our preferred partitioned 90%-0.98-spruceup analysis, as well as untrimmed partitioned and unpartitioned of 90% and 80% ML analyses (Supporting Information, Figs S1, S3) and coalescent analyses (Supporting Information, Fig. S6), place this clade as sister to *C. hespera* + *C. cerasi* (Fitch, 1855), the remaining analyses recover it sister to *C. vermiculata* Emery, 1895, *C. sanguinea* Roger, 1863 and *C. lucayana* Wheeler, 1905 (Supporting Information, Figs S2, S4, S5). Coalescent analyses also disagree with ML analyses with regard to the position of *C. navajoa* and *C. lucayana*. In addition, untrimmed analyses of the 90% matrix (Supporting Information, Fig. S1) and coalescent analyses (Supporting Information, Fig. S6) recover *C. lineolata* (Say, 1836) as paraphyletic with regard to *C. emeryana*.

Divergence age and biogeographic history

The most recent common ancestor (MRCA) of the North American *C. scutellaris* group is estimated to be of Late Miocene age (~7.3 Mya, node 4; Table 1; Fig. 2), with a broad distribution range across the eastern and western US and north-east to north-west Mexico obtaining highest probability in the DEC model. The *C. coarctata* subgroup subsequently diverged sometime before ~5.9 Mya (node 33; Table 1 and Fig. 2) and became restricted to the western US and north-west Mexico. The MRCAs of the remaining two subgroups most likely retained the broad distribution across the US and northern Mexico. Whereas the *C. opaca* subgroup diverged shortly after the establishment of the *C. scutellaris* group in the Nearctic region, the MRCA of the *C. lineolata* subgroup is estimated to be somewhat younger, with a Pliocene age around 4 Mya (nodes 20 and 6, respectively; Table 1 and Fig. 2). Within the *C. opaca* subgroup, one lineage subsequently became restricted to the western US and north-west Mexico (node 21; Table 1 and Fig. 2), while its sister-lineage dispersed to eastern Mexico and Mesoamerica (node 32; Table 1 and Fig. 2). Most of the earlier biogeographic history of the *C. lineolata* subgroup is reconstructed with an unresolved broad distribution across the US and northern Mexico (nodes 8, 12, 13, 14; Table 1 and Fig. 2), but two clades (nodes 7 and 16; Table 1 and Fig. 2) and two species (*C. vermiculata* and *C. lineolata*) within this subgroup either dispersed to, or became restricted to, the eastern US fairly recently, during the Pleistocene (< 2.5 Mya). A Pleistocene age is also inferred for the dispersal of *Crematogaster* to the Caribbean (2.5–1.6 Mya, nodes 18 to 19; Table 1; Fig. 2).

Nesting preference

Ancestral state reconstructions suggest a ground-dwelling habit for the MRCA of the North American *C. scutellaris* group ($P = 0.71$, node 4; Table 1; Fig. 2). This ground-dwelling habit appears to have been retained in the *C. opaca* and *C. coarctata* subgroups, in which most species are considered ground-dwelling, except for three isolated transitions to an arboreal nesting preference in *C. isolata*, *C. rifelna* Buren, 1968 and *C. marioni*. The ancestral nesting preference for the *C. lineolata* subgroup remains equivocal, with almost equal probability between an arboreal and a ground-dwelling habit (node 6; Table 1; Fig. 2). In this subgroup, the majority of species are considered arboreally nesting, but only two transitions are inferred to account for the current distribution of this trait. First, the lineage comprising *C. ashmeadi* Mayr, 1886 and *C. pinicola* Deyrup & Cover, 2007, which is sister to all others in the *C. lineolata* subgroup, clearly made an early transition to arboreal nesting (node 7; Table 1; Fig. 2). Second, a transition happened sometime in a larger subclade of eight species, including the Caribbean and most of the species occuring in the eastern United States (nodes 12 to 13; Table 1; Fig. 2). Overall, these results indicate

Table 1. Dating, biogeographic inference and nesting biology. Results from divergence date estimations with mcmctree, summarized as median ages and their 95% HPD for all nodes. Nodes marked with * were calibrated for dating analyses. Ancestral ranges and ancestral nesting preferences are further given for each node; for nesting preference, states with the highest probability are given in bold; for ancestral ranges, only the most probable range and its relative probability is listed for each node. Node numbers refer to Figure 2. Geographic ranges are C = Caribbean, E = Eastern US, ne Mexico, W = Western US, nw Mexico, M = southern Mexico to Honduras, EW = combined distribution of E and W, EC = combined distribution of E and C, EM = combined distribution of E and M

Divergence Dating			**Nesting preference**			**Biogeographic reconstructions**		
Node	Median age (Ma)	95% HPD	Node	Ground	Arboreal	Node	Range	Rel. Prob.
***1**	15.70	13.2, 20.0	1			1		
***2**	8.06	5.4, 9.7	2			2		
3	4.16	1.9, 6.7	3			3		
4	7.35	5.0, 9.2	4	**0.71**	0.29	4	EW	0.65
5	6.92	4.7, 8.7	5	**0.73**	0.27	5	EW	0.66
6	4.05	2.6, 6.9	6	0.47	**0.53**	6	EW	0.85
7	2.49	1.2, 4.5	7	0.13	**0.87**	7	E	1.00
8	3.70	2.4, 6.1	8	0.50	0.50	8	EW	0.88
9	3.26	2.1, 5.2	9	**0.83**	0.17	9	W	0.86
10	2.91	1.8, 4.6	10	**0.90**	0.10	10	W	0.77
11	1.38	0.6, 2.6	11	**0.99**	0.01	11	EW	1.00
12	3.33	2.1, 5.4	12	0.38	**0.62**	12	EW	0.88
13	3.09	2.0, 4.9	13	0.12	**0.88**	13	EW	0.77
14	2.86	1.8, 4.5	14	0.11	**0.89**	14	EW	0.78
15	2.27	1.3, 3.6	15	0.15	**0.85**	15	EW	0.86
16	1.78	1.0, 2.9	16	0.01	0.99	16	E	1.00
17	1.17	0.6, 2.1	17	0.00	1.00	17	E	1.00
18	2.51	1.5, 4.0	18	0.04	**0.96**	18	EC	1.00
19	1.61	0.9, 2.7	19	0.01	**0.99**	19	C	1.00
20	6.52	4.4, 8.2	20	**0.77**	0.23	20	EW	0.70
21	6.03	4.0, 7.7	21	**0.82**	0.18	21	W	1.00
22	5.14	3.4, 6.7	22	**0.92**	0.08	22	W	1.00
23	3.79	2.5, 5.2	23	**0.99**	0.01	23	W	1.00
24	2.99	2.0, 4.2	24	**1.00**	0.00	24	W	1.00
25	2.71	1.7, 3.8	25	**1.00**	0.00	25	W	1.00
26	2.13	1.3, 3.1	26	**1.00**	0.00	26	W	1.00
27	1.39	0.7, 2.3	27	**1.00**	0.00	27	W	1.00
28	2.45	1.5, 3.5	28	**1.00**	0.00	28	W	1.00
29	1.83	1.0, 2.8	29	**1.00**	0.00	29	W	1.00
30	3.13	1.9, 4.4	30	**0.99**	0.01	30	W	1.00
31	3.10	1.5, 5.0	31	**0.69**	0.31	31	W	1.00
32	4.58	2.6, 6.4	32	**0.69**	0.31	32	EM	0.99
33	5.92	3.4, 8.0	33	**0.66**	0.34	33	W	1.00

an interesting association of nesting preference with biogeography. A ground-dwelling habit appears more common in the species restricted to the arid western United States (15 species ground-dwelling vs. three arboreal), whereas species restricted to the eastern United States show a preference for the arboreal habitat (seven species arboreal vs. one ground-nesting). The two species that straddle the east–west divide (*C. cerasi* and *C. punctulata* Emery, 1895) are ground-nesting.

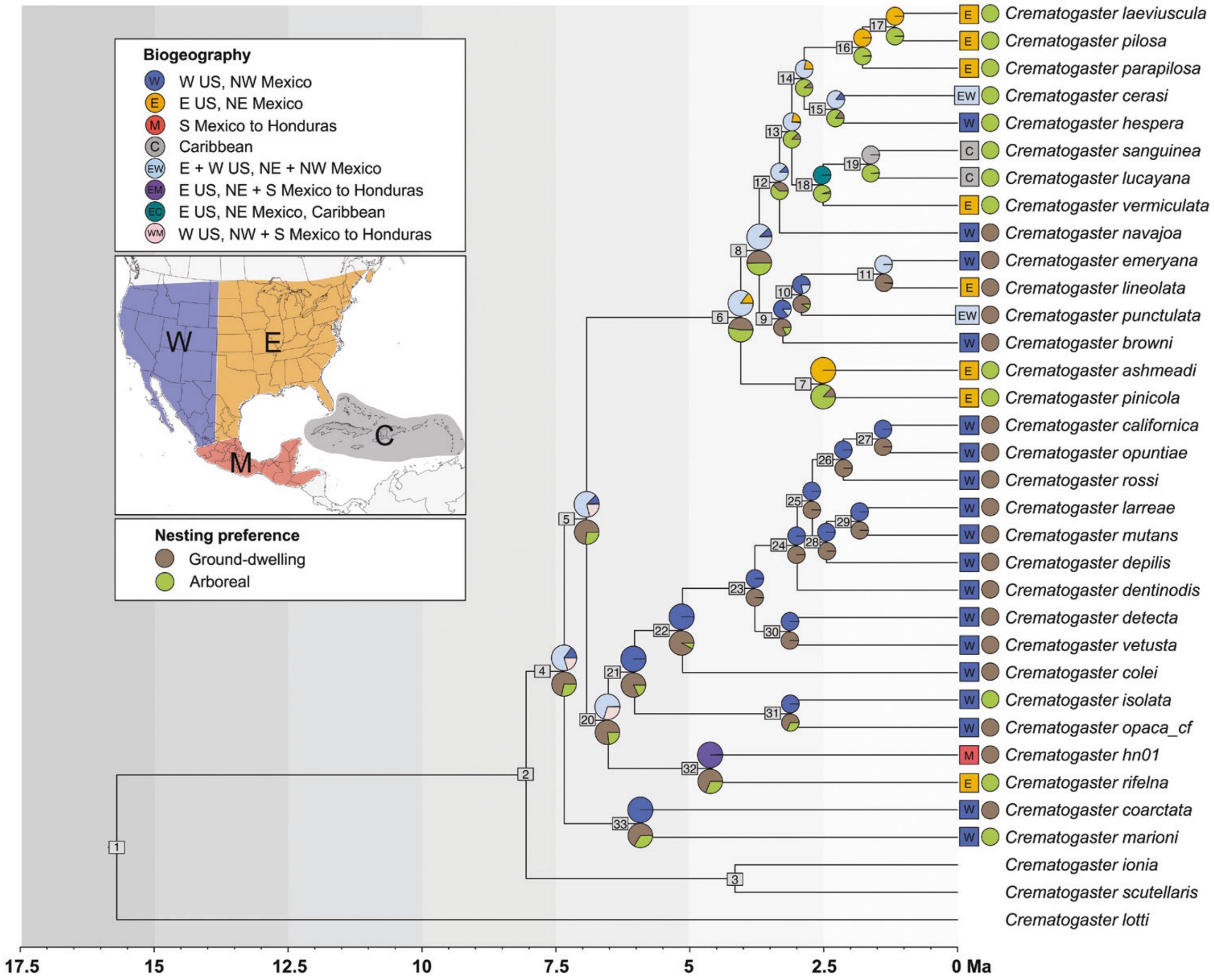


Figure 2. Biogeography and nesting preference of the *Crematogaster scutellaris* group. Time-calibrated phylogeny estimated with mcmctree and codeml in PAMLv.4.9. The analysis is based on the 90% completeness matrix after application of spruceup trimming with a cut-off of 0.98 (90%-0.98-spruceup), and the best maximum likelihood tree resulting from SWSC-EN partitioning of this matrix. This matrix and tree was pruned to a reduced dataset of 34 taxa for dating analysis. Node numbers refer to Table 1, where median ages and 95% highest posterior densities (HPD) are given. Biogeographic range reconstructions with BioGeoBEARS v.1.1.2 are mapped on this chronogram as E = eastern US and north-east Mexico (orange), W = western US and north-west Mexico (dark blue), C = the Caribbean (grey), M = southern Mexico to Honduras (red), EW = combined E and W distributions (light blue), EM = combined E and M distributions (purple), EC = combined E and C distributions (dark green), WM = combined W and M distributions (peach). Respective probabilities for ancestral ranges are given in Table 1. Ancestral states for nesting preference, estimated with the R package corHMM v.2.5, are further mapped on the phylogeny; pie colours are: light green = arboreal; brown = ground-dwelling.

TAXONOMY

SYNONYMIC LIST OF *CREMATOGASTER* SPECIES IN AMERICA NORTH OF MEXICO

CREMATOGASTER (CREMATOGASTER)

C. ashmeadi Mayr, 1886: 463
= *C. ashmeadi matura* Wheeler, 1932: 8 (synonymy by Creighton, 1950: 206)

C. browni Buren, 1968: 100 **stat. rev.**
C. californica Wheeler, 1919: 111 **stat. rev.**
C. cerasi (Fitch, 1855: 835)
= *C. kennedyi* Wheeler, 1930: 58 (synonymy by Buren in Smith, 1958: 126)

C. coarctata Mayr, 1870: 992
= *C. mormonum* Wheeler, 1919: 111 (synonymy by Morgan & Mackay, 2017: 105)

C. colei Buren, 1968: 108 **stat. rev.**
C. dentinodis Forel, 1901: 130
C. depilis Wheeler, 1919: 111
C. detecta **sp. nov.**
C. emeryana Creighton, 1950: 213
C. hespera Buren, 1968: 98 **stat. rev.**
C. isolata Buren, 1968: 106
C. laeviuscula Mayr, 1870: 993
  = *C. arborea* (Buckley, 1867: 349) (synonymy by Buren in Smith, 1958: 126)
  = *C. bicolor* (Buckley, 1867: 350) (junior homonym, replaced by *Crematogaster clara* Mayr 1870)
  = *C. clara* Mayr, 1870: 993 (synonymy by Mayr, 1886: 463 and Johnson, 1988: 322)
C. larreae Buren, 1968: 117 **stat. rev.**
C. lineolata (Say, 1836: 290)
  = *C. columbiana* (Buckley, 1867: 340) (synonymy by Mayr, 1886: 462)
  = *C. marylandica* (Buckley, 1867: 339) (synonymy by Mayr, 1886: 462)
  = *C. novaeboracensis* (Buckley, 1867: 337) (synonymy by Mayr, 1886: 462)
  = *C. lineolata lutescens* Emery, 1895: 282 (synonymy by Creighton, 1950: 213)
  = *C. lineolata subopaca* Emery, 1895: 283 (synonymy by Johnson, 1988: 320)
C. marioni Buren, 1968: 105 **stat. rev.**
C. mutans Buren, 1968: 115
C. navajoa Buren, 1968: 102
C. nocturna Buren, 1968: 112
C. opuntiae Buren, 1968: 120 **stat. rev.**
C. parapilosa **sp. nov.**
C. pilosa Emery, 1895: 285
  = *C. atkinsoni* Wheeler, 1919: 108 **syn. nov.**
  = *C. atkinsoni helveola* Wheeler, 1919: 109 **syn. nov.**
  = *C. creightoni* Wheeler, 1933: 86 (synonymy by Buren in Smith, 1958: 127)
C. pinicola Deyrup & Cover, 2007: 101
C. punctulata Emery, 1895: 287
  = *C. opaca texana* Santschi, 1929: 91 **syn. rev.**
C. rifelna Buren, 1968: 96
C. vermiculata Emery, 1895: 286
C. vetusta **sp. nov.**

CREMATOGASTER (ORTHOCREMA)

C. corvina Mayr, 1870: 994
C. crinosa Mayr, 1862: 767 (for list of junior synonyms see Longino, 2003: 49)
C. minutissima Mayr, 1870: 995
C. missouriensis Emery, 1895: 287
  = *C. minutissima smithi* Creighton, 1950: 205 (synonymy by Shattuck & Cover, 2016: 15)
C. obscurata Emery, 1895: 287
  = *C. agnita* Wheeler, 1934b: 175 (synonymy by Longino, 2003: 97)
C. torosa Mayr, 1870: 404
  = *C. arizonensis* Wheeler, 1908: 482 (synonymy by Longino, 2003: 120)
  = *C. brevispinosa tumulifera* Forel, 1899: 84 (synonymy by Longino, 2003: 120)

From the preceding list, the *Crematogaster* fauna of the United States and Canada is seen to comprise 33 species: 27 species of *Crematogaster* (*Crematogaster*), all members of the *C. scutellaris* group, and six species of *Crematogaster* (*Orthocrema*). An additional species in the *C. scutellaris* group, of uncertain identity, occurs in southern Arizona. It is referred to as *Crematogaster* sp. cf. *opaca* in the key and in remarks below.

The following *Crematogaster* (*Crematogaster*) taxa are treated in individual species accounts after the key: *Crematogaster browni*, *C. californica*, *C. cedrosensis*, *C. cerasi*, *C. colei*, *C. depilis*, *C. detecta*, *C. hespera*, *C. larreae*, *C. marioni*, *C. opaca*, *C. opuntiae*, *C. parapilosa*, *C. pilosa*, *C. punctulata*, *C. rossi*, *C. vermiculata* and *C. vetusta*.

WORKER-BASED KEY TO SPECIES OF *CREMATOGASTER* IN AMERICA NORTH OF MEXICO

This key is broadly based on Buren (1968), but updated to incorporate recent discoveries and more quantitative measures of species differences. The user is cautioned that the species-level taxonomy of these ants has not been fully resolved, especially among the complex of species related to *Crematogaster californica* and *C. depilis*, and among taxa found in Mexico (the latter not treated here). In some couplets we have been forced to characterize species based on several features, no single one of which is diagnostic by itself. The second lug of such couplets is often of the form 'without this combination of characters', followed by a series of conditional statements. This makes the key somewhat cumbersome but we can find no other way to accurately account for the variation observed within and among species.

Features of pilosity assume importance in many couplets, and they will be difficult or impossible to assess accurately in specimens that are badly worn or covered in glue. Use of soft (fluorescent) light and an effective specimen manipulator that permits viewing from all angles and with varying degrees of backlighting will greatly assist in discerning differences in pilosity and sculpture. Accurate linear measurements are also critical for identification of many of these species. Differences among species are sometimes less pronounced in the smallest workers, so if the choice exists, it is advisable to use the larger workers of a series for identification.

To assist the user we provide images of some of the more salient morphological features that are cited in the key (Figs 3–12), as well as standard views of the worker caste of each species in the *C. scutellaris* group (Figs 13–39). However, images of single specimens do not provide information about the variability of each species. Linear measurements, ratios of measurements and setal counts more accurately capture such variation. Bivariate plots of these measurements can sometimes be helpful for distinguishing species (Figs 40–47).

Following Buren (1968), the nominate subgenus of *Crematogaster*, represented in the Nearctic region by the *Crematogaster scutellaris* group, is divided by geography into those species occurring in eastern and western North America, here defined arbitrarily as east and west of 102°W longitude. Only two species (*C. cerasi* and *C. punctulata*) occur in both regions. The last portion of the key (couplets 31–35) covers the six species of *Crematogaster* (*Orthocrema*) occurring in the United States and is based on Longino (2003) and Shattuck & Cover (2016). Two other Neotropical species of the subgenus *Orthocrema*, *C. sotobosque* Longino, 2003 and *C. curvispinosa* Mayr, 1862, have been reported from the United States (Morgan & Mackay, 2017), but we do not consider these records credible.

1. Petiole as wide as, or wider than, long and broadened anteriorly (Fig. 3A); postpetiole bilobed, wider than long and with distinct median sulcus; *Crematogaster* (*Crematogaster*) 2
- Petiole rectangular or ovorectangular, longer than wide and not widened anteriorly (Fig. 3B); postpetiole subglobular and lacking a distinct median sulcus, except in one species (*C. corvina*); *Crematogaster* (*Orthocrema*) 31

2. Species occurring in the western United States, west of 102°W 3
- Species occurring east of 102°W in the United States and Canada 22

3. Mesosoma dorsum densely reticulate-foveolate and opaque, with some overlying rugulae in larger workers; declivitous face of propodeum completely covered with reticulate-foveolate sculpture (Fig. 4A); seta-bearing posterolateral extremity of petiole in form of small acute tooth; standing pilosity short and stout, relatively sparse on mesosoma (MSC 4–12), but abundant on gaster (A4SC 48–80) (Fig. 13A); relatively small species (HW 0.73–1.02), with broad petiole (PTW/HW 0.37–0.41) (Fig. 13C); Arizona, New Mexico and Mexico .... *C. dentinodis*
- Mesosoma sculpture variable, but declivitous face of propodeum usually weakly reticulate and sublucid, or smooth and shining (Fig. 4B); seta-bearing posterolateral extremity of petiole usually blunter and not in the form of a small acute tooth; standing pilosity almost never in the combination of sparse on the mesosoma and abundant on the gaster, but if this condition applies (see couplet 4 below) then larger, on average (HW 0.96–1.27), with narrow petiole (PTW/HW 0.32–0.34) 4

4. Mesosoma predominantly reticulate-foveolate and opaque, with overlying rugulae (Fig. 14C); promesonotum with short, standing hairs that grade into, and are sometimes difficult to distinguish from, uplifted pubescence (MSC 6–24); gaster with abundant, short, standing pilosity (A4SC 38–70) (Fig. 14A); larger species (HW 0.96–1.27) with moderately long scapes (SI 0.74–0.83, SL/HL 0.82–0.92) and propodeal spines (SPL/HW 0.20–0.23) and narrow postpetiole (PPW/HW 0.27–0.30) (Fig. 14C); southern Arizona, Sonora .... *C. vetusta*
- Sculpture and pilosity variable but not in the above combination; if standing pilosity abundant on gaster (A4SC > 35) then species smaller, on average (HW 0.71–1.10), and *either* with more conspicuous mesosomal pilosity (MSC 16–30) and broader postpetiole (PPW/HW 0.29–0.35) (*C. navajoa*, *C. punctulata*) *or* mesosoma with reticulate-striate sculpture and scapes shorter (SL/HL 0.73–0.81) (*C. marioni*)........ 5

5. Standing pilosity abundant, present on most of the dorsal surface of the mesosoma and gaster (MSC 16–30, A4SC 20–55) (Figs 5A, 15A); scape and legs of moderate length relative to mesosoma length (SL/WL 0.69–0.82, MtFL/WL 0.77–0.85) 6
- Standing pilosity varying from sparse to common, but not present on the entire dorsal surface of the mesosoma and gaster (MSC 0–15, A4SC 0–38), if present on mesosoma dorsum then usually confined to the pronotal humeri and the mesonotal declivity (Fig. 5B); rarely (some workers of *C. marioni*) one or two standing hairs on middle of promesonotum but in that case scape and legs short relative to mesosoma length (SL/WL 0.64–0.69, MtFL/WL 0.72–0.76) 7

6. Standing pilosity on head and mesosoma relatively long and slender, giving worker a shaggy appearance (Fig. 15A, B); PP-SL/HW 0.17–0.25; promesonotum with weak reticulate-foveolate to reticulostriate sculpture, the surface sublucid; legs longer (MtFL/HW 0.89–0.92); southern Utah, northern Arizona, New Mexico (with a divergent, outlying population in southern California) .... *C. navajoa*
- Standing pilosity on head and mesosoma relatively short and stout (Fig. 16A, B); PP-SL/HW 0.13–0.18; promesonotum reticulate-foveolate, subopaque; legs shorter (MtFL/HW 0.82–0.87); Great Plains south to northern Mexico, west to Arizona .... *C. punctulata*

7. Sides of propodeum convex in dorsal view, the bases of the propodeal spines not inserted at the widest portion (Fig. 6A); propodeal spines short (SPL/HW 0.15–0.19, SPL/WL 0.13–0.17); standing pilosity sparse, each pronotal humerus with one or no seta (MSC 0–3), and abdominal tergite 4 with none to several short setae, along or near the posterior margin (A4SC 0–4) (Fig. 17A, C); arboreal species occurring in Arizona, Utah, New Mexico, west Texas and northern Mexico .... *C. isolata*
- Propodeum not configured as described above, bases of propodeal spines inserted at widest portion (as in Fig. 6B); *either* propodeal spines longer *and/or* standing pilosity more common 8

8. Dorsum of head (except small shiny median patch, of variable size) and mesosoma densely reticulate-striate to reticulate-foveolate and opaque (Fig. 18B, C); eye relatively small (OI 0.23–0.25, ED/HL 0.24–0.27); propodeal spines and legs relatively short (SPL/HW 0.18–0.22, MtFL/HW 0.87–0.93); standing pilosity sparse on mesosoma, restricted to 1–3 setae on each pronotal humerus (MSC 2–5), better developed on gaster (A4SC 10–18); southern Arizona, Mexico; part of an unresolved complex of forms related to *C. opaca* Mayr, 1870...*C.* sp. cf. *opaca*
- Head sculpture less densely developed, not rendering head fully opaque; if promesonotum predominantly reticulate-foveolate and opaque, then either propodeum with contrastingly coarse longitudinal rugulae *and/or* eye larger (OI 0.25–0.31, ED/HL 0.27–0.32) *and/or* standing pilosity sparser on gaster (A4SC 0–6)...9

9. Petiole broad (PTW/HW 0.36–0.42) (Figs 7, 19C) with prominent anteroventral tooth (Fig. 8); promesonotum predominantly reticulate-foveolate and opaque, variably overlain by weak striae; dorsal face of propodeum with contrastingly coarse longitudinal rugulae, on a reticulate-foveolate background; declivitous face of propodeum with moderate to weak reticulate sculpture, subopaque to sublucid; scape short (SI 0.75–0.81, SL/WL 0.69–0.75); standing pilosity sparse on mesosoma, with one or no seta on each pronotal humerus (MSC 0–2) and sparse but long on gaster (A4SC 0–6) (Fig. 19A); Oregon, Nevada and California, suspected of being a temporary social parasite of other *Crematogaster* species........ *C. mutans*
- Without the above combination of characters; petiole usually less broad and with anteroventral tooth normal in size or absent; mesosoma usually without the contrasting pattern of sculpture described above, but if present (some workers of *C. californica, C. opuntiae* and *C. depilis*) then petiole generally narrower (PTW/HW 0.31–0.37); declivitous face of propodeum mostly unsculptured and shiny; scape length and standing pilosity variable 10

10. Promesonotum predominantly reticulate-foveolate and subopaque (Fig. 20C); scapes, propodeal spines and legs relatively long (SI 0.82–0.92, SPL/HW 0.21–0.26, MtFL/HW 0.94–1.00) compared to related species (Fig. 42); standing pilosity sparse (MSC 0–2, A4SC 0–11); paired postpetiolar setae usually lacking, if present then short (PP-SL 0.12–0.15); hemilobes of postpetiole sharply angulate in profile (Fig. 20A); southern Utah, Arizona, New Mexico and west Texas .... *C. colei*
- Without the above combination of characters; if promesonotum predominantly reticulate-foveolate then scapes and legs shorter (SI 0.72–0.84, MtFL/HW 0.80–0.91) 11

11. Promesonotum predominantly reticulate-foveolate and generally opaque, sometimes with weak overlying rugulae or striae anteriorly (Fig. 9A); standing pilosity sparse on mesosoma, usually restricted to a single hair (rarely two) on each pronotal humerus, or entirely absent (MSC 0–4); eye large and legs relatively short, such that ED/MtFL 0.29–0.37 12
- Promesonotum reticulate-striate, often with smooth, shiny interspaces (Fig. 9B), or predominantly smooth and shiny; standing pilosity more common on mesosoma, usually with two or more (rarely one) hairs on each pronotal humerus (MSC 1–15); eye size and leg length variable.......................................17

12. Standing pilosity absent from mesosoma dorsum and sparse on the gaster (MSC 0, A4SC 0–4), if present on abdominal tergite 4 then short (~0.08 mm long or less) and confined to posterior border (Figs 21A, 22A, 23A); postpetiolar seta either lacking or present but short (PP-SL/HW 0.10–0.13).........................13

- Standing pilosity usually present on mesosoma dorsum as a single hair on each pronotal humerus (MSC 1–4) and more common on gaster (A4SC 5–25) (Figs 14A, 15A); postpetiolar seta present and usually longer (PP-SL/HW 0.12–0.21 15

13. Pubescence on scape relatively conspicuous, decumbent to suberect (Fig. 21B); in larger workers (HW > 1.05) legs longer (MtFL/HW 0.87–0.91, MtTL/HW 0.77–0.79) (Figs 43, 44), eye tending to be smaller (ED/MtFL 0.29–0.32) and body more slender (WL/HW 1.08–1.17) than in related species (see remarks under 'Species accounts') (Fig. 21); south-eastern California, southern Nevada and southern Utah .... *C. detecta*

- Pubescence on scape variable, usually less conspicuous, predominantly decumbent to appressed; legs shorter (MtFL/HW 0.80–0.87, MtTL/HW 0.71–0.77), eye larger (ED/MtFL 0.32–0.37) and body more robust (WL/HW 0.97–1.09); widespread 14

14. Head and mesosoma dark brown, gaster blackish-brown (Fig. 22); queen: posterior quarter of pronotum smooth and shiny; male: small (3.0 to 3.2 mm long), head largely smooth and shining, suberect pubescence sparse on mesosoma; west Texas to eastern California, nesting among lower stems and roots of *Larrea divaricata* Cav. (creosote bush); workers not always separable from those of *C. depilis* (see remarks under 'Species accounts') .... *C. larreae*

- Head and mesosoma yellowish-brown to reddish-brown (head may be darker than mesosoma), gaster medium to dark brown (Fig. 23); queen: pronotum largely or entirely reticulate-foveolate; male: larger (5.5 to 6.0 mm long), head reticulate-foveolate, suberect pubescence conspicuous on mesosoma; south-western United States and northern Mexico; ground-nesting species, in desert and semi-desert regions, not specifically associated with *Larrea divaricata* .... *C. depilis*

15. Mesosoma sublucid, the reticulate-foveolate sculpture weakened, except on lower mesopleuron; dark reddish-brown with black gaster; described from males and queens from northern Arizona; putative workers from southern Utah have not been definitively linked to this species (see Buren 1968: 114) .... *C. nocturna*

- Mesosoma opaque, with dense reticulate-foveolate sculpture, overlain by longitudinal rugae on dorsal face of propodeum; variable in colour; widespread in the south-western United States and north-western Mexico 16

16. Pubescent hairs suberect on scapes and head (Fig. 24B), long on body (Fig. 24A); central-southern California and Baja California .... *C. californica*

- Pubescent hairs appressed on scapes and head (Fig. 25B) and shorter and less noticeable on all surfaces (Fig. 25A); desert locations in Arizona and adjacent regions; possibly conspecific with *C. californica* (see under 'Species accounts') .... *C. opuntiae*

17. Small species (HW 0.72–1.05) with short scapes (SL/WL 0.64–0.71) (Fig. 26B) and legs (MtFL/WL 0.72–0.78); side of pronotum usually reticulate and lower mesopleuron usually longitudinally striate; standing pilosity present on pronotum and mesonotal declivity (MSC 4–15) and common on gaster (A4SC 19–38); most standing pilosity short, grading into (and sometimes difficult to distinguish from) subdecumbent pubescence (Fig. 26A); PP-SL/HW 0.08–0.14; California, Baja California .... *C. marioni*

- Scapes and legs generally longer (SL/WL 0.69–0.83, MtFL/WL 0.75–0.92); *either* side of pronotum and lower mesopleuron with weaker sculpture *and/or* pattern of standing pilosity different from that described above; PP-SL/HW 0.12–0.25 18

18. Lower mesopleuron reticulate-foveolate, overlain with conspicuous longitudinal striae (Fig. 27A); scape and legs relatively long in relation to head length (SL/HL 0.87–0.96, MtFL/HL 0.97–1.07); Utah, Nevada, Oregon, California, Baja California .... *C. coarctata*

- Lower mesopleuron reticulate-foveolate, usually lacking conspicuous longitudinal striae; scape and legs shorter (SL/HL 0.78–0.90, MtFL/HL 0.84–0.98) 19

19. Side of pronotum predominantly smooth and shiny, the dorsum of promesonotum similar but overlain with fine longitudinal striae (Fig. 28A, C); in profile promesonotum evenly and notably convex, lacking a prominent mesonotal declivity posteriorly (Fig. 28A); often bicoloured, with dark gaster contrasting with reddish-brown head, mesosoma, petiole and postpetiole (dark unicoloured populations occur on the Pacific Coast); west Texas and Chihuahua west to California and Baja California .... *C. hespera*

- Promesonotum, including side of pronotum, more strongly sculptured, reticulate or reticulate-striate; in profile promesonotum somewhat flattened with a notable mesonotal declivity (Fig. 29A) or gently convex (Fig. 30A); unicoloured to weakly bicoloured 20

20. Upper-third of head predominantly smooth and shiny, with relatively coarse punctures (> 0.01 mm diameter); standing pilosity long and abundant, especially on the gaster (A4SC 14–30) (Fig. 29A); longest postpetiolar seta about two-thirds of postpetiole width (PP-SL/PPW 0.59–0.75) (Fig. 10A; see also Fig. 40); west Texas, New Mexico, Arizona and adjacent Mexico...*C. browni*

- Upper-third of head with smaller punctures (< 0.01 mm diameter) and often with greater incursion of finely reticulate surface sculpture; standing pilosity shorter and less abundant on gaster (A4SC 4–16) (Fig. 30A); longest postpetiolar seta about one-half of postpetiole width or less (PP-SL/PPW 0.38–0.54) (Fig. 10B).....21

21. Standing pilosity present on pronotal humeri and on mesonotal declivity (MSC 6–13) (Figs 5B, 30A); scape relatively long (SI 0.82–0.89); propodeal spines short (SPL/HW 0.18–0.22); Colorado and Utah to northern Mexico...*C. emeryana*

- Standing pilosity on mesosoma restricted to pronotal humeri (MSC 2–7) (Fig. 31A); scapes shorter (SI 0.72–0.81); propodeal spines longer (SPL/HW 0.22–0.25); eastern Canada, south to Florida and west to the Great Plains and Rocky Mountain foothills...*C. cerasi*

22. Promesonotum with distinct rugulose sculpture, imparting a vermiculate (worm-like) appearance (Fig. 32C); small species (HW 0.67–0.85), with short scapes and legs (SI 0.72–0.78, MtFL/HW 0.79–0.84) (Fig. 32B); propodeal spines short and stout (SPL/WL 0.15–0.19), inwardly curved and directed posterad (SPTD/HW 0.39–0.48) (Figs 32A, 32C); swamp-inhabiting species from south-eastern United States ....*C. vermiculata*

- Promesonotum lacking distinct rugulose-vermiculate sculpture; other characters variable..................23

23. Pronotum with smooth or weakly sculptured median impression, flanked on each side by ruguloreticulate sculpture; in anterior view median impression of pronotum enhancing the distinctness of the median carina of the mesonotum (likened to a gun sight); small, dark-coloured arboreal species (HW 0.88–1.06) with conspicuous standing pilosity on mesosoma and gaster (MSC 12–17, A4SC 20–40) (Fig. 33A, C); south-eastern Texas, north-eastern Mexico.. *C. rifelna*

- Pronotum without a smooth median depression, flanked by ruguloreticulate sculpture; size, pilosity and nesting habits variable...24

24. Propodeal spines short and distinctly incurved (SPL/HW 0.14–0.18; SPTD/HW 0.39–0.47) (Fig. 6B); mesosoma smooth to weakly foveolate; standing pilosity relatively sparse on mesosoma and gaster (MSC 2–6, A4SC 5–13); small, arboreal species (HW 0.74–0.92)..25

- Either propodeal spines longer and less incurved, or mesosoma more densely sculptured; standing pilosity and size variable..26

25. Uniformly dark brown (fresh specimens) (Fig. 34); arboreal species, with variable nesting habits, south-eastern United States... *C. ashmeadi*

- Bicoloured, gaster black and other body parts ferrugineus-red (Fig. 35); nesting in pine branches and under pine bark in open habitats; Florida and adjacent states .... *C. pinicola*

26. Standing pilosity conspicuous on head (Fig. 36B), with numerous short subdecumbent and suberect hairs (uplifted pubescence), in addition to several pairs of longer setae flanking the midline; standing pilosity also present as numerous fine hairs of varying degrees of inclination and length on mesosoma and gaster (MSC 10–30, A4SC 20–60) (Fig. 36A); propodeal spines long (SPL/HW 0.22–0.29) (Fig. 36C); south-eastern United States..*C. pilosa*

- Standing pilosity generally less common and more distinct from the appressed pubescence (at least on the mesosoma and gaster), *or* present as short bristle-like hairs; propodeal spine length variable........27

27. Propodeal spines long and divergent (SPL/HW 0.26–0.34, usually > 0.27) (Fig. 37A, C); dorsal face of propodeum smooth or weakly sculptured; standing pilosity sparse (MSC 0–8, A4SC 11–24) (Fig. 37A); marsh-inhabiting species from south-eastern United States, often building carton nests.....*C. parapilosa*

- Propodeal spines shorter (SPL/HW 0.19–0.27); dorsal face of propodeum usually distinctly sculptured; standing pilosity variable; carton nests rarely or never constructed...28

28. Standing pilosity relatively sparse on mesosoma dorsum, confined to a clump of flexuous setae on the pronotal humeri and occasionally one or two setae on the mesonotal declivity, always lacking on propodeum (MSC 2–14) (Figs 31A, 38A)...29

- Standing pilosity common and well distributed across the mesosoma dorsum, often including the propodeum (MSC 15–28) (Figs 5A, 39A) 30

29. Side of pronotum and dorsum of promesonotum smooth and shining (Fig. 38A, C); midwestern species, occurring from Kansas and Missouri to north-eastern Mexico *C. laeviuscula*

- Side of pronotum usually distinctly foveolate-striate, dorsum of mesosoma striate (Fig. 31A, C); widely distributed, from eastern Canada, south to Florida and west to the Great Plains and Rocky Mountain foothills .... *C. cerasi*

30. Mesosoma dorsum reticulate-foveolate and opaque, lacking striae or rugulae (Fig. 16C); propodeal spines directed posteriorly, such that SPTD/HW 0.39–0.46 and SPTD/PPW 1.11–1.36 (Fig. 47); Great Plains south to northern Mexico, west to Arizona; see remarks under 'Species accounts' .... *C. punctulata*
- Mesosoma dorsum usually with longitudinal rugulae or striae, on a weak reticulate or reticulate-foveolate sublucid background (Fig. 39C); propodeal spines directed more posterolaterally such that SPTD/HW 0.46–0.63 and SPTD/PPW 1.38–1.76 (Fig. 47); eastern Canada to southern United States and west to the Great Plains .... *C. lineolata*

31. Dorsum of head with dilute appressed pubescence and six or fewer standing hairs (Fig. 11A 32
- Dorsum of head with abundant standing pilosity and no underlying short, appressed pubescence (Fig. 11B) 34

32. Postpetiole bilobed, much wider than long and with a distinct median sulcus; head reticulate-foveolate and opaque .... *C. corvina* (southern Texas to Honduras)
- Postpetiole globular to subquadrate, slightly broader than long, and lacking a distinct median sulcus; head less densely sculptured, mostly smooth and shiny, at least medially 33

33. In profile promesonotum usually broadly convex (Fig. 12A); anteroventral petiolar tooth relatively well-developed and sharp; gaster with abundant, evenly distributed standing pilosity; southern Texas to Argentina .... *C. crinosa*
- In profile promesonotum tending to be somewhat flattened (Fig. 12B); anteroventral petiolar tooth usually less well-developed, forming a right or weakly acute angle; standing pilosity moderately common on gaster, denser anterolaterally and often leaving a median strip relatively clear of setae; southern United States to South America .... *C. torosa*

34. Standing pilosity on head short and bluntly clavate; body dark brown; Florida and Texas, south to Venezuela .... *C. obscurata*
- Standing pilosity on head long and flexuous; body yellow to orange-brown, sometimes with darker head 35

35. Queen small (4–4.8 mm long); worker with short propodeal spines (SPL/HW 0.10–0.19); promesonotum with scattered longitudinal carinulae; mesopleuron predominantly smooth and shiny; eastern United States, west to Texas, south to Costa Rica .... *C. minutissima*
- Queen larger (5–6 mm long); where sympatric with *C. minutissima* in eastern United States, worker with longer propodeal spines (SPL/HW 0.20–0.24), promesonotum tending to have fewer carinulae, mostly on sides, and mesopleuron often reticulate-foveolate and opaque (in allopatry these worker differences do not apply; further study required); eastern United States, west to Utah, Arizona and northern Mexico .... *C. missouriensis*

SPECIES ACCOUNTS

In this section we discuss species for which taxonomic clarification is required, mostly those that were synonymized in Morgan & Mackay (2017) but that are here reinstated. We document differences between these species and their closest relatives and the species with which they were synonymized (usually not the same thing), using quantitative criteria whenever possible. We also discuss a few other taxa, and describe three new species. A full treatment of all species is beyond the scope of this paper, but current understanding of the remaining North American species is captured in the preceding worker-based key.

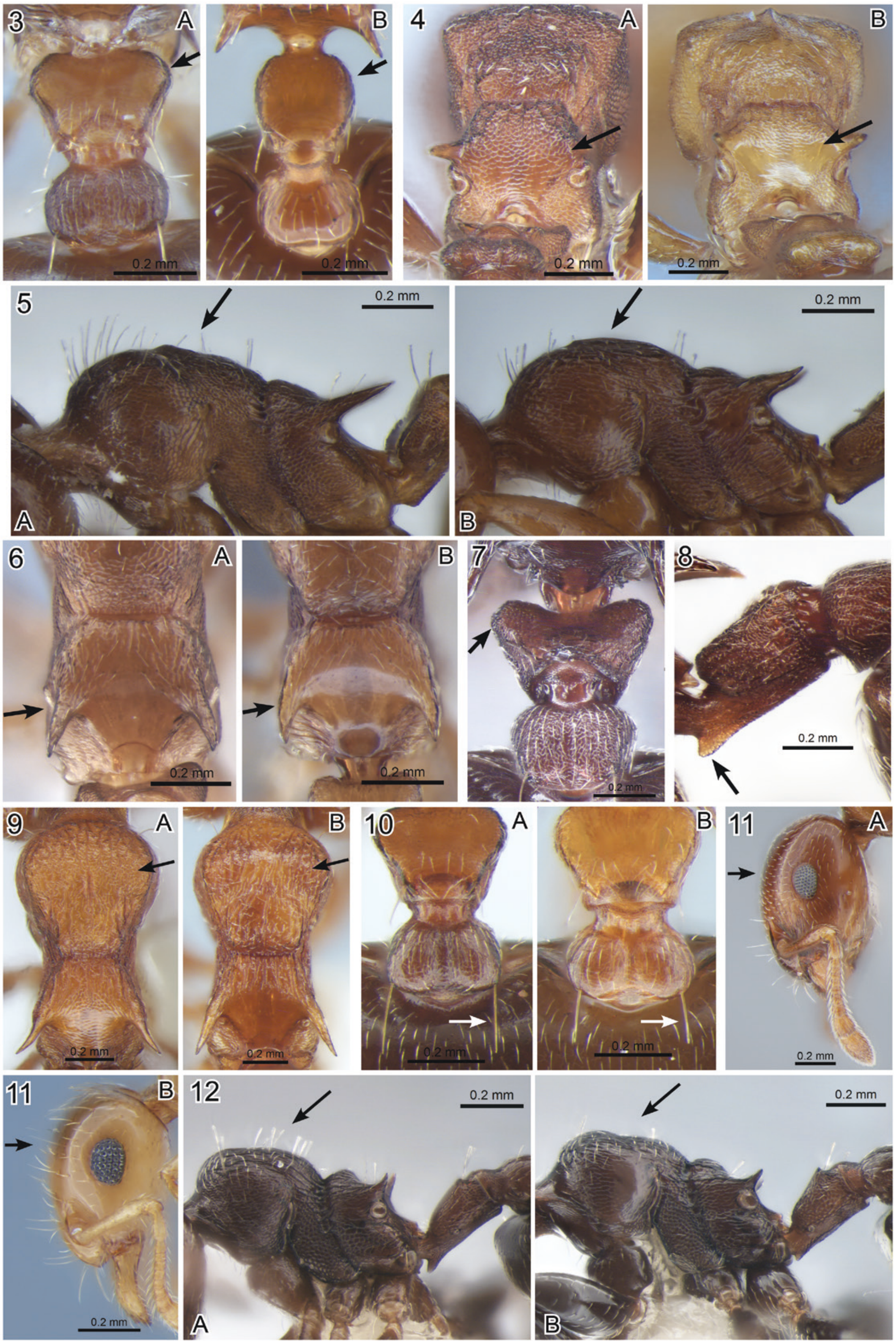
CREMATOGASTER BROWNI BUREN, 1968, **STAT. REV.**

(FIGS 10A, 29)

Crematogaster browni Buren, 1968: 100. Holotype worker, Garden Canyon, Huachuca Mts., Arizona (W. S. Creighton) (LACM) (examined).

Junior synonym of *C. cerasi*: Morgan & Mackay, 2017: 91; here overturned.

Worker measurements (N = *16*)*:* HW 0.69–1.01, HL 0.67–0.94, SL 0.57–0.75, WL 0.74–1.08, MtFL 0.60–0.84, MSC 2–9, A4SC 14–30, PP-SL/HW 0.19–0.25, CI 0.98–1.09, OI 0.22–0.25, SI 0.75–0.85, MtFL/HW 0.84–0.89, SPL/HW 0.18–0.24, SPTD/HW 0.44–0.53.



Figures 3–12. *Crematogaster* worker features useful for identification. 3, petiole shape, dorsal view, *C. lineolata* (CASENT0863235) (3A) and *C. torosa* (CASENT0795540) (3B); 4, sculpture on declivitous face of propodeum, *C. dentinodis* (CASENT0863070) (4A) and *C. depilis* (CASENT0863478) (4B); 5, mesosomal pilosity, *C. punctulata* (CASENT0863277) (5A) and *C. emeryana* (CASENT0863099) (5B); 6, position and shape of propodeal spines, dorsal view, *C. isolata* (CASENT0863072) (6A) and *C. pinicola* (CASENT0882129) (6B); 7, petiole shape, dorsal view, *C. mutans* (CASENT0862488); 8, subpetiolar tooth, lateral view, *C. mutans* (CASENT0862488); 9, promesonotal sculpture, *C. californica* (CASENT0221085) (9A) and *C. coarctata* (CASENT0221962) (9B); 10, postpetiolar seta, *C. browni* (CASENT0863144) (10A) and *C. cerasi* (CASENT0795541) (10B); 11, cephalic pilosity, *C. torosa* (CASENT0795540) (11A) and *C. missouriensis* (CASENT0221041) (11B); 12, mesosomal profile, *C. crinosa* (CASENT0795543) (12A) and *C. torosa* (CASENT0863226) (12B).

Discussion: Neither morphological nor molecular evidence supports the synonymy of *C. browni* under *C. cerasi*. The phylogenomic UCE results show that these two species are not sister-taxa; *C. browni* is more closely related to *C. emeryana*, *C. lineolata* and *C. punctulata*, while *C. cerasi* is the sister-species of *C. hespera* (Fig. 1). *Crematogaster browni* and *C. cerasi* can be readily distinguished by differences in sculpture and pilosity. In workers of *C. browni*, the upper-third of the head is predominantly smooth and shiny, with relatively coarse punctures (greater than 0.01 mm in diameter), while in workers of *C. cerasi*, this region tends to have a greater incursion of reticulate sculpture and finer punctures (< 0.01 mm in diameter). As Buren (1968) observed, the standing hairs on workers of *C. browni* are unusually long. Measurement of the postpetiolar seta affords a simple way to separate the two species: in *C. browni* the length of this seta is about two-thirds of the width of the postpetiole (0.59–0.75× postpetiole width) (Fig. 10A), whereas in *C. cerasi*, the same hairs are about one-half the width (0.42–0.54× postpetiole width) (Fig. 10B). A plot of postpetiole setal length against head width clearly distinguishes the two taxa (Fig. 40). In addition, the first gastric (fourth abdominal) tergite has greater amounts of standing pilosity in *C. browni* (A4SC 14–30) compared to *C. cerasi* (A4SC 4–14). Buren (1968) distinguished workers of *C. browni* from those of *C. cerasi* by their shorter, stouter and less divergent propodeal spines, and a narrow petiole that was said to be only slightly wider than the postpetiole. Metric measurements reveal average differences in these directions, but also indicate broad overlap in both propodeal spine length (SPL/HW 0.18–0.24 in *C. browni* and 0.22–0.25 in *C. cerasi*) and the postpetiolar/petiolar width ratio (PPW/PTW 0.83–0.96 in *C. browni* and 0.81–0.91 in *C. cerasi*). *Crematogaster browni* can be distinguished from *C. emeryana*, the only closely related congener with an overlapping geographic range, by the coarser cephalic punctures, longer postpetiolar seta, greater contrast between abundant pilosity on the gaster and relatively sparse standing pilosity on the mesososma (A4SC >> MSC) and somewhat smaller eyes (worker ED/MtFL 0.25–0.28, vs. 0.28–0.32 in *C. emeryana*).

Distribution and biology: Crematogaster browni is found in mountainous regions of west Texas, New Mexico, Arizona and adjacent northern Mexico. Colonies are found in the ground, under stones, in high-elevation desert, oak savanna, juniper woodland and open oak-pine-juniper woodland. Buren (1968) provides additional details on habitat preferences and co-occurrence with other species of *Crematogaster*.

CREMATOGASTER CALIFORNICA WHEELER, 1919, STAT. REV.

(FIGS 9A, 24)

Crematogaster lineolata subsp. *laeviuscula* var. *californica* Emery, 1895: 285 (unavailable name).

Crematogaster laeviuscula var. *californica* Wheeler, W.M., 1919: 111 (first available use of name). Syntype worker, Los Angeles, California (MSNG) (examined), here designated **lectotype** (CASENT0923319).

Crematogaster lineolata subsp. *californica* Wheeler; Wheeler, W. M., 1934a: 135.

Junior synonym of *C. coarctata* Mayr: Creighton, 1950: 207.

Status as species: Smith, M. R. 1951: 808; Buren, 1968: 94.

Junior synonym of *C. coarctata* Mayr: Morgan & Mackay 2017: 105; here overturned.

*Worker measurements (*N *= 22):* HW 0.86–1.30, HL 0.81–1.19, SL 0.72–0.97, WL 0.93–1.41, MtFL 0.76–1.15, MSC 1–4, A4SC 6–25, PP –SL/HW 0.08–0.21, CI 1.04–1.14, OI 0.25–0.28, SI 0.75–0.84, MtFL/HW 0.83–0.91, SPL/HW 0.19–0.25, SPTD/HW 0.47–0.56.

Discussion: It is unclear why Morgan & Mackay (2017) synonymized *C. californica* under *C. coarcata*. There are reliable morphological differences between these two species and our phylogenetic analyses show that they are found in distant parts of the tree: *C. coarctata* and *C. marioni* form a well-supported clade, sister to all other New World species of the *C. scutellaris* group, while *C. californica* belongs to a subcomplex of species in the *C. opaca* clade that includes *C. opuntiae* (see below) and related species (Fig. 1). In workers of *C. californica*, the dorsum of the promesonotum is densely reticulate-foveolate and opaque, with variable incursion of weak longitudinal striae or rugulae (Fig. 9A); standing pilosity is relatively sparse, with each pronotal humerus typically furnished with a single isolated seta; the eye is relatively large; and the appendages (scapes, legs) are relatively short. By contrast, in workers of *C. coarctata* (including its recently proposed junior synonym, *C. mormonum*), the promesonotum is longitudinally striate, with shiny interspaces intermingled with weak reticulate-foveolate sculpture (Fig. 9B), or it is predominantly smooth and shiny with weak irregular striae; standing pilosity is more common, usually manifested as two to three setae on each pronotal humerus; the eye is relatively smaller; and the appendages longer. Buren (1968) and Snelling & George (1979) employed pronotal pilosity to separate *C. californica* from *C. coarctata* (in the broad sense, including *C. mormonum*) but this distinction sometimes breaks down. There are occasional worker specimens of *C. californica*

Figures 13–18. *Crematogaster* workers, showing lateral view of body (A), full-face view of head (B) and dorsal view of body (C). 13, *C. dentinodis* (CASENT0102830); 14. *C. vetusta* holotype (CASENT0863254); 15, *C. navajoa* worker (CASENT0064826); 16, *C. punctulata* lectotype (CASENT0923318); 17, *C. isolata* (CASENT0922731); 18, *C.* sp. cf. *opaca* (MCZENT00589113). Images courtesy of *AntWeb* (www.antweb.org); photographers Jen Fogarty (13), Michele Esposito (14, 16), April Nobile (15), Wade Lee (17), Zachary Griebenow (18).

with no seta or two setae on one of the humeri and specimens of *C. coarctata* with a single hair on one of the pronotal humeri. More reliable are the differences in sculpture, eye size and metafemur length (Table 2). An index calculated as ED/MtFL ranges from 0.25 to 0.28 in *C. coarctata*, and 0.29–0.32 in *C. californica*, and a bivariate plot of ED and MtFL highlights this distinction between the two species (Fig. 41).

Type notes: Crematogaster californica was described by Emery on the basis of two workers, one from Los Angeles and the other from Encinitas (San Diego County), California. Morgan & Mackay (2017: 111) claimed that the two syntype workers of *C. californica* are deposited in 'MNHG', apparently a misspelling of MHNG, but the types are not present in the Geneva collection (Bernard Landry, pers. comm.). The syntype from Los Angeles is in MSNG and has been examined by us. The second syntype, from Encinitas, is not in MSNG (Maria Tavano, pers. comm.) and must be presumed lost or misplaced. It was apparently examined by Morgan & Mackay (2017), so the loss is a recent one. Nevertheless, the Los Angeles syntype agrees well with the species that has come to be known as *C. californica*, and it serves as a suitable lectotype.

Distribution and biology: Crematogaster californica is a ground-nesting species that occurs from central California to Baja California Sur, in desert, chaparral, coastal sage scrub and open woodland. The eastern limits are unclear because of confusion with *C. opuntiae* (see discussion under that species). *Crematogaster coarctata* (type locality: San Francisco; syntype worker imaged on AntWeb: CASENT0902143) has a more northerly distribution than *C. californica*, but the ranges of the two species overlap in southern California and northern Baja California, and there is no evidence of intergradation where they co-occur.

CREMATOGASTER CEDROSENSIS WHEELER, 1934A
STAT. REV., STAT. NOV.

Crematogaster lineolata cedrosensis Wheeler, 1934a: 136. Eight syntype workers, Cedros Island, Baja California, Mexico, 5 June 1925 (Keifer) (CASC, LACM, MCZC) (four workers in CASC, two workers in LACM and one worker in MCZC examined); one worker in CASC here designated **lectotype** (CASENT0863153).

Crematogaster opaca cedrosensis Wheeler; Enzmann, 1946: 94.

Crematogaster opaca cedrosensis a junior synonym of *C. laeviuscula*: Morgan & Mackay, 2017: 197; here overturned.

*Worker measurements (*N = *6):* HW 0.82–0.96, HL 0.83–0.94, SL 0.66–0.77, WL 0.93–1.05, MtFL 0.71–0.83, MSC 0, A4SC 0–2, PP-SL/HW 0.09–0.12, CI 1.00–1.05, OI 0.25–0.27, SI 0.73–0.81, MtFL/HW 0.83–0.88, SPL/HW 0.18–0.21, SPTD/HW 0.43–0.50.

Discussion: Described from Cedros Island off the west coast of Baja California, *C. cedrosensis* was originally treated as a subspecies of *C. lineolata*, then combined with *C. opaca* by Enzmann (1946: 94) and finally synonymized under *C. laeviuscula* by Morgan & Mackay (2017: 197). In fact, *C. cedrosensis* shows little similarity to those three species. It can be characterized as follows: relatively small species (HW 0.82–0.96), with little standing pilosity (MSC 0, A4SC 0–2); frons and mesosoma dorsum strongly shining, with weak reticulate-striate sculpture on parts of the latter; promesonotum joining the dorsal face of the propodeum without a distinct step (lateral view); and propodeal spines relatively short and directed posterad (SPL/HW 0.18–0.21, SPTD/HW 0.43–0.50). *Crematogaster cedrosensis* is most similar in appearance to certain West Coast populations of *C. hespera* with dark-coloured workers (see below). Metric measurements and indices do not allow unequivocal separation of the two, but *C. cedrosensis* workers tend to have a less broad head (CI 1.00–1.05 vs. 1.04–1.11 in *C. hespera*). A more reliable distinguishing trait is the scarcity of standing pilosity in *C. cedrosensis*: there are no setae on the mesosoma dorsum and almost none on the fourth abdominal (first gastric) tergite (MSC 0, A4SC 0–2 vs. MSC 3–14, A4SC 9–26 in *C. hespera*). In addition, the postpetiolar seta is disporportionately

Table 2. Differences between workers of *Crematogaster coarctata* and *C. californica*

Trait	*C. coarctata*	*C. californica*
Predominant promesonotal sculpture	longitudinally striate, sublucid	reticulate-foveolate, opaque
Eye size	smaller, ED/SL 0.28–0.32	larger, ED/SL 0.32–0.37
Metafemur length	longer, MtFL/WL 0.83–0.92	shorter, MtFL/WL 0.78–0.84
Eye size/metafemur length ratio	smaller, ED/MtFL 0.25–0.28	larger, ED/MtFL 0.29–0.32
Standing pilosity on pronotum	more common, MSC 1–8	sparser, MSC 1–4
Typical number of setae on each humerus	2–3	1

shorter in *C. cedrosensis* (PP-SL/HW 0.09–0.12, versus 0.13–0.21 in *C. hespera*).

Distribution and biology: This species is known only from the type locality (Cedros Island) and a few adjacent locations on the mainland of Baja California. The nearest known samples of *C. cedrosensis* and *C. hespera* were collected less than 50 km apart, and they show no evidence of converging in appearance. No genetic sequence data are available for *C. cedrosensis*, nor is anything known about its biology.

CREMATOGASTER CERASI (FITCH, 1855)

(FIGS 10B, 31)

Myrmica cerasi Fitch, 1855: 835. Four syntype workers, New York (USNM) (examined); one worker here designated **lectotype** (USNMENT00529078) (image on AntWeb).

Crematogaster cerasi (Fitch, 1855); Roger, 1863: 37.

Junior synonym of *Crematogaster lineolata* (Say): Dalla Torre, 1893: 83; Creighton 1950: 213.

Crematogaster lineolata var. *cerasi* (Fitch): Emery, 1895: 282.

Crematogaster lineolata cerasi (Fitch): Smith, 1951: 809.

Status as species: Buren in Smith, 1958: 125; Buren, 1968: 92; Johnson, 1988: 318.

Senior synonym of *Crematogaster kennedyi*: Buren in Smith, 1958: 125.

Senior synonym of *Crematogaster browni*: Morgan & Mackay, 2017: 91; here overturned (see above).

*Worker measurements (*N = *17):* HW 0.77–1.05, HL 0.74–0.99, SL 0.62–0.82, WL 0.83–1.17, MtFL 0.67–0.95, MSC 2–7, A4SC 4–14, PP-SL/HW 0.15–0.19, CI 1.03–1.13, OI 0.22–0.25, SI 0.72–0.81, MtFL/HW 0.81–0.92, SPL/HW 0.22–0.25, SPTD/HW 0.45–0.59.

Discussion: This is a common species in eastern North America that overlaps broadly in distribution with *C. lineolata*. It is distinguished from the latter by having the standing pilosity on the mesosoma dorsum restricted to one to several setae on each pronotal humerus (MSC 2–7 vs. 15–26 in *C. lineolata*). The pilosity on the gaster is also sparser in *C. cerasi* (A4SC 4–14 vs. 16–42 in *C. lineolata*) but the postpetiolar seta is longer (PP-SL/PPW 0.42–0.54 vs. 0.28–0.43 in *C. lineolata*). For differences between *C. cerasi* and *C. browni*, see under the latter species.

Type notes: The four syntypes of *C. cerasi* in USNM are old and in poor condition; each is on a separate pin and labeled 'N. Y.', 'Collection | T Pergande' and 'No 53583 | U.S.N.M. | Cotype'. The specimens have also been assigned recent USNMENT specimen codes: 00921679, 00921680, 00921681 and 00529078. The last is in best condition and is here designated lectotype. Specific measurements of the lectotype are as follows: HW 1.05, HL 0.94, SL 0.80, ED 0.26, WL 1.14, MtFL 0.92, SPL 0.26, SPTD 0.61.

Distribution and biology: Crematogaster cerasi is widespread in eastern North America, from southern Canada to Florida. It occurs as far west as North Dakota (Wheeler & Wheeler, 1977), Colorado (Gregg, 1963; as '*Crematogaster lineolata*') and northern New Mexico (material examined in LACM). Records on AntWeb of '*C. lineolata*' from Montana (FMNHINS0000108303) and South Dakota (FMNHINS0000109880) almost certainly refer to *C. cerasi*. This species nests in rotten logs, in stumps, under stones and directly in the soil, in both open habitats (grasslands, fields) and in woodlands (Wheeler & Wheeler, 1963; Johnson, 1988; Ellison *et al.*, 2012; Deyrup, 2017). It is also known to colonize wooden structures in houses (Smith, 1965).

CREMATOGASTER COLEI BUREN, 1968, STAT. REV.

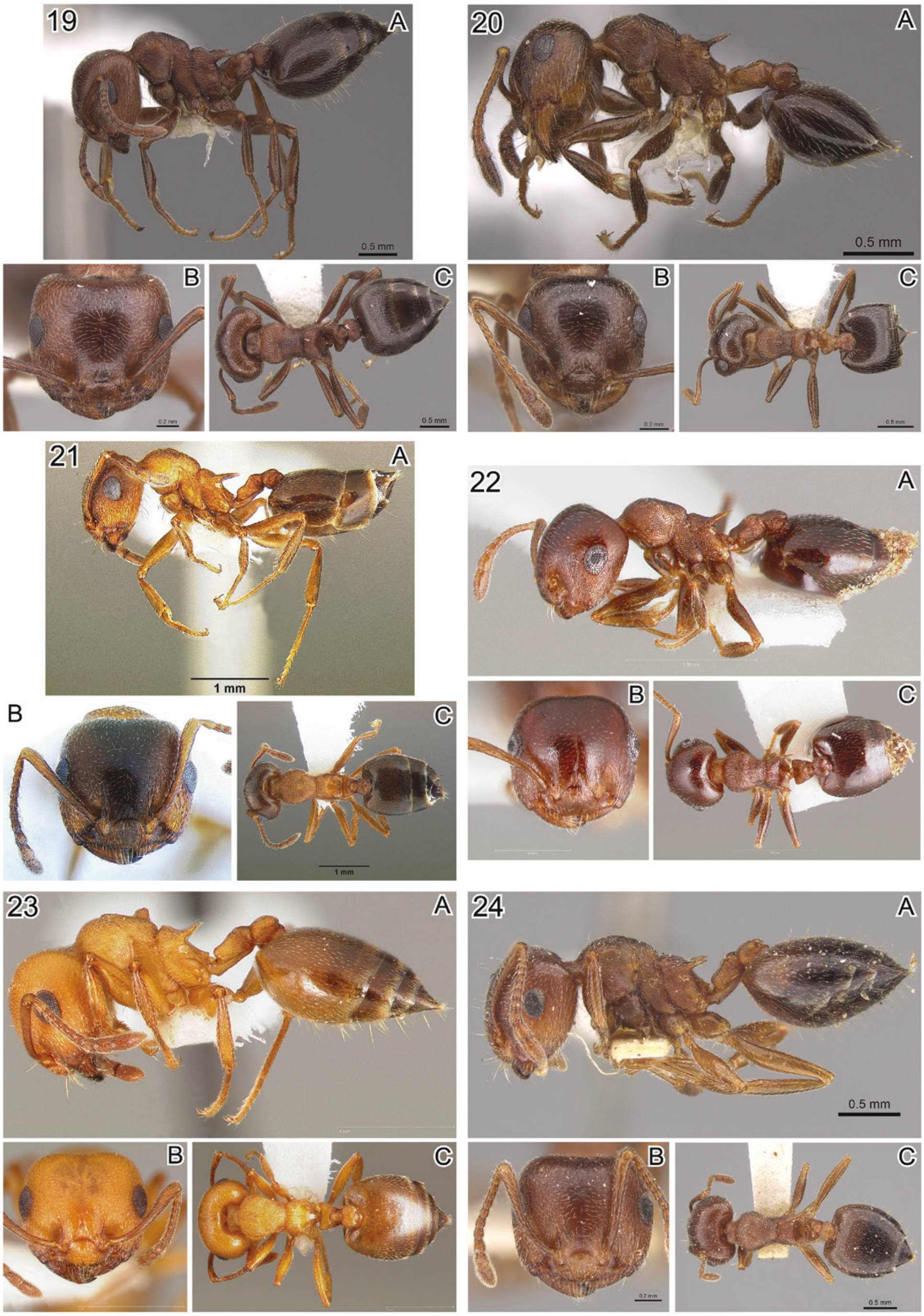
(FIG. 20)

Crematogaster colei Buren, 1968: 108. Holotype worker, Wooten, Sacramento Mts., New Mexico, 7500 ft, 4 July 1917 (Wheeler) (USNM) (USNMENT00528846) (examined).

Junior synonym of *C. vermiculata*: Morgan & Mackay, 2017: 396; here overturned.

*Worker measurements (*N = *12):* HW 0.73–1.06, HL 0.71–0.99, SL 0.68–0.89, WL 0.82–1.19, MtFL 0.71–1.01, MSC 0–2, A4SC 0–11, PP-SL/HW 0.12–0.15, CI 1.03–1.09, OI 0.25–0.28, SI 0.82–0.92, MtFL/HW 0.94–1.00, SPL/HW 0.21–0.26, SPTD/HW 0.48–0.60.

Discussion: Morphological and phylogenomic data affirm that *C. colei* and *C. vermiculata* are distantly related, falling in the *C. opaca* clade and *C. lineolata* clade, respectively (Fig. 1). *Crematogaster colei* can be recognized by the features mentioned by Buren (1968), particularly the relatively elongate scapes (SI 0.82–0.92, SL/HL 0.88–0.96) and well-developed hemilobes of the postpetiole that are sharply angulate in profile. This species is also characterized by relatively long legs (MtFL/HW 0.94–1.00, MtFL/HL 0.99–1.08), long propodeal spines (SPL/HW 0.21–0.26), sparse standing pilosity (MSC 0–2, A4SC 0–11) and predominantly reticulate-foveolate sculpture on the mesosoma, overlain by weak rugulae. *Crematogaster*



Figures 19–24. *Crematogaster* workers, showing lateral view of body (A), full-face view of head (B) and dorsal view of body (C). 19, *C. mutans* worker (CASENT0922736); 20, *C. colei* (CASENT0922726); 21, *C. detecta* holotype (CASENT0863461); 22, *C. larreae* paratype (CASENT0005943); 23, *C. depilis* (CASENT0005668); 24, *C. californica* lectotype (CASENT0923319). Images courtesy of *AntWeb* (www.antweb.org); photographers Wade Lee (19, 20), Zachary Griebenow (21), April Nobile (22, 23), Michele Esposito (24).

vermiculata is different: it has relatively short scapes (SI 0.72–0.78), short legs (MtFL/HW 0.79–0.84), short propodeal spines (SPL/HW 0.17–0.21), more abundant standing pilosity (MSC 3–9, A4SC 9–20) and distinctive rugulose sculpture on the promesonotum (see further discussion under that species). *Crematogaster colei* is actually more similar to *C. californica*, *C. depilis* and *C. opuntiae* (see below) than to *C. vermiculata*. It can be distinguished from those three taxa by the longer legs (see measurements cited above, compared to MtFL/HW 0.80–0.91 and MtFL/HL 0.84–0.98 in *C. californica*, *C. depilis* and *C. opuntiae*) (Fig. 42), smaller eye size (ED/MtFL 0.26–0.28 in *C. colei*, compared to ED/MtFL 0.29–0.37 in the other three taxa) and by the hemilobes of the postpetiole being weakly sculptured and sublucid (usually reticulate-foveolate and subopaque in the other three taxa). In addition, the postpetiolar seta is either absent or short in *C. colei* (PP-SL/HW 0–0.15) and usually present and longer (PP-SL/HW 0.12–0.21) in *C. californica* and *C. opuntiae*. For differences between *C. colei* and the newly described *C. detecta*, see under the latter species.

Distribution and biology: Crematogaster colei is a denizen of desert grassland and oak-pine-juniper woodland of the American South-West. It is known from west Texas, New Mexico, southern Utah, Arizona and northern Mexico. Colonies have been collected under stones and (once) in a dead branch of live oak.

CREMATOGASTER DEPILIS WHEELER, 1919

(FIGS 4B, 23)

Crematogaster lineolata opaca var. *depilis* Wheeler, 1908: 478 (unavailable name).
Crematogaster opaca var. *depilis* Wheeler, W.M. 1919: 111 (first available use of name). Lectotype worker, Cerro Carrizal, Chihuahua, Mexico (Townsend) (MCZC) (MCZENT00303629) (examined).
Crematogaster (*Acrocoelia*) *lineolata* subsp. *opaca* var. *depilis* Wheeler; Emery, 1922: 141.
Crematogaster (*Acrocoelia*) *punctulata* var. *depilis* Wheeler; Enzmann, 1946: 93.
Crematogaster (*Acrocoelia*) *depilis* Wheeler; Creighton, 1950: 209.
Crematogaster (*Crematogaster*) *depilis* Wheeler; Buren, 1968: 93.
Senior synonym of *C. larreae* Buren: Morgan & Mackay, 2017: 155; here overturned (see below).

*Worker measurements (*N = *15):* HW 0.85–1.18, HL 0.79–1.12, SL 0.69–0.89, WL 0.88–1.27, MtFL 0.74–1, MSC 0, A4SC 0–3, PP-SL/HW 0.07–0.12, CI 1.02–1.15, OI 0.27–0.30, SI 0.72–0.81, MtFL/HW 0.80–0.87, SPL/HW 0.16–0.24, SPTD/HW 0.42–0.56.

Discussion: Our phylogenomic results indicate that *C. depilis* is sister to (*C. larreae* + *C. mutans*) (Fig. 1), but further study of this complex is needed. Workers of *C. depilis* can be characterized as follows: mesosoma, petiole and postpetiole densely reticulate-foveolate and opaque, with overlying irregular rugulae on the promesonotum and dorsal face of propodeum; standing pilosity sparse: absent from mesosoma dorsum and usually lacking on fourth abdominal tergite (if present on the latter then restricted to 1–3 short hairs on the posterior margin); legs relatively short and eye relatively large (MtFL/HW 0.80–0.87, ED/MtFL 0.32–0.37); head and mesosoma light yellowish- to reddish-brown (head may be darker than mesosoma), gaster medium to dark brown.

Type notes: From a series of 11 syntype workers in the MCZC, attached to two cards on a single pin, Morgan & Mackay (2017: 160) chose a lectotype worker, identifying it as 'worker on far right of top card designated by red dot and labeled as lectotype'. Upon examining this pin, we found that no lectotype label had been affixed to it, but there is a red dot on the card, so we have printed and attached a label that confirms the lectotype designation. Despite their labelling oversight, Morgan & Mackay's (2017) published statement would appear to meet the requirements for lectotype designation, under Article 74.7.3. of the International Code of Zoological Nomenclature. The lectotype worker and ten paralectotype workers are part of a nest series collected by Townsend in beetle-bored branches of mesquite in which the ants were observed tending coccids (Wheeler, 1908: 479).

Distribution and biology: Material corresponding to the above description comes from a wide variety of arid locations, from Texas to California and south to northern Mexico. Nevertheless, there is some uncertainty about whether all such populations are conspecific, and there are closely similar taxa that are difficult to distinguish from *C. depilis* (see *C. detecta* and *C. larreae*, below). Most collections are from desert habitats, with foragers frequently collected on cacti, and colonies located under stones, directly in the soil and in buried wood and roots.

CREMATOGASTER DETECTA SP. NOV.

(FIG. 21)

Zoobank registration: urn:lsid:zoobank.org:act:4508D17A-F49A-4092-942B-89F3431E117A.

Type material: Holotype worker, US, Nevada, Clark Co.: 4 km NW Calico Basin, 1330 m, 36.16514 –115.44926 ± 5m, 21 Apr 2016, P. S. Ward PSW17509, under stone, oak-pine woodland (CASENT0863461) (USNM). Paratypes: nine workers, same data as holotype (CASENT084433, CASENT0863074, CASENT0863459, CASENT0863460, CASENT0863462, CASENT0863463, CASENT0863464, CASENT0863465) (CASC, LACM, MCZC, UCDC).

Non-type material: Four workers, *US, California*, San Bernardino Co.: Teutonia Peak, 1720 m, 35°18′N 115°34′W, 30 Mar 2004, P. S. Ward PSW15191, under stone, juniper woodland (UCDC); four alate queens, one male, *US, Utah*, Washington Co.: Springdale, 1180 m, 37.18449 −113.00067 ± 5 m, 3 Aug 2019, P. S. Ward PSW18243, at light, roadside (UCDC).

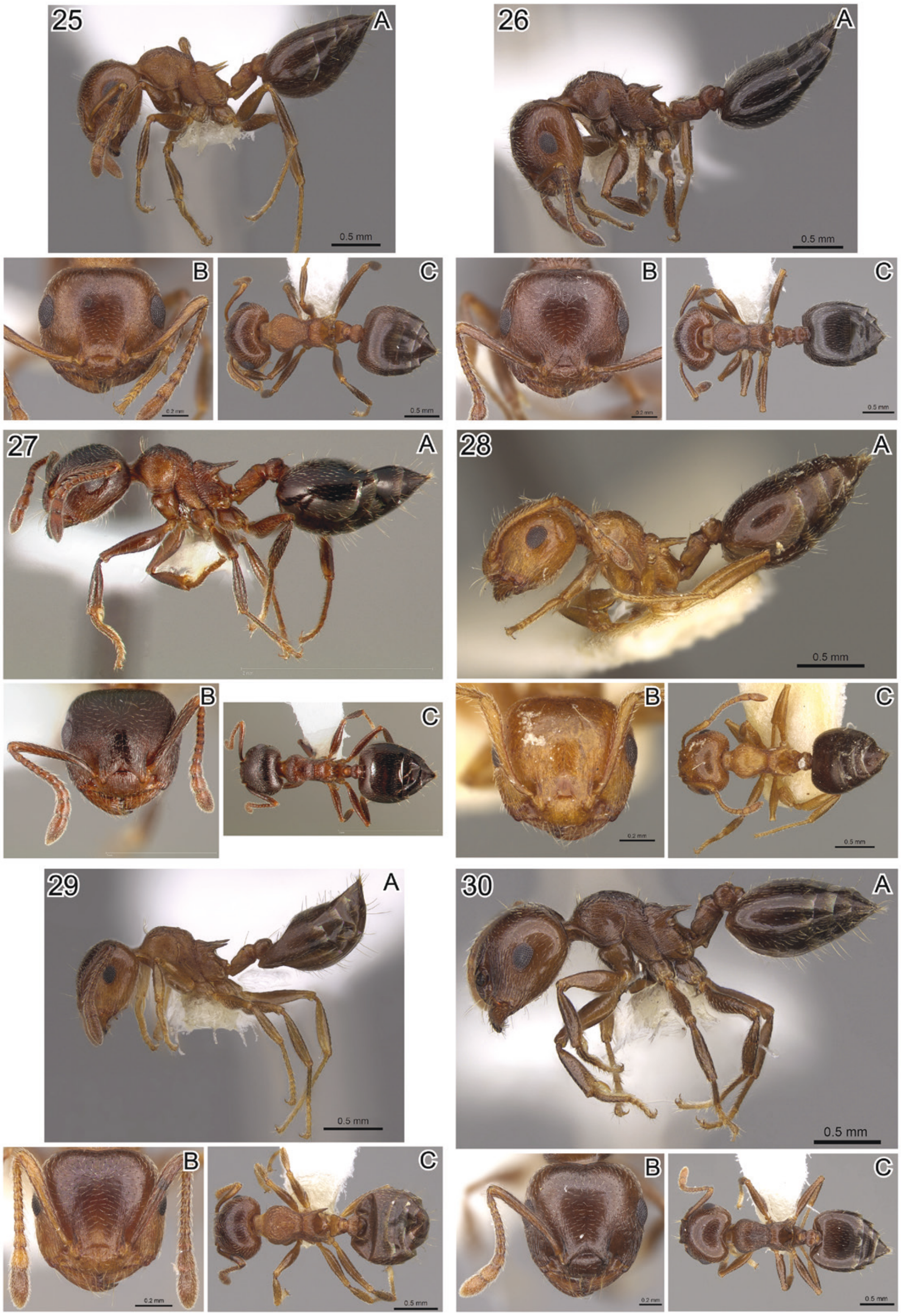
*Worker measurements (*N = *11):* HW 0.95–1.17, HL 0.93–1.14, SL 0.76–0.95, WL 1.00–1.37, MtFL 0.80–1.05, MSC 0, A4SC 0–3, PP-SL/HW 0.08–0.12, CI 1.02–1.06, OI 0.26–0.30, SI 0.79–0.83, MtFL/HW 0.84–0.93, SPL/HW 0.20–0.24, SPTD/HW 0.43–0.55.

Worker diagnosis: Head slightly broader than long, the sides convex and the posterior margin flat to weakly concave; scapes surpassing the posterior margin of head by less than distal scape width (SI 0.79–0.83, SL/HL 0.80–0.87, SL/WL 0.67–0.79); eye moderately large (OI 0.26–0.30, ED/HL 0.27–0.31, ED/MtFL 0.28–0.36); promesonotum lacking well-marked pronotal humeri and mesonotal declivity; propodeal spines relatively long (SPL/HW 0.20–0.24, SPL/WL 0.18–0.21) and divergent (SPTD/HW 0.43–0.55); petiole subtrapezoidal, broadened anteriorly (PTW/HW 0.32–0.39); postpetiole relatively broad (PPW/HW 0.28–0.32), the hemilobes not strongly angulate in profile; legs relatively long (MtFL/HW 0.84–0.93, MtFL/HL 0.86–0.95, MtTL/HW 0.77–0.81). Mandibles striate; head reticulate to reticulate-striolate, becoming effaced and sublucid medially; mesosoma predominantly reticulate-foveolate and opaque, with overlying irregular rugulae on pronotum and dorsal face of propodeum; declivitous face of propodeum mostly smooth and shiny; petiole and postpetiole reticulate to reticulate-foveolate, subopaque. Standing pilosity sparse on head and absent from mesosoma dorsum; scape with relatively conspicuous decumbent pubescence; postpetiolar seta short (PP-SL/HW 0.08–0.12); standing pilosity absent from most of fourth abdominal (first gastric) tergite, confined to 0–3 short hairs on the posterior margin. Light reddish-brown, head and gaster darker.

Comments: The workers of this species are similar to those of *C. depilis* yet phylogenomic data place *C. detecta* as sister to *C. vetusta* and more distant from *C. depilis* (Fig. 1). As in *C. depilis*, the mesosoma dorsum of *C. detecta* is densely reticulate-foveoleate and opaque and lacks standing pilosity (MSC 0); standing pilosity is correspondingly sparse on the head and gaster and confined on the fourth abdominal tergite to a few or no (0–3) short standing hairs on the posterior margin. *Crematogaster detecta* differs from *C. depilis* by the less strongly developed rugulose sculpture on the dorsal face of the propodeum which contrasts less with the sculpture on the mesonotum than in *C. depilis*, and by a tendency to have more conspicuously uplifted pubescence on the scape. These features are somewhat difficult to evaluate, however, and they show considerable variation among putative workers of *C. depilis*. Larger workers (HW > 1.05 mm) can be separated by morphometric differences: *C. detecta* exhibits longer legs and a more slender mesosoma than both *C. depilis* and the closely similar *C. larreae* (Figs 43, 44) such that, for these larger workers of *C. detecta*, MtFL/HW 0.87–0.91, MtTL/HW 0.77–0.79, ED/MtFL 0.29–0.32 and WL/HW 1.08–1.17. Corresponding combined values for *C. depilis* and *C. larreae* (of all sizes) are: MtFL/HW 0.80–0.87, MtTL/HW 0.71–0.77, ED/MtFL 0.32–0.37 and WL/HW 0.97–1.09. However, small workers of *C. detecta* cannot be recognized on this basis (Figs 43, 44). *Crematogaster detecta* can be distinguished from *C. colei* by its shorter scapes (SL/HL 0.80–0.87 vs. 0.88–0.96 in *C. colei*) and legs (MtFL/HL 0.86–0.95 vs. 0.99–1.08 in *C. colei*); denser sculpture on the mesosoma, petiole and postpetiole; and more rounded (less angulate) hemilobes of the postpetiole, as seen in lateral view.

Distribution and biology: The type series from Clark County, Nevada (PSW17509) consists of a series of workers collected under a stone in a sandy wash with *Pinus monophylla* Torr. & Frém., *Quercus turbinella* Greene, *Arctostaphylos pungens* Kunth, *Garrya flavescens* S.Watson, *Fraxinus anomala* Torr. ex S.Watson, *Purshia* DC. sp. and various cacti. Otherwise this species is known only from (1) workers collected under a stone in juniper woodland in San Bernardino County, California (PSW15191) and (2) four alate queens and one male collected at light in southern Utah (PSW18243). These specimens were identified as conspecific with the type series through phylogenomic (UCE) data. Other material undoubtedly exists in collections, masquerading as *C. depilis*. Based on limited locality data it seems that *C. detecta* prefers more wooded habitats than *C. depilis*.

Etymology: The name is derived from Latin detectus, past participle of *detegere*, to discover or disclose, referring to the initial detection of this cryptic species from DNA sequence data.



Figures 25–30. *Crematogaster* workers, showing lateral view of body (A), full-face view of head (B) and dorsal view of body (C). 25, *C. opuntiae* (CASENT0922738); 26, *C. marioni* (CASENT0922734); 27, *C. coarctata* (CASENT0005667); 28, *C. hespera* holotype (USNMENT00529501); 29, *C. browni* (CASENT0922722); 30, *C. emeryana* (CASENT0922729). Images courtesy of *AntWeb* (www.antweb.org); photographers Wade Lee (25, 26, 29, 30), April Nobile (27), Michele Esposito (28).

CREMATOGASTER HESPERA BUREN, 1968, **STAT. REV.**
(FIG. 28)

Crematogaster hespera Buren, 1968: 98. Holotype worker, Phoenix, Arizona, 20 Jul 1918 (A. W. Morrill) (USNM) (USNMENT00529501) (examined).

Crematogaster hespera a junior synonym of *C. laeviuscula*: Morgan & Mackay, 2017: 197; here overturned.

Worker measurements (N = *18*)*:* HW 0.82–1.16, HL 0.79–1.05, SL 0.67–0.90, WL 0.90–1.20, MtFL 0.72–1.03, MSC 3–14, A4SC 9–26, PP-SL/HW 0.13–0.21, CI 1.04–1.11, OI 0.22–0.26, SI 0.76–0.83, MtFL/HW 0.82–0.89, SPL/HW 0.19–0.22, SPTD/HW 0.42–0.52.

Discussion: The synonymy of *C. hespera* under *C. laeviuscula* is not supported by our phylogenomic analyses, which indicate that *C. hespera* is sister to *C. cerasi* and more distantly related to *C. laeviuscula* (Fig. 1). Buren (1968: 99) described differences in sculpture and shape between *C. hespera* and *C. laeviuscula* as follows: 'This form [*hespera*] may be easily distinguished from *laeviuscula* by the finely striate thorax, the evenly but not strongly convex profile of the promesonotum without mesonotal declivity, the less divergent, often incurved epinotal [= propodeal] spines with the little oblique impressions at base, the differently shaped postpetiole and by the fact that the larger workers do not exhibit as much allometry as in *laeviuscula*.' Buren noted the apparent allopatry of the two species while at the same time identifying areas in northern Mexico and west Texas that could be investigated to determine if the two taxa overlap. We have found that larger workers of *C. laeviuscula* (HW > 1.00 mm) differ from those of *C. hespera* by the greater relative length of their propodeal spines: SPL/HW 0.23–0.27 and SPL/WL 0.22–0.25, compared to SPL/HW 0.19–0.22 and SPL/WL 0.18–0.21 in *C. hespera* (Fig. 45). In smaller workers this distinction does not hold up. *Crematogaster hespera* differs from its sister-species, *C. cerasi*, by having a more smooth and shiny promesonotum which is, moreover, convex not flattened, in profile.

Crematogaster hespera is typically a bright, bicoloured ant with orange-brown or reddish-brown head and mesosoma and dark brown gaster, but in coastal California there is a tendency for workers to become more uniformly dusky in colour. These could be confused with workers of *C. coarctata* from southern California that have comparable coloration and a similarly shiny head and mesosoma (more typical *C. coarctata* from northern California have dense reticulate-foveolate sculpture on the head, which readily distinguishes them from shiny-headed *C. hespera*). Workers of *C. hespera* can generally be distinguished from those of *C. coarctata* by their shorter legs (MtFL/HL 0.89–0.98 vs. 0.97–1.07 in *C. coarctata*) and shorter scapes (SL/HL 0.79–0.89 vs. 0.87–0.96 in *C. coarctata*). Measurements taken from throughout the ranges of the two species overlap slightly, but in south-central California and northern Baja California, where the two species might be confused, the differences in leg length are diagnostic (MtFL/HL 0.90–0.96 in *C. hespera* and 0.97–1.03 in *C. coarctata*). In addition, *C. hespera* workers usually lack the longitudinal striae on the lower mesopleuron that are present in *C. coarctata*, and they have a mesosoma dorsum that is more convex in profile and without a pronounced mesonotal declivity, compared to workers of *C. coarctata*.

Distribution and biology: Crematogaster hespera has a wide distribution across the South-West, from Chihuahua and west Texas to California and Baja California. It is commonly found in riparian woodland; other recorded habitats include coastal scrub, maritime chaparral, sand dunes, grassland, sagebrush-riparian vegetation and mixed coniferous forest. Colonies are typically located under tree bark, in dead branches of trees and shrubs or in dead stalks of perennial plants. Although this species is predominantly arboreal, nests are sometimes found in or under fallen logs on the ground and under stones.

CREMATOGASTER LARREAE BUREN, 1968, **STAT. REV.**
(FIG. 22)

Crematogaster larreae Buren, 1968: 117. Holotype male, Franklin Mts., El Paso, Texas (W. F. Buren) (LACM) (examined).

Junior synonym of *C. depilis*: Morgan & Mackay, 2017: 155; here overturned.

Worker measurements (N = *5*)*:* HW 0.74–1.05, HL 0.71–0.99, SL 0.59–0.78, WL 0.80–1.09, MtFL 0.63–0.87, MSC 0, A4SC 0, PP-SL/HW 0.10–0.13, CI 1.00–1.06, OI 0.27–0.31, SI 0.74–0.80, MtFL/HW 0.83–0.85, SPL/HW 0.19–0.23, SPTD/HW 0.48–0.53.

Discussion: Crematogaster larreae was described by Buren (1968) as a 'cryptic' species closely related to and sympatric with *C. depilis*, having distinctive queens and males but workers that are very similar to those of *C. depilis*. The primary difference between the workers of the two species is their colour: *C. larreae* workers have the head and mesosoma dark brown and the gaster brownish-black, while in *C. depilis* the head and mesosoma vary from yellowish-brown to reddish-brown (the head may be darker than the mesosoma), and the gaster is medium to dark brown. However, this distinction is tenous and difficult to ascertain in older, faded specimens. Buren (1968) also provided evidence of differences in biology, with *C. larreae* apparently confined to nesting at the base of creosote bush (*Larrea tridentata*), in contrast to the generalized ground-nesting habits of *C. depilis*. Because they could not distinguish the workers of these two forms, Mackay & Morgan (2017) synonymized *C. larreae* under *C. depilis*, while making no comment about the male and queen differences. We have sequenced sympatric samples taken in Chihuahuan desert near Portal, Arizona, corresponding to the *C. depilis* colour phenotype (PSW14684) and the *C. larreae* colour phenotype (PSW15960 and PSW16636), and we find that they are positioned in different parts of the UCE phylogeny (Fig. 1). The *C. larreae*-like samples are sister to *C. mutans*, while the *C. depilis*-like sample clusters with other *C. depilis* populations from New Mexico, Arizona and California. Thus we have provisional evidence that there are indeed two species, with *C. larreae* actually being more closely related to *C. mutans* (with which it is allopatric) than to *C. depilis*. On the basis of univariate observations and bivariate plots we have been unable to discover diagnostic morphometric differences between the workers of *C. depilis* and *C. larreae*, but it is possible that a more detailed, multivariate analysis would permit discrimination of the workers of these two species. This was found to be effective, for example, to separate two closely similar sister-species in Europe, *C. scutellaris* and *C. schmidti* (Mayr, 1853) that also differ subtly in colour (Seifert, 2018).

Distribution and biology: Crematogaster larreae was recorded by Buren (1968) from desert localities in west Texas, Arizona and California, nesting in the lower stems and roots of *Larrea divaricata*. The one nest series that we have collected (PSW15960) was in a similar situation in south-eastern Arizona. Buren (1968) further noted that *C. larreae* was often absent from localities with *Larrea*, and he suggested that competition with other desert-dwelling ants may restrict it to harsher, rockier sites. It is also interesting to note that the queens and males of *C. larreae* are smaller and shinier than those of *C. depilis*, suggesting perhaps an unusual mode of colony foundation.

CREMATOGASTER MARIONI BUREN, 1968, STAT. REV. (FIG. 26)

Crematogaster marioni Buren, 1968b: 105. Holotype worker, Morena Lake, San Diego Co., California (W. F. Buren) (LACM) (examined).

Junior synonym of *C. emeryana*: Morgan & Mackay, 2017: 171; here overturned.

*Worker measurements (*N *= 18):* HW 0.72–1.05, HL 0.71–0.98, SL 0.56–0.73, WL 0.81–1.14, MtFL 0.60–0.82, MSC 4–15, A4SC 19–38, PP-SL/HW 0.08–0.14, CI 1.01–1.09, OI 0.24–0.28, SI 0.69–0.80, MtFL/HW 0.78–0.89, SPL/HW 0.16–0.23, SPTD/HW 0.43–0.56.

Discussion: Crematogaster emeryana and *C. marioni* exhibit notable differences in morphology, biology and distribution. They also have no close phylogenetic relationship to one another, with *C. marioni* being sister to *C. coarctata*, while *C. emeryana* appears to be a western offshoot of *C. lineolata* (Fig. 1). The most noticeable distinctions between the two species are as follows:

- Scape length: shorter in *C. marioni* (SI 0.69–0.80, SL/HL 0.73–0.81, SL/WL 0.64–0.71; *N* = 18), longer in *C. emeryana* (SI 0.82–0.89, SL/HL 0.84–0.90, SL/WL 0.74–0.79; *N* = 12) (Fig. 46).
- Conspicuous striae on lower mesopleuron: usually present in *C. marioni*, absent in *C. emeryana*.
- Standing pilosity on gaster: common in *C. marioni* (A4SC 19–38), sparser in *C. emeryana* (A4SC 8–16).
- Nesting habits: arboreal (*C. marioni*) vs. ground-dwelling (*C. emeryana*).

Distribution and biology: Crematogaster marioni is endemic to the California floristic province and occurs from northern California to northern Baja California. It has been recorded from a variety of low- to medium-elevation habitats, including oak woodland, riparian woodland, *Quercus–Pinus–Pseudotsuga* forest, pine forest/woodland, chaparral and coastal scrub. Nest site records include oak galls; dead branches of *Arctostaphylos*, *Baccharis*, *Pinus* and *Quercus* and rotten pine logs.

CREMATOGASTER OPACA MAYR, 1870

Crematogaster opaca Mayr, 1870: 992. Syntype worker, Tabukaya, Mexico, 1865 (Bilimek) (NHMW) (examined via AntWeb image: CASENT0919705) and syntype worker, Mexico (Sichel) (BMNH) (examined via AntWeb image: CASENT0902152); latter **here designated lectotype**.

Crematogaster lineolata subsp. *opaca* Mayr; Emery, 1895: 283.

Crematogaster opaca Mayr; Wheeler, 1919: 111.

Crematogaster (*Acrocoelia*) *lineolata* subsp. *opaca* Mayr; Emery, 1922: 141.

Crematogaster (*Acrocoelia*) *opaca* Mayr; Wheeler, 1934a: 139.

Crematogaster (*Crematogaster*) *opaca* Mayr; Smith, 1958: 126.

Discussion: Morgan & Mackay (2017) refer to a syntype worker of *C. opaca* in NHMW 'collected by Professor Bilimek and Dr Sichel in México'. This statement is misleading because there is no single syntype collected by Bilimek and Sichel; their collections were separate. In the BMNH there is a syntype worker (here designated lectotype) (CASENT0902152) labelled 'Mex. | Sichel', while the NHMW syntype (now paralectotype) is labelled 'Mexico | Takubaya | Bilim. 65'. However, the important point is that these two specimens are almost certainly not conspecific. The Sichel specimen has the head, mesosoma, petiole and postpetiole densely reticulate-foveolate and opaque, and the gaster finely reticulate and sublucid; the promesonotum is evenly convex in profile and broad in dorsal view (pronotum width/head width ~0.62); the propodeal spine distance is relatively large (SPTD/HW ~0.49); and standing pilosity appears to be sparse (not visibly present on the mesosoma dorsum). The Bilimek specimen is more weakly sculptured with a correspondingly shinier integument, especially on the petiole, postpetiole and gaster; the promesonotum is somewhat flattened in profile and narrower in dorsal view (pronotum width/head width ~0.53); the propodeal spine tips are less distant (SPTD/HW ~0.44); and standing pilosity is more conspicuous, being present on the mesosoma dorsum on both the pronotal humeri and the mesonotal declivity. Although in this study we are concerned primarily with the *Crematogaster* of America north of Mexico, we have decided to select a lectotype of *C. opaca* to assist future work. We designate the BMNH specimen as lectotype because it better matches the original description, which emphasizes the densely reticulate-punctate sculpture and the scarcity of standing pilosity (Mayr, 1870). Unfortunately the provenance of this specimen – other than Mexico – is unknown. Sichel evidently supplied the specimen to Mayr, but there is no evidence that he visited Mexico or anywhere else outside Europe during his lifetime (Mulsant, 1869), so the specimen would have been acquired from another collector, possibly de Saussure. The non-conspecific paralectotype is from Takubaya (= Tacubaya), a district of Mexico City, near Bilimek's place of residence during his stay in Mexico (Roth, 1965: 346).

There is a confusing array of *C. opaca*-like forms found in Mexico and Central America, showing considerable variation in sculpture, pilosity, configuration of the promesonotum, size of propodeal spines and petiole shape. More comprehensive sampling and careful study is necessary to determine how many species are present in this complex. These ants just barely enter the United States, in southern Arizona. Because of taxonomic uncertainty, we refer to the Arizona populations as *Crematogaster* sp. cf. *opaca*. These specimens are similar to the *C. opaca* lectotype with respect to integument sculpture, promesonotal shape (pronotum width/head width 0.59–0.62) and propodeal spine distance (SPTD/HW 0.45–0.51), but they have more abundant standing pilosity (MSC 2–5, A4SC 10–18).

CREMATOGASTER OPUNTIAE BUREN, 1968, **STAT. REV.**

(FIG. 25)

Crematogaster opuntiae Buren, 1968: 120. Holotype worker, Santa Rita Experimental Range, Arizona (Buren) (LACM) (examined).

Junior synonym of *C. vermiculata*: Morgan & Mackay, 2017: 396; here overturned.

*Worker measurements (*N = *10):* HW 0.86–1.21, HL 0.80–1.11, SL 0.72–0.94, WL 0.89–1.27, MtFL 0.74–1.05, MSC 1–3, A4SC 5–16, PP-SL/HW 0.14–0.19, CI 1.05–1.11, OI 0.26–0.29, SI 0.75–0.84, MtFL/HW 0.85–0.89, SPL/HW 0.19–0.25, SPTD/HW 0.50–0.59.

Discussion: Crematogaster opuntiae bears little similarity or close phylogenetic relationship (Fig. 1) to the eastern, swamp-inhabiting species *C. vermiculata*, under which it was synonymized by Morgan & Mackay (2017). Among obvious differences, it has longer scapes and legs (SL/HL 0.83–0.90 and MtFL/HL 0.91–0.95 compared to SL/HL 0.75–0.82 and MtFL/HL 0.84–0.89 in *C. vermiculata*), predominantly reticulate-foveolate sculpture on the promesonotum, more divergent propodeal spines (SPTD/PPW 1.71–1.96 compared to 1.15–1.48 in *C. vermiculata*) and lesser amounts of standing pilosity (MSC 1–3 and A4SC 5–16, compared to MSC 3–9 and A4SC 9–20 in *C. vermiculata*). As noted by Buren (1968), *C. opuntiae* is similar to *C. californica*, differing primarily by the shinier head and by the more appressed pubescence on the scapes and head. The relationship of *C. opuntiae* to *C. californica* remains to be clarified – they may well prove to be conspecific. *Crematogaster opuntiae* has similar eye, scape, leg (Fig. 42) and propodeal spine dimensions as *C. californica*, and in our phylogenomic analyses the two are sister-taxa (Fig. 1).

Distribution and biology: Buren (1968) recorded *C. opuntiae* from desert and semi-desert regions of Arizona and considered *C. californica* to be restricted to California and Baja California. Both taxa are ground-nesting.

CREMATOGASTER PARAPILOSA SP. NOV.

(FIG. 37)

Zoobank registration: urn:lsid:zoobank.org:act:529E00DF-E3E5-4087-BA6E-0E9E037EFE6A.

Crematogaster atkinsoni; Buren, 1968: 92 (nec Wheeler, 1919:108).
Crematogaster atkinsoni; Johnson, 1988: 316 (nec Wheeler, 1919:108).
Crematogaster atkinsoni; Deyrup 2017: 61 (nec Wheeler, 1919:108).
Crematogaster laeviuscula; Morgan & Mackay, 2017: 197 (nec Mayr, 1870: 993) (in part).

Type material: Holotype worker, US, Florida, Sarasota Co.: Longino Ranch, 10 m, 27.15564 −82.11670 ± 3 m, 1 October 2016, P. S. Ward PSW17790, on low vegetation, *Cephalanthus* swamp (CASENT0863386) (USNM). Paratypes: ten workers, same data as holotype (CASENT0842343, CASENT0863137, CASENT0863387, CASENT0863388, CASENT0863389, CASENT0863390, CASENT0863391, CASENT0863392) (CASC, FSCA, LACM, MCZC, UCDC).

Non-type material: US, Alabama, Baldwin Co.: Bon Secour River, 16 km SW Foley (D. E. Read) (CASC); *US, Florida*, Collier Co.: Big Cypress Natl. Preserve, Concho Billy Trail (D. M. Olson) (UCDC); Collier Co.: Collier-Seminole State Park (P. S. Ward) (UCDC); Leon Co.: Tall Timbers Plant. (B. V. Travers) (LACM); Monroe Co.: Big Pine Key (T. Daccy) (NCSU); Palm Beach Co.: West Palm Beach (W. F. Buren) (LACM); Sarasota Co.: Albee Farm & Laurel Rd. (W. Rodriguez-Cayro) (UCDC); Sarasota Co.: Myakka River St. Pk. (J. Longino) (CASC).

*Worker measurements (*N = *15):* HW 0.83–1.13, HL 0.78–1.01, SL 0.67–0.85, WL 0.93–1.22, MtFL 0.74–0.95, MSC 0–8, A4SC 11–24, PP-SL/HW 0.14–0.20, CI 1.04–1.12, OI 0.23–0.25, SI 0.76–0.87, MtFL/HW 0.84–0.92, SPL/HW 0.26–0.34, SPTD/HW 0.56–0.71.

Worker diagnosis: Head broader than long, with convex sides, posterior margin straight to weakly concave; scapes moderately long, surpassing the posterior margin of head by distal scape width or more (SI 0.76–0.87, SL/HL 0.84–0.91, SL/WL 0.70–0.79); eye of moderate size (OI 0.23–0.25, ED/HL 0.24–0.27, ED/MtFL 0.25–0.29); pronotal humeri weakly developed; anteromedial mesonotal carina prominent in profile; dorsal face of mesonotum flat, then rounding gently into mesonotal declivity; propodeal spines long and slender (SPL/HW 0.26–0.34, usually > 0.27, SPL/WL 0.23–0.31), strongly divergent (SPTD/HW 0.56–0.71); petiole subtrapezoidal, with moderate lateral expansion (PTW/HW 0.35–0.41); postpetiole broad (PPW/HW 0.31–0.35), with prominent median furrow; legs of moderate length (MtFL/HW 0.84–0.92, MtFL/HL 0.92–1.00). Mandibles striate; head and mesosoma dorsum predominantly smooth and shiny, excepting usual anterolateral striae on head and weak reticulate to reticulate-striate sculpture on promesonotum, mostly laterally and on mesonotal declivity; mesopleuron reticulate-foveolate, opaque, overlain by rugulae on upper-third; petiole, postpetiole and gaster smooth and shining, with weak reticulation on postpetiole and side of petiole. Standing pilosity moderately developed, present as two to six hairs in a row on each side of the midline of the front of the head, as none to four hairs on each pronotal humerus (MSC 0–8), as paired setae on the petiole and postpetiole (PP-SL/PPW 0.38–0.54), and as scattered setae on the first gastric (fourth abdominal) tergite (A4SC 11–24). Pubescence present on most of body, appressed or decumbent and generally distinct from the standing pilosity (i.e. not becoming suberect). Medium to dark brown (workers in some populations bicoloured to reddish brown).

Comments: This is a marsh-inhabiting species of the south-eastern United States that has been masquerading under the name of a different species, *Crematogaster atkinsoni* (here considered a junior synonym of *C. pilosa* – see below). It has been recognized for some time that workers of *C. parapilosa*, going by the name '*C. atkinsoni*', can be distinguished from those of the closely related species, *C. pilosa*, by their lesser amount of standing pilosity and more consistently appressed pubescence, especially on the head (Johnson, 1988; Deyrup, 2017). A lateral or posterodorsal view of the head is the best way to appreciate this difference: in *C. parapilosa* there are two to six pairs of long, standing hairs flanking the midline of the head, and these stand apart from the shorter appressed and decumbent pubescence, whereas in *C. pilosa* the pubescence tends to be uplifted (suberect or subdecumbent), contrasting less with the longer paired setae, and imparting a hairier appearance to the head (see Johnson, 1988; Fig. 6). Examination of the type workers of *C. atkinsoni* reveals that they have the pilosity characteristics of *C. pilosa*, and a new name is therefore required for the less pilose species. The two species are broadly sympatric in much of Florida (Deyrup, 2017) and they apparently co-occur – or previously co-occurred – at the type locality of *C. atkinsoni* (Fort Myers, Florida). Wheeler (1919) described the biology of what is probably *C. parapilosa* – in particular, the carton nest construction – yet the workers that were designated type specimens appear to be *C. pilosa*.

Morgan & Mackay (2017: 197) considered *C. parapilosa* (as '*C. atkinsoni*') to be a junior

Figures 31–36. *Crematogaster* workers, showing lateral view of body (A), full-face view of head (B) and dorsal view of body (C). 31, *C. cerasi* lectotype (USNMENT00529078); 32, *C. vermiculata* (CASENT0914534); 33, *C. rifelna* holotype (LACMENT164556); 34, *C. ashmeadi* (CASENT0922720); 35, *C. pinicola* (CASENT0172943); 36, *C. pilosa* (CASENT0914530). Images courtesy of *AntWeb* (www.antweb.org); photographers Michele Esposito (31, 33), Zach (Ziv) Lieberman (32, 36), Wade Lee (34), April Nobile (35).

synonym of *C. laeviuscula*, a midwestern species that nests in dead stems, branches and logs, and occurs from Kansas and Missouri south to Texas and north-eastern Mexico (Creighton, 1950; Buren, 1968; Johnson, 1988). Apart from biological and distributional differences, all but the smallest workers of *C. parapilosa* can be distinguished from those of *C. laeviuscula* by their disporportionately longer propodeal spines (Fig. 45) (for worker HW > 0.85 mm, SPL/HW 0.29–0.34 in *C. parapilosa* vs. 0.21–0.27 in *C. laeviuscula*). Our phylogenomic (UCE) data indicate that *C. parapilosa* is sister to *C. laeviuscula* + *C. pilosa* (Fig. 1).

Distribution and biology: Crematogaster parapilosa is an arboreal species found in marsh habitats of the south-eastern United States. We have examined material from Florida and Alabama, and there are also records (as '*C. atkinsoni*') from as far north as North Carolina (Guénard *et al.*, 2012). This species typically constructs carton nests on vegetation (Wheeler, 1919; Deyrup, 2017), but Johnson (1988: 317) reported variation in this behaviour, with some nests being found in plant cavities without the use of carton. The apparent biological and morphological differences between *C. parapilosa* and *C. pilosa*, and the extent of intraspecific variation in both taxa, need further study.

Etymology. The name '*parapilosa*' alludes to the close relationship of this species to *C. pilosa*, using the Greek preposition *παρα*-, meaning near or beside.

CREMATOGASTER PILOSA EMERY, 1895

(FIG. 36)

Crematogaster lineolata subsp. *pilosa* Emery, 1895: 285. Syntype workers, District of Columbia and New Jersey (Pergande) (MHNG, NHMB). Syntype worker from New Jersey examined as image on AntWeb (CASENT0919707).

Status as species: Wheeler, 1919: 111; Creighton, 1950: 216; Buren, 1968: 92; Johnson, 1988: 321.

Crematogaster atkinsoni Wheeler, 1919: 108. Six syntype workers, Fort Myers, Florida (J. W. Youngs) (LACM, MCZC) (examined). One worker in LACM (LACMENT182007) here designated as **lectotype**. **Syn. nov.**

Crematogaster atkinsoni var. *helveola* Wheeler, 1919: 109. Three syntype workers, five males, one dealate queen, Okefenokee Swamp, Georgia (J. C. Bradley) (MCZC). One syntype worker (MCZENT00020823) here designated as **lectotype**. **Syn. nov.**

Crematogaster atkinsoni var. *helveola* as junior synonym of *C. atkinsoni*: Creighton, 1950: 207.

Crematogaster atkinsoni as junior synonym of *C. laeviuscula*: Morgan & Mackay, 2017: 197; here overturned.

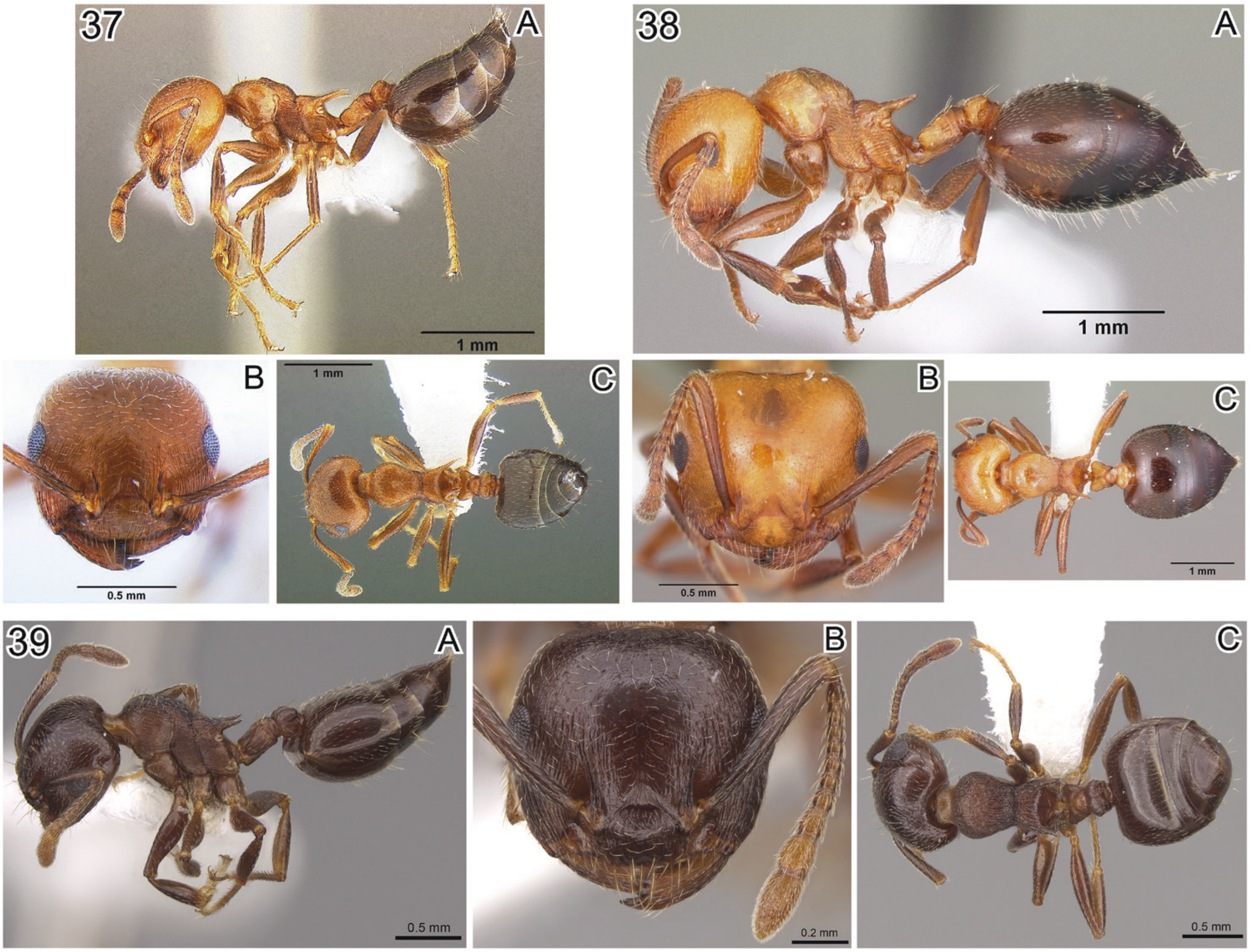
Crematogaster atkinsoni helveola (misspelled as '*haeveola*') as junior synonym of *C. laeviuscula*: Morgan & Mackay, 2017: 197; here overturned.

Crematogaster (*Acrocoelia*) *creightoni* Wheeler, 1933: 86. Syntype alate queens, Roanoke, Virginia, 10 September 1932 (W. S. Creighton) (FMNH, MCZC, NHMB, USNM). Syntype queens examined as images on AntWeb: FMNHINS0000062697, FMNHINS0000062698, CASENT0912712 and CASENT0105566. Synonymy by Buren in Smith, 1958: 127.

*Worker measurements (*N = *11).* HW 0.85–1.04, HL 0.75–0.96, SL 0.69–0.84, WL 0.89–1.16, MtFL 0.71–0.88, MSC 10–30, A4SC 20–60, PP-SL/HW 0.17–0.23, CI 1.05–1.17, OI 0.22–0.25, SI 0.78–0.83, MtFL/HW 0.82–0.88, SPL/HW 0.22–0.29, SPTD/HW 0.55–0.68.

Discussion: As the name implies, this species is characterized by its conspicuous standing pilosity. In particular, the pubescence on the head, mesosoma and gaster of the worker has a tendency to become uplifted (suberect or subdecumbent) and grade into the longer erect hairs, increasing the total amount of standing pilosity (MSC 10–30, A4SC 20–60). The length of the longest postpetiolar seta is half or more the width of the postpetiole (PP-SL/PPW 0.49–0.60). The propodeal spines are usually long (SPL/HW 0.22–0.29) and divergent (SPTD/HW 0.55–0.68). As noted by others (Johnson 1988), this species is variable and specimens from the northern part of the range, including the *C. pilosa* syntypes, tend to be more pilose than those from farther south. Examination of type specimens and other material indicates that *C. atkinsoni* and *C. atkinsoni helveola*, described from Florida and Georgia, respectively, are junior synonyms of *C. pilosa*, not *C. laeviuscula* (cf. Morgan & Mackay, 2017). If the southern *pilosa*-like populations prove to be specifically distinct from the more setose northern populations of *C. pilosa*, then the name *C. atkinsoni* is available for them. For the moment we are treating them as conspecific. Phylogenomic data show that *C. pilosa* and *C. laeviuscula* are closely related – they are sister-species in our UCE tree (Fig. 1). Some samples of putative *C. laeviuscula* from eastern Texas have workers that are atypically dark and hairy, suggesting the possibility of gene flow between these taxa.

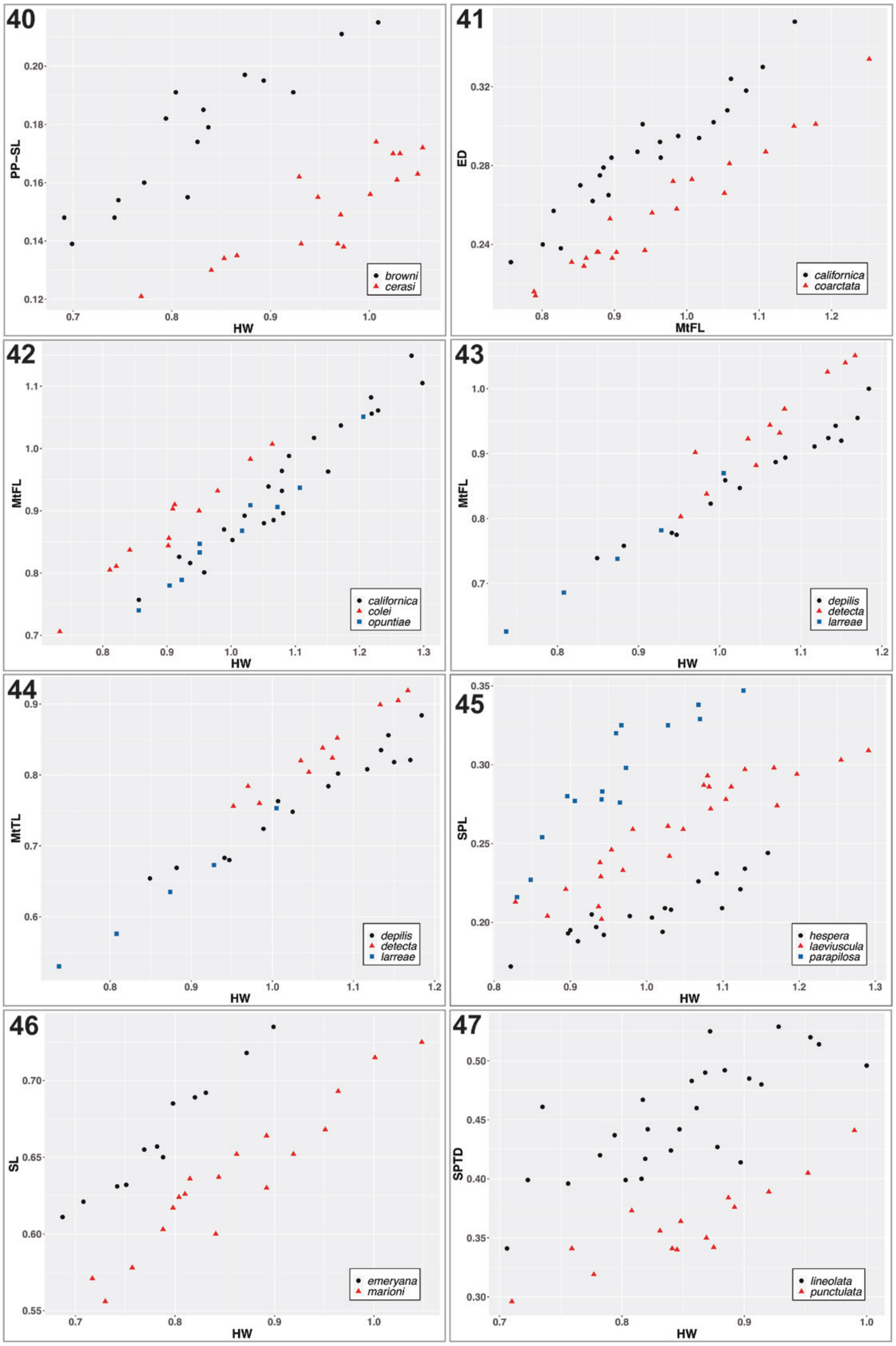
Type notes: The syntype workers of *C. atkinsoni* are in poor condition: over-glued, greasy and abraded. The least degraded specimen is one of the LACM workers and it has been been selected as lectotype. It shows the uplifted pubescence on the head that



Figures 37–39. *Crematogaster* workers, showing lateral view of body (A), full-face view of head (B), and dorsal view of body (C). 37, *C. parapilosa* holotype (CASENT0863386); 38, *C. laeviuscula* (CASENT0104828); 39, *C. lineolata* (CASENT0922733). Images courtesy of *AntWeb* (www.antweb.org); photographers Zachary Griebenow (37), April Nobile (338), Wade Lee (39).

characterizes *C. pilosa*, although it is on the less pilose end of the spectrum (MSC ~10, A4SC ~25) for this species. Creighton (1950) found that the type series of *C. atkinsoni* var. *helveola* was mixed, with the males, dealate queen and some workers being *C. ashmeadi*, while the remaining workers were a second species that Creighton (1950) considered to be *C. atkinsoni*. We examined three worker syntypes of *Crematogaster atkinsoni helveola* in the MCZC from Okefenokee Swamp. All of these have long propodeal spines and conspicuous standing pilosity that grades into subdecumbent pubescence, making them conspecific with *C. atkinsoni* and hence also *C. pilosa*. We have selected as lectotype the worker imaged on MCZbase (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:20823). A label on this specimen indicates that it had been chosen as a lectotype of *C. helveola* by Buren in 1982, but this action was never published. The Okefenokee series also includes a small, headless dealate queen (WL ~2.10, MtFL 1.04) with short propodeal spines, and five small males (HW, including eyes, 0.67–0.73 mm); the queen and males appear to be *C. ashmeadi* (non-conspecific paralectotypes). Also labelled as 'co-types' of *C. helveola* are three workers, on a single pin, from Pinnacle, Georgia, collected by Bradley; two of these are *C. ashmeadi* and one is *C. atkinsoni* (= *C. pilosa*). Because Okefenokee Swamp was explicitly cited as the type locality in the original description (Wheeler, 1919: 110), we do not consider these Pinnacle specimens to be paralectotypes.

Distribution and biology: Crematogaster pilosa occurs along the east coast of the United States from New Jersey to Florida, west to at least Mississippi and



Figures 40–47. Bivariate plots of selected worker measurements in the *Crematogaster scutellaris* group. 40, PP-SL (postpetiole seta length) by HW (head width) in *C. browni* (*N* = 16) and *C. cerasi* (*N* = 17); 41, ED (eye diameter) by MtFL (metafemur length) in *C. californica* (*N* = 22) and *C. coarctata* (*N* = 21); 42, MtFL (metafemur length) by HW (head width) in *C. californica* (*N* = 22), *C. colei* (*N* = 12) and *C. opuntiae* (*N* = 10); 43, MtFL (metafemur length) by HW (head width) in *C. depilis* (*N* = 15), *C. detecta* (*N* = 11) and *C. larreae* (*N* = 5); 44, MtTL (metatibia length) by HW (head width) in *C. depilis* (*N* = 15), *C. detecta* (*N* = 11) and *C. larreae* (*N* = 5); 45, SPL (propodeal spine length) by HW (head width) in workers of *C. hespera* (*N* = 18), *C. laeviuscula* (*N* = 25) and *C. parapilosa* (*N* = 15); 46, SL (scape length) by HW (head width) in *C. emeryana* (*N* = 12) and *C. marioni* (*N* = 18); 47, SPTD (propodeal spine tip distance) by HW (head width) in *C. lineolata* (*N* = 26) and *C. punctulata* (*N* = 15).

Louisiana. The species is predominantly arboreal, nesting in logs, branches, dead stems and grass clumps, and it has been recorded from a variety of habitats, including marshes, coastal dunes, old fields and forested sites (Johnson, 1988; Deyrup, 2017).

CREMATOGASTER PUNCTULATA EMERY, 1895
(FIGS 5A, 16)

Crematogaster punctulata Emery, 1895: 287. Syntype workers, Colorado (Pergande) (MHNG, MSNG, NHMW) (MHNG and MSNG workers examined). One worker from MHNG here designated **lectotype** (CASENT0923318).

Crematogaster opaca var. *punctulata* Emery; Wheeler, 1919: 111.

Crematogaster lineolata punctulata Emery; Creighton, 1950: 214.

Senior synonym of *Crematogaster opaca texana* Santschi: Buren in Smith, 1958: 127; here affirmed (**syn. rev.**); see discussion below.

Junior synonym of *Crematogaster lineolata* (Say): Johnson, 1988: 319.

Status as species: Enzmann, 1946: 33; Smith, 1958: 127; Buren, 1968: 92; Bolton, 1995: 160; Mackay & Mackay, 2002: 100; Morgan & Mackay, 2017: 330.

*Worker measurements (*N = *15):* HW 0.71–0.99, HL 0.67–0.92, SL 0.58–0.75, WL 0.75–1.05, MtFL 0.62–0.83, MSC 16–28, A4SC 28–55, PP-SL/HW 0.13–0.19, CI 1.00–1.11, OI 0.22–0.25, SI 0.74–0.82, MtFL/HW 0.82–0.87, SPL/HW 0.17–0.21, SPTD/HW 0.39–0.46.

Discussion: This species is characterized by its relatively small size (HW 0.71–0.99), reticulate-foveolate sculpture on the mesosoma dorsum, posteriorly directed propodeal spines (SPTD/HW 0.39–0.46, SPTD/PPW 1.11–1.40) and abundant, short, standing pilosity (MSC 16–28, A4SC 28–55). *Crematogaster lineolata* is similar, but usually has some striae or rugulae on the mesosoma dorsum, generally oriented longitudinally and often intermingled with reticulate-foveolate sculpture. In addition the propodeal spines of *C. lineolata* are directed more posterolaterally (SPTD/HW 0.46–0.63, SPTD/PPW 1.38–1.76) (Fig. 47). There are reports of intergradation between the two taxa in the midwestern and south-eastern United States (Creighton, 1950; Johnson, 1988; Morgan & Mackay, 2017), however, so the status of *C. punctulata* remains uncertain.

We provisionally treat *C. punctulata* as a species, recognized by the combination of features cited above, and largely confined to the midwestern states. In populations of *C. lineolata* from south-eastern United States there is considerable (and seemingly continuous) variation in the degree of development of rugulae or striae on the mesosoma dorsum, such that at one end of the spectrum the sculpture is essentially like that of *C. punctulata*. However, in south-eastern *punctulata*-like workers that we have examined, the propodeal spines conform to the *C. lineolata* pattern (SPTD/HW > 0.46, SPTD/PPW > 1.36). Does *C. punctulata* occur in the south-eastern States, where it introgresses with *C. lineolata*, or is this just part of the natural variation of *C. lineolata* in areas where it is allopatric to the midwestern *C. punctulata*? Is there gene flow between the two forms where they meet in the midwest? These questions cannot be answered without further study. It is worth noting that both species have been reported from overlapping regions in Kansas (DuBois, 1985) and Texas (O'Keefe *et al.*, 2000).

There are two infraspecific forms that had been considered synonyms of *C. punctulata*, namely *C. lineolata subopaca* Emery (type locality Virginia) and *C. opaca texana* Santschi (type locality Bonham, Texas) (synonymy by Buren in Smith, 1958: 127). Johnson (1988: 320) cited the former as a synonym of *C. lineolata*, when he synonymized *C. punctulata* under *C. lineolata*, but he made no statement about *C. opaca texana*. Morgan & Mackay (2017) treated *C. punctulata* as a good species, but placed its two former synonyms under *C. lineolata*, without explanation. An imaged syntype worker on AntWeb of *C. opaca texana* (CASENT0912717) has the posteriorly directed propodeal spines (SPTD/HW ~0.41) and sculptural features of *C. punctulata*, not *C. lineolata*. Therefore, it is here removed from synonymy under *C. lineolata*,and again placed under synonymy of *C. punctulata* (syn. rev.).

The form described as *C. lineolata subopaca* from Virginia is part of that complex variation described above in south-eastern populations of *C. lineolata*. A syntype worker (CASENT0904537) imaged on AntWeb has a reticulate-foveolate mesosoma, but the propodeal spines are divergent (SPTD/HW ~0.49), like those of *C. lineolata*. We leave this as a synonym of *C. lineolata*, while emphasizing that the *C. lineolata/punctulata* complex needs a thorough genetic investigation.

Although larger sample sizes are desirable, our UCE phylogeny (Fig. 1) provides support for treating *C. lineolata* and *C. punctulata* as different species. Based on three population samples of *C. lineolata* and two each of *C. punctulata* and *C. emeryana*, we find that *C. emeryana*, a south-western species, is the sister-taxon of *C. lineolata*, while *C. punctulata* is more distantly related (sister to these two).

Type notes: Morgan & Mackay (2017) reported examining 30 syntype workers of *C. punctulata* in a collection cited as 'MNHG', an apparent misspelling of MHNG (Muséum d'Histoire Naturelle, Geneva). We have located and examined a total of 24 syntype workers, but only four are in MHNG. The remaining 20 specimens are in MSNG (Genoa). There is also an image on AntWeb (CASENT0919708) of a syntype worker in NHMW. The four workers in MHNG are labelled 'Cotypus', 'Crematogaster | punctulata Em | Colorado', and 'Sp. C. punctulata | Em', while those in MSNG bear the labels: 'TYPUS | Crematogaster | punctula ta | det. Emery, 1895' and 'MUSEO GENOVA | coll. C. Emery | (dono 1925)'. Each type label is red, and has a large question mark handwritten at the right side of the first three lines. The MSNG workers (20 workers on five pins) also bear different handwritten numbers on each pin (N. 5Ga, N. 562, N. 513a, N. 513 and 513) that possibly refer to different nest series. This would be consistent with Emery's (1895: 287) statement that Pergande had supplied him with four nests. The workers from MHNG and MSNG are all similar and match Emery's original description. Nevertheless, because no locality is given on the labels of the MSNG specimens and because there is a question mark on the type labels, we have chosen a lectotype from one of the four syntype workers in MHNG.

Distribution and biology: Based on our current concept of *C. punctulata*, this is a midwestern species occurring from the Great Plains south to northern Mexico, and west to Arizona. We have not seen definitive records east of Mississippi, but the status of some eastern samples remains ambiguous (see above). This species is ground-nesting and occurs in woodlands, grasslands and other open habitats.

CREMATOGASTER ROSSI BUREN, 1968, STAT. REV.

Crematogaster rossi Buren, 1968: 111. Holotype worker, San Jose del Cabo, Baja California Sur, Mexico (USNM) (USNMENT00531965) (examined).
Junior synonym of *C. vermiculata*: Morgan & Mackay, 2017: 396; here overturned.

Worker measurements (N = 6)*:* HW 0.90–1.1, HL 0.83–1.04, SL 0.76–0.86, WL 0.95–1.25, MtFL 0.80–0.99, MSC 0–8, A4SC 25–34, PP-SL/HW 0.15–0.19, CI 1.06–1.13, OI 0.25–0.27, SI 0.78–0.85, MtFL/HW 0.87–0.92, SPL/HW 0.24–0.26, SPTD/HW 0.53–0.60.

Discussion: Phylogenomic (UCE) data reveal a close relationship of *C. rossi* to *C. californica* and *C. opuntiae*; it has no close affinity to *C. vermiculata* (Fig. 1). *Crematogaster rossi* is recognizable by the combination of a predominantly shiny head, conspicuously rugulose promesonotum on a reticulate-foveolate background and abundant standing pilosity on the gaster. The mesosomal sculpture is superficially similar to that of *C. vermiculata*, but the two species differ in numerous ways. *Crematogaster rossi* is larger (HW 0.90–1.10, WL 0.95–1.25), with disproportionately longer scapes (SI 0.78–0.85) and legs (MtFL/HW 0.87–0.92) and with propodeal spines that are straight, longer and more divergent posteriorly (SPL/WL 0.22–0.24, SPTD/HW 0.53–0.60) (compare with equivalent measurements for *C. vermiculata* below). There are up to two isolated standing hairs on each pronotal humerus and usually a few short standing hairs on the mesonotal declivity (MSC 0–7), but the pilosity on the gaster is particularly well-developed (A4SC 25–34, compared with A4SC 9–20 in *C. vermiculata*). From the closely related species, *C. californica* and *C. opuntiae*, *C. rossi* can be distinguished primarily by its promesonotal sculpture and abundant standing pilosity on the gaster.

Distribution and biology: Crematogaster rossi is known from the Mexican states of Baja California Sur and Baja California, and (more doubtfully) Nayarit. Specimens with habitat information come from 'oak woodland' and 'dry wash next to oak woodland' but others have been collected from sites in more xeric locations. The species is apparently a ground-nester.

CREMATOGASTER VERMICULATA EMERY, 1895
(FIG. 32)

Crematogaster vermiculata Emery, 1895: 286. Two syntype workers, 'Los Angeles' (Pergande) (MSNG) (examined). One worker here designated **lectotype** (CASENT0923320). See comments below about type locality.
Crematogaster coarctata subsp. *vermiculata* Emery; Creighton 1950: 209.
Crematogaster vermiculata Emery; Buren 1968: 91, 112.
Senior synonym of *Crematogaster colei* Buren, *C. opuntiae* Buren and *C. rossi* Buren (Morgan & Mackay 2017: 396); here reversed.

Worker measurements (N = 10)*:* HW 0.67–0.85, HL 0.64–0.81, SL 0.52–0.63, WL 0.72–0.93, MtFL 0.56–0.7, MSC 3–9, A4SC 9–20, PP-SL/HW 0.14–0.21, CI 1.01–1.08, OI 0.23–0.26, SI 0.72–0.78, MtFL/HW 0.79–0.84, SPL/HW 0.17–0.21, SPTD/HW 0.39–0.48.

Discussion: This is a distinctive arboreal species of *Crematogaster* restricted to cypress and hardwood swamps of the south-eastern United States. It belongs to the *C. lineolata* clade, and its closest relatives are the Caribbean species, *C. lucayana* and *C. sanguinea*

(Fig. 1). Workers of *C. vermiculata* are easily recognized by the striking rugulose sculpture on the promesonotum that imparts a vermiculate (worm-like) appearance, a feature not seen in any other species in the United States. *Crematogaster vermiculata* also has notably short scapes and legs (SI 0.72–0.78, SL/HL 0.75–0.82, MtFL/HW 0.79–0.84, MtFL/HL 0.84–0.89) and moderately conspicuous standing pilosity on the mesosoma (uo to four hairs on each pronotal humerus and one to three on the mesonotal declivity) and on the gaster (MSC 3–9, A4SC 9–20). The propodeal spines are relatively short and stout (SPL/HW 0.17–0.21, SPL/WL 0.15–0.19) and, in dorsal view, inwardly curved and directed posterad (SPTD/HW 0.39–0.48). Although the type locality is Los Angeles, California, the type specimens agree in all respects with the well-known swamp-inhabiting species of the south-eastern United States, and there is no species in California – or indeed in all of western North America – that matches *C. vermiculata*. Hence we concur with Buren (1968) and Johnson (1988) that the type locality cited in the original description (Los Angeles) is an error. This is by no means the only locality or labelling error that can be attributed to Pergande; see other examples cited by Gregg (1969: 101), Ward (2000: 89) and Wetterer (2015: 132). Buren's (1968) findings were overlooked by Morgan & Mackay (2017), who reverted to an outdated concept of *C. vermiculata* as a western Nearctic species, with outlying populations in south-eastern United States, and they synonymized three western species (*C. colei*, *C. opuntiae* and *C. rossi*) under *C. vermiculata*. These three taxa are not closely related to *C. vermiculata* (Fig. 1), nor do they bear any close morphological resemblance to that species.

Type notes: The two syntype workers of *C. vermiculata* are deposited in MSNG [not MHNG, as indicated by Morgan & Mackay (2017)] and are labelled 'Los Angeles | Calif.' and 'SYNTYPUS | Crematogaster | ver miculata | det. Emery, 1895'. One of the two workers also has a label with 'No. | 372'. The latter worker has been designated lectotype. There are four similar workers in the USNM labelled 'Los Angeles | Calif.', 'No. | 372' and 'Collection | T Pergande', and one of these is additionally labelled 'Cremastogaster | vermiculata | Em. (372) Em.' in Pergande's handwriting. These four workers in USNM are not true types, since Emery's (1895: 286) description is based on two workers only, but they appear to be part of the same series. All six workers agree closely with Emery's (1895) original description, particularly his mention of the almost parallel propodeal spines and the 'peculiar worm-like sinuous wrinkled sculpture of the promesonotum'.

Distribution and biology: Crematogaster vermiculata occurs from North Carolina to Florida and west to Louisiana and Arkansas. It is a strictly arboreal species, inhabiting cypress and hardwood swamps (Johnson, 1988; Deyrup, 2017).

CREMATOGASTER VETUSTA SP. NOV.

(FIG. 14)

Zoobank registration: urn:lsid:zoobank.org:act:E2ACD687-1F5C-4EAA-BB19-A75C215C3670.
Type material: Holotype worker, US, Arizona, Cochise Co.: 11 km NNW Portal, 1430 m, 32.00293 −109.18198 ± 3 m, 8 Aug 2011, P. S. Ward PSW16646, ground forager, Chihuahuan desert (CASENT0863254) (USNM).

Paratypes: Five workers, same data as holotype (CASENT0221037, CASENT0863251, CASENT0863252, CASENT0863253, CASENT0863255) (CASC, MCZC, UCDC).

Non-type material: MX, Sonora, 36.6 km SE El Golfo de Santa Clara, 15 m, 31°31.6′N 114°9.8′W, 27 Feb 2017, T. Van Devender, two workers (CASENT0882151) (UCDC); ten workers, same data but without specimen codes (RAJC); *US, Arizona*, Pima Co.: Brown Cañon, Baboquivari Mtns., 5000 ft., 17 Sept. 1951, W. S. Creighton, three workers (LACMENT403634) (LACM); Cochise Co.: Chiricahua Mtns., Cave Creek Canyon, Sunny Flat Campground, 4950 ft., 2-VII-1986, S. P. Cover #862, 18 workers (MCZENT00588704, MCZENT00589124, MCZENT00589125, MCZENT00589126, MCZENT00589127, MCZENT00589128, MCZENT00589129, MCZENT00589130, and CASENT0173014 with redundant specimen code MCZENT00589131) (MCZC); Cochise Co.: Chiricahua Mtns., SWRS, 8 km W Portal, 1650 m, 31°53′N 109°12′W, 4–14.viii.2005, Ant Course, two workers (MCZENT00589132) (MCZC).

*Worker measurements (*N = *11):* HW 0.96–1.27, HL 0.89–1.17, SL 0.80–1.02, WL 1.04–1.40, MtFL 0.86–1.16, MSC 6–24, A4SC 38–70, PP-SL/HW 0.10–0.13, CI 1.06–1.12, OI 0.24–0.25, SI 0.74–0.83, MtFL/HW 0.87–0.94, SPL/HW 0.20–0.23, SPTD/HW 0.46–0.55.

Worker diagnosis: Head broader than long, with convex sides, and weakly concave posterior margin (more strongly so in larger workers); scapes moderately long, surpassing the posterior margin of head by distal scape width or more (SI 0.74–0.83, SL/HL 0.82–0.92, SL/WL 0.68–0.79); eye of moderate size (OI 0.24–0.25, ED/HL 0.26–0.28, ED/MtFL 0.27–0.29); promesonotum lacking well-marked pronotal humeri and mesonotal declivity; propodeal spines relatively long (SPL/HW 0.20–0.23, SPL/WL 0.18–0.21) and divergent (SPTD/HW 0.46–0.55); petiole subtrapezoidal, narrow (PTW/

HW 0.32–0.35); postpetiole relatively narrow (PPW/HW 0.27–0.30), the hemilobes not strongly angulate in profile; legs relatively long (MtFL/HW 0.87–0.94, MtFL/HL 0.96–1.02). Mandibles striate; head reticulate to reticulate-striolate, with shiny median patch (more extensively smooth and shiny in smallest workers); mesosoma predominantly reticulate-foveolate and opaque, with overlying irregular rugulae on the promesonotum, and better developed longitudinal rugulae on the dorsal face of the propodeum; declivitous face of propodeum weakly reticulate to smooth and shiny; petiole and postpetiole reticulate to reticulate-foveolate, subopaque. Head, including scapes, and mesosoma with short but conspicuous standing pilosity, grading into (and sometimes difficult to distingush from) decumbent pubescence (MSC 6–24); postpetiolar seta short (PP-SL/HW 0.10–0.13), and flanked by several adjacent setae of almost equal length; short standing pilosity especially common on gaster (A4SC 38–70). Dark reddish-brown, gaster and appendages lighter.

Comments: The key distinguishing features of the worker of *C. vetusta* are the dense reticulate-foveoleate sculpture of the mesosoma, overlain by weak rugulae; short standing pilosity of the head and mesosoma which grades into uplifted pubescence (MSC 6–24); abundant, short, standing pilosity on the gaster (A4SC 38–70); relatively long and divergent propodeal spines (SPL/HW 0.20–0.23); and narrow petiole (PTW/HW 0.32–0.35) and postpetiole (PPW/HW 0.27–0.30). Other species from the south-western United States with similarly abundant pilosity on the gaster (A4SC > 35 in at least some workers) differ as follows: *C. dentinodis* is darker, with smaller eyes (ED/HL 0.24–0.26) and a broader petiole (PTW/HW 0.37–0.41) and postpetiole (PPW/HW 0.32–0.35); *C. punctulata* is smaller and darker, with more conspicuous mesosomal pilosity (MSC 16–28), shorter legs (MtFL/HL 0.82–0.96) and less divergent propodeal spines (SPTD/HW 0.39–0.46); *C. navajoa* has a much shinier integument, much longer standing pilosity (PP-SL/HW 0.17–0.25), more abundant pilosity on the mesosoma (MSC 18–29) and a broader postpetiole (PPW/HW 0.29–0.35); and *C. marioni* has a shinier integument, shorter scapes and legs (SL/HL 0.73–0.81, MtFL/HL 0.83–0.90) and generally less standing pilosity on the gaster (A4SC 19–38). All of the above species, except *C. navajoa*, also have more appressed pubescence on the scapes than *C. vetusta*, although this character shows considerable variation among and within species. The UCE phylogenetic tree (Fig. 1) reveals that *C. vetusta* is a member of the *C. opaca* clade and sister to *C. detecta*. The latter species is easily distinguished from *C. vetusta* by its scarcity of standing pilosity (MSC 0, A4SC 0–3).

Biology and distribution: This species is known only from southern Arizona and northern Sonora. The type series (PSW16646) consists of daytime foragers collected in the Chihuahuan desert, on a rocky quartzite hill with *Vachellia*, *Fouquieria*, *Yucca*, *Agave* and scattered *Juniperus* and *Sapindus saponaria* L.. Stefan Cover's collection #862 was taken under a rock in an open gap, in creek floodplain forest with *Quercus grisea* Liebm., *Q. emoryi* Torr. and *Platanus occidentalis* L. The collection from Sonora, Mexico was taken from sand dunes in Sonoran desert-scrub.

Etymology: The name refers to the position of this species in a lineage (containing one other known species) that is sister to all other members of the *C. depilis* complex, from Latin *vetustus*, old or antiquated.

DISCUSSION

DELIMITING *CREMATOGASTER* SPECIES

In investigating the taxonomy of *Crematogaster*, we adopt the viewpoint that for sexual organisms, such as these ants, the biological species concept (Mayr, 1942) provides a useful framework for understanding the nature of species and their morphological cohesiveness (Coyne & Orr, 2004; Barraclough, 2019). At the same time, widely distributed species with large effective population sizes can be expected to harbour considerable phenotypic variation, distributed non-randomly across the landscape. Delimiting species then involves the discovery of phenotypic or genetic gaps that indicate the occurrence of reproductive isolation among these population assemblages. This exercise requires comprehensive geographic sampling and a careful consideration of the observed variation. Morereover, because speciation is a continuous process, with complex dynamics at intermediate stages (Noor & Bennett, 2009; Roux *et al.*, 2016; Taylor & Larson, 2019) the findings may be properly ambiguous.

The results presented here, based primarily on morphology, should be considered tentative and subject to refinement with further study, especially more detailed genetic analyses. Whereas our morphological study of these Nearctic *Crematogaster* is based on examination of thousands of workers, the phylogenomic sample sizes are much smaller, in the range of one to four individuals per species. Nevertheless, we chose a geographically representative set of specimens for sequencing and there were instances in which the two sources of data were reciprocally illuminating. For example, our reinstatement – based on morphological evidence – of previously synonymized *Crematogaster* species was bolstered by the discovery that they did not have a close phylogenetic relationship to the species under which they had been synonymized. Conversely, where the molecular data indicated that two forms were sister-taxa – as we found for *C. emeryana* and *C. lineolata* – this directed attention to their geographical distributions, because maintenance of morphological differences in sympatry provides a more compelling case for treating two taxa as different species than if they are allopatric (Galtier, 2019). In one instance, the phylogenomic data revealed more than one species among samples that we initially treated as conspecific: collections of *C. detecta* were originally misidentified as *C. depilis*, a species situated several nodes distant in the phylogeny (Fig. 1). Once their genetic distinctness was discovered, this motivated a search for morphological differences.

CONTINUING CHALLENGES IN *CREMATOGASTER* TAXONOMY

Because the *C. scutellaris* group is relatively young, with most diversification in the New World occurring within the last 5 Myr (Fig. 2), one can expect there to be ongoing differentiation of populations and incomplete reproductive isolation between some taxa, making clear delineation of species boundaries challenging. The preceding species accounts and the worker-based key to the North American representatives of the *C. scutellaris* group serve to summarize our current understanding of these ants, but there is still considerable taxonomic uncertainty about species limits.

The distinction between the allopatric taxa *C. californica* and *C. opuntiae* is a tenuous one, relying on a character (appressed scape pubescence in *C. opuntiae*) that shows substantial variation. *Crematogaster opuntiae* may prove to be nothing more than a desert-dwelling variant of *C. californica*. Resolution of this issue requires further genetic and morphological studies, especially of populations from geographically intermediate areas and from farther south in Baja California. Another problematic taxon in this complex is *C. nocturna*, described from distinctive-looking males and alate queens from northern Arizona, but without associated workers. Buren (1968) identified a small series of six workers from southern Utah (not seen by us) as being possibly conspecific. Until the phylogenetic position of *C. nocturna* is determined, and queens and males are collected in association with workers, there will be ongoing uncertainty about the status of this species. There is also the challenging problem of distinguishing workers of *C. depilis*, *C. detecta* and *C. larreae*, discussed above but not fully resolved.

We let stand the synonymy by Morgan & Mackay (2017) of *C. mormonum* (type locality Utah) under *C. coarctata* (type locality San Francisco, California). This is one of the few synonymies in Morgan & Mackay (2017) that appears to be justified. The putative distinction in cephalic sculpture between these two forms – with shiny heads of *C. mormonum* workers being contrasted with the densely reticulate-foveolate heads of *C. coarctata* workers (Buren, 1968) – is undermined by intermediate conditions among many individuals from northern California and Nevada. Nevertheless, among samples that we are now calling *C. coarctata*, there is considerable variation in shape, pilosity and sculpture. In particular, workers from southern California and northern Baja California tend to have reduced pronotal pilosity, a weakly sculptured promesonotum and shiny (*C. mormonum*-like) heads. Further study of this complex of populations is warranted.

Several investigators have commented on the extensive variation in colour and other features (pilosity, sculpture) that occurs within some species of *Crematogaster* from the eastern United States (Creighton, 1950; Johnson, 1988; Deyrup, 2017). One such colour variant has been cleaved from *C. ashmeadi* and described as a distinct species, *C. pinicola* (Deyrup & Cover, 2007), which differs in colour and nesting habits from the more widespread *C. ashmeadi*. The taxonomic significance of colour variation in other species, such as *C. laeviuscula*, *C. parapilosa* and *C. pilosa*, remains unclear. Among other problems affecting *Crematogaster* from eastern and central United States, the relationship of *C. punctulata* to *C. lineoleata* also requires further scrutiny, as discussed above.

The species-level taxonomy of the Caribbean representatives of *Crematogaster* (*Crematogaster*) is a further source of confusion. There are seven valid species or subspecies names (*C. lucayana*, *C. lucayana etiolata* Wheeler, 1905, *C. manni* Buren, 1968, *C. sanguinea*, *C. sanguinea atavista* Mann, 1920, *C. sanguinea sotolongoi* Mann, 1920 and *C. sanguinea torrei* Wheeler, 1913), but we have no clear understanding of the number of species or their relationship to one another. Our knowledge of the *C. scutellaris* group in Mexico and Central America is even more fragmentary. There are five valid names of taxa occurring almost entirely south of the United States in this region (*C. cedrosensis*, *C. opaca*, *C. patei* Buren, 1968, *C. rossi* and *C. saussurei* Forel, 1899), but this belies a greater diversity that remains undersampled and understudied. The *C. opaca* complex, discussed above, is particularly troublesome and requires comprehensive morphological and phylogenetic investigation to clarify how many species exist and their boundaries.

Finally, there is a mysterious species, *C. clydia* Forel, 1912, known only from the holotype (unique syntype) worker collected more than one-hundred years ago in São Paulo state, Brazil. This is a *Crematogaster*

(*Crematogaster*) species and presumably a member of the *C. scutellaris* group, and yet it represents an extraordinary out-of-range occurrence. Assuming that it has not been mislabelled, the rediscovery of *C. clydia* and clarification of its relationship to other congeners poses an intriguing challenge to Brazilian myrmecologists.

LOCATION OF TYPE SPECIMENS

In his treatment of the North American representatives of *Crematogaster s.s.* (i.e. the *C. scutellaris* group), Buren (1968) described 14 new species. He stated his intention to deposit the holotypes of the new species in the USNM, except those of *C. nocturna* and *C. rossi*, which were destined for CASC, and that of *C. opuntiae*, for which no place of deposition was indicated. However, Buren did not follow through for most species, so the information in his paper is misleading. Most holotypes were retained in his collection and that collection was acquired by the LACM in 1983, after Buren's death. Through visits and loans we have determined the location of the holotypes of all 14 species and we provide this information here (Table 3) for the benefit of future researchers. It will be noted that eight of the holotypes are in LACM, five in USNM and one in CASC.

Statements in Morgan & Mackay (2017) about the location of type specimens should also be viewed with caution. The authors use at least four collection acronyms (MNHG, NHMG, NMHG and NNHW) that are nowhere explained and are not part of the list of collections cited in the 'Material and methods' section. 'MNHG' appears to be a misspelling of MHNG (Muséum d'Histoire Naturelle, Genève), but some claims about types existing in that collection are incorrect, as documented above.

In fact, there are many errors and mistatements in the Morgan & Mackay (2017) monograph, particularly regarding the distribution and biology of particular species. The paper was published by a print-on-demand publisher, whose policy is to print without peer review or editorial supervision (Fang, 2014; Stromberg, 2014; Anonymous, 2015). Taxonomy inevitably suffers if researchers pursue this kind of publication strategy, bypassing editor-mediated peer review and even the most perfunctory editing, and burdening other taxonomists with the task of correcting their mistakes.

NEW INSIGHTS INTO THE COMPOSITION AND ORIGIN OF THE *CREMATOGASTER SCUTELLARIS* GROUP

The *Crematogaster scutellaris* group was circumscribed by Blaimer (2012b) as likely encompassing all Nearctic and Palaearctic representatives within the subgenus *Crematogaster*, as well as a few species distributed in the northern Neotropical realm. This assumption was based on phylogenetic data from multiple nuclear loci (Blaimer, 2012a) and morphological similarities of eight species (six Nearctic and two Palaearctic) within the *C. scutellaris* group. That study indicated a clear phylogenetic division between a Nearctic and a Palaearctic clade (Blaimer, 2012a). Our phylogenomic study has expanded taxon sampling within the *C. scutellaris* group to include nearly all the Nearctic members of the group and a representative sampling of Caribbean and northern Neotropical taxa. Our results reveal a strongly

Table 3. Place of deposition of holotypes of *Crematogaster* species described by Buren (1968)**.** The species are listed in the order in which they appear in the paper. All specimens were examined physically by PSW or BBB

Species	Repository	Type locality	Specimen Code, Caste
manni	USNM	Cuba: Herradura	USNMENT00533156, worker
rifelna	LACM	USA Texas: Riviera	LACMENT164556, worker
hespera	USNM	USA Arizona: Phoenix	USNMENT00529501, worker
browni	LACM	USA Arizona: Garden Canyon	LACMENT164546, worker
navajoa	LACM	USA Arizona: 8 mi E Seligman	LACMENT164488, worker
marioni	LACM	USA California: Morena Lake	LACMENT164545, worker
isolata	LACM	USA Texas: McDonald Observatory	LACMENT164496, worker
patei	USNM	Mexico: Tamaulipas: Tampico	USNMENT00533046, worker
colei	USNM	USA New Mexico: Wooten	USNMENT00528846, worker
rossi	USNM	Mexico: B.C.S.: San Jose del Cabo	USNMENT00531965, worker
nocturna	CASC	USA Arizona: Rainbow Lodge	CASTYPE11424, male
mutans	LACM	USA California: Morena Lake	LACMENT164534, queen
larreae	LACM	USA Texas: El Paso	LACMENT164548, male
opuntiae	LACM	USA Arizona: Santa Rita Exper. Range	LACMENT164544, worker

supported New World clade, which is sister to the two sequenced Palaearctic species. A comprehensive overview of the *C. scutellaris* group will only be possible once the phylogenetic affinities of the Mexican/Mesoamerican and remaining Palaearctic *Crematogaster* (*Crematogaster*) species are tested. In contrast to the tight relationships of the subgenus in the New World, it appears likely that some Palaearctic species are not members of the *C. scutellaris* group (*sensu* Blaimer, 2012b), but more closely related to African *Crematogaster* lineages (Blaimer, unpublished data).

A single origin of the Nearctic diversity of the subgenus *Crematogaster* (*Crematogaster*) had already been inferred by Blaimer (2012a). This study had estimated a dispersal of the *C. scutellaris* group to the Nearctic from the Palaearctic region sometime between 5.2–7.4 Mya. Our divergence analyses tighten this estimate somewhat, by inferring a slightly older median crown age of the Nearctic *C. scutellaris* group with 7.35 Mya (node 4; Fig. 2 and Table 1) and suggesting a dispersal to North America thus shortly after the divergence with the Palaearctic ancestor of the group around 8 Mya (node 2; Fig. 2 and Table 1). Our results hence confirm the relatively recent, Late Miocene origin of the Nearctic *C. scutellaris* group. However, the crown *C. scutellaris* group node was calibrated with an age range taken from the earlier study (Blaimer, 2012a), and we would, therefore, not expect large deviations from the previous estimates. The previous study (Blaimer, 2012a) was not able to distinguish between a transatlantic dispersal or a terrestrial dispersal via the Bering Strait landbridge between the Palaearctic and Nearctic region. Both the previous and current age estimates are older than the earliest estimated opening of the Bering Strait around 5 Mya (Gladenkov *et al.*, 2002) and agree with a possible dispersal via the second Beringian landbridge (*sensu* Sanmartín *et al.*, 2008). Our biogeographic reconstructions were equivocal with regard to the ancestral range of the most recent common ancestor of the *C. scutellaris* group, and due to minimal sampling of Palaearctic species (as outgroups), we are also not able to pinpoint the exact source of the colonization event. Nonetheless, given that that the first split in the Nearctic *C. scutellaris* group is between an exclusively western lineage, the *C. coarctata* clade, and all other taxa, we suggest that a trans-Beringian dispersal from the eastern Palaearctic could be a likely scenario, as has been suggested for other ant taxa (Jansen *et al.*, 2010; Schär *et al.*, 2018) and several groups of insects (Sanmartín *et al.*, 2008). More decisive evidence will have to await a larger biogeographic analysis including the Palaearctic members of the *C. scutellaris* group and further outgroup sampling.

BIOGEOGRAPHY AND BIOLOGY OF NEARTIC *CREMATOGASTER* – FROM WESTERN GROUND-NESTERS TO EASTERN TREE-DWELLERS

Our phylogenomic analyses recovered well-resolved species-level phylogenies for the Nearctic *C. scutellaris* group. We found the group to be separated into three major clades: the small western USA and north-western Mexico endemic *C. coarctata* clade, and the two species-rich *C. opaca* and *C. lineolata* clades, which have a predominantly western or eastern distribution, respectively. Interestingly, morphological characteristics to distinguish these three clades are lacking, at least in the workers, but perhaps this is not so surprising given their recent divergences (4–8 Mya; Fig. 2; Table 1). The biogeography and diversification history of the Nearctic *C. scutellaris* group is thus characterized by a 'western to eastern' geographical pattern of range evolution, potentially dominated by the Rocky Mountain Range and the Great Plains as major dispersal barriers. Our range reconstructions are ambiguous about the early evolutionary history of the *C. scutellaris* group and show a broad eastern and western North American distribution (EW, nodes 4, 5 and 20; Fig. 2). From these broad ancestral reconstructions, the subsequent limitation of *Crematogaster* lineages to a western or eastern distribution would have to be interpreted as range restrictions rather than dispersal events. However, since the *C. coarctata* subclade, which is sister to all other New World taxa, has a western North American distribution, it appears also probable that the MRCA of the entire Nearctic *C. scutellaris* group was distributed only in western North America during their early diversification.

Under the latter scenario, only one dispersal from western into eastern North America would have occurred within the *C. opaca* clade, when the ancestor of *C. rifelna* and an undescribed species migrated east sometime in the Late Miocene or Early Pliocene (branch leading to node 32; Fig. 2), and then further south into Mexico and Mesoamerica. Considering the present distribution of these two sister-species in south-eastern Texas and southern Mexico to Mesoamerica, this dispersal could have happened via migration through the low-elevation break between the Rocky Mountains/Colorado Plateau and the Sierra Madre Occidental. Alternatively, a widespread MRCA for the *C. opaca* clade may have diverged from the western lineage as populations became isolated geographically and speciated. Judging by our phylogeny, it appears that most of the diversification of the *C. opaca* clade remained restricted to the western USA and north-west Mexico, west of the Great Plains. However, as we discussed above, several morphologically similar taxa occur south of the United States, in what we term the

'*C. opaca* complex', which were not sampled here. Until the number of species and their phylogenetic affinities have been determined, the evolutionary history of the *C. opaca* clade cannot be fully resolved.

In contrast to the pattern seen in the *C. opaca* clade, there appears to have been a surprising amount of connectivity or exchange between biogeographic regions within the *C. lineolata* clade. If we accept a widespread Nearctic ancestor for this clade, as inferred in the present analysis and Fig. 2 (node 6), we have to assume several subsequent range reductions – four to eastern North America (plus one dispersal to the Caribbean) and three to western North America. If we consider a possible western MRCA, five dispersals to the eastern realm and two range reductions from an EW to a W state would be necessary to explain current distribution patterns. We had recovered some phylogenetic incongruence between analyses in this clade, where some ML analyses placed *C. laeviuscula*, *C. pilosa* and *C. parapilosa* as sister to *C. vermiculata*, *C. sanguinea* and *C. lucayana*, instead of sister to *C. hespera* and *C. cerasi*, as in the main analysis. This is noteworthy as this topology would require fewer dispersal events or range reductions from western to eastern North America to explain the species distributions within this clade.

Regardless of this remaining uncertainty, we overall note a dominance of dispersals or range restrictions directed from the western Nearctic to the eastern Nearctic region, rather than vice versa. This is in line with previous findings. Sanmartín *et al.* (2008) analysed dispersal patterns across 57 animal clades in the Holarctic and also observed a statistically significant dominance of west to east dispersals. Several palaeoclimatic changes are discussed by these authors that could explain this trend (Sanmartín *et al.*, 2008), albeit not all apply to the time frame of our present study. Relevant for range evolution within the Nearctic *C. scutellaris* group may have been the increasing aridification of the central Great Plains in North America throughout the Pliocene (Eronen *et al.*, 2012). This process may have been an essential force in driving humid- and forest-adapted species eastwards, as mixed mesophytic forests shifted eastwards and were replaced by more xerophytic plant species (Tiffney, 1985). Further climatic cooling and glaciation events during the Pleistocene probably reinforced this pattern, and the Great Plains are assumed to have continued to act as a dispersal barrier to the west for less arid-adapted insects (Howden, 1969). Among Nearctic members in the *C. scutellaris* group, only two species with a predominantly eastern distribution (*C. cerasi* and *C. punctulata*) traverse the Great Plains and marginally enter the west. It is also noteworthy that no western species penetrates the Great Plains to any significant degree.

The ancestor of North American *C. scutellaris group* is estimated to have a ground-dwelling habit, and this nesting preference was retained largely within the *C. coarctata* and *C. opaca* clades. Within members of the *C. lineolata* clade, the preference for ground-dwelling is further retained largely in members with a western distribution. In fact, most western species are ground-dwellers, mainly nesting under stones, and only three species with a western distribution – one in each of the three main clades – are arboreal nesters: *C. marioni*, *C. isolata* and *C. hespera*. From the standpoint of biogeographic and climatic range evolution discussed above, the association of ground-dwelling with the western range seems logical. The MRCA of the Nearctic *C. scutellaris* group must have been relatively cold-adapted to migrate across the trans-Beringian Bridge that was then covered by taiga (Sanmartín *et al.*, 2008). Climatic fluctuations during the Pliocene and Pleistocene would have then prevented, or at least disfavoured an invasion of the tree canopy as a nesting space by the ants. It is, therefore, plausible that the arboreal nesting habit was relatively recently acquired in the three western arboreal species. By contrast, all but one of the exclusively eastern or Caribbean species have an arboreal nesting preference. These arboreal inhabitants of mixed hardwood, subtropical forests and coastal scrublands may have survived the Pleistocene in glacial refugia, which occurred in eastern Texas/western Louisiana and Florida (Swenson & Howard, 2005). The exception, the ground-dwelling *C. lineolata*, is one of the most widely distributed species within the Nearctic *C. scutellaris* group, occuring from eastern Canada to the southern United States and west to the Great Plains. A generalist ground-nesting habit may have facilitated the success of this species, by possibly allowing a more widespread distribution even during glacial maxima or a more rapid post-glaciation range expansion.

CONCLUSIONS

Our study emphasizes, as many others before, the value of integrating multiple sources of data in taxonomy. Using a cross-validation approach between molecular and morphological evidence, we were able to improve the taxonomy of a clade of *Crematogaster* ants, a genus whose species boundaries are notoriously challenging to delimit. In this case, there was an immediate urgency for our study, because a poorly executed recent revision left this group in a chaotic state. We cannot overstate the negative impact that unedited and non-peer reviewed publishing can have on the quality of taxonomic knowledge. Non-experts may not be able to critically evaluate such works and automatic harvesting of the literature by data compilers results in wide dissemination of misinformation. Moreover, such unrefereed publications degrade the reputation of taxonomy as a scientific field.

On the positive side, a long-overdue treatment of *Crematogaster* in North America, in a molecular phylogenetic context, has now been accomplished. Remarkably, our findings demonstrate that even in temperate regions, new species of ants are still to be discovered and, moreover, they may be hiding among specimens already deposited in collections. The same is undoubtly true for most insect groups. Our biogeographic results fall in line with previously proposed dispersal scenarios for taxa with Holarctic distributions, and they support common dispersal patterns within the Nearctic region that may have been mediated by climatic niche evolution during the Pliocene and Pleistocene. Expanded analyses of the *C. scutellaris* group, including a majority of the Palaearctic species and better representation of the Mesoamerican taxa, are needed to improve support for biogeographic hypotheses. To conclude, our work has contributed to a better understanding of the evolutionary history of temperate insects, yet at the same time highlighted how crucial taxonomic and phylogenetic information is still lacking even for seemingly better-studied insect taxa, such as ants, in regions with a long tradition of scientific collecting.

ACKNOWLEDGEMENTS

We are grateful to the following curators for access to material in the indicated collections: Brian Fisher (CASC), Kevin Williams (CSCA), Jack Longino (JTLC), Brian Brown and Weiping Xie (LACM), Stefan Cover (MCZC), Bernard Landry (MHNG), Maria Tavano (MSNG), Bob Blinn (NCSU), Matthew Gimmel (SBMN), Ted Schultz and Eugenia Okonski (USNM) and Alex Wild (UTIC). We also received useful material from Mark Deyrup, David Holway, Jim des Lauriers, Joe MacGown, Lloyd Morrison, Ida Naughton, David Olson, Matthew Prebus, Karl Roeder and Mark Trepanier. Special acknowledgement is due to Brian Fisher, Michele Esposito and collaborators, whose development and maintenance of AntWeb (www.antweb.org) is a godsend to ant taxonomy. For assistance with lab work and DNA sequencing we thank Jill Oberski, Zach Griebenow and Brendon Boudinot. Discussion and comments on the manuscript were kindly provided by Brendon Boudinot, Stefan Cover, Jack Longino and two anonymous reviewers. This research was supported by the University of California, Davis, the Museum für Naturkunde and the National Science Foundation (DEB-1932405 and DEB-2019431).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Voucher information for sequenced specimens.
Table S2. Comprehensive data for sequenced specimens.
Table S3. Alignment statistics calculated with AMAS (Borowiec, 2016).
Table S4. Worker measurements of Nearctic species in the *Crematogaster scutellaris* group.
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Figure S2. Maximum likelihood phylogenies estimated from the SWSC-partitioned, 90% taxon completeness matrix using a combined best tree and bootstrap (*N* = 1000) in IQ-TREE v.1.6.12.
Figure S3. Maximum likelihood phylogenies estimated from the SWSC-partitioned, 80% taxon completeness matrix using a combined best tree and bootstrap (N = 1000) in IQ-TREE v1.6.12.

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Figure S6. Species trees estimated from UCE gene trees with ASTRAL-III.