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A subgeneric revision of *Crematogaster* and discussion of regional species-groups (Hymenoptera: Formicidae)

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Abstract

Crematogaster ants are diverse, widespread and abundant in tropical, subtropical and warm-temperate climates throughout the world. The species diversity of this genus has been notoriously difficult to manage based upon morphology alone, and former attempts have generated a vaguely defined subgeneric system. I propose an improvement of the previous subgeneric classification and recognize two subgenera based upon a concurrent molecular study of the global diversity of these ants. Five of 13 former subgenera of *Crematogaster* are hereby synonymised under the subgenus *Orthocrema* Santschi: *Neocrema* Santschi **syn. nov.**, *Eucrema* Santschi **syn. nov.**, *Rhachiocrema* Mann **syn. nov.**, *Mesocrema* Santschi **syn. nov.** and *Apterocrema* Wheeler **syn. nov.**. The eight remaining subgenera are synonymised under the subgenus *Crematogaster* sensu stricto: *Decacrema* Forel **syn. nov.**, *Oxygyne* Forel **syn. nov.**, *Atopogyne* Forel **syn. nov.**, *Sphaerocrema* Santschi **syn. nov.**, *Colobocrema* Wheeler **syn. nov.**, *Paracrema* Santschi **syn. nov.**, *Physocrema* Forel **syn. nov.** and *Xiphocrema* Forel **syn. nov.**. I present keys, morphological diagnoses and illustrations for the two revised, globally distributed subgenera *Orthocrema* and *Crematogaster* sensu stricto, based upon the worker caste. The two subgenera can be distinguished from each other by a combination of features of the petiole, postpetiole and propodeal spiracle. I also provisionally circumscribe a number of species-groups within the subgenus *Crematogaster* and discuss the utility of species-groups for further taxonomic, phylogenetic and ecological research on the genus *Crematogaster.*

Key words: *Crematogaster* ants, *Orthocrema*, infrageneric classification, subgenera, species-groups, taxonomy, Myrmicinae

Introduction

The genus *Crematogaster* Lund 1831 is a global, widespread and species-rich clade within the largest subfamily of ants, the Myrmicinae. Worldwide this genus comprises currently about 467 described nominal species and about 300 subspecies names (cf. Bolton, 2011), and therefore constitutes one of the 'giant genera of ants' (Bolton, 1995a:1043). *Crematogaster* reaches its highest diversity and abundance in tropical and subtropical forest and savannah habitats, both in the Neotropical and the Palaeotropical regions. It is also well represented in warmer temperate climates of the southern Holarctic region. Its distribution can roughly be characterized as between latitudes ~50° N and ~40° S (see Fig. 1); notable gaps in this broad occurrence are absences from New Zealand, Fiji and Chile (Brown, 1973; Guénard *et al.*, 2010).

In the tropics and subtropics, *Crematogaster* ants nest predominantly arboreally in dead branches or twigs, or under tree bark or moss. A few species are known to be obligate plant-ants (see e.g. Fiala *et al.*, 1999; Feldhaar 2003a & b; Quek *et al.*, 2007). Many species further have the ability to form 'carton' from masticated wood fibres and use this carton material to various extents in nest construction or to shelter trophobionts. For example, some species use carton to seal openings of nest cavities in dead wood, and others to achieve within-nest partitioning (Longino, 2003). A subset of these carton-making species builds more elaborate independent carton nests around branches or on tree trunks. The distribution and biology of carton making in *Crematogaster* is poorly understood and requires further investigation. Ground and leaf-litter nesting also is observed in the genus, but is generally less common in tropical and subtropical species and occurs more frequently among species in temperate regions (Creighton, 1950).

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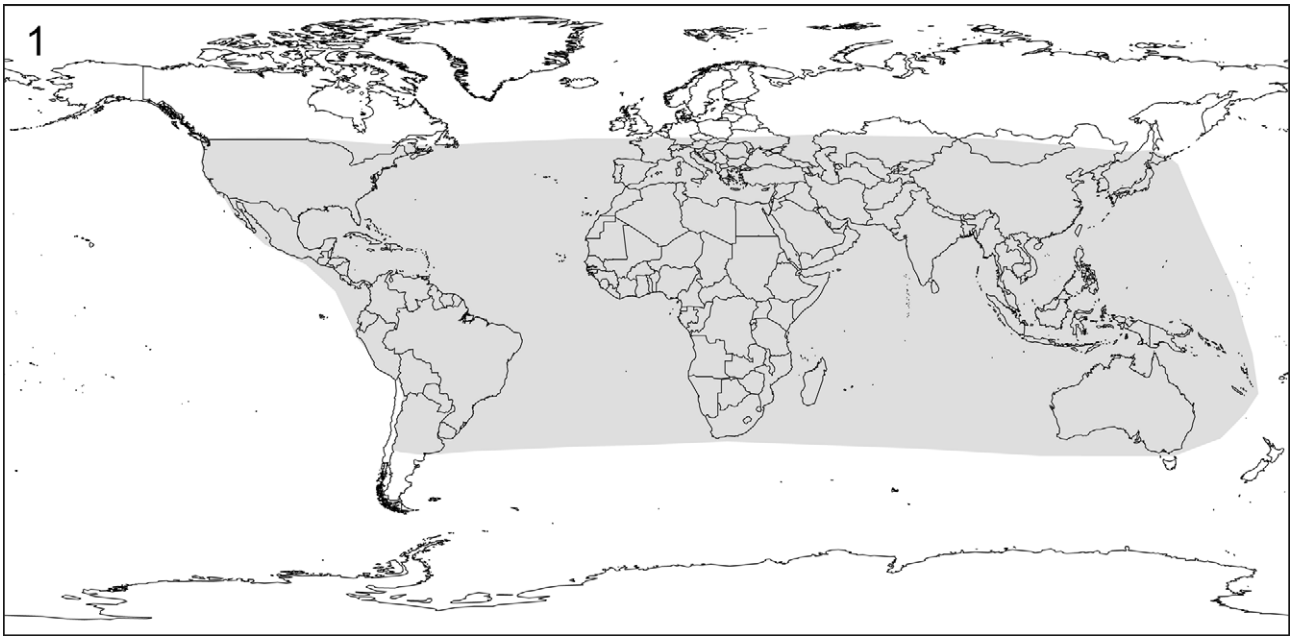


FIGURE 1. Distribution of the genus *Crematogaster*, as indicated by the shaded area, after Guénard *et al.* (2010).

Crematogaster ants are morphologically clearly defined by the distinct dorsal attachment of the postpetiole to the 4th abdominal segment, the first segment of the gaster. This arrangement lends great flexibility to the gaster, which can be brought high up over the rest of the mesosoma so that the petiole is more or less flush with the posterior face of the propodeum (Longino, 2003). This position is often assumed by the ants upon disturbance, either as a defensive or aggressive gesture, and most likely has earned the genus its common name of 'acrobat ants'. Another exceptional morphological characteristic of the genus is its sting: this has a spatulate form and is used to apply venom by contact rather than by injection (Buren, 1959; Marlier, 2004).

Species boundaries in these ants are in contrast usually less clearly demarcated, due to high intraspecific variation in widespread species on the one hand, coupled with often only slight variation among species on the other hand. This has created a chaotic species-level taxonomy within the genus, burdened by countless intraspecific names and likely synonyms (Brown, 1973). A large number of species is therefore in need of taxonomic revision (Longino, 2003; Ward, 2007 & 2010). Regional taxonomic work on the genus has been accomplished for some parts of the world (e.g. Longino, 2003; Hosoishi & Ogata, 2009 & in press; Blaimer, 2010 & 2012), and especially the integration of molecular and morphological data presents a promising approach to improve the state of the species-level taxonomy of *Crematogaster*. The genus is currently subdivided into 15 subgenera on the basis of morphological characteristics; these were mainly erected by Forel (1901, 1910a, 1911, 1912, 1913) and Santschi (1918, 1928), and complemented by some descriptions of Wheeler (1927, 1936) and Mann (1919). However, these groupings provide minimal aid in managing the large genus. They are vaguely defined – thus adding more to the confusion than ameliorating the situation (Brown, 1973).

A solid basis for the improvement of *Crematogaster* systematics and the subgeneric classification has now been presented by a molecular phylogenetic approach (Blaimer, in press). In this study, a broad-scale framework phylogeny for the genus was reconstructed to investigate the internal structure of the genus and its biogeographic history, but a full treatment of morphology was beyond the scope of that paper. The purpose and objective of the following study is to complement these molecular results with the available morphological data, and to revise the subgeneric classification of *Crematogaster* based upon both molecular and morphological data. Moreover, in the following, I aim to introduce a finer, informal organization system for the species diversity of the genus that is based upon the definition of several species-groups. My intention hereby is to identify monophyletic species groupings that can be targeted more easily for taxonomic revision. While the present study certainly cannot achieve a comprehensive treatment of the entire genus and has to leave many gaps, I hope that this contribution nonetheless will encourage others to investigate the taxonomy, biology and evolution of these ecologically dominant and important ants.

Material and methods

Taxon sampling. For the molecular study (Blaimer, in press), 124 *Crematogaster* species were chosen to represent most of the suggested phylogenetic diversity of the whole genus worldwide, taking subgeneric assignments and geographic distribution as indicators. Further included in the study as outgroup taxa were eight members of other ant genera (*Metapone*, *Vollenhovia*, *Tetramorium*, *Recurvidris*, *Leptothorax*, *Temnothorax*, *Aphaenogaster*, *Stenamma*) within the subfamily Myrmicinae, ranging from moderately to distantly related to *Crematogaster.* For further details, including a list of voucher specimens, refer to Blaimer (in press). Images of all molecular voucher specimens are available on AntWeb (www.antweb.org). In the molecular study (Blaimer, in press), specimens were identified using existing identification keys, reference collections, images or original species descriptions. Taxa denoted with "cf" before the species name in Fig. 2 usually have been identified with original literature only. This label indicates that the identification may not be fully accurate, but that the specimen is expected to have close morphological affinity to the applied name. Taxa with code names represent undescribed or unidentifiable species; the code names are hereby not intended for use in formal nomenclatural purposes. Species code names consist of a combination of abbreviations of the previously assigned subgenus, the country of collection, and a number; Malagasy taxa lack the country abbreviation, but possess a locality code. Morphological observations are based upon the molecular voucher species, and on a range of species in several collections (see below); all statements given below refer to the worker caste.

Morphological analysis. All morphological observations were made with a Leica MZ12.5 stereomicroscope. Colour images were created with a JVC KY-F75U digital camera, a Leica MZ16A stereomicroscope, Syncroscopy Auto-Montage (v5.0) software and Zerene Stacker (v1.02) software. All images presented here are publicly available on AntWeb (www.antweb.org). Specimens were examined in the following collections.

CASC	California Academy of Sciences, San Francisco, CA, USA
MCZC	Museum of Comparative Zoology, Harvard, USA
MHNG	Muséum d'Histoire Naturelle, Genève, Switzerland
NHMB	Naturhistorisches Museum, Basel, Switzerland
PSWC	P. S. Ward Collection, University of California at Davis, CA, USA
UCDC	Bohart Museum of Entomology, University of California, Davis, USA
ZMBH	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
MSNG	Museo Civico di Storia Naturale, Genova, Italy
BBBC	B.B. Blaimer Collection

Molecular analysis. DNA was extracted using a DNeasy Tissue Kit (Qiagen Inc., Valencia, California, U.S.A.), performing either non-destructive or destructive methods on the entire ant specimens. Molecular data were obtained from five nuclear protein-coding genes: long wavelength rhodopsin (LW Rh, 856bp exon /199bp intron), arginine kinase (ArgK, 390bp exon), carbomoylphosphate synthase (CAD, 535bp exon/193bp intron), wingless (Wg, 409bp exon) and topoisomerase (Top 1, 802bp exon). A total of 3384bp of aligned sequence data was included in the phylogenetic inference. Amplifications of LW Rh, ArgK, CAD, Top 1 and Wg were performed using standard PCR methods outlined in Ward and Downie (2005) and sequencing reactions were analyzed on an ABI 3730 Capillary Electrophoresis Genetic Analyzer with ABI BigDye Terminator v3.1 Cycle Sequencing chemistry (Applied Biosystems Inc., Foster City, CA). For a more detailed description of molecular methods and for GenBank accession numbers of sequences refer to Blaimer (in press).

Phylogenetic inference. The following is only a brief summary of inference methods performed to generate the phylogeny replicated in Fig. 2; for a full account of phylogenetic methods that were used within the molecular phylogenetic study see Blaimer (in press). All sequence data were assembled and edited in the program Sequencher 4.6 (Gene Codes Corporation, 2006, Ann Arbor, MI) and aligned in Muscle 3.7 (Edgar, 2004) accessed through the CIPRES science gateway (Miller *et al.,* 2010). Phylogenetic analyses were performed within a Bayesian framework using MrBayes v3.1 (Ronquist & Huelsenbeck, 2003), accessed through the CIPRES science gateway (Miller *et al.,* 2010) and the University of Oslo Bioportal (www.bioportal.uio.no). Analyses within a maximum likelihood framework (ML) used RAxML-GUIv.0.93 (Stamatakis, 2006), performed on an IMac desktop computer.

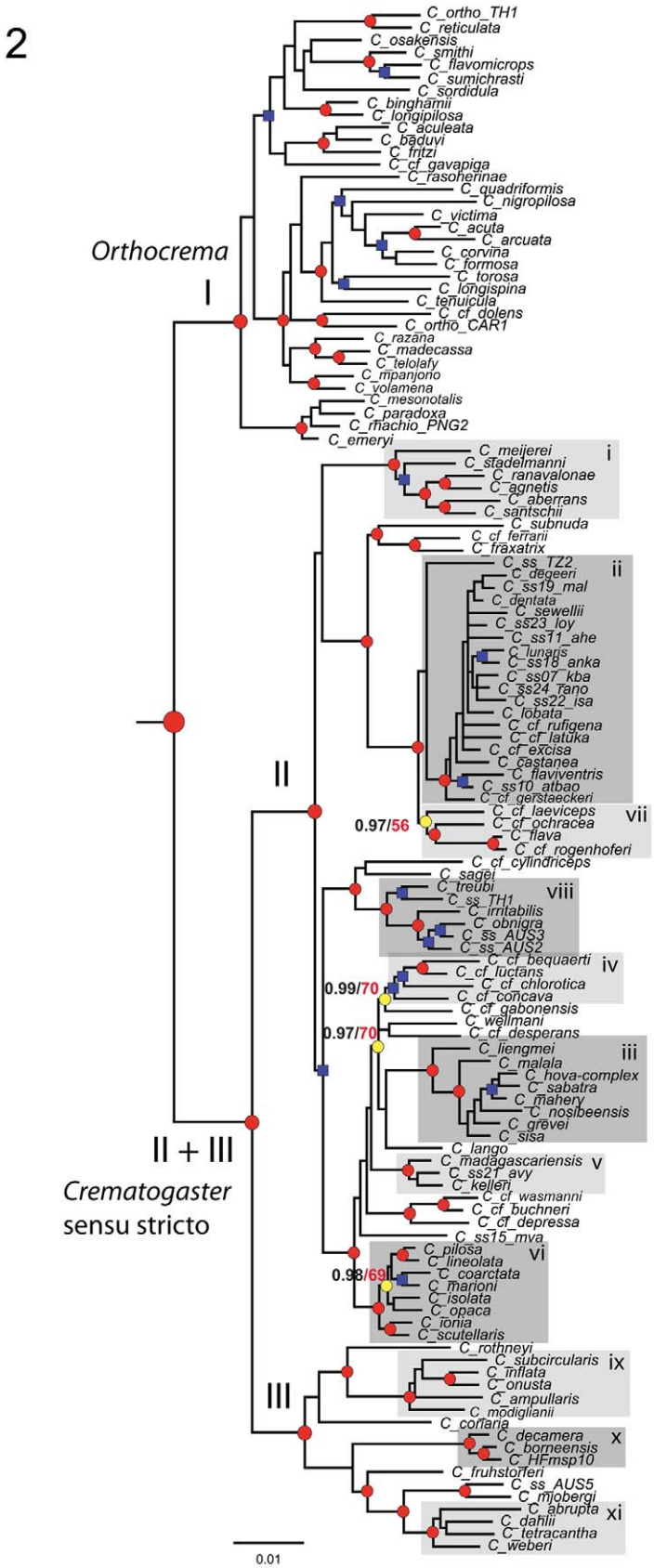


FIGURE 2. Bayesian phylogeny of *Crematogaster* as reconstructed by Blaimer (in press); this analysis was based upon 3384bp from five nuclear genes. Outgroups have been pruned. Red circles indicate PP=1.0 and bootstrap > 94; blue squares indicate PP>0.94 and bootstrap > 74; yellow circles indicate where bootstrap ≤74 and PP>0.94, in these cases both values are shown. Clade labels indicate I: subgenus *Orthocrema*, II+III: subgenus *Crematogaster* sensu stricto, II: Global *Crematogaster* clade, III: Australo-Asian *Crematogaster* clade. Labels i-xi refer to species-groups as outlined in the text.

Bayesian and ML analyses were performed on a concatenated data matrix of the five loci. The data matrix was divided into 17 biologically sensible subsets by gene, translational pattern (exon, intron) and codon position. To test the effect of data partitioning on phylogenetic results, four other partitioning schemes were also originally applied, ranging from simple to more complex, and Bayesian inference was also performed on single-locus data sets (see Blaimer, in press). Best-fitting models of nucleotide sequence evolution were selected for each of these partitions using the Akaike information criterion (AIC) in the program MrModeltest v2.3 (Posada & Crandall, 1998; Nylander, 2004), executed through PAUP* 4.0b10 (Swofford, 2000). RAxML analyses applied a GTRGAMMA model uniformly to all partitions. MrBayes analyses employed two runs of Metropolis-coupled Markov Chain Monte Carlo (MCMCMC) consisting of four chains (temp=0.05) and sampling every 1000 generations, and followed steps outlined in Ward *et al.* (2010) to improve MCMCMC performance. Chain convergence and performance of diagnostic parameters was assessed in MrBayes, Tracer v1.5 (Rambaut & Drummond, 2007) and with the AWTY-online server (Wilgenbusch et al, 2004). Final analyses were run for a length of 30 million generations and the posterior distribution of trees was summarized as majority-rule consensus tree in MrBayes after discarding the first 20% of samples as burnin. Trees were rooted applying the outgroup method, using one of the two most distantly related taxa to *Crematogaster* (*Aphaenogaster and Stenamma*) included in the analyses, *Stenamma dyscheres*.

Results

Based on the molecular results that are concurrently published elsewhere (Blaimer, in press), and on morphological observations that are outlined below, the subgenera of *Crematogaster* are revised to represent the mutually exclusive phylogenetic clades shown in Fig. 2. These clades were robustly recovered across all analyses; tree topology was not affected by different treatments of the data (e.g. partitioning schemes; see Blaimer, in press).

Observing the "principle of priority" under ICZN (Article 23.3), the following two subgeneric names have priority and are recognized hereafter: *Orthocrema* Santschi 1918 (clade I) and *Crematogaster* sensu stricto Lund 1831 (clade II + III). *Orthocrema* is hereby chosen preferentially over the simultaneously published subgeneric names *Neocrema* Santschi 1918 and *Eucrema* Santschi 1918, in accordance with the "principle of the first reviser" (ICZN, Article 24.2.2).

The type species of the subgenus *Orthocrema*, *C. sordidula* Nylander, and the nominotypical subgenus *Crematogaster*, *C. scutellaris* Olivier, have been sequenced and included in the molecular study (Blaimer, in press). I have further confirmed that the type species of each of the previously recognized subgenera belongs to the respective revised subgenera by taking the following measures. **1)** I have morphologically examined primary type material for the species *C. daisyi* Forel (*Oxygyne*), *C. schencki* Forel (*Decacrema*), *C. tetracantha* Emery (*Xiphocrema*), *C. spengeli* Forel (*Paracrema*), *C. wheeleri* Mann (*Rhachiocrema*) and *C. rasoherinae* Forel (*Mesocrema*). **2)** *Crematogaster schencki*, *C. tetracantha*, *C. inflata* Smith (*Physocrema*), *C. stadelmanni* Mayr (*Nematocrema*), *C. acuta* Fabricius (*Eucrema*), *C. rasoherinae*, a species close to (or conspecific with) *C. cylindriceps* Wheeler (*Colobocrema*) and *C. sumichrasti* Mayr (senior synonym of *C. atitlanica* Wheeler, type species of *Apterocrema*) have been included in the molecular phylogeny (Blaimer, in press). **3)** I have further examined non-type material (with reliable identification) for the species *C. distans* Mayr (*Neocrema*) and *C. kneri* Mayr (*Sphaerocrema*). Not examined was *C. hellenica* Forel [currently *C. lorteti hellenica*], the type species of the former subgenus *Atopogyne*. It is clear from Forel's (1911) description, however, that this species has close affinities with *C. depressa* Latreille, a species that was included in the molecular study (Blaimer, in press).

Taxonomic history and synonymic list of subgenera

Orthocrema Santschi 1918: 182: *Orthocrema* as subgenus of *Crematogaster*. Type-species: *Myrmica sordidula*, by original designation. Also listed as subgenus of *Crematogaster* by: Emery, 1922: 130; Wheeler, W.M. 1922b: 662; subsequent authors except those below; Bolton, 1995b: 40. *Orthocrema* as junior synonym of *Crematogaster*: Brown, 1973: 183 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. *Orthocrema* as genus: Soulié, 1964: 398.

= *Tranopeltoides* Wheeler, W.M. 1922a: 10. Type-species: *Tranopelta huberi*, by original designation. *Tranopeltoides* as junior synonym of *Crematogaster* (*Orthocrema*): Bolton, 2003: 239. *Tranopeltoides* as junior synonym of *Crematogaster*: Kempf, 1960: 173.

= *Neocrema* Santschi 1918: 182: *Neocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster distans*, by original designation. Also listed as subgenus of *Crematogaster* by: Wheeler, W.M. 1922b: 662; Kempf, 1972: 82; Bolton, 1995b: 39. *Neocrema* as junior synonym of *Orthocrema*: Emery, 1922: 130. *Neocrema* as genus: Soulié, 1964: 398. *Neocrema* as junior synonym of *Crematogaster*: Brown, 1973: 183 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Eucrema* Santschi 1918: 182: *Eucrema* as subgenus of *Crematogaster*. Type-species: *Formica acuta*, by original designation. Also listed as subgenus of *Crematogaster* by: Kempf, 1972: 82; Bolton, 1995b: 29. *Eucrema* as junior synonym of *Crematogaster*: Brown, 1973: 180 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. [Note: Emery, 1919: 62, Emery, 1922: 137, Soulié, 1964: 389 and Soulié, 1965: 78 incorrectly treat *Eucrema* as a junior synonym of subgenus *Crematogaster* sensu stricto. This stems from Emery's 1912: 272 unjustified subsequent designation of *Formica acuta* as type-species of *Crematogaster* (Bolton, 2011).] **Syn. nov.**

= *Rhachiocrema* Mann 1919: 318: *Rhachiocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster (Rhachiocrema) wheeleri*, by original designation. Also listed as subgenus of *Crematogaster* by: Wheeler, W.M. 1922b: 662; subsequent authors except for those below; Bolton, 1995b: 45. *Rhachiocrema* as genus: Soulié, 1964: 398. *Rhachiocrema* as junior synonym of *Crematogaster*: Brown, 1973: 184 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Mesocrema* Santschi 1928: 33 *Mesocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster rasoherinae*, by subsequent designation of Donisthorpe, 1943: 661. Also listed as subgenus of *Crematogaster* by Bolton, 1995b: 35. *Mesocrema* as junior synonym of *Crematogaster*: Brown, 1973: 182 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Apterocrema* Wheeler 1936: 45 (in text): *Apterocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster (Apterocrema) atitlanica*, by monotypy. Also listed as subgenus of *Crematogaster* by: Kempf, 1972: 81; Bolton, 1995b: 21. *Apterocrema* as junior synonym of *Crematogaster*: Brown, 1973: 178 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

Crematogaster Lund, 1831: 132. Nominotypical subgenus of *Crematogaster*; type-species (as genus): *Formica scutellaris*, by subsequent designation of Bingham, 1903: 124.[Note: The type-species is not *Formica acuta*, which was an unjustified subsequent designation by Emery, 1912: 272; this error has been subsequently repeated by other authors (Bolton, 2011).]

= *Acrocoelia* Mayr, 1853: 147. Type-species: *Acrocoelia ruficeps* (junior synonym of *Formica scutellaris*), by subsequent designation of Wheeler, W.M. 1911: 158. *Acrocoelia* as genus: Mayr, 1853: 147; Soulié, 1964: 398. *Acrocoelia* as subgenus of *Crematogaster*: Emery, 1922: 140; Donisthorpe, 1943: 619; Creighton, 1950: 206; Chapman & Capco, 1951: 86.

Acrocoelia as junior synonym of *Crematogaster*: Roger, 1863: 36; Mayr, 1863: 404; Emery & Forel, 1879: 464; Dalla Torre, 1893: 79; Wheeler, W.M. 1911: 158; Wheeler, W.M. 1922c: 828; Buren, 1959: 126; Kempf, 1972: 81; Brown, 1973: 178.

= *Decacrema* Forel 1910a: 18: *Decacrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster schencki*, by subsequent designation of Wheeler, W.M. 1911: 161. Also listed as subgenus of *Crematogaster* by: Forel, 1917: 242; Arnold, 1920: 547; Emery, 1922: 137; Wheeler, W.M. 1922b: 661; subsequent authors except for those below; Bolton, 1995b: 26.

[Note: *Decacrema* also described as new by Forel, 1910b: 9. Type-species is not *Crematogaster decamera*, which was an unjustified subsequent designation by Wheeler, W.M. 1922c: 860. (Bolton, 2011)]. *Decacrema* as genus: Soulié, 1964: 398. *Decacrema* as junior synonym of *Crematogaster*: Brown, 1973: 179 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Oxygyne* Forel 1901: 375: *Oxygyne* as subgenus of *Crematogaster*. Type-species: *Crematogaster (Oxygyne) daisyi*, by subsequent designation of Wheeler, W.M. 1911: 169. Also listed as subgenus of *Crematogaster* by: Forel, 1917: 242; Arnold, 1920: 542; Emery, 1922: 156; Wheeler, W.M. 1922: 662; subsequent authors except those below; Bolton, 1995b: 40. *Oxygyne* as genus: Soulié, 1964: 398. *Oxygyne* as junior synonym of

Crematogaster: Brown, 1973: 183 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Atopogyne* Forel 1911: 343: *Atopogyne* as subgenus of *Crematogaster*. Type-species: *Crematogaster (Atopogyne) hellenica*, by subsequent designation of Wheeler, W.M. 1911: 159. Also listed as subgenus of *Crematogaster* by: Forel, 1917: 242; Arnold, 1920: 545; Emery, 1922: 153; Wheeler, W.M. 1922b: 662; subsequent authors except those below; Bolton, 1995b: 21. [Note: Type-species is not *Crematogaster depressa*, which was an unjustified subsequent designation by Emery, 1912: 272; this error is repeated by other authors (Bolton, 2011)] *Atopogyne* as genus: Soulié, 1964: 398. *Atopogyne* as junior synonym of *Crematogaster*: Brown, 1973: 178 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Sphaerocrema* Santschi 1918: 182: *Sphaerocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster kneri*, by original designation. Also listed as subgenus of *Crematogaster* by: Emery, 1922: 152; Wheeler, W.M. 1922b: 662; subsequent authors except for those above; Bolton, 1995b: 46. *Sphaerocrema* as genus: Soulié, 1964: 398. *Sphaerocrema* as junior synonym of *Crematogaster*: Brown, 1973: 185 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Colobocrema* Wheeler 1927: 31 *Colobocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster (Colobocrema) cylindriceps*, by monotypy. Also listed as subgenus of *Crematogaster* by: Bolton, 1995b: 24. *Colobocrema* as junior synonym of *Crematogaster*: Brown, 1973: 179 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Paracrema* Santschi 1918: 182: *Paracrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster spengeli*, by original designation. Also listed as subgenus of *Crematogaster* by: Emery, 1922: 155; Wheeler, W.M. 1922b: 662; subsequent authors except those below; Bolton, 1995b: 41. *Paracrema* as genus: Soulié, 1964: 398. *Paracrema* as junior synonym of *Crematogaster*: Brown, 1973: 183 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Physocrema* Forel 1912: 220: *Physocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster inflata*, by subsequent designation of Wheeler, W.M. 1913: 82. Also listed as subgenus of *Crematogaster* by: Forel, 1917: 242; Emery, 1922: 139; Wheeler, W.M. 1922b: 662; subsequent authors except for those below; Bolton, 1995b: 42. *Physocrema* as genus: Soulié, 1964: 398. *Physocrema* as junior synonym of *Crematogaster*: Brown, 1973: 183 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Xiphocrema* Forel 1913: 80: *Xiphocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster tetracantha*, by subsequent designation of Emery, 1922: 138. Also listed as subgenus of *Crematogaster* by: Forel, 1917: 242; Emery, 1922: 138; Wheeler, W.M. 1922b: 662; subsequent authors except for those below; Bolton, 1995b: 50. *Xiphocrema* as genus: Soulié, 1964: 398. *Xiphocrema* as junior synonym of *Crematogaster*: Brown, 1973: 185 [provisional]; Smith, D.R. 1979: 1376; Hölldobler & Wilson, 1990: 13. **Syn. nov.**

= *Nematocrema* Santschi 1918: 182: *Nematocrema* as subgenus of *Crematogaster*. Type-species: *Crematogaster stadelmanni*, by original designation. Also listed as subgenus of *Crematogaster* by: Emery, 1922: 157; Wheeler, W.M. 1922b: 662; Bolton, 1995b: 38. *Nematocrema* as junior synonym of Oxygyne: Blaimer, 2012: 249.

Morphological diagnoses

Orthocrema Santschi
(Fig. 2, clade I)

Distribution: GLOBAL (same as genus). Former members of subgenera *Orthocrema* (except *C. irritabilis* Smith, *C. polita* Smith), *Neocrema*, *Eucrema*, *Rhachiocrema*, *Mesocrema* (in part) and *Apterocrema* (note that this subgenus was monotypic and its only species member was synonymised previously by Longino (2003) under *C. sumichrasti* Mayr).

1. Petiole in dorsal view rectangular (Fig. 3), ovo-rectangular (Fig. 4), or (much less commonly, seen in some Asian, Australian or Neotropical taxa) more or less elongate-rectangular (Fig. 5).
2. Petiole with dorsoposterior lateral denticles or tubercules that each bear an erect seta (Fig. 6). Denticles may be absent or reduced, but dorsoposterior setae are always present.

3. Postpetiole usually globular, without (Fig. 7), or with a faint median longitudinal impression only (Fig. 8). Some species in the Neotropical and Malagasy regions have a more pronounced longitudinal impression on the postpetiole, which then appears bilobed (Fig. 9).
4. Occipital carina usually sharp and distinct (Fig. 10).
5. Propodeal spiracle circular or subcircular (Fig.11).
6. Antennae 11-segmented. Antennal scapes often surpassing head margin, and antennae usually with a 2-segmented club, or lacking distinct club.
7. Posterior head margin usually rounded (Fig. 12), rarely straight or medially depressed with subangular corners (Fig. 13) (e.g. Neotropical *C. crinosa*-group (after Longino, 2003), or Malagasy *C. volamena*-group).

***Crematogaster* sensu stricto**
(Fig. 2, clade II + III)

Distribution: GLOBAL (same as genus). Former members of subgenera *Crematogaster* sensu stricto, *Decacrema*, *Oxygyne* (incl. *Nematocrema*), *Mesocrema* (in part), *Atopogyne*, *Sphaerocrema*, *Colobocrema*, *Paracrema*, *Physocrema*, *Xiphocrema*, and a few previously misassigned *Orthocrema* species (*C. irritabilis* and *C. polita*).

1. Petiole shape (in dorsal view) highly variable: moderately flared (Fig. 14a), broadly flared (Fig. 15a), sharply flared (Fig.16a), greatly flared (Fig. 17a), oval (Fig. 18a) or suboval (Fig. 19a), elongate rectangular (Fig. 20), circular (Fig. 21a), or hexagonal (Fig. 22a), but **not** rectangular or ovo-rectangular (as in Fig. 3 or 4). **If** petiole elongate-rectangular (Fig. 20) and thus similar to some *Orthocrema* species (as in Fig. 5), **then** propodeal spiracle compressed oval.
2. Petiole with dorsoposterior denticles/tubercules and dorsoposterior erect setae (e.g. Figs 14a, 16a) or lacking denticles/tubercules (e.g. Figs 15a, 18a–19a, 20, 22a), while setae may still be present.
3. Postpetiole varying from distinctly (Figs 16b-17b, 19b, 22b) to weakly bilobed (Figs 14b–15b, 18b), with a broad (Fig. 16b) to thin median longitudinal impression (Fig. 23). More rarely postpetiole only with faint posterior impression (Figs 18b, 25) or lacking impression entirely (Fig. 24). *Probably ~80% of the species diversity in this clade has a clearly bilobed postpetiole with a distinct median longitudinal impression.*
4. Propodeal spiracle often oval or compressed oval (Fig. 26).
5. Occipital carinae variable, but often reduced (Fig. 27).
6. Antennae usually 11-segmented, rarely 10-segmented or (one species) 9-segmented. Antennal scapes of variable length; if antennae distinctly clubbed, then usually club 3-segmented.
7. Head shape highly variable, but often with a straight (Fig. 28) or medially depressed posterior head margin (Fig. 29) and with suboval or subangular corners.

Key to the subgenera *Orthocrema* and *Crematogaster*

1 Postpetiole globular, lacking median impression (Figs 7, 24), or merely impressed posteriorly (Figs 8, 21b, 25) 2
– Postpetiole bilobed, with a broad or sharp, more or less distinct median impression (Figs 9, 14b–19b, 22b, 23). 4
2(1) Petiole rectangular or ovo-rectangular (Figs 3 and 4); dorsoposterior setae and/or denticles usually present on petiole; propodeal spiracle circular or subcircular (Fig. 11); *global* . . . . . *Orthocrema*
– Petiole of different form (Figs 5, 14a–19a, 20, 21a–22a); dorsoposterior setae and denticles present or absent; propodeal spiracle variable 3
3(2) Petiole elongate rectangular (Fig. 5); propodeal spiracle circular or subcircular (Fig. 11); *global* . . . . . *Orthocrema*
– Petiole of variable form (Figs 14a–19a, 20, 21a–22a), **if** elongate rectangular (Fig. 20), **then** propodeal spiracle compressed oval (Fig. 26); *Old World* . . . . . *Crematogaster*
4(1) Petiole rectangular or ovo-rectangular (Figs 3 and 4); dorsoposterior setae and/or denticles usually present on petiole; *Neotropical and Malagasy region.*. . . . . *Orthocrema*
– Petiole of different form (Figs 14a–19a, 20, 21a–22a); dorsoposterior setae and denticles present or absent; *global*. . . . . *Crematogaster*

Species membership in revised subgenera

Nominal species as listed currently by Bolton (2011) are assigned to the revised subgenera. Anticipated taxonomic changes on the species level have been incorporated where this seemed appropriate and does not violate ICZN rules. Type species are in bold font.

Crematogaster* (*Orthocrema*):** *abstinens, aculeata, acuta, aitkenii, amapaensis, ampla, arata, arcuata, atra, baduvi, binghamii, bingo, biroi, boera, bogojawlenskii, boliviana, brasiliensis, brevidentata, brevimandibularis, brevis, bruchi, bryophilia, carinata, chodati, cisplatinalis, corticicola, corvina, crassicornis, crinosa, cristata, crucis, cubaensis, curvispinosa, delitescens, dispar, distans, dolens, dorsidens, egregior, emeryi, erecta, euterpe, evallans, flavomicrops, flavosensitiva, foliocrypta, formosa, fritzi, gavapiga, goeldii, gratiosa, heathi, huberi, iheringi, indefensa, insularis, iridipennis, jardinero, javanica, jeanneli, laevis, levior, limata, littoralis, longipilosa, longispina, lutzi, madecassa, magnifica, mancocapaci, masukoi, mesonotalis, minutissima, moelleri, montana, monteverdensis, montezumia, mpanjono, muralti, myops, natalensis, nigropilosa, nitidiceps, obscurata, osakensis, overbecki, oxygynoides, pallida, pallipes, paradoxa, parallela, pauciseta, pauli, peristerica, peruviana, polymnia, pulchella, pygmaea, quadriformis, quadrispinosa, queenslandica, ralumensis, raptor, rasoherinae, razana, rectinota, resulcata, reticulata, rochai, rudis, rufotestacea, russata, russoi, scapamaris, scelerata, schimmeri, scita, sericea, snellingi,* ***sordidula*, sotobosque, steinheili, stigmatica, stollii, subtonsa, suehiro, sumichrasti, telolafy, tenuicula, thalia, torosa, transvaalensis, udo, unciata, uruguayensis, ustiventris, vicina, victima, volamena, wardi, wheeleri, xerophila.*

Crematogaster* (*Crematogaster*):** *abdominalis, aberrans, abrupta, acaciae, adrepens, aegyptiaca, affabilis, afghanica, africana, agnetis, agniae, algirica, alluaudi, aloysiisabaudiae, alulai, amabilis, ambigua, amita, ampullaris, ancipitula, angulosa, angusticeps, antaris, anthracina, apicalis, arnoldi, aroensis, arthurimuelleri, ashmeadi, atkinsoni, auberti, augusti, aurita, australis, bakeri, batesi, bequaerti, betapicalis, bicolor, biformis, bison, borneensis, bouvardi, breviventris, browni, brunnea, brunneipennis, brunnescens, buchneri, buddhae, butteli, californica, capensis, captiosa, castanea, censor, cephalotes, cerasi, chiarinii, chlorotica, chopardi, chungi, cicatriculosa, clariventris, clydia, coarctata, coelestis, colei, concava, constructor, coriaria, cornigera, cornuta, corporaali, cuvierae, cylindriceps, dahlii, daisyi, dalyi, decamera, degeeri, delagoensis, dentinodis, depilis, depressa, desecta, desperans, difformis, diffusa, dohrni, donisthorpei, dubia, ebenina, edentula, egidyi, elegans, elysii, emeryana, enneamera, ensifera, eurydice, excisa, ferrarii, flava, flavicornis, flavitarsis, flaviventris, foraminiceps, foxi, fraxatrix, frivola, fruhstorferi, fuentei, fusca, gabonensis, gallicola, gambiensis, gerstaeckeri, gibba, gordani, grevei, gutenbergi, hemiceros, hespera, hezaradjatica, himalayana, hogsoni, homeri, hottentota, hova, ilgii, impressa, impressiceps, inconspicua, incorrecta, inermis, inflata, innocens, ionia, irritabilis, isolata, jacobsoni, jehovae, jullieni, juventa, kachelibae, karawaiewi, kasaiensis, kelleri, kirbii, kneri, kohlii, kojimai, kutteri, laestrygon, laeviceps, laevissima, laeviuscula, lamottei, lango, larrae, latuka, laurenti, ledouxi, libengensis, liengmei, lineolata, lobata, longicephala, longiceps, longiclava, lorteti, lotti, lucayana, luctans, macaoensis, macracantha, madagascariensis, magitae, mahery, major, malala, manni, margaritae, marioni, marthae, matsurumai, meijerei, melanogaster, menilekii, microspina, mimosae, misella, mjobergi, modiglianii, montenigrina, monticola, moqorensis, mormonum, motazzi, mucronata, mutans, navajoa, nawai, nesiotis, neuvillei, nigeriensis, nigrans, nigriceps, nigronitens, nocturna, nosibeensis, oasium, obnigra, obscura, , ochracea, ochraceiventris, onusta, opaca, opaciceps, opuntiae, orobia, oscaris, painei, paolii, patei, pellens, perelegans, peringueyi, petiolidens, phoenica, phoenix, physothorax, pia, pilosa, pinicola, polita, politula, popohana, pradipi, pseudinermis, pythia, ranavalonae, ransonneti, recurva, retifera, rifelna, rivai, rogenhoferi, rogeri, ronganensis, rossi, rothneyi, rufa, rufigena, rugosa, rugosior, ruspolii, rustica, sabatra, sagei, sanguinea, santschii, saussurei, schencki, schmidti, schultzei,* ***scutellaris*, semperi, senegalensis, sewardi, sewellii, similis, simoni, sisa, skounensis, solenopsides, solers, sorokini, soror, spengeli, stadelmanni, stenocephala, stigmata, striatula, subcircularis, subdentata, subnuda, tanakai, tarsata, teranishii, tetracantha, theta, togoensis, transiens, trautweini, tranvancorensis, treubi, tumidula, urvijae, vacca, vagula, vandeli, vandermeermohri, vermiculata, vidua, vitalisi, vulcania, walshi, warburgi, wasmanni, weberi, wellmani, werneri, whitei, wilwerthi, wroughtonii, yamanei, yappi, zavattarii, zoceensis, zonacaciae.*

Incertae sedis: *consternens, mimicans, obscurior, terminalis.*

Major lineages within the subgenus *Crematogaster*

The '*Crematogaster* in the strict sense' consist of a globally distributed and an Australo-Asian endemic clade, which on molecular basis form highly supported divergent lineages (Fig. 2). Diagnostic morphological characters for these two clades have not been uncovered however. The type species of the genus *Crematogaster*, *C. scutellaris* belongs in the global clade.

The global *Crematogaster* clade

(Fig. 2, clade II)

Comprises former members of subgenera *Crematogaster* sensu stricto (in part), *Decacrema* (part), *Oxygyne* (incl. *Nematocrema*), *Mesocrema* (in part), *Colobocrema*, *Atopogyne* and *Sphaerocrema*.

1. Petiole shape varying from moderately (Fig. 14), broadly (Fig. 15) or sharply flared (Fig. 16), oval (Fig. 18) or suboval (Fig. 19), elongate oval (Fig. 20) or hexagonal (Fig. 22).
2. Postpetiole usually more or less bilobed (Figs 14b–19b, 22b), with a distinct longitudinal impression (e.g. Figs 14b–16b, 23); exception is the African *C. kneri*-group (see below), here postpetiole globular with at most a weak posterior impression (Figs 24–25).

The Australo-Asian *Crematogaster* clade

(Fig. 2, clade III)

Includes former members of subgenera *Crematogaster* sensu stricto (in part), *Decacrema* (in part), *Paracrema*, *Physocrema* and *Xiphocrema*.

1. Petiole shape in dorsal view circular (Fig. 21a), oval (Fig. 18a), suboval (Fig. 19a), or greatly flared (Fig. 17a).
2. Postpetiole usually globular, with at most faint posterior impression (Figs 24–25); less commonly postpetiole bilobed (Fig. 17b).

Species groups

With further sampling it will be possible to structure the subgenera *Orthocrema* and *Crematogaster* into smaller species-groups, which should then be targeted for taxonomic revisions. At this point, I recognize several species-groups within the subgenus *Crematogaster* that are supported by the current data (see Fig. 2), and that I deem likely to form natural, monophyletic groups even when further data, i.e. more taxa, are added to the molecular phylogeny. They should however be regarded as hypotheses to be tested. Not all taxa sampled in the molecular study (Blaimer, in press) fit into the defined groupings below, so some species remain unassigned. In addition these species-groups reflect morphological observations of the author on *Crematogaster* species beyond the molecular sampling. Groups are named after the oldest available species name(s) *known* to be associated with that group, and thus do not necessarily reflect the most commonly observed morphology.

Within the global clade (II)

PALAEOTROPICAL

i. *Crematogaster ranavalonae*-group

This group is equivalent to the former subgenus *Oxygyne*. A full diagnosis for this group was given in Blaimer (2012); main features are summarized below. Since then, one additional character (reduced palp formula) has been discovered.

1. Number of maxillary and labial palps reduced in workers: palp formula 3,3, 3,2 or 2,2 (versus 5,3 in other examined members of the genus).
2. In lateral view, median portion of clypeus more or less prominently convex and in fullface view medially protruding over mandibles.
3. Fronto-clypeal suture impressed, often anterior portion of frons (above suture) transversely concave.
4. Head usually rounded and equally long as wide or slightly wider than long.
5. Promesonotal suture often complete and distinct.
6. Subpetiolar process absent.
7. Postpetiole with median impression.

The *C. ranavalonae*-group is a strongly supported and highly divergent lineage within the global *Crematogaster* clade. Relationships to other clades however are poorly resolved (Fig. 2). Members of this group are: *Crematogaster agnetis* Forel, *C. marthae* Forel, *C. ranavalonae* Forel, *C. breviventris* Santschi, *C. donisthorpei* Santschi, *C. magitae* Forel, *C. margaritae* Emery, *C. oscaris* Forel, *C. santschii* Forel, *C. stadelmanni* Mayr, *C. trautweini* Viehmeyer, *C. aberrans* Forel, *C. augusti* Emery, *C. butteli* Forel, *C. daisyi* Forel, *C. dalyi* Forel, *C. ebenina* Forel, *C. pia* Forel, *C. soror* Forel, *C. tumidula* Emery, *C. vandermeermohri* Menozzi and *C. meijerei* Emery after Blaimer (2012).

AFRICA AND MADAGASCAR

ii. *Crematogaster castanea*-group

1. Petiole usually broadly (Fig. 15a) or moderately flared (Fig. 14a) and distinctly wider than long, rarely reduced to a suboval form (Figs 18a–19a).
2. Postpetiole distinctly and broadly bilobed, usually with deep and broad median impression.
3. Head usually broad, often wider than long, with straight (Fig. 28) or medially depressed posterior margin (Fig. 29) and subangular corners.

This group includes members of the subgenus *Crematogaster* (as defined prior to this study) from Africa and Madagascar. At the moment the following described species are assigned to this group: *C. degeeri* Forel, *C. sewellii* Forel, *C. dentata* Dalla Torre, *C. lunaris* Santschi, *C. lobata* Emery, *C. castanea* Smith, *C. rufigena* Arnold, *C. latuka* Weber, *C. excisa* Mayr, *C. flaviventris* Santschi and *C. gerstaeckeri* Dalla Torre. A number of yet undescribed species from Madagascar also belong in this grouping. Note that the Malagasy clade within this group is elsewhere (Blaimer, in press) further defined as the *C. degeeri-sewellii*-group, in order to highlight the endemism of this latter grouping to the Malagasy region.

iii. *Crematogaster hova*-group

1. Antennae 10-segmented (vs. 11-segments in most other species).
2. Petiole broadly or moderately flared, suboval or hexagonal (Figs 15a, 14a, 18a, 22a, respectively).
3. Postpetiole bilobed, with a more or less distinct median impression (e.g. Figs 14b &15b).

Includes members of previous subgenus *Decacrema* from Africa and Madagascar as follows. *Crematogaster hova*-complex (*C. hova* Forel, *C. schencki* Forel, *C. ensifera* Forel), *C. sisa* Blaimer, *C. mahery* Blaimer, *C. malala* Blaimer, *C. grevei* Forel, *C. sabatra* Blaimer, *C. nosibeensis* Forel and *C. liengmei* Forel.

CONTINENTAL AFRICA

iv. *Crematogaster kneri*-group

1. Petiole moderately to sharply flared, or suboval (Figs 14a, 16a)
2. Postpetiole globular, with at most weak posterior impression (Figs 24, 25).

3. Pronotum often with angular or tuberculate lateral margins (Fig. 30).
4. Mesonotum often postero-laterally angulate or denticulate (Fig. 31).

This group will probably contain a large part of the former subgenus *Sphaerocrema*, but this remains to be tested. At the moment the following species are assigned to this grouping: *C. kneri* Mayr, *C. bequaerti* Forel, *C. concava* Emery, *C. luctans* Forel and *C. chlorotica* Emery.

MADAGASCAR

v. *Crematogaster kelleri*-group

1. Petiole oval or suboval (Figs 19a & 18a).
2. Postpetiole bilobed, with distinct median longitudinal impression (e.g. Figs 14b & 15b).
3. Mesonotum posterolaterally angulate (Fig. 32a) and with distinct dorsal face (Fig. 32b).
4. Head shape quadrate.
5. Sculpture overall reduced, aciculate and shiny.

To date this group comprises three species: *C. kelleri* Forel, *C. madagascariensis* André and one yet undescribed morphospecies.

HOLARCTIC & NEOTROPICS

vi. *Crematogaster scutellaris*-group

1. Petiole moderately (Fig. 14a) to broadly flared (Fig. 15a), rarely suboval (Fig. 18a).
2. Postpetiole bilobed, with distinct median longitudinal impression (e.g. Figs 14b & 15b); rarely only with faint impression and postpetiole indistinctly bilobed (e.g. Fig. 18b).

Definitive members are: *C. scutellaris* Olivier, *C. ionia* Forel, *C. opaca* Mayr , *C. isolata* Buren, *C. marioni* Buren, *C. coarctata* Mayr, *C. lineolata* Say , *C. pilosa* Emery. It seems likely that all of the (non-*Orthocrema*) Nearctic and Palaearctic taxa belong to this clade, as well as a few members of the subgenus *Crematogaster* that have entered the margins of the northern Neotropics.

SOUTH-EAST ASIA, NEW GUINEA & AUSTRALIA

vii. *Crematogaster rogenhoferi*-group

1. Petiole sharply (Fig. 16a) or broadly flared (Fig. 15a), often with sharp dorsolateral margin (Fig. 16c).
2. Postpetiole bilobed, with a broad median longitudinal impression.
3. Pronotum with acute or angular margins (Fig. 33a).
4. Mesonotum convex and posterolaterally margined (Fig. 33b).

At the moment, the following species are assigned to this group: *C. rogenhoferi* Mayr, *C. flava* Forel, *C. ochracea* Mayr and *C. laeviceps* Smith.

viii. *Crematogaster irritabilis*-group

1. Petiole hexagonal (Fig. 22a), suboval (Fig. 18a), or elongate-rectangular (Fig. 20).
2. Postpetiole varying from narrowly bilobed (Fig. 23) with sharp but narrow median impression, to strongly bilobed with broad median impression (e.g. Fig. 16b).

3. Pronotum laterally rounded or subangular (Fig. 34).
4. Mesonotum in lateral view rounded, and without distinct posterior face (Fig. 35).
5. Fairly abundant erect pilosity over entire body.
6. Propodeal spines, if present, often with a downward curve.

Members of this group are currently: *C. irritabilis* Smith, *C. polita* Smith, *C. obnigra* Mann, *C. treubi* Emery and several yet unidentified (or undescribed) species.

Within the Australo-Asian endemic clade

SOUTH-EAST ASIA

ix. *Crematogaster inflata*-group

1. Members either with propodeum greatly inflated (Fig. 36), or posterolateral denticles on the mesonotum (Fig. 37).
2. Head large and broad, often medially depressed.
3. Petiole elongate-rectangular (Fig. 20), oval (Fig. 19a) or circular (Fig. 21a).
4. Postpetiole of globular shape (Figs 21b, 24, 25), a faint posterior impression may be present.

This group most likely includes members of the former subgenera *Physocrema* and *Paracrema* (as listed by Bolton, 2011), as well as probably a number of species that have previously been associated with the subgenus *Crematogaster* sensu stricto. Definitive membership of species is, however, difficult to assess at this point and only certain for the following: *C. subcircularis* Mayr, *C. inflata* Smith, *C. onusta* Stitz, *C. ampullaris* Smith and *C. modiglianii* Emery.

x. *Crematogaster borneensis*-group

1. Antennae 10-segmented.
2. Head shape rectangular, longer than wide .
3. Petiole in dorsal view suboval (Fig. 18a), circular (Fig. 21a) or hexagonal (Fig. 22a).
4. Postpetiole globular (e.g. Figs 21b, 24, 25), a faint posterior impression may be present.

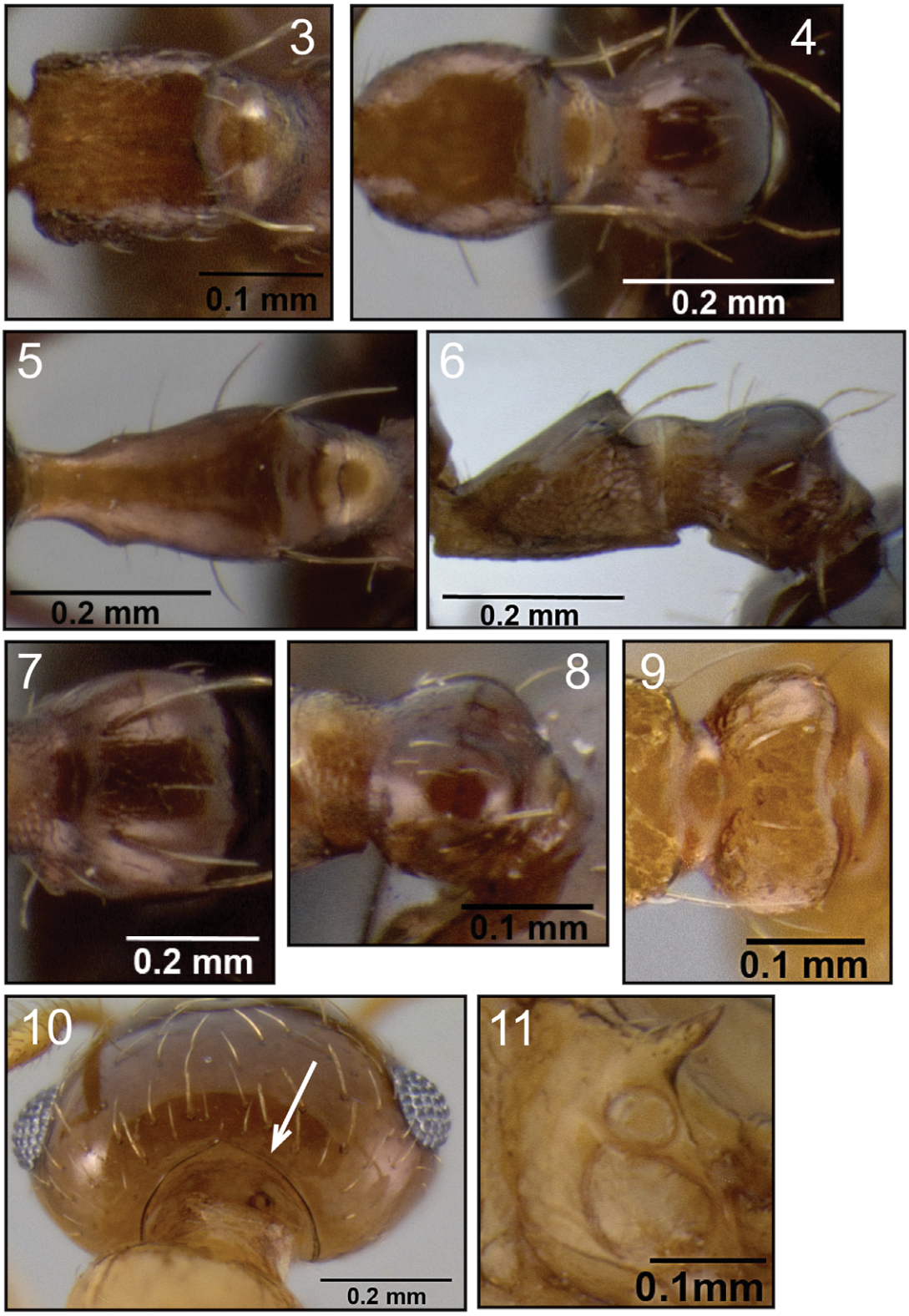
Most members of this group are obligate inhabitants of *Macaranga* plants. Species associated with this clade are *C. borneensis* André, *C. decamera* Forel, *C. captiosa* Forel and several undescribed species (Feldhaar *et al.*, in prep.).

NEW GUINEA (incl. SOLOMON ISL.)

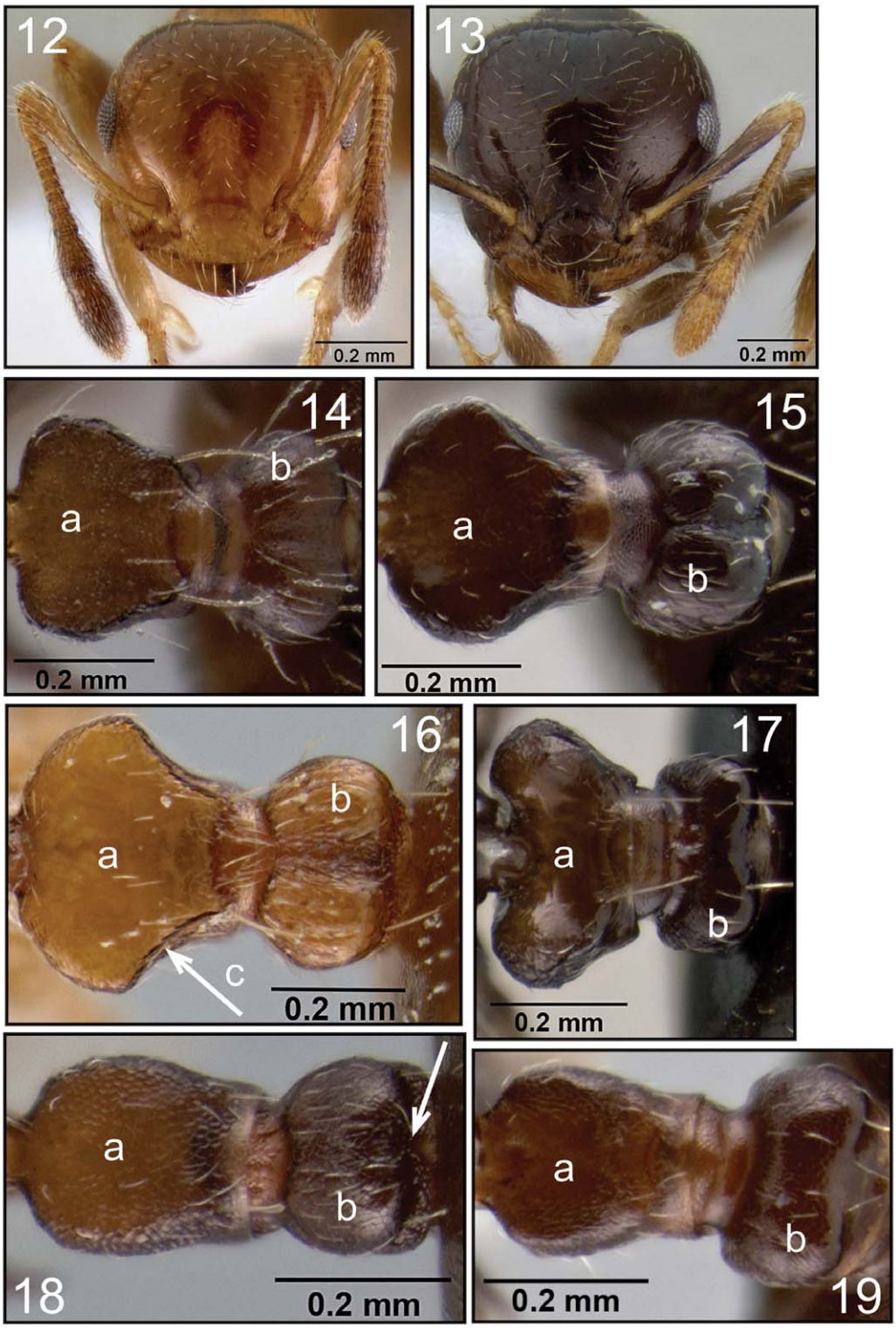
xi. *Crematogaster tetracantha*-group

1. Pronotum antero-laterally with distinct sharp margins or denticles (Fig. 38) or spinose protuberances (Fig. 39).
2. Petiole in dorsal view either greatly flared (Fig. 17a) and transversely convex, or suboval (Fig. 18a).

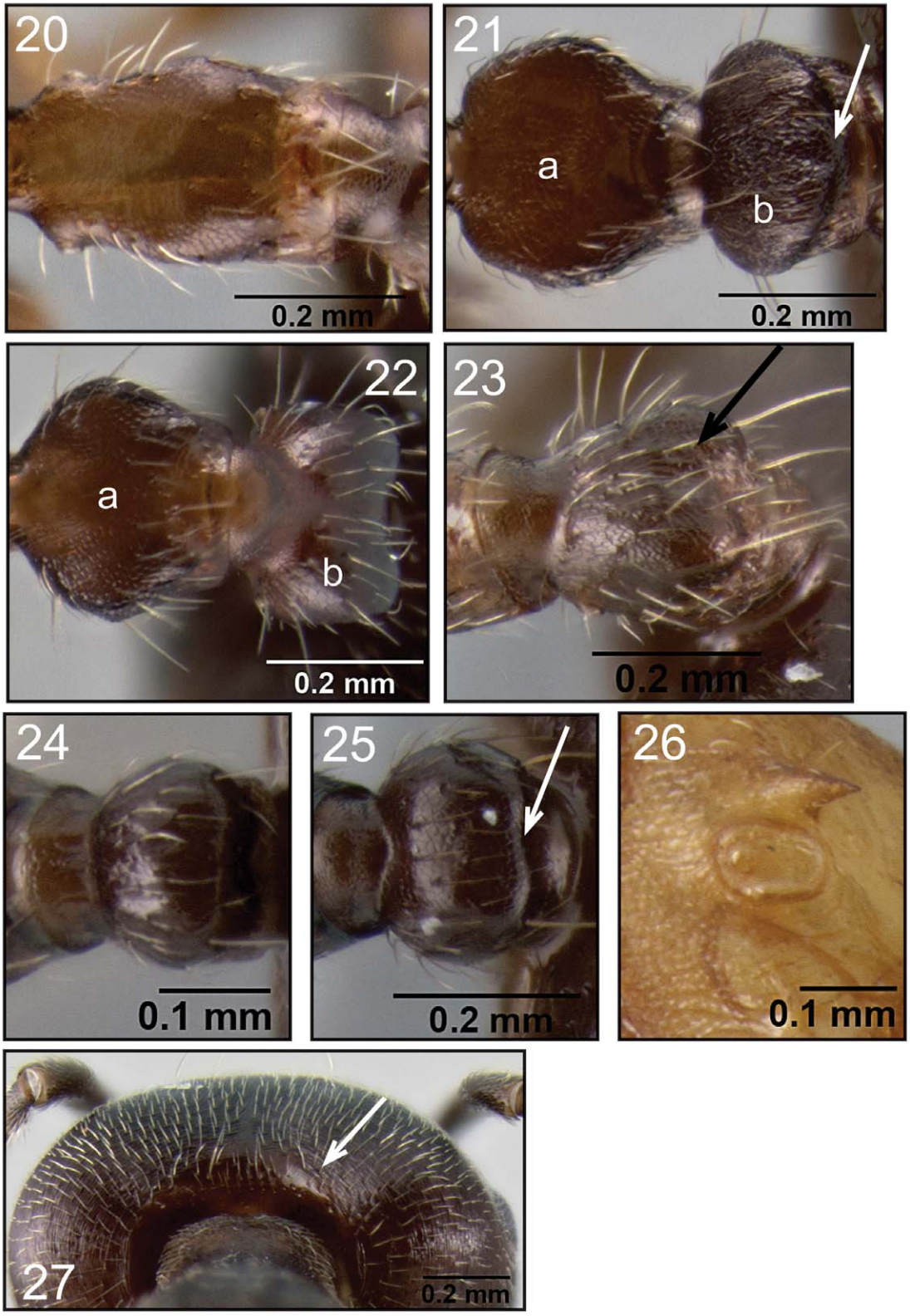
This group comprises all members of the previous subgenus *Xiphocrema* and some additional species from *Crematogaster*, and thus to date has the following members: *C. dahlii* Forel, *C. tetracantha* Emery, *C. recurva* Emery, *C. elegans* Smith, *C. flavitarsis* Emery, *C. weberi* Emery, *C. elysii* Mann, *C. abrupta* Mann and *C. tarsata* Smith.



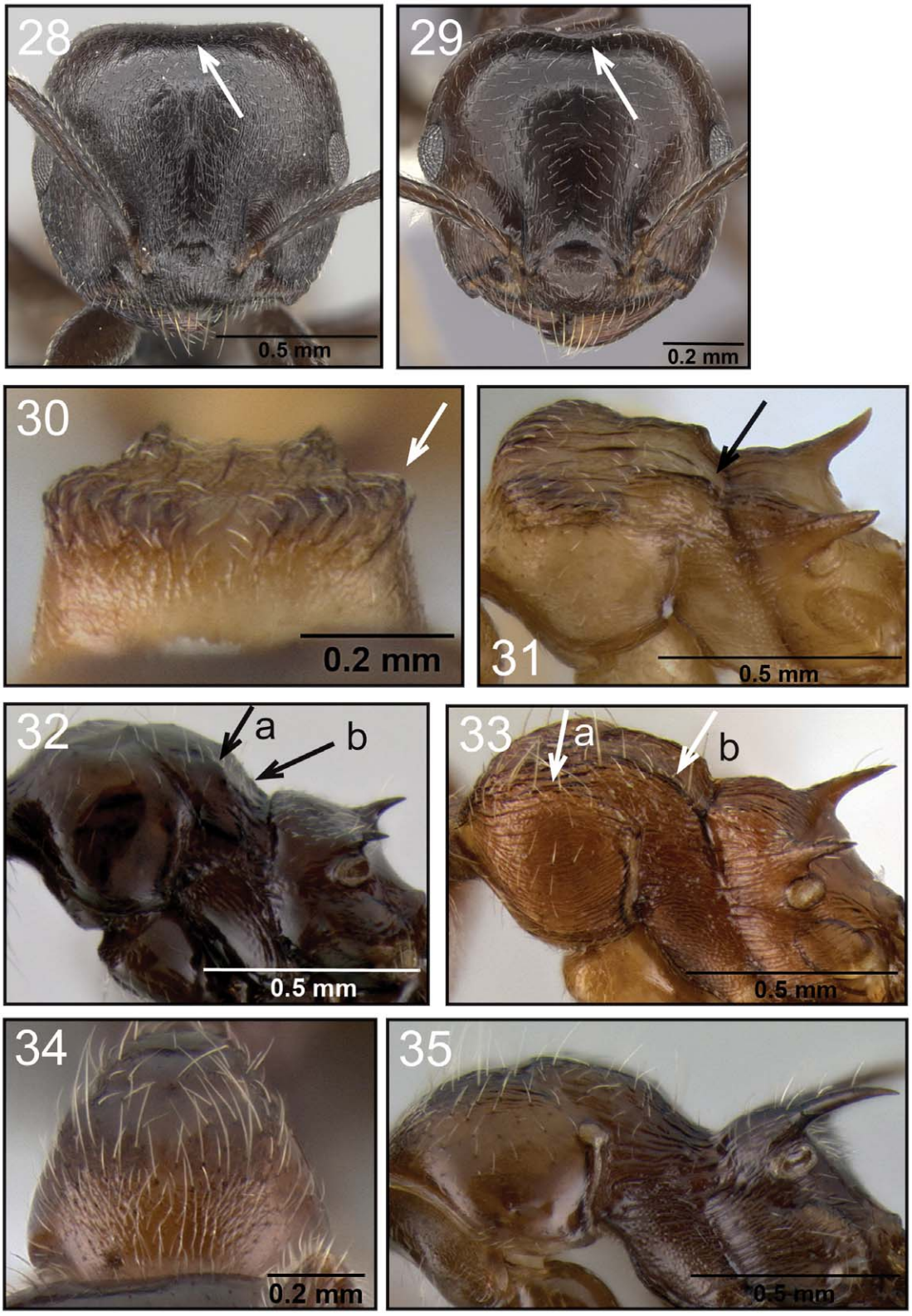
FIGURES 3–11. 3: Petiole rectangular (dorsal view) [*Crematogaster* (*Orthocrema*) *rasoherinae*, CASENT0070841]; **4**: petiole ovo-rectangular (dorsal view) [*C.* (*Orthocrema*) *baduvi*, CASENT0193723]; **5**: petiole elongate-rectangular (dorsal view) [*C.* (*Orthocrema*) *longispina*, CASENT0193767]; **6**: petiole with dorsoposterior lateral denticles or tubercules, bearing erect setae (lateral view) [*C.* (*Orthocrema*) *baduvi*, CASENT0193723]; 7: postpetiole globular and without impression (dorsal view) [*C.* (*Orthocrema*) *longispina*, CASENT0193767]; **8**: postpetiole globular with faint median impression (angled view) ; **9**: postpetiole with median impression and bilobed (dorsal view) [*C.* (*Orthocrema*) *rasoherinae*, CASENT0070841]; **10**: occipital carinae sharp and distinct [*C.* (*Orthocrema*) *smithi*, CASENT0193697]; **11**: propodeal spiracle circular or subcircular [*C.* (*Orthocrema*) *smithi*, CASENT0193697].



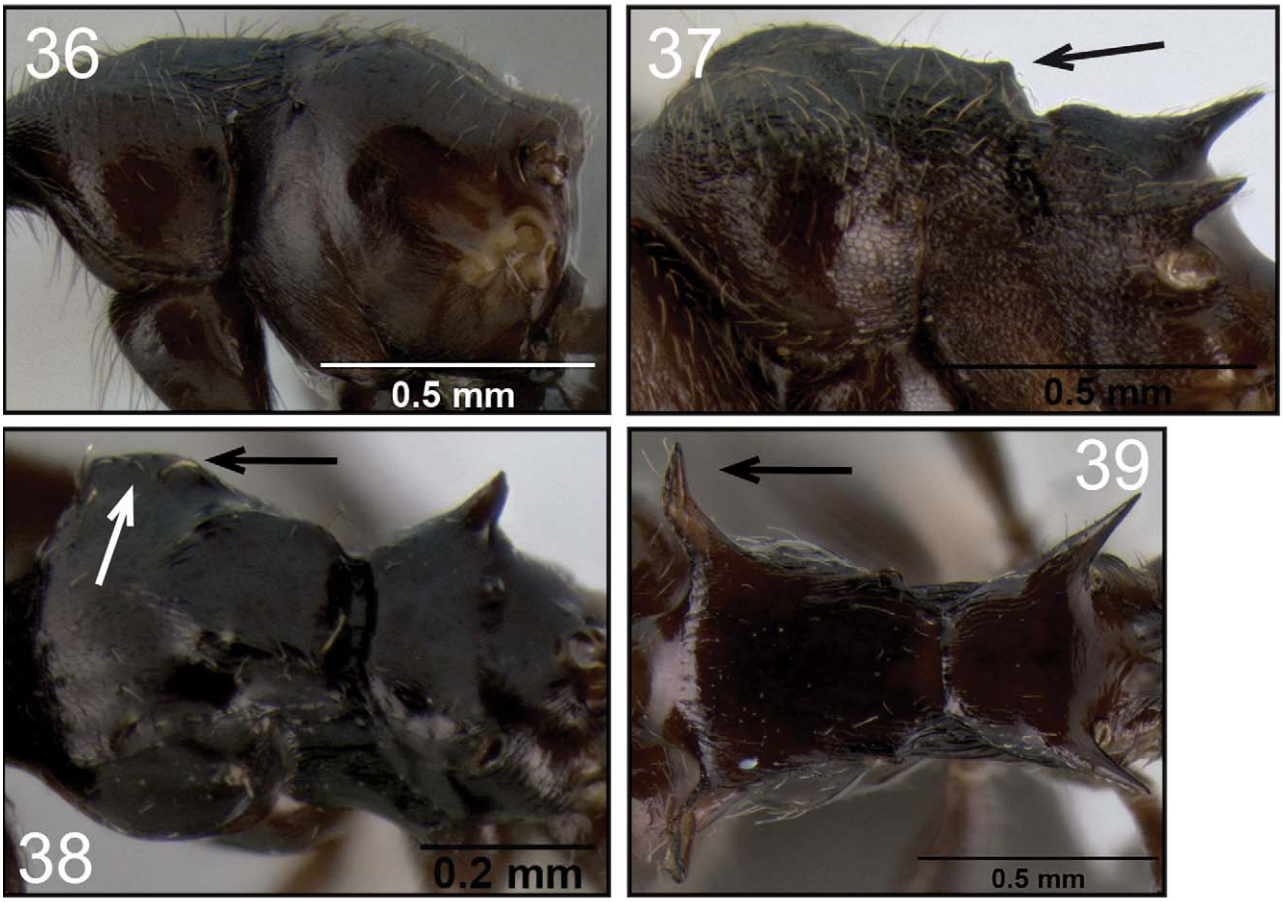
FIGURES 12–19. 12: posterior head margin rounded [*Crematogaster* (*Orthocrema*) *rasoherinae*, CASENT0193412]; **13**: posterior head margin with subangular corners [*C.* (*Orthocrema*) *volamena*, CASENT0012744]; **14a:** petiole moderately flared, **b**: postpetiole weakly bilobed (dorsal view) [*C.* (*Crematogaster*) *pilosa*, CASENT0193165]; **15a**: petiole broadly flared, **b**: postpetiole weakly bilobed (dorsal view) [*C.* (*Crematogaster*) *lobata*, CASENT0193045]; **16a**: petiole sharply flared, **b**: postpetiole distintly bilobed with broad median impression (dorsal view) [*C. (Crematogaster*) *flava*, CASENT0193691]; **17a**: petiole greatly flared, **b**: postpetiole distintly bilobed (dorsal view) [*C.* (*Crematogaster*) *dahlii*, CASENT0193602]; **18a**: petiole oval, **b**: postpetiole weakly bilobed and with faint median impression (dorsal view) [*C.* (*Crematogaster*) *cf. mjobergi*, CASENT0193799]; **19a**: petiole suboval, **b**: postpetiole distintly bilobed (dorsal view) [*C.* (*Crematogaster*) *ranavalonae*, CASENT0193425].



FIGURES 20–27. 20: petiole elongate rectangular (dorsal view) [*Crematogaster* (*Crematogaster*) *irritabilis*, CASENT0193598]; **21**: petiole circular (dorsal view) [*C.* (*Crematogaster*) *subcircularis*, CASENT0193915]; **22a**: petiole hexagonal, **b**: postpetiole distintly bilobed (dorsal view) [*C.*_ss_AUS3, CASENT0193798]; **23**: postpetiole with a thin median impression [*C.* (*Crematogaster*) *irritabilis*, CASENT0193598]; **24**: postpetiole lacking median impression (dorsal view) [*C.* (*Crematogaster*) *treubi*, CASENT0193783]; **25**: postpetiole with faint median impression (dorsal view) [*C.* (*Crematogaster*) *onusta*, CASENT0193714]; **26**: propodeal spiracle compressed oval [*C.*_ss11 (=bbb43), CASENT0193399]; **27**: occipital carinae reduced [*C.* (*Crematogaster*) *cf. buchneri*, CASENT0193750].



FIGURES 28–35. 28: posterior head margin straight (*Crematogaster* (*Crematogaster*) ss07 [=bbb38], CASENT0141219); **29**: posterior head margin medially depressed (*C.* (*Crematogaster*) *madagascariensis*, CASENT0127516); **30**: pronotum with tuberculate lateral margins [*C.* (*Crematogaster*) *cf. luctans*, CASENT0193747]; **31**: mesonotum postero-laterally denticulate [*C.* (*Crematogaster*) *cf. luctans*, CASENT0193747]; **32a**: mesonotum postero-laterally angulate, **b**: mesonotum with distinct dorsal face [*C.* (*Crematogaster*) *madagascariensis*, CASENT0193580]; **33a**: pronotum with acute margins, **b**: mesonotum convex and postero-laterally margined [*C.* (*Crematogaster*) *flava*, CASENT0193691]; **34**: pronotum laterally rounded [*C.* (*Crematogaster*) *irritabilis*, CASENT0193598]; **35**: mesonotum in lateral view rounded and without distinct posterior face [*C.* (*Crematogaster*) *irritabilis*, CASENT0193598].



FIGURES 36–39. 36: propodeum greatly inflated [*Crematogaster* (*Crematogaster*) *onusta*, CASENT0193714]; **37**: mesonotum with postero-lateral denticles [*C.* (*Crematogaster*) *subcircularis*, CASENT0193915]; **38**: pronotum antero-laterally with distinct sharp margins [*C.* (*Crematogaster*) *weberi*, CASENT0193599]; **39**: pronotum antero-laterally with spinose protuberances [*C.* (*Crematogaster*) *dahlii*, CASENT0193602].

Discussion

A subgeneric revision of *Crematogaster* based on phylogenetic relationships was long overdue, and is based here on a framework phylogeny that has been established in a concurrent, complementary molecular and biogeographic study of these ants (Blaimer, in press). The new two-subgenera system as proposed follows a deep molecular divergence event between *Orthocrema* and *Crematogaster* sensu stricto, tracing back into the Mid-Eocene (ca. 40–45 Mya) when these two clades last shared a common ancestor (Blaimer, in press). Recognizing these two groups from each other on a morphological basis is fairly easily achieved, although a diagnosis of the *Crematogaster* sensu stricto is more problematic given the high morphological variability. An obvious further improvement to the system presented here would have been the recognition of the global *Crematogaster* clade and the Australo-Asian *Crematogaster* clade as separate subgeneric entities, as they certainly show enough molecular divergence to justify a three-subgenera-approach. I refrained from such a formal distinction since it was not possible to assign species to these groups on a morphological basis. I primarily aimed to develop a practical, 'user-friendly' classification. Petiole and postpetiolar characters that are useful for the distinction of *Crematogaster* sensu stricto and *Orthocrema* become hypervariable within the two sensu stricto clades and are not informative at deeper phylogenetic levels. Similar character patterns, such as for example the presence/absence of a median longitudinal impression on the postpetiole appear to have evolved multiple times within the genus, but the selective pressures acting on morphological evolution in *Crematogaster* have yet to be revealed. More biological data will need to be collected to investigate these questions.

Although I chose not to give the two clades within the *Crematogaster* sensu stricto a formal subgenus rank, I nonetheless like to encourage the use of the terms “global clade” and “Australo-Asian clade” for these lineages. With more molecular data becoming available over time, we will eventually know the affinities of all species with one or the other clade (assuming that no species are discovered that lie outside these clades). At that point, morphological characters to diagnose and distinguish members of these clades from each other could possibly be revealed.

The proposed species-groups are intended as a guideline on how to structure the large *Crematogaster* sensu stricto clade more finely, given the phylogenetic framework. I did not attempt to assign every species sampled within the phylogeny (or otherwise known to me) to a species-group. Many more natural groups will only become apparent when the phylogeny of the genus is extended and should thus be established sequentially as data become available. For very similar reasons, I have not yet proposed species-groups for *Orthocrema*. The molecular sampling for *Orthocrema* in Blaimer (in press) is too sparse to make predictions on species-groups, as is obvious from the overall long phylogenetic branches that separate species in this clade from each other (Fig. 2). Finally, I conclude that the main advantage of recognizing monophyletic species-groups as suggested here is, that these present manageable subunits for taxonomic revisions. In addition, these species-groups will pose excellent subjects for (needed) comparative ecological and behavioural studies within *Crematogaster.*

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