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A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*

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Abstract

The classification of the ant subfamily Formicinae is revised to reflect findings from a recent molecular phylogenetic study and complementary morphological investigations. The existing classification is maintained as far as possible, but some tribes and genera are redefined to ensure monophyly. Eleven tribes are recognized, all of which are strongly supported as monophyletic groups: Camponotini, Formicini, Gesomyrmecini, Gigantiopini, Lasiini (= Prenolepidii **syn. n.**), Melophorini (= Myrmecorhynchini **syn. n.**; = Notostigmatini **syn. n.**), Myrmelachistini **stat. rev.** (= Brachymyrmicini **syn. n.**), Myrmoteratini, Oecophyllini, Plagiolepidini, and Santschiellini **stat. rev.** Most of the tribes remain similar in content, but the generic composition of Lasiini, Melophorini, and Plagiolepidini is changed substantially. Species that have been placed in the genus *Camponotus* belong to three separate lineages. To ensure monophyly of this large, cosmopolitan genus we institute the following changes: *Colobopsis* and *Dinomyrmex*, both former subgenera of *Camponotus*, are elevated to genus level (**stat. rev.**), and two former genera, *Forelophilus* and *Phasmomyrmex*, are demoted to subgenus status (**stat. n.** and **stat. rev.**, respectively) under *Camponotus*; two erstwhile subgenera of *Phasmomyrmex*, *Myrmorhachis* and *Myrmacantha*, become junior synonyms (**syn. n.**) of *Camponotus* (*Phasmomyrmex*); and the *Camponotus* subgenus *Myrmogonia* becomes a junior synonym (**syn. n.**) of *Colobopsis*. *Dinomyrmex*, represented by a single species from southeast Asia, *D. gigas*, is quite distinctive, but *Camponotus* and *Colobopsis* exhibit more subtle differences, despite being well separated phylogenetically. We identify morphological features of the worker caste that are broadly useful for distinguishing these two genera. *Colobopsis* species on the islands of New Caledonia and Fiji—regions with few native *Camponotus* species—tend to exceed these diagnostic bounds, but in this case regionally applicable character differences can be used to distinguish the two clades. Despite confusing similarities in the worker caste *Colobopsis* and *Camponotus* retain diagnostic differences in their larvae and pupae.

Key words: ant taxonomy, phylogenomics, morphology, convergence, divergence, *Camponotus*

Introduction

The ant subfamily Formicinae is a large and successful group, comprising about 3030 described species, distributed globally across a wide range of terrestrial environments (Brown 2000; Bolton 2003; AntCat 2015). The subfamily includes such well-known taxa as wood ants and their relatives (*Formica*), carpenter ants (*Camponotus*), weaver ants (*Oecophylla*), and honeypot ants (*Myrmecocystus*), and a diverse array of about fifty other genera. The females (workers and gynes) of this subfamily are readily distinguished from all other ants by the presence of an acidopore, a nozzle-shaped structure at the apex of the seventh abdominal sternum used to spray formic acid (Bolton 1994). Formicine workers have a flexible promesonotal suture (secondarily immobile in a few taxa), closed metacoxal cavities, single petiolar node, complete tergosternal fusion of the petiole (second abdominal segment), and no functional sting; abdominal segments 4–6 are very large relative to the sternites, which they overlap laterally and usually also ventrally (Bolton 2003). A diagnosis of Formicinae males is provided by Boudinot (2015).

Early attempts at a higher classification of Formicinae (e.g., Forel 1912; Emery 1925) were based largely on the features of the proventriculus, an internal organ regulating movement of liquids from the crop to the midgut (Eisner 1957). A more synthetic approach, involving a larger suite of morphological characters, was initiated by Agosti (1991) and further developed and expanded by Bolton (2003), who recognized nine tribes and two informal tribe groups: the lasiine tribe group (with Lasiini, Myrmoteratini and Plagiolepidini) and the formicine tribe group (with Camponotini, Formicini, Gigantiopini, Melophorini, Notostigmatini and Oecophyllini). Two tribes, Gesomyrmecini and Myrmecorhynchini, were unplaced to tribe group. This classification has been accepted to the present day, with 51 extant genera being distributed among these eleven tribes (AntCat 2015).

The first molecular phylogenetic analysis of Formicinae, based on two mitochondrial genes (Johnson *et al.* 2003), yielded results that were mostly concordant with the Bolton (2003) classification, but taxon and gene sampling was quite limited. Later studies based on multiple nuclear genes and more extensive taxon sampling (Brady *et al.* 2006; Moreau *et al.* 2006; Moreau & Bell 2013) indicated that some of the recognized formicine taxa, such as the genus *Camponotus* and tribes Lasiini and Plagiolepidini, are not monophyletic. A recent study of Formicinae, employing a phylogenomic data set of almost 1000 genes and a broad sampling of taxa, has given a much more comprehensive and robust picture of the evolution of this group (Blaimer *et al.* 2015). We propose a revised classification of the subfamily based on the results of this study and on complementary morphological investigations of the tribe Camponotini.

Material and methods

Taxon sampling, gene sampling, and methods of phylogenetic analysis are detailed in Blaimer *et al.* (2015). For the phylogenomic study we sequenced 959 UCE (ultraconserved element) loci in 82 formicines, representing 48 of 51 currently recognized genera, and in eight outgroup taxa. For the same set of taxa we also generated a more "traditional" dataset of 10 nuclear genes, by Sanger sequencing. Bayesian and maximum likelihood (ML) analyses were carried out on both datasets, yielding similar results but with notably better resolution and stronger node support in the phylogenomic tree, which we use as the reference phylogeny.

Morphological analysis focused on the tribe Camponotini, in which we introduce several genus-level changes. We examined specimens of approximately 85 species of *Camponotus* (*Colobopsis*) and about 200 species of *Camponotus* sensu stricto, in an effort to discern diagnostic differences between the two lineages. Most specimens were examined directly but we also took advantage of images, especially on AntWeb (www.antweb.org), to scrutinize taxa for which direct examination was not possible.

The following metric measurements and indices were employed:

HW	Head width: maximum width of head, excluding the eyes.
HL	Head length: midline length of head from the posterior margin to a line across the anterior clypeal margin (medial indentations on either margin do not decrease length).
EL	Eye length: length of eye measured in a full-face view of the head.
ASM	Minimum distance between the antennal sclerites (inter-torular distance).
CLW	Clypeus width: width of clypeus, taken at the anterior tentorial pits.
CLL	Clypeus length: maximum measurable length of clypeus, taken along the midline, from a line drawn across posterior margin to a line across the anterior margin (medial indentations on either margin do not decrease length).
CI	Cephalic index: HW/HL
REL	Relative eye length: EL/HL

The first three measurements were taken in a full-face (dorsal) view of the head, with the posterior margin of the head and the anterior clypeal margin in the same focal plane. The last three measurements (ASM, CLW, CLL) were taken in an anterodorsal view of the head, such that the measurement of clypeus length was maximized.

Voucher specimens from molecular and morphological studies are deposited in UCDC (Bohart Museum of Entomology, University of California, Davis), CASC (California Academy of Sciences, San Francisco) and USNM (National Museum of Natural History, Washington, DC).

Results

Phylogeny. The new phylogeny of the Formicinae (Figure 1) reveals six strongly supported, species-rich clades, and five other species-poor, long-branched lineages whose positions in the tree are less certain. This pattern is obtained with both the 10-gene and 959-gene data sets, but the latter provides greater resolution across the tree and stronger branch support (Blaimer *et al.* 2015). Of the six well-supported clades, Myrmelachistini is sister to all other Formicinae, and Lasiini is consistently recovered as sister to the remaining taxa. The phylogenomic data support Melophorini as the next branch in this series, but the relationships among the three remaining groups (Plagiolepidini, Formicini, and Camponotini) are less clear. Phylogenetic relationships within each of these six clades are quite well resolved, however, with most nodes having 100% bootstrap support.

The five taxonomically isolated lineages correspond to the genera *Gesomyrmex*, *Gigantiops*, *Myrmoteras*, *Oecophylla*, and *Santschiella*. The phylogenomic data do suggest partial resolution of their positions in the formicine tree, including placement of *Myrmoteras* as sister to Camponotini, and a sister-group relationship of *Oecophylla* and *Gesomyrmex* as well as *Gigantiops* and *Santschiella* (Figure 1). All of these taxa are situated on long branches, however, and the nodes where they join the tree are subtended by very short branches. Some of the putative sister group relationships might therefore be artifacts of long-branch attraction (Bergsten 2005), base frequency heterogeneity (Jermiin *et al.* 2004), or other confounding factors.

Revised tribal classification. The tribal classification of Formicinae is modified in accordance with these molecular phylogenetic results. The new classification was briefly outlined in Blaimer *et al.* (2015) and is here given a more formal treatment. We strive to maintain the existing classification as far as possible, while also ensuring that all recognized tribes are monophyletic. The major clades are treated as six tribes (Camponotini, Formicini, Lasiini, Melophorini, Myrmelachistini, Plagiolepidini) whose composition is discussed below. The five taxonomically isolated genera are each assigned to their own tribe; this is a cautionary approach, justified by the uncertainty of their relationships to one another, and to other Formicinae. The resulting schema comprises 11 tribes, with high confidence in the monophyly of each one. This provides a framework for future work on the morphological and social characteristics of each clade.

We cite the author and year of publication of each tribe name; equivalent information for genus names is available in AntCat (http://antcat.org/). Genera known only from fossils are signified with a dagger (†); most of these are unplaced to tribe and treated as *incertae sedis* within the subfamily.

Tribe Camponotini Forel 1878

= Polyrhachidini Ashmead 1905

Genera: *Calomyrmex*, *Camponotus*, †*Chimaeromyrma*, *Colobopsis*, *Dinomyrmex*, *Echinopla*, *Opisthopsis*, *Overbeckia*, *Polyrhachis*, †*Pseudocamponotus*.

Comments. The composition of this tribe remains unchanged, although some generic boundaries have been modified (see below). *Overbeckia*, not sequenced in this study, is likely a junior synonym of *Camponotus* (Bolton 2003). All members of this tribe have a unique, vertically inherited bacterial symbiont, *Blochmannia*, whose evolutionary history mirrors that of the ants (Wernegreen *et al.* 2009). Morphologically the workers of Camponotini can be recognized by the combination of distinctive mandibular dentition (5–8 teeth, with the third tooth from apex not reduced in size), antennal insertions well separated from the posterior clypeal margin, and twelve antennal segments (Bolton 1994, 2003).
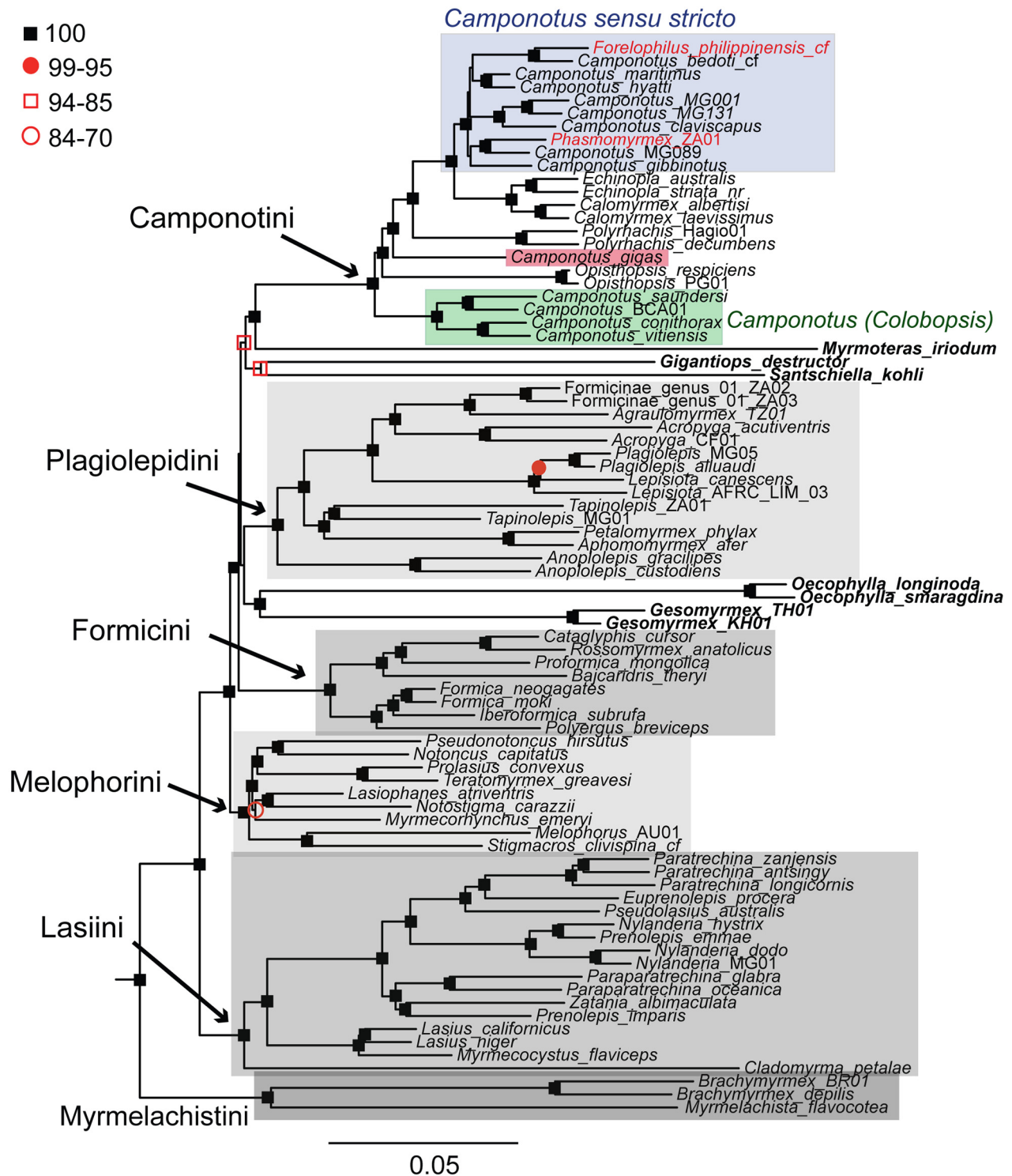
FIGURE 1. Phylogeny of the ant subfamily Formicinae based on 959 UCE (ultraconserved element) loci (Blaimer *et al.* 2015). Support values are maximum likelihood bootstrap percentages. The tree depicts six major clades, here treated as tribes, and five isolated genera subtended by long branches (*Gesomyrmex*, *Gigantiops*, *Myrmoteras*, *Oecophylla*, and *Santschiella*, in bold font). Note that species assigned to *Camponotus* occur as three separate lineages within the tribe Camponotini, and that *Phasmomyrmex* and *Forelophilus* are embedded within *Camponotus* (sensu stricto).

Tribe Formicini Latreille 1809

Genera: *Alloformica, Bajcaridris, Cataglyphis, †Cataglyphoides, †Conoformica, Formica, Iberoformica, Polyergus, Proformica, †Protoformica, Rossomyrmex.*

Comments. This is another distinctive group whose composition is unchanged. These ants are characterized by closely approximated metacoxae, elliptical to slit-shaped propodeal spiracle, presence of ocelli in workers, and a double row of stout setae on the metatibia (Bolton (2003). This clade is mostly confined to the Palearctic and Nearctic regions.

Tribe Gesomyrmecini Ashmead 1905

= Dimorphomyrmii Emery 1895
= Gesomyrmini Forel 1912
= †Sicelomyrmicini Wheeler 1929

Genera: *Gesomyrmex, †Prodimorphomyrmex, †Sicilomyrmex.*

Comments. The tribe Gesomyrmecini is here restricted to *Gesomyrmex* and two similar fossil taxa (Wheeler 1915). Bolton (2003) also placed *Santschiella* in Gesomyrmecini, but the molecular results do not support a close relationship between *Gesomyrmex* and *Santschiella* (Blaimer *et al.* 2015). The similarities between the two—very large eyes, widely separated antennal insertions, and scapes that pass below the eyes (Bolton 2003)—must be interpreted as due to convergence.

Tribe Gigantiopini Ashmead 1905

Genus: *Gigantiops.*

Comments. This remains a monotypic tribe, represented by a single taxonomically isolated species, *Gigantiops destructor*, restricted to northern South America. The molecular phylogeny recovers *Gigantiops* as sister to *Santschiella* (Figure 1), a monotypic African genus, but support for this relationship is not strong, so we retain a separate tribe for *Santschiella*. Although both genera share distinctively large eyes, they differ markedly in configuration of the frontoclypeal complex, with the antennal insertions of *Gigantiops* being located close to one another and between the eyes (Bolton 2003).

Tribe Lasiini Ashmead 1905

= Acanthomyopsini Donisthorpe 1943
= Prenolepidii Forel 1912 **syn. n.**

Genera: *Cladomyrma, Euprenolepis* (tribal transfer), *†Glaphyromyrmex, Lasius, Myrmecocystus, Nylanderia* (tribal transfer), *Paraparatrechina* (tribal transfer), *Paratrechina* (tribal transfer), *Prenolepis* (tribal transfer), *Pseudolasius* (tribal transfer), *Zatania* (tribal transfer).

Comments. Apart from retention of *Cladomyrma, Lasius* and *Myrmecocystus*, the composition of this tribe is greatly changed. It is now comprised of those three genera and a cluster of taxa known as the *Prenolepis* genus group. *Lasius* and *Myrmecocystus* are each other's closest relatives, and in turn they are the sister group of the *Prenolepis* genus group. The latter has been the subject of recent phylogenetic and taxonomic studies by LaPolla and colleagues (e.g., LaPolla *et al.* 2010, 2012).

Tribe Melophorini Forel 1912

= Myrmecorhynchini Wheeler 1917 **syn. n.**
= Notostigmatini Bolton 2003 **syn. n.**

Genera: *Lasiophanes* (tribal transfer), *Melophorus, Myrmecorhynchus* (tribal transfer), *Notoncus* (tribal transfer), *Notostigma* (tribal transfer), *Prolasius* (tribal transfer), *Pseudonotoncus* (tribal transfer), *Stigmacros* (tribal transfer), *Teratomyrmex* (tribal transfer).

Comments. This tribe formerly contained *Melophorus* only, but that genus is now known to be embedded within a larger, well-supported clade of ants (Figure 1), which is confined to southern South America, Australia, New Zealand, and New Guinea, and for which the oldest available tribal name is Melophorini. A satisfactory morphological circumscription of this group awaits further study.

Tribe Myrmelachistini Forel 1912 stat. rev.

= Brachymyrmicini Emery 1925 **syn. n.**

Genera: *Brachymyrmex* (tribal transfer), *Myrmelachista* (tribal transfer).

Comments. These two genera form a robustly supported clade that is sister to all other Formicinae (Figure 1). Shared worker characters include a reduced antennal count (9–10 segments), five mandibular teeth, petiole inclined anteriorly and/or with long posterior peduncle, and anterior tergosternal fusion of the third abdominal segment (Bolton 2003). Both genera have the plesiomorphic palp formula 6,4 but this has been reduced to five maxillary palp segments in some *Myrmelachista* species (Longino 2006).

Tribe Myrmoteratini Emery 1895

= Myrmoteratini Forel 1912

Genus: *Myrmoteras*.

Comments. This is another isolated genus, with numerous distinctive features including elongate, trap-jaw mandibles and very large eyes (Bolton 2003). It appears to be sister to the tribe Camponotini (Figure 1), but this requires confirmation.

Tribe Oecophyllini Emery 1895

= Oecophyllini Forel 1912

Genus: *Oecophylla*.

Comments. The placement of the genus *Oecophylla* (weaver ants) in the formicine phylogeny remains uncertain, and we continue to maintain tribal status for this taxonomically distinctive group. A sister group relationship with *Gesomyrmex* (Figure 1) is plausible and deserves further investigation.

Tribe Plagiolepidini Forel 1886

= Bregmatomyrminii Wheeler 1929

Genera: *Acropyga* (tribal transfer), *Agraulomyrmex*, *Anoplolepis* (tribal transfer), *Aphomomyrmex*, *Bregmatomyrma, Lepisiota*, *Petalomyrmex*, *Plagiolepis*, *Tapinolepis*.

Comments. A number of genera previously placed in Plagiolepidini, such as *Brachymyrmex*, *Myrmelachista*, *Nylanderia*, and *Prenolepis*, are here transferred elsewhere (to either Lasiini or Myrmelachistini), and the tribe is now comprised exclusively of Old World taxa, except for the cosmopolitan *Acropyga*. The placement of *Bregmatomyrma* has not been evaluated with sequence data, and its retention in Plagiolepidini remains provisional. A taxonomic revision of the plagiolepidine genera is overdue.

Tribe Santschiellini Forel 1917 stat. rev.

Genus: *Santschiella* (tribal transfer)

    Comments. We resurrect the tribe Santschiellini for this monotypic West African genus due to uncertainty about its position within the formicine tree (Blaimer *et al.* 2015). It appears to be the sister group of the Neotropical genus *Gigantiops* but there is only moderate support for this hypothesis. See previous discussion under Gesomyrmecini and Gigantiopini.

Unplaced to tribe

The following fossil genera cannot be placed with confidence in any of the 11 extant tribes and are here considered *incertae sedis* in Formicinae: †*Camponotites*, †*Curtipalpulus*, †*Drymomyrmex*, †*Eoleptocerites*, †*Eurytarsites*, †*Fushuniformica*, †*Heeridris*, †*Huaxiaformica*, †*Imhoffia*, †*Kyromyrma*, †*Leptogasteritus*, †*Leucotaphus*, †*Liaoformica*, †*Longiformica*, †*Magnogasterites*, †*Orbicapitia*, †*Ovalicapito*, †*Ovaligastrula*, †*Protrechina*, †*Sinoformica*, †*Sinotenuicapito*, †*Wilsonia*.

Genus-level changes in the tribe Camponotini

The new phylogeny has important implications for the classification of Camponotini. *Camponotus* itself is non-monophyletic, appearing as three separate lineages: *Camponotus* sensu stricto, *Camponotus gigas*, and *Camponotus* (*Colobopsis*). *C.* (*Colobopsis*) is sister to all other members of the tribe, and is well separated from true *Camponotus*. The latter remains technically non-monophyletic, however, because two taxa, *Forelophilus* and *Phasmomyrmex*, are found to be nested within it (Figure 1).

    The following changes are made to ensure monophyly of each recognized genus in Camponotini. New and revived combinations implicitly include the junior synonyms of the species names transferred below. Author and year of publication for species names can be found in AntCat (http://antcat.org/).

***Camponotus* Mayr 1861**

Type species: *Formica ligniperda*, designated by Bingham (1903: 347).
For generic synonymy see Bolton (2003) and AntCat (2015).

As a result of new phylogenetic findings we institute the following genus-level changes to *Camponotus*.

1   *Forelophilus* Kutter (type species *Forelophilus overbecki*, by monotypy) is demoted to subgenus (**stat. n.**) under *Camponotus*, creating the following **new combinations** in *Camponotus*: *overbecki*, *philippinensis*, *stefanschoedli*. One of these new combinations, *C. overbecki* (Kutter), becomes a secondary junior homonym, here replaced with *C. javaensis* (**nom. n.**).

2   *Phasmomyrmex* Stitz (type species *Phasmomyrmex sericeus* (=*P. buchneri*), by monotypy) is demoted to subgenus (**stat. rev.**) under *Camponotus*, creating the following **revived combinations** (unless noted as new) in *Camponotus*: *aberrans*, *buchneri*, *buchneri griseus* (**comb. n.**)*, paradoxus* (**comb. n.**)*, paradoxus cupreus* (**comb. n.**)*, wolfi*. One of these new combinations, *C. buchneri griseus* (Santschi), becomes a secondary junior homonym, here replaced with *C. buchneri camerounensis* (**nom. n.**). The two erstwhile subgenera of *Phasmomyrmex*, *Myrmorhachis* Forel and *Myrmacantha* Emery, are here treated as junior synonyms (**syn. n.**) of *Camponotus* (*Phasmomyrmex*).

3   The subgenera *Colobopsis* Mayr and *Dinomyrmex* Ashmead are removed from *Camponotus*, and treated as separate genera (see below). The *Camponotus* subgenus *Myrmogonia* Forel becomes a junior synonym of *Colobopsis*.

    With these changes *Camponotus* now comprises 45 valid subgenera (including the nominate subgenus), with three losses (*Colobopsis, Dinomyrmex, Myrmogonia*; see below) and two gains (*Forelophilus, Phasmomyrmex*).

As others have commented (Bolton 1995), many of the *Camponotus* subgenera are poorly defined and undoubtedly represent artificial groupings (Brady *et al.* 2000; Clouse *et al.* 2015). Nevertheless, until a global revision of the genus is carried out, we prefer to retain the subgeneric classification—at least some of the groups are distinctive and evidently monophyletic, and thus serve to keep clusters of closely related species together.

Colobopsis Mayr 1861 stat. rev.

Type species: *Formica truncata*, designated by Bingham (1903: 342).
Myrmogonia Forel (as subgenus of *Camponotus*). Type species *Camponotus laminatus*, designated by Wheeler (1913: 81). **Syn. n.**
Dolophra Wu & Wang. Type species *Dolophra politae*, by original designation. Junior synonym of *Camponotus*: Bolton (1995: 27); of *Camponotus* (*Colobopsis*): Bolton (2003: 113).

Diagnosis, minor worker. Generally small, HW 0.65–1.10 (exceptions: *cylindrica* group and the Fijian radiation, where HW 0.90–1.70), with rounded head and relatively small eyes, REL 0.20–0.32; head width three-quarters of more of head length (CI 0.75–0.98; except one Fijian species, *C. polynesica*, where CI ~0.72); antennal insertions—and hence also the frontal carinae—relatively relatively well separated, ASM/HW 0.36–0.47 (except *cylindrica* group, New Caledonia radiation and the Fijian radiation, where ASM/HW 0.31–0.39), ASM/CLW usually 0.66–0.98 (except some New Caledonian and most Fijian species where ASM/CLW is in the range of 0.60–0.66); frontal carinae relatively short, usually not strongly sinuate, the antennal insertions occurring at about midlength of the frontal carinae; clypeus more or less subquadrate, as long as wide or slightly wider than long (CLW/CLL 0.96–1.32), with sides parallel or diverging moderately towards the anterior margin (clypeus broader in Fijian species of the *bryani* and *dentata* groups where CLW/CLL ~ 1.46, and in the *conica* and *vitrea* groups, sensu Emery (1925), where CLW/CLL 1.40–1.50 and clypeus more trapezoidal in form); anterolateral extremities of clypeus differentiated from rest of clypeus by a sulcus or impression running from the anterior tentorial pit to the clypeal margin, the suture between clypeus and malar region of head often weak here, so that the clypeus appears to lack the anterolateral extensions often conspicuous in *Camponotus* minors (compare Figures 2–5 with Figure 15).

Diagnosis, major worker. Head generally phragmotic, varying from strongly truncate and marginate (Figure 6) to weakly truncate (Figure 7), the truncated portion incorporating part of the clypeus, the malar region of the head capsule and the upper surface of the mandibles. Clypeus elongate-rectangular, the anterolateral extremities separated from the clypeus by a well-marked sulcus and appearing to form an independent triangular sclerite.

Additional diagnostic features. Dimorphic worker caste, with few or no intermediates between major and minor workers, except in the *cylindrica* group (Emery 1925); larva with distinctive ventral trough (praesaepium), overhung posteriorly by a protruding welt of the second abdominal segment (Wheeler & Wheeler 1953, 1982); pupa naked (Wheeler 1904). Brendon Boudinot has recently found that male *Colobopsis* have distinctive genitalia, with the shape of the digitus distinguishing them from *Camponotus* males (Boudinot, in prep.).

The elevation of *Colobopsis* to the rank of genus generates the following **new combinations** (unless noted as revived) in *Colobopsis*: *abdita, anderseni, annetteae, aruensis, aurata, aureliana, badia* (unresolved junior primary homonym), *badia saginata, brachycephala, †brodiei, bryani, calva, camela, cerberula, ceylonica, clerodendri, conica* (**comb. rev.**), *conithorax, corallina* (**comb. rev.**), *cotesii, cristata, culmicola, culmicola haweisi, custodula, cylindrica* (**comb. rev.**), *dentata* (**comb. rev.**), *desecta* (**comb. rev.**), *elysii, equa, etiolata, excavata, fijiana, flavolimbata, gasseri* (**comb. rev.**), *gundlachi, guppyi, horrens, horripila, hosei, hosei mima, howensis, hunteri, impressa* (**comb. rev.**), *kadi, karawaiewi, laminata, laotsei, lauensis, leonardi, leonardi gracilenta, leonardi grisea, levuana, loa, loa belli, longi, maafui, macarangae, macrocephala, manni, markli, mathildeae, mississippiensis, mutilata, mutilata stitzi, newzealandica, nigrifrons* (**comb. rev.**), *nipponica, obliqua, oceanica, papago, perneser, phragmaticola, politae, polynesica, pylartes, pylartes fraxinicola, pylora, quadriceps, quadriceps convexior, quadriceps curvata, quadriceps nanula, reepeni, riehlii* (**comb. rev.**), *rothneyi, rothneyi krafti, rothneyi makilingi, rothneyi taivanae, rotunda, rufifrons* (**comb. rev.**), *rufifrons leucopa, sadina, sanguinifrons, saundersi, saundersi krama, schmeltzi, schmitzi, severini, shohki, smithiana, solenobia, sommeri* (**comb. rev.**), *stricta* (**comb. rev.**), *trajana, tricolor* (**comb. rev.**), *triton, truncata* (**comb. rev.**), *umbratilis, vitiensis, vitrea, vitrea angustula, vitrea carinata, vitrea latinota* (unresolved junior primary homonym), *vitrea oebalis, vitrea praelutea, vitrea praerufa, vitrea vittatula*, and *wildae*.

Comments. As now conceived the genus *Colobopsis* comprises 94 valid species (93 extant, 1 fossil) and 23 subspecies. Based on original descriptions and images, *Camponotus bifossus* and *Camponotus tritschleri*, nominally *Colobopsis*, are retained in *Camponotus*, subgenus indeterminate; and *Camponotus cordincola* is retained in *Camponotus*, and transferred to subgenus *Pseudocolobopsis*. The eight Fijian species in the subgenus *Myrmogonia* (Sarnat & Economo 2012) are transferred to *Colobopsis*, based on both genetic (e.g., Clouse *et al.* 2015) and morphological evidence. Three Australian species, *armstrongi*, *cameratus*, and *macareaveyi*, previously assigned to subgenus *Myrmogonia*, are retained in *Camponotus*, subgenus indeterminate. McArthur's (2012) treatment of *Colobopsis*, which involved numerous ad hoc and poorly justified transfers of species from other *Camponotus* subgenera into *Camponotus* (*Colobopsis*), is here ignored.

Biology. Most species of *Colobopsis* are strictly arboreal, nesting in cavities in dead branches or twigs and employing phragmotic major workers to block the nest entrance (Forel 1892; Wheeler 1904; Creighton 1967). In some Fijian species, with reduced phragmosis, nests can also be found in rotten wood and in epiphytic ant-plants (Sarnat & Economo 2012). Phragmosis is also reduced in some Southeast Asian species nesting in live stems; at least one species, *Colobopsis macarangae*, apparently lacks a major worker subcaste (Dumpert 1996). In the field, collections of *Colobopsis* can be readily distinguished from those of *Camponotus* if pupae are available: these are always naked in *Colobopsis* (Wheeler 1904; Ward, pers. obs.), while those of *Camponotus* are enclosed in cocoons.

Distribution. *Colobopsis* occurs in the New World from southern United States to Costa Rica; across the southern and central Palearctic from the western Mediterranean to Japan; throughout the Oriental and Australian biogeographic regions as far south as Tasmania; and into the Pacific as far east as New Caledonia, Vanuatu, and Fiji. The genus is notably absent from the Afrotropics and most of the Neotropics.

Distinguishing *Colobopsis* from *Camponotus*. Despite their phylogenetic distance, morphological distinctions between *Colobopsis* and *Camponotus* have been obscured by extensive evolution within each group, including convergent evolution of phragmotic heads in the major workers of some *Camponotus*, and variable development of phragmosis in *Colobopsis* (Figures 5–6). Some recent taxonomic treatments have confused the two lineages. For example, of the 11 species assigned by McArthur & Shattuck (2001) to the "*Camponotus macrocephalus* group" eight are *Colobopsis* (*anderseni*, *annetteae*, *conithorax*, *gasseri*, *howensis*, *macrocephala*, *sanguinifrons, vitrea*) and three are *Camponotus* (*janeti*, *janforrestae*, *mackayensis*). Similarly, of the four newly described species of phragmotic "*Camponotus*" from New Guinea in Klimes & McArthur (2014), one is *Colobopsis* (*rotunda*), while the other three are *Camponotus*.

To reduce future confusion we provide a key for separating minor workers of *Colobopsis* from those of *Camponotus*. It is helpful to segregate the New Caledonian and Fijian species, since *Colobopsis* tends to "break the rules" in these island situations (Figures 8–13).

1 Not occurring in Fiji or New Caledonia 2
- Occurring in Fiji 3
- Occurring New Caledonia 4
2 Generally small species, HW 0.65–1.10 (except *cylindrica*-group of Southeast Asia with HW 1.20–1.70, and facies as in Figures 4 and 5); either antennal insertions relatively well separated, such that ASM/HW 0.36–0.47 and ASM/CLW 0.66–0.98, *and/or* clypeus relatively narrow, such that CLW/CLL 0.96–1.32; antennal insertions occurring at about midlength of frontal carinae; anterolateral extremities of clypeus set off from rest of clypeus by a sulcus or impression, so clypeus appears to lack prominent anterolateral extensions (Figures 2–5) . . . . *Colobopsis*
- Small to large species, HW 0.70–3.00; antennal insertions less well separated, such that ASM/HW 0.22–0.35 and ASM/CLW 0.35–0.68; clypeus variable in shape but in smaller species with HW 0.70–1.35 (e.g., *Camponotus* (*Myrmamblys*), *C.* (*Myrmentoma*) and *C.* (*Pseudocolobopsis*)) clypeus tending to be relatively broad, such that CLW/CLL 1.25–1.62, although exceptions occur (e.g., in some *C.* (*Pseudocolobopsis*) species) (Figures 14–15); antennal insertions usually occurring in front of midlength of frontal carinae; clypeus typically with prominent anterolateral extensions (Figure 15) . . . . *Camponotus*
3 With conspicuous long setae, gracile legs, and a shield-shaped clypeus with prominent anterolateral extensions (Figure 16). . . . . *Camponotus chloroticus*
- Without the combination of conspicuous long setae and gracile legs; clypeus lacking prominent anterolateral extensions (Figures 8–11) . . . . *Colobopsis*
4 Small species, HW 0.68–1.04; antennal insertions more widely separated (ASM/HW 0.34–0.39 and ASM/CLW 0.64–0.77) (Figures 18–19); clypeus tending to be less broad (CLW/CLL 1.15–1.40) . . . . *Colobopsis*
- Small to medium-sized species, HW 0.75–2.10; antennal insertions less well separated (ASM/HW 0.25–0.29 and ASM/CLW 0.46–0.55); clypeus varying in shape, but if HW < 1.05 (e.g., *Camponotus pulchellus* complex) (Figure 17) then clypeus tending to be broader (CLW/CLL 1.25–1.60) . . . . *Camponotus*
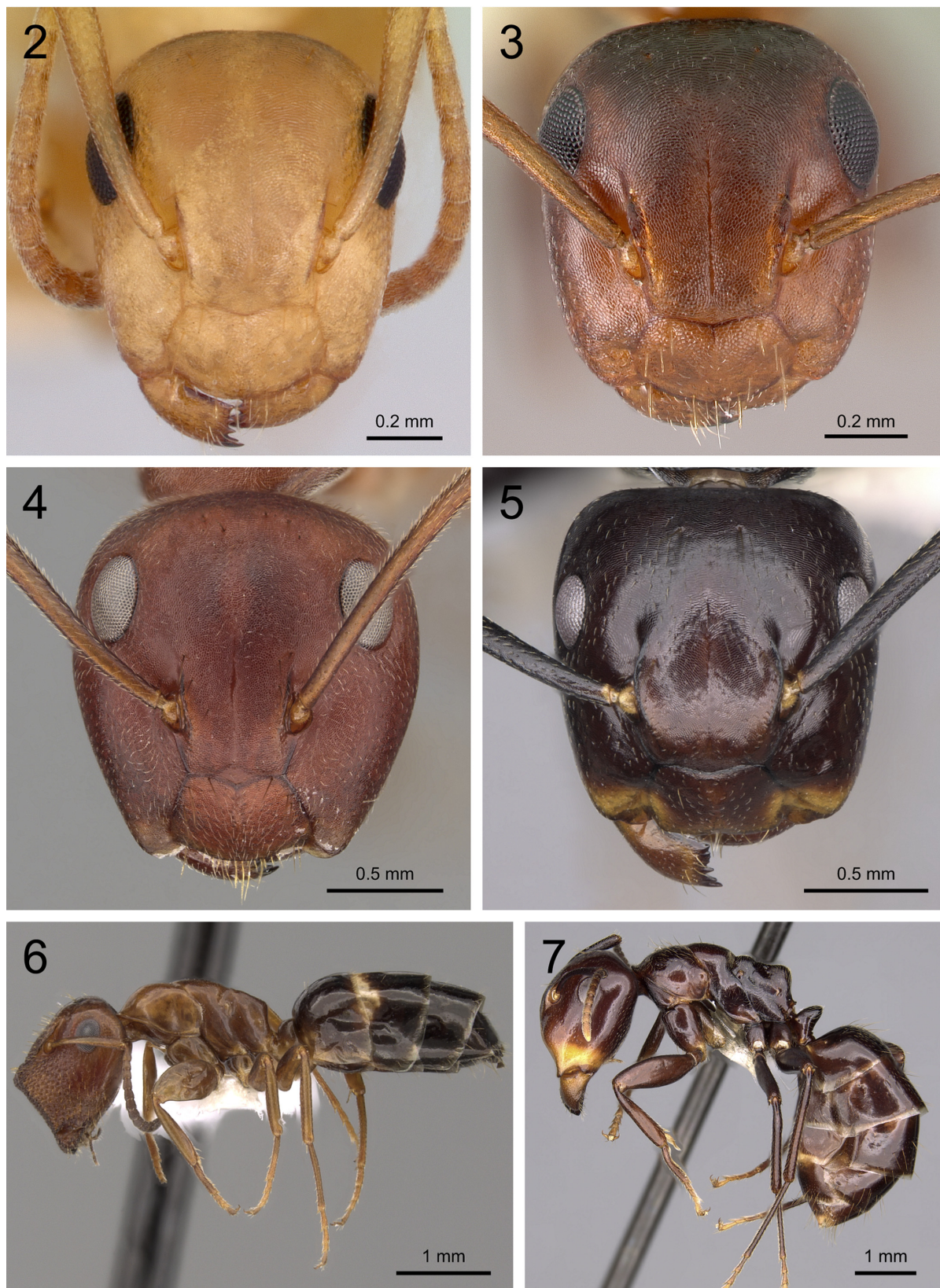
FIGURES 2–7. Selected species of *Colobopsis*, full-face view of head of minor worker (Figs. 2–5) and lateral view of soldier (Figs. 6–7). 2, *Colobopsis etiolata*, Texas, USA (CASENT0104949); 3, *C. truncata*, Bulgaria (CASENT0179881); 4. *C. cylindrica* group, Brunei (CASENT0280269); 5, *C. quadriceps*, Papua New Guinea (CASENT0280264); 6, *C. truncata*, Italy (CASENT0249998); 7, *C. quadriceps*, Papua New Guinea (CASENT0280263). Images from AntWeb (www.antweb.org); photographers Aprile Nobile (2), Erin Prado (3), Estella Ortega (4, 5, 7) and Ryan Perry (6).
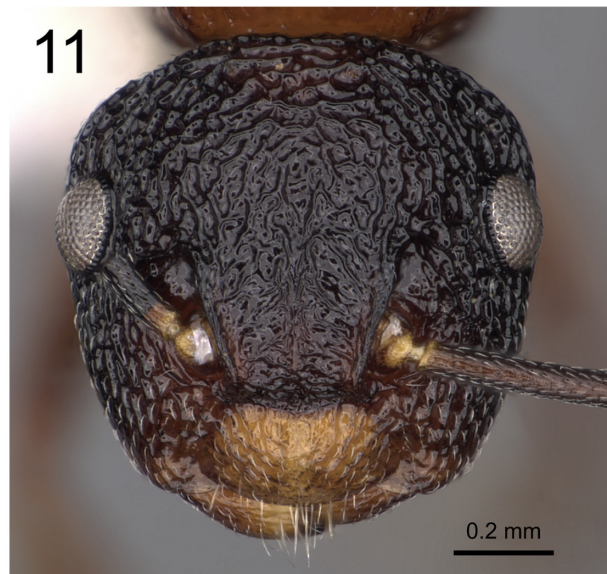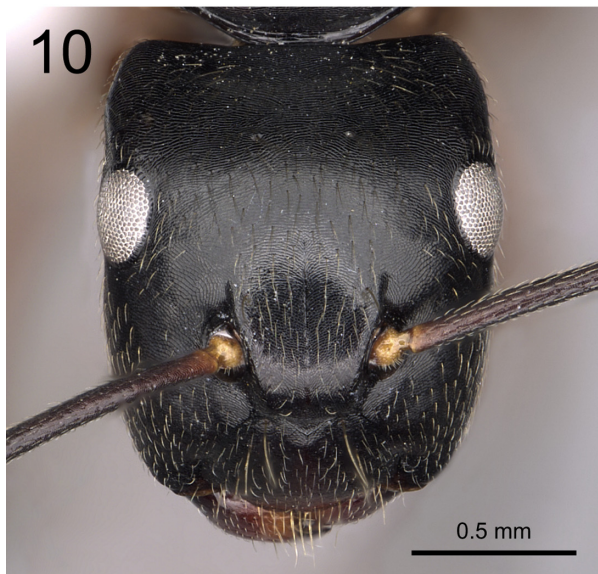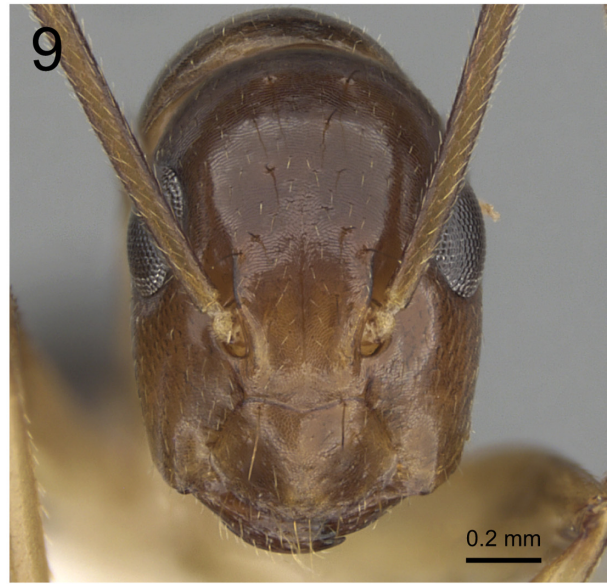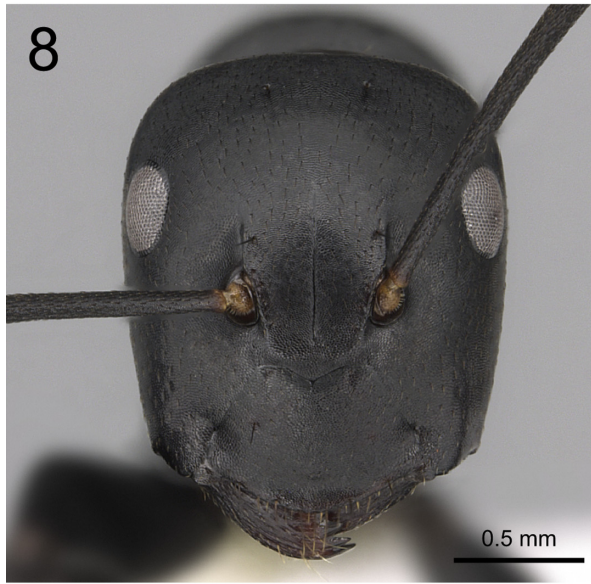
FIGURES 8–13. Species of *Colobopsis* from Fiji. Full-face view of head of minor worker (Figs. 8–11) and lateral view of minor worker (Figs. 12–13). 8, *Colobopsis vitiensis* (CASENT0280250); 9, *C. polynesica* (CASENT0280252); 10. *C. schmelzi* (CASENT0280259); 11, *C. bryani* (CASENT0280258); 12, *C. schmelzi* (CASENT0280259); 13, *C. bryani* (CASENT0280258). Images from AntWeb (www.antweb.org); photographers Shannon Hartman (8–9) and Estella Ortega (10–13).
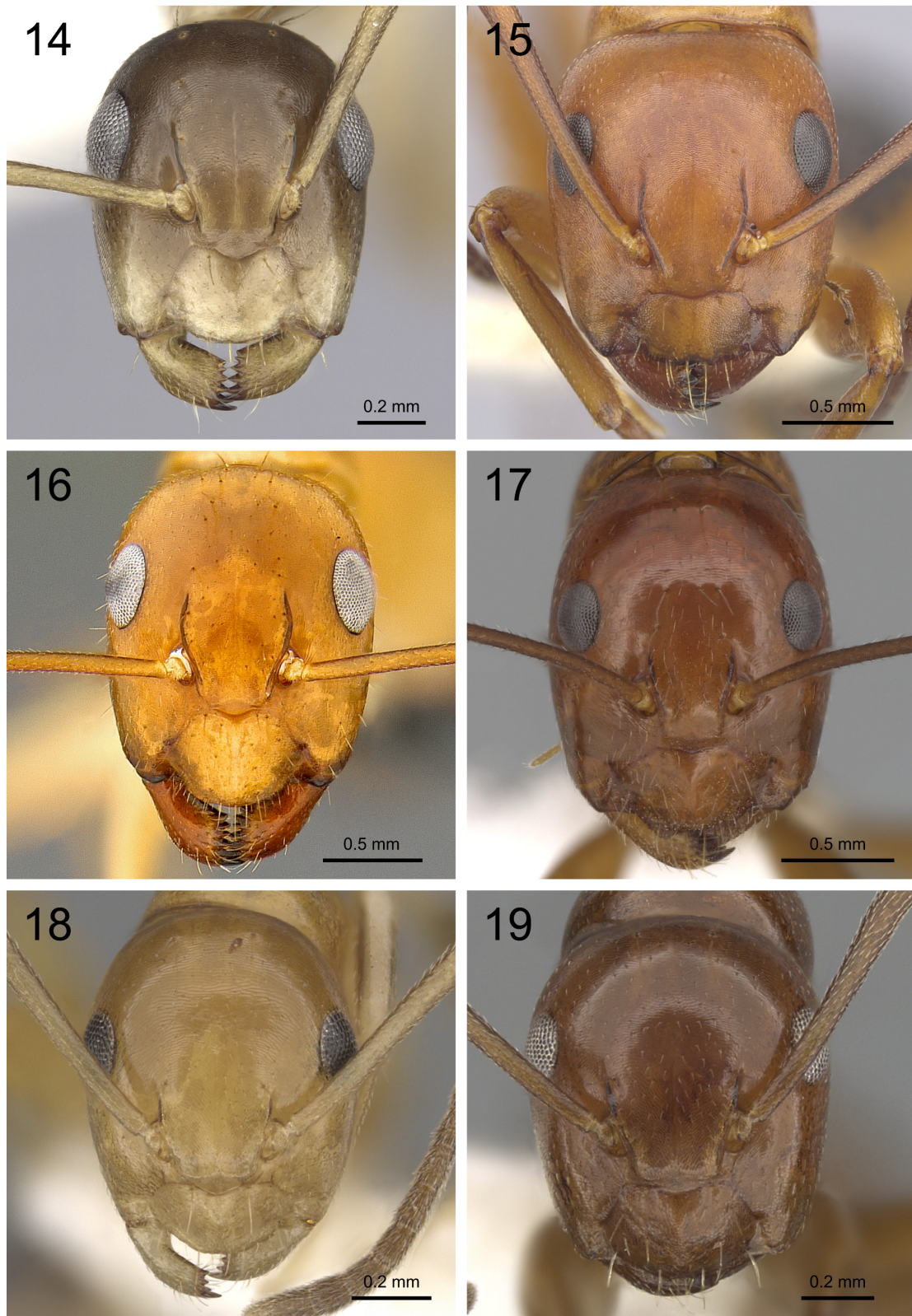
FIGURES 14–19. Selected species of *Camponotus* (Figs. 14–17) and New Caledonia *Colobopsis* (Figs. 18–19), full-face view of head of minor worker. 14, *Camponotus* (*Pseudocolobopsis*) *claviscapus*, Costa Rica (CASENT0249388); 15, *C.* (*Myrmentoma*) *decipiens*, Texas, USA (CASENT0249367); 16. *C.* (*Tanaemyrmex*) *chloroticus*, Fiji (CASENT0171139); 17, *C.* (*Myrmamblys*) *pulchellus*_cf, New Caledonia (CASENT0280237); 18, *Colobopsis* indet. (CASENT0280248); 19, *Colobopsis camela* (CASENT0280242). Images from AntWeb (www.antweb.org); photographers Will Ericson (14–15), Eli Sarnat (16) and Shannon Hartman (17–19).

Dinomyrmex Ashmead 1905 stat. rev.

Type species: *Formica gigas*, by original designation.

Based on its phylogenetic position, as a lineage separate from both *Camponotus* and *Colobopsis*, and sister to all other camponotines except *Opisthopsis* and *Colobopsis*, *Dinomyrmex* is here resurrected as a genus. This generates the following **revived combinations**: *gigas*, *gigas borneensis*.

Dinomyrmex is a distinctive camponotine, confined to southeast Asia, and recognized by the combination of very large size (HW 3.25–5.35), elongate antennae and legs, and the presence of a metapleural gland. The species also has characteristic mandibular dentition, with teeth occurring on both the masticatory and basal margins of the mandible (Emery 1925).

Concluding remarks

This study continues a series of attempts to revise the higher classification of ants in accordance with new molecular phylogenetic information, with the goal of promoting a ranked phylogenetic classification (Ward *et al.* 2010, 2015; Brady *et al.* 2014; Schmidt & Shattuck 2014), just as systematists are doing for other groups such as flowering plants (Stephens 2015). Establishing higher taxa that are monophyletic, diagnosable, and—for any given rank—mutually exclusive can be challenging in the face of variable evolutionary rates and extensive convergence (Ward 2011), but such classifications are likely to be more stable and informative over the long term than non-phylogenetic alternatives.

It is important, however, to avoid the trap of essentialist thinking (Hillis 2006). The features that evolved along a particular branch of the tree of life—the synapomorphies of the clade that succeeds that branch—are not always easily discovered, nor immutable. Such features may undergo further evolution to the point where they are no longer recognizable. Thus the higher taxa that we decide to name (as genera, tribes, etc.) will not always be readily diagnosable by "gold standard" synapomorphies. Morphological circumscription may require conditional statements and subclauses that account for exceptions. We encountered this situation when attempting to define *Colobopsis* on the basis of worker morphology. Diagnostic attributes that hold up under most circumstances for this genus do not apply to the island radiations that have occurred in New Caledonia and Fiji. Here there are few or no species of *Camponotus* (sensu stricto), and *Colobopsis* appears to have expanded into regions of morphospace not occupied elsewhere. Any diagnosis of *Colobopsis* needs to take these exceptions into account.

Our solution was to insert qualifying clauses for the island species, and to treat them separately in the key. While this might be considered rather arbitrary, it is an effective way to deal with the vagaries of adult worker morphology. For practical reasons worker morphology is the basis of most ant taxonomy, even though worker features can be prone to deceptive convergence and divergence. In this instance the larval, pupal, and genetic (DNA sequence) characteristics of *Colobopsis* continue to distinguish it globally from *Camponotus*, so we can be confident that these island radiations are correctly attributed to *Colobopsis*.

There are still some issues remaining to be addressed in the higher classification of the Formicinae. The genus *Prolasius* may be paraphyletic relative to *Teratomyrmex*, based on cox1 (cytochrome c oxidase I) sequence data (Alan Andersen, pers. comm.). The new molecular phylogeny of the subfamily reveals three other genera that are likely non-monophyletic (*Nylanderia*, *Prenolepis* and *Lepisiota*) as well as an apparently undescribed genus related to *Agraulomyrmex* (Blaimer *et al.* 2015). More detailed scrutiny of these taxa, including more comprehensive taxon sampling, is needed to resolve the taxonomic problems presented. We can therefore anticipate some additional changes at the genus level, but it is hoped that the basic framework adopted here for the Formicinae remains robust and useful.

Acknowledgments

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