Insect Systematics and Diversity, 9(4), 11; 2025, ixaf025
https://doi.org/10.1093/isd/ixaf025
Invited Article

ENTOMOLOGICAL SOCIETY OF AMERICA
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Taxonomy

Ant systematics: past, present, and future

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Nagoya Protocol: No specimens were included in this project that required permits of any kind.

Subject Editor: Hojun Song

Received on 12 August 2024; revised on 7 May 2025; accepted on 20 August 2025

The classification of ants (Hymenoptera: Formicidae) has progressed in waves since the first 17 species were described by Linnaeus in the 1758 edition of *Systema Naturae*. Since then, over 18,000 species-rank names have accumulated for the global myrmecofauna, of which ~14,260 living and ~810 fossil species are valid. Here, we provide a synopsis of ant biodiversity and review the history and classification of the family, while highlighting the massive growth of the field in the new millennium. We observe that major transformation has occurred for ant classification due to advances in DNA sequencing technologies, model-based hypothesis testing, and imaging technologies. We therefore provide a revised and illustrated list of diagnostic character states for the higher clades of Formicidae, recognizing that vastly more work is to be done. To facilitate discussion and the systematic accumulation of evolutionary knowledge for the early evolution of the ants, we suggest an informal nomenclatural system for the higher clades of ants, based on names currently in use and a set of names that have been democratically selected by the authors. To guide future work on ant systematics, we summarize currently available databases and present perspectives on regions in need of biodiversity exploration, challenges facing the field, and the future of ant taxonomy.

Keywords: phylogenetics, micro-computed tomography, taxonomy, myrmecology, evolution.

Scope of the Review

Among all insects, the ants (Hymenoptera: Formicidae) are arguably unmatched in their abundance, ubiquity, and ecological importance. Originating in the Late Jurassic to Early Cretaceous, ants have become the most species-rich and ecologically diverse group of social insects (Romiguier et al. 2022, Sosiak et al. 2024, Boudinot 2024, see also Borowiec et al. 2021). Ants constitute about 2% of the world's described insect species but represent over 50% of insect biomass in tropical forests globally (Wilson and Hölldobler 2005). They encompass over 14,000 valid species, although the actual diversity maybe 2 or 3 times higher (Ward 2014), and their numbers are conservatively estimated at twenty quadrillion (2×10^{16}) individuals (Schultheiss et al. 2022).

Ants dominate a diversity of ecosystems, ranging from subpolar forests to tropical deserts (Kaspari 2005), and play crucial roles in ecosystem functioning through interactions with various organisms (eg plants, fungi, hemipterans, a myriad of soil organisms, and even vertebrates) (Vander Meer 2012, Chomicki and Renner 2017, Avilés 2024), regulation of arthropod populations (Parker and Kronauer 2021), plant dispersal (Leal and Koski 2024), and environmental structuring (Folgarait 1998, Elizalde et al. 2020). The factors influencing their evolution and diversity are numerous, multifaceted, and intersecting, operating on every scale from molecules to ecosystems. At the individual, colonial, and ecological scales, social insects—especially ants—offer great advantages for the study of evolution; their intrinsic biological organization and "exuberant" diversity make correlative analyses of adaptation and differentiation easier and more rigorous (Hölldobler and Wilson 1990; Fig. 1).

Here, we provide a multipart review of the past, present, and future of ant systematics. We start with a synopsis of the natural history and biodiversity of living Formicidae, define the major clades

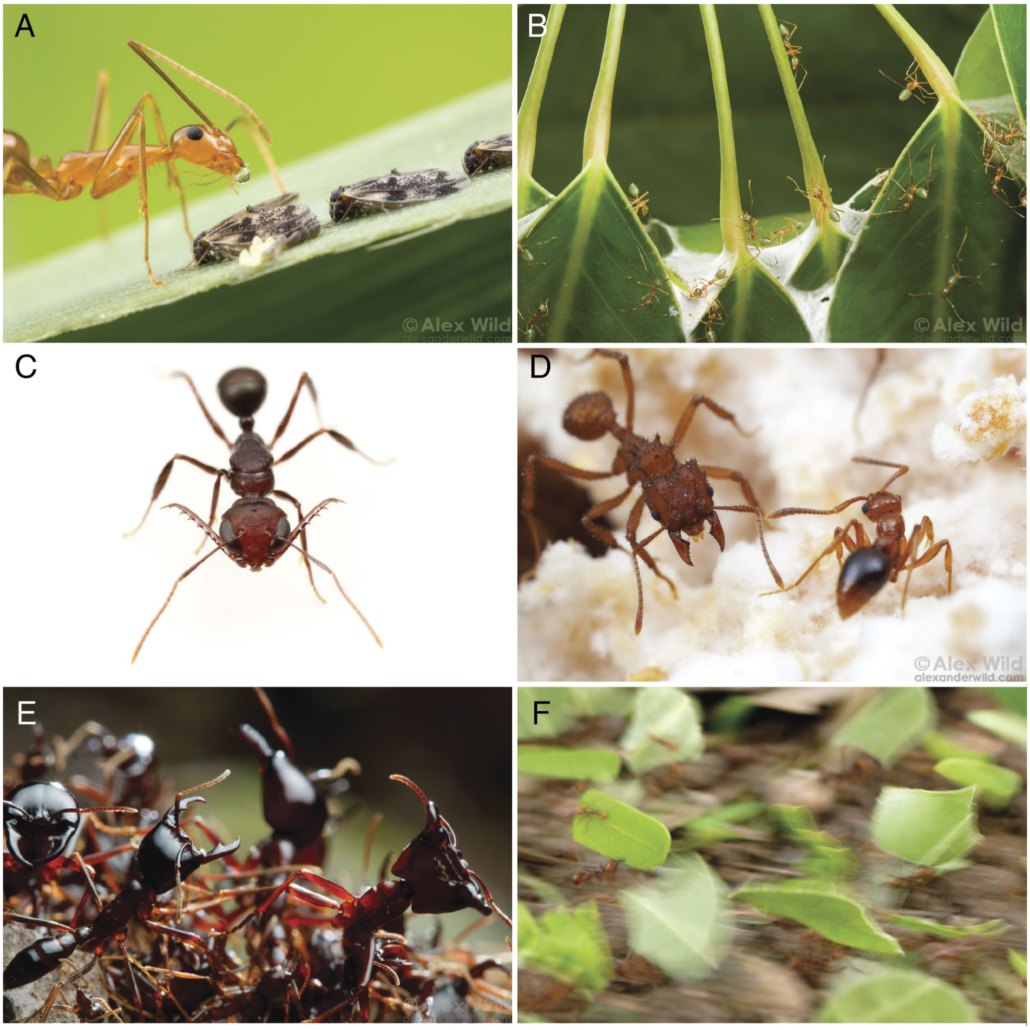


Fig. 1. A tiny fraction of the diversity in natural history of ants. A) The critically invasive "yellow crazy ant," *Anoplolepis gracilipes* (Smith 1857), tending hemipterans, showcasing the important symbiosis of ants and plant-sucking insects. B) The dominant arboreal "green tree ants," *Oecophylla smaragdina* (Fabricius 1775), guard the stems of their woven silk leaf nest, likely one of the hundreds of such nests in the tree. C) The trap-jaw ant *Myrmoteras iriodum* Moffett 1985, one of several lineages to independently evolve power amplification mechanisms for swift mandibular closure. D) A *Mycetomoellerius* Solomon et al. 2019 worker (left) wanders the fungal blooms of its colony and encounters a socially parasitic ant, *Megalomyrmex adamsae* Longino 2010b (right). E) Aggressive and polymorphic "siafu," or African driver ants (*Dorylus* Fabricius 1793), make a heavily defended tunnel with their bodies to transport prey. F) A blur of leaf-cutting ants (*Atta cephalotes* [Linnaeus 1758]) captures the frantic pace of colony life and extreme locomotory capacity of ants, and size-based behavioral specialization (note the small worker being carried on the leaf in the left-hand side of the frame). All photographs by Alex Wild, www.alexanderwild.com.

of ants with illustrations of key synapomorphies, and review the history of ant classification and phylogenetic hypothesis testing. We end by summarizing the available databases for the systematic study of ants, outlining regions in need of biodiversity exploration, and addressing the challenges and future of ant taxonomy. We also propose an informal system of higher ant classification that captures well-supported results from phylogenomic studies, and that provides a framework for the continued discovery of morphological patterns in the early evolutionary history of ants (Fig. 2).

Ant Biology and Natural History

Ants are eusocial insects: individuals of multiple generations live together and cooperate in brood care, with nonreproductive individuals effectively working on behalf of reproductives (Wilson 1971, 1979, Steiner et al. 2010, see also Boomsma and Gawne 2018). Division of labor and developmental polyphenism ("castes") are the foundations of colonial organization (Oster and Wilson 1978, Wilson 1979) and are included in the colony structure concept along with demography, genealogy, and spatial arrangement (Steiner et al. 2010). The ancestral ant colony structure likely consisted of 2 female forms—winged queens and wingless workers—plus the winged male (Boudinot et al. 2022b). Usually, the queen mates once (monandry), founds a new colony, and remains the only reproductive over the colony lifespan (monogyny) together with dozens to hundreds of monomorphic or size-varying workers specialized for nonreproductive tasks (Hölldobler and Wilson 1990).

However, there are derived systems across the ant phylogeny (Heinze 2008, Boudinot et al. 2025). For instance, the subfamily Ponerinae includes some species that show only subtle morphological differences between reproductive and nonreproductive females, with

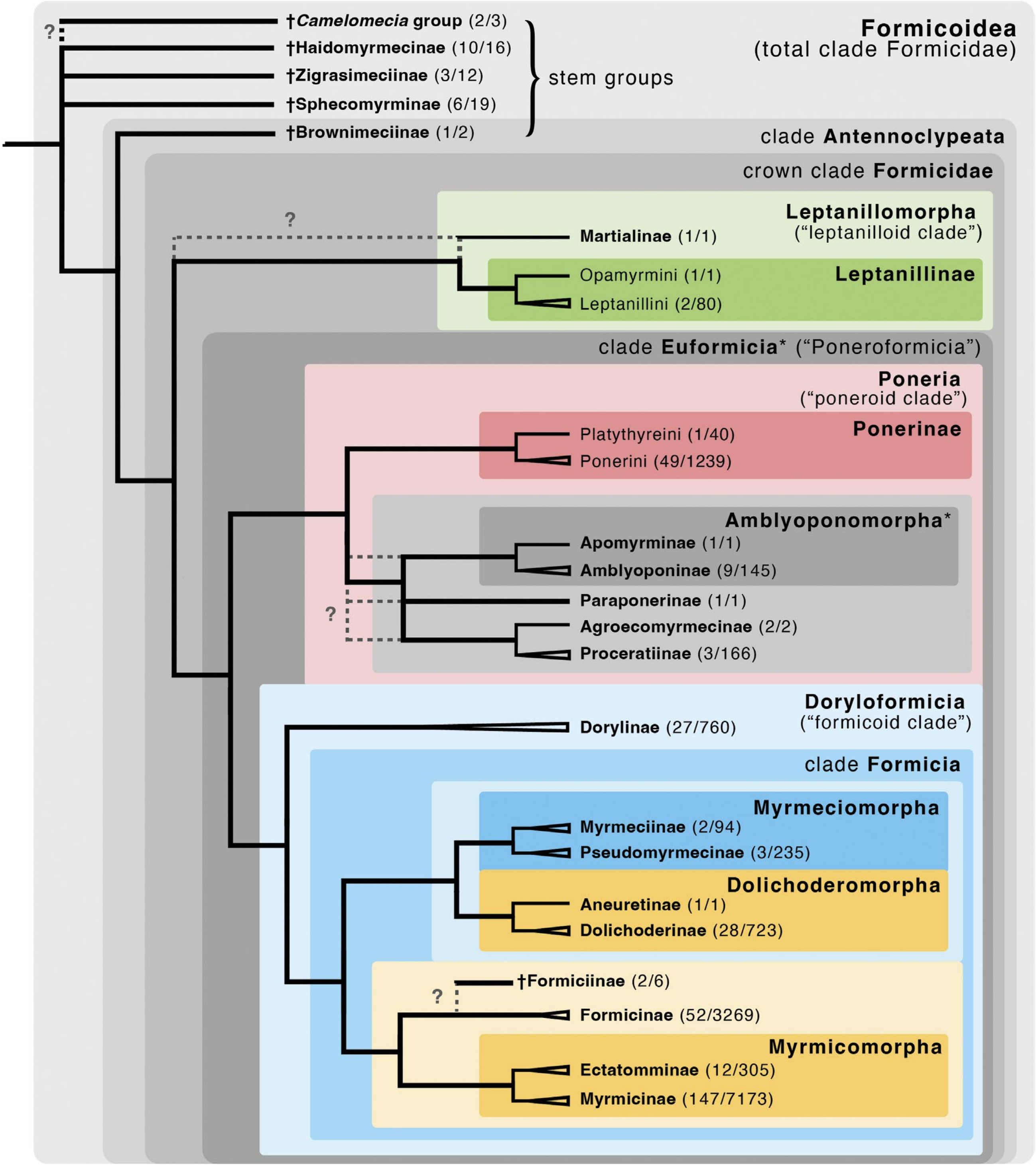


Fig. 2. Currently accepted phylogenetic hypothesis for the higher taxa of Formicoidea and Formicidae based on the phylogenomic analyses of Romiguier et al. (2022) and Borowiec et al. (2025), supplemented by Boudinot et al. (2022a) for extinct taxa. Numbers of valid genera and species per taxon, respectively, are indicated in parentheses "()" for living and square brackets "[]" for extinct taxa. Outstanding phylogenetic uncertainties above the subfamily level include: (i) the relationship of the †*Camelomecia* genus-group to the remainder of the Formicoidea; (ii) the relationships of the definitive stem ants relative to one another and the crown clade; (iii) the monophyly of Leptanillomorpha; (iv) the relationships among clade Poneria / the poneroid clade; and (v) the placement of †Formiciinae. Informal clade names between subfamily and family level have been used in prior studies (Supplementary Appendix I); the names "Euformicia" and "Amblyoponomorpha" (indicated by an asterisk [*]) were selected by a poll among the authors.

reproduction performed by mated egg-laying workers (gamergates) (Peeters 2012, Boudinot et al. 2025). Furthermore, short-winged (brachypterous) queens are known only within Doryloformicia (the "formicoid" clade–ie the clade that includes both Dorylinae and its sister clade, Formicia; see Fig. 2), but wingless queens have evolved many times across the Formicidae (Peeters 2012). Several ant

Fig. 3. Comparison of resources exploited by ant symbionts and 5 categories of social parasites (detailed in Supplementary Appendix II).

species with flightless female reproductives also have winged queens (Johnson et al. 2007, General et al. 2020) or lack these entirely (Ulysséa et al. 2024). Wingless (ergatoid) males are rarer and can be polymorphic (Yamauchi et al. 1996, 2005). Besides sexual reproduction, unmated workers in numerous species may reproduce by laying unfertilized eggs, which develop into males because of haplodipoid sex determination (arrhenotoky) (Crozier 1971). Less commonly, a few species may reproduce via parthenogenesis, in which unfertilized eggs develop into more female workers (thelytoky) (Schilder et al. 1999). For instance, the queenless ant *Ooceraea biroi* (Forel 1907) is exclusively parthenogenetic (Kronauer et al. 2012). In other species (eg *Monomorium triviale* Wheeler 1906), males are absent, and unmated queens produce workers and queens via thelytoky (Idogawa et al. 2021).

In small colonies, each worker generally performs many tasks (eg brood care, foraging, defense, nest construction). In large colonies, each worker tends to specialize in fewer tasks. Even in ant societies without morphological specialization, division of labor manifests as temporal polyethism: young workers stay within the nest, caring for the queen and brood, while older workers take on riskier duties such as guarding the nest and foraging (Oster and Wilson 1978). Temporal polyethism is flexible: workers can shift to different tasks following changes in colony composition or environmental factors (Gordon 1996). In addition, many ant genera show continuous worker polymorphism, suggesting there are adaptive advantages to a flexible worker developmental pathway and size variation. For example, in the harvester ant *Messor barbarus* (Linnaeus 1767), the size range of workers is correlated with the size range of seeds they can carry, providing an advantage to colonies with higher polymorphism (Bernadou et al. 2016). In a few ant genera across the clade Doryloformicia (Fig. 2), division of labor is further specialized with an additional worker caste—called major workers or soldiers—which follows a different developmental pathway than workers and queens (Molet et al. 2012). Major workers often perform defensive tasks, such as defending foraging columns (Kronauer 2009) or protecting the nest entrance through phragmosis (Ward et al. 2016). Major workers can also fill other functions, like seed milling and food storage in *Pheidole* Westwood 1839 and *Acanthomyrmex* Emery 1893 (Tsuji 1990, Gobin and Ito 2000). The evolution of major workers likely improved division of labor, and may have contributed to the diversification of the 2 most species-rich ant genera, *Pheidole* and *Camponotus* Mayr 1861 (Moreau 2008, Moreau and Bell 2013). A few ants display a third worker caste ("supersoldiers") with a distinctive behavioral repertoire. This is known in *Gesomyrmex* Mayr 1868 and some *Pheidole* (Gordon et al. 2017, Peeters et al. 2017a), as well as in some *Carebara* Westwood 1840, which have multiple discrete worker castes performing different tasks in their foraging raids (Moffett 2019).

The complexity and sheer diversity of ant societies have given rise to many instances of social parasitism—ie one social species living regularly in dependency on another social species—among the ants (Forel 1898). Depending on definition, there are >400 socially parasitic ant species, with the phenomenon evolving >90 times in the Formicidae (Rabeling 2021, Gray and Rabeling 2023). Social parasites exploit various resources unique to social animals through a diverse range of strategies, including inquilinism, temporary parasitism, dulosis, thief, and guest parasitism (highlighted in Supplementary Appendix II). Figure 3 contrasts the 5 categories of social parasites with myrmecophiles (nonant organisms that obligately associate with the Formicidae) and parabiotic ants (which live independently from, but side by side with, another ant species). Parabiosis is not necessarily associated with parasitism, and is often difficult to identify in nature, manifesting as "eavesdropping" or trail- or nest-sharing (Hölldobler and Wilson 1990, Sanhudo et al. 2008).

Prevailing theory posits that workerless social parasites evolve from reproductively isolated populations of facultative parasites through a series of steps that lead to a parasitic phenotype (Wilson 1971, Hölldobler and Wilson 1990). However, experimental evidence from free-living *Ooceraea biroi* suggests that genetic change in a single generation can underlie the evolution of social parasitism (Trible et al. 2023). Host specialization varies across social parasites: inquilines and guest ants tend to parasitize a single host species (Adams et al. 2013); dulotic ants, temporary parasites, and thief ants are more generalized in host preference, exploiting multiple host species (Wheeler 1901, Huang and Dornhaus 2008). Moreover, transmission of social parasites is largely horizontal (between colonies). There are exceptions in which vertical transmission (from mother to daughter colony) occurs, eg in the *Solenopsis phoretica* species group (Davis and Deyrup 2006).

Ants inhabit arboreal (tree) to epigeic (ground surface) and subterranean strata, utilizing resources differently to build their nests (Hölldobler and Wilson 1990, Steiner et al. 2010). Species with relatively small nests may be located within fallen hollow branches (eg some *Strumigenys* Smith 1860, *Wasmannia* Forel 1893), hollow nut shells (eg some *Temnothorax* Mayr 1861), or rock crevices. Others, such as *Thaumatomyrmex* Mayr 1887, may nest in natural cavities like abandoned solitary wasp nests or snail shells, and spaces between dried bromeliad leaves (Brandão et al. 1991, Delabie et al. 2000). Soil is used both as a nesting substrate and the entire zone of daily life by many ants, such as the subterranean Apomyrminae and Leptanillinae, and most Amblyoponinae and Dorylinae. Tree-dwelling ants, such as *Cephalotes* Latreille 1802 (Powell et al. 2014, Oliveira et al. 2021) and most Pseudomyrmecinae (Ward 1991), usually nest in wood galleries previously excavated by other insects. Ants of the genera *Azteca* Forel 1878, *Dolichoderus* Lund 1831, *Camponotus*, and *Crematogaster* Lund 1831 may nest in epiphytic plants, forming mutualistic associations called "ant gardens" (Hölldobler and Wilson 1990, Rico-Gray and Oliveira 2007). Nests are most complex in the fungus-farming ant genus *Atta* Fabricius 1804, with several entrances surrounded by large mounds and thousands of chambers that together may reach depths of 6 m (Forti et al. 2018).

Nest quantity and stability vary as much as site (Hölldobler and Wilson 1990, Steiner et al. 2010). Colonies may live permanently in a single nest (monodomy) or more than one nest at a time (polydomy). Propensity for nest relocation can be categorized as follows (McGlynn 2012): (a) adventitious: species that are capable of moving their nests in response to trauma, such as *Pogonomyrmex barbatus* (Smith 1858) (Gordon 1992); (b) intrinsic: species that periodically move their nest to avoid predators (like the serially monodomous *Stenamma expolitum* Smith 1962 [Longino 2005]), for thermoregulation (like the seasonally polydomous *Linepithema humile* [Mayr 1868] [Heller and Gordon 2006]), or to escape from local competition (as in *Veromessor andrei* [Mayr 1886] [Brown 1999]); (c) unstable nesting: species that nest in ephemeral environments (eg *Nylanderia steinheili* [Forel 1893] [McGlynn 2006]); and (d) nomadism: observed in army ants (*Dorylus*, *Eciton* Latreille 1804, etc.), but also in *Leptanilla* Emery 1870 (Masuko 1990), some Ponerinae (eg *Neoponera marginata* [Roger 1861] [Leal and Oliveira 1995]), Formicinae (*Euprenolepis procera* [Emery 1900] [Witte and Maschwitz 2008]), and Dolichoderinae (*Dolichoderus cuspidatus* species-group [Dill and Maschwitz 1994]).

Diet and social ecology are inextricably linked for eusocial insects, making nutrition a critical factor in their evolution (Wheeler 1918, Meurville and LeBoeuf 2021). Diets are diverse across the Formicidae: ants may be predators, scavengers, herbivores, seed harvesters, fungus or hemipteran farmers, or omnivores. Ants of the subfamilies Formicinae, Pseudomyrmecinae, and Dolichoderinae tend to acquire much of their nutrition from plant sources, while the Myrmicinae, Ponerinae, and Dorylinae are predominantly carnivorous (Blüthgen and Feldhaar 2010). Protein requirements may vary seasonally with brood cycles (eg Tschinkel 2013, Zakharov and Zakharov 2022), or may in some cases be provided or recycled by endosymbionts (eg *Camponotus* [Rafiqi et al. 2020]; *Cephalotes* [Hu et al. 2018]). Several predators of specific and rare prey feed on the hemolymph of their larvae (larval hemolymph feeding) (Masuko 2019). Many of the ants belonging to the clade Formicia (Fig. 2) feed on the waste of sap-feeding Hemiptera (suborders Auchenorrhyncha and Sternorrhyncha) (Klimes et al. 2018). This trophobiosis is one of the main factors underlying the numerical abundance of this clade (Delabie 2001). Trophobiosis often takes the form of ants "herding" their trophobionts, and this mutualism may or may not be obligatory for one or both parties. For example, *Melissotarsus* Emery 1877b and *Rhopalomastix* Forel 1900 (Myrmicinae) eat wax and protein secretions from armored scale insects (Hemiptera: Sternorrhyncha: Coccoidea: Diaspididae), plus exuviae and old individuals (Peeters et al. 2017b, Yong et al. 2019). These ants chew galleries through live wood, where they then host their independently feeding trophobionts (Yong et al. 2021). Diaspidids can live freely on the tree surface, but cohabiting with *Melissotarsus* and *Rhopalomastix* probably provides direct access to the inner cambium layers of trees on which the diaspidids feed. Conversely, subterranean *Acropyga* Roger 1862 (Formicinae) ants feed on the honeydew of mealybugs and ensign scales (Coccoidea: Pseudococcidae and Ortheziidae), trophobionts which in turn require the ants for survival (Weber 1944, LaPolla 2021). Unmated, colony-founding *Acropyga* queens carry a single mealybug which serves as a fundatrix for a new herd (LaPolla et al. 2002, LaPolla 2004). This behavior dates back >15 to 30 Mya, based on amber inclusions (LaPolla 2005) and phylogenomic divergence dating analyses (Blaimer et al. 2016). Another notable instance of obligate trophobiotic mutualism is the nomadic *Dolichoderus cuspidatus* species group (Dolichoderinae), ants which move their mealybug (Pseudococcidae: Allomyrmococcini) herds to new "pastures" with such regularity that they do not form permanent nests (Dill and Maschwitz 1994).

Fungus-farming ants (Myrmicinae: Attini: Attina; hereafter "attine ants") represent remarkable examples of mutualism and coevolution (Weber 1972, Mehdiabadi and Schultz 2010). Attine ants form a monophyletic group, currently consisting of 248 described extant and 5 extinct species in 20 genera (Bolton 2024), that originated approximately 56 to 65 Mya in South America (Branstetter et al. 2017a, Hanisch et al. 2022, Schultz et al. 2024). Distributed in the New World, primarily in the Neotropics, attine ants depend on the cultivation of fungi (Agaricales: Agaricaceae and Pterulaceae), which serve as their primary food source (Schultz et al. 2022, 2024). The ants, in exchange, provide their fungal cultivars with nourishment, protect them from pathogens, and facilitate dispersal (Fernández-Marin et al. 2006, Kyle et al. 2023). The fungus-farming ant symbiosis also includes fungal pathogens, mostly in the genus *Escovopsis* (Ascomycota: Hypocreales: Hypocreaceae) (Montoya et al. 2021, Gotting et al. 2022, Berasategui et al. 2024), and symbiotic filamentous bacteria that grow in specialized structures on attine integument (Li et al. 2018, Goldstein and Klassen 2020). Additional microbial symbionts are continuously being discovered within the fungus-farming ant systems (Ronque et al. 2020, Bizarria Jr. et al. 2023). Fungus-farming ants and their fungal cultivars represent a valuable resource for a rich array of myrmecophiles, including commensals, parasites, predators, and parasitoids (Adams et al. 2020, Hölldobler and Kwapich 2022).

Interesting behavioral and morphological syndromes in the Formicidae have also arisen from predatory diets. A chief example is the army ant syndrome, characterized by obligate collective foraging, nomadism, and highly specialized wingless queens (Gotwald 1995, Kronauer 2009). Additional traits of some army ants include phasic reproduction, advanced division of labor, and male-biased sex ratios (Kronauer 2009). The army ant syndrome is most prevalent in the Dorylinae, where it has evolved twice (Borowiec 2019), but is also found in Amblyoponinae (*Onychomyrmex* Emery 1895 [Miyata et al. 2003]), Leptanillinae (*Leptanilla japonica* Baroni Urbani 1977 [Masuko 1990]), Ponerinae (*Simopelta* Mann 1922 [Gotwald and Brown 1966] and *Leptogenys processionalis* [Jerdon 1851, Maschwitz et al. 1989]), and Myrmicinae (*Carebara* spp.; Moffett 1988). The army ant syndrome tends to co-occur with specialization on patchy or transient food sources, whether the brood of other ants (Dorylinae) or centipedes (*Onychomyrmex*, *Leptanilla*), but some tropical doryline army ants—*Dorylus* of the former subgenus *Anomma* Shuckard 1840 (Afrotropics), *Eciton* and *Labidus* Jurine 1807 (Neotropics), and *Aenictus* Shuckard 1840 (Indomalaya)—have become generalists. These lineages are notorious for massive epigeic foraging trails that give the "army ant" syndrome its name. Analogous generalization occurs in *Carebara diversa* (Jerdon 1851) and *L. processionalis*.

Another well-studied predatory syndrome is that of trap-jaw ants. Trap-jaw morphology occurs in the Ponerinae (*Odontomachus* Latreille 1804 and *Anochetus*, Mayr 1861), Formicinae (*Myrmoteras* Forel 1893), and Myrmicinae (Dacetina and *Strumigenys*), evolving 7 to 10 times within *Strumigenys* (Attini) alone (Larabee and Suarez 2014, Booher et al. 2021). These ants use a power-amplifying spring-latch mechanism to shut their mandibles at some of the fastest speeds recorded in the Metazoa (Patek et al. 2006), sometimes outspeeding springtails (Gronenberg 1996). Trap-jaw mandibles in some lineages were a key innovation that fueled diversification (Moreau and Bell 2013, Booher et al. 2021). Even though the morphological structures acting as latch, spring and trigger differ among trap-jaw genera, physiological properties of muscles and neurons are highly conserved: adductor muscle fibers are slow-contracting, while trigger muscles are fast-contracting and innervated by large fast-conducting axons (Gronenberg and Ehmer 1996, Larabee et al. 2017). The remarkable diversity of natural history of ants sets the stage for an exploration of their evolutionary history, which we begin by defining the major clades and their key synapomorphies in the following section.

Definitions of Major Clades

Currently, the family Formicidae comprises >14,000 extant species sorted into 342 genera and 16 subfamilies, and >800 extinct species from 172 genera across 6 subfamilies. (Bolton 2024). The subfamilial classification has been largely stable since Bolton (2003) (excepting Dorylinae), with major advancements in the robust recognition of higher clades resulting from multi-gene to genome-scale phylogenetic analysis. This section outlines the status of morphological knowledge for the higher clades of ants, which has been substantially informed by molecular phylogenetic results, detailed scanning electron microscopy (SEM) (Keller 2011), and the application of micro-computed tomography (µ-CT). Here, we also suggest the use of informal names for robust clades above subfamily rank (Fig. 2), given the emerging need to discuss patterns of evolution in the deeper history of Formicidae. Most of these informal names have been used in previous studies, but we have collectively enumerated them in Supplementary Appendix I and summarized their diagnostic features in Supplementary Appendix III. Our intent is for these names to ease communication of alternative phylogenetic hypotheses and aid comparative discussion of evolution and biology, while also avoiding nomenclatural confusion (eg "formicoids" ambiguously referring either to a subclade of the Formicidae vs. all members of the superfamily Formicoidea) or circuitous definitions ("formicoids minus Dorylinae" for the clade Formicia). These names are not regulated by the International Code of Zoological Nomenclature, and their use here is neither prescriptive or proscriptive. Future authors are therefore free to use, modify, or forgo these labels according to their own preferences and needs, although we do recommend keeping stability in mind if adjustments are made.

We recognize the **superfamily Formicoidea** to harmonize with the superfamilial classification of Aculeata. The Formicoidea—ie the "total clade Formicidae", or Formicidae in the broadest possible sense, are here recognized according to the current classification of the Aculeata (eg Pilgrim et al. 2008, Branstetter et al. 2017b, Peters et al. 2017, Boudinot et al. 2022a, Blaimer et al. 2023). These include not only the **crown Formicidae**, or all ants descended from the most recent common ancestor (MRCA) of the living ants, but also extinct lineages that are not descended from that same MRCA—ie the **stem Formicidae**. All adult Formicoidea—male and female, extant and extinct—are recognizable by modification of the articulation between the procoxa and trochanter, where the membrane between these sclerites is completely concealed (Boudinot 2015, Boudinot et al. 2022a). Female ants are further recognizable by (i) the presence of the metapleural gland ("fovea metathoracica": Meinert 1861, "metasternal gland": Wheeler 1910, references therein; Wilson et al. 1967, Gauld and Bolton 1988, Rasnitsyn 2002) (note that this gland may be lost [Bolton 2003] and also that a similar gland occurs in the Pelecinidae [Apocrita: Proctotrupoidea]:, Ulmer et al. 2023), (ii) petiolation between the mesosoma and gaster (eg Latreille 1802, Wilson et al. 1967, Gauld and Bolton 1988, Rasnitsyn 2002, Bolton 2003) (independently derived in other Aculeata, eg Bradynobaenidae, †Falsiformicidae), and (iii) at least some degree of ventral elongation of the head (Bolton 2003, Richter et al. 2022) (also occurring in the Ampulicidae and other lineages). For further definition of the Formicoidea and illustrations, see section *Summary of apomorphies of total and crown clade Formicidae* and Figs. 4 and 5.

Most stem ant lineages appear in the fossil record during the Cenomanian–Turonian (100.5 to 89.8 Mya) in the Northern Hemisphere, but the South American †*Vulcanidris cratensis* Lepeco, Brandão and Camacho 2025 (†Haidomyrmecinae) is the earliest known definitive stem member of the Formicidae, dating from the Aptian (121.4 to 113 Mya). However, none of these ant-wasp intermediates survived into the Cenozoic (Boudinot 2024, Sosiak et al. 2024). Of these, the †***Camelomecia* genus-group** (†*Camelomecia* Barden and Grimaldi 2016, †*Camelosphecia* Boudinot et al. 2020) from Kachin amber (~99 Mya) have been recovered as sister to all other Formicoidea (Boudinot et al. 2022a). Whether these truly belong to that clade (Fig. 2) or had a worker caste remains uncertain (Boudinot et al. 2022a). Among the remaining stem ants, the †**Armaniinae**, known from often-incomplete Late Cretaceous compression fossils of alates from both Northern and Southern Hemispheres, may not form a clade and are incertae sedis in the family (Barden and Engel 2019, Boudinot et al. 2022a). All other stem subfamilies are known from Northern Hemisphere amber alone. The †**Brownimeciinae** (2 species from ~90–77 Mya; Grimaldi et al. 1997, Sosiak et al. 2024) are supported as sister to the crown Formicidae based on antennal proportions (eg Borysenko 2017), mesonotal simplification (eg Grimaldi et al. 1997), and by the form of the antennotorular complex (Boudinot et al. 2020). Regarding the latter, the posterior clypeal margin extends between the antennal toruli, a condition that is unique among stem groups and synapomorphically shared with crown Formicidae, hence the name **Antennoclypeata** has been suggested for this clade (Boudinot et al. 2020, affirmed by phylogenetic analyses in Barden et al. 2020, Boudinot et al. 2022a, Sosiak et al. 2024). Lineages outside the Antennoclypeata represent a range of extinct phenotypes, from the possibly paraphyletic †**Sphecomyrminae** (19 spp., 6 genera; Boudinot et al. 2022b, Richter et al. 2022), to the extremely derived †**Haidomyrmecinae** (16 spp., 10 genera; Perrichot et al. 2020) and †**Zigrasimeciinae** (12 spp., 3 genera; Cao et al. 2020). The phylogeny of these lineages is unclear, but their fossils indicate that eusociality evolved in the Formicoidea prior to the origin of the crown Formicidae (eg Perrichot et al. 2008, Barden et al. 2016, Boudinot et al. 2022b).

The oldest definitive, undisputed fossil of **crown Formicidae** is the formicine †*Kyromyrma neffi* Grimaldi and Agosti 2000 from Turonian-aged amber, which implies a mid- to Early Cretaceous origin of the crown subfamilies (Perrichot 2019, Sosiak et al. 2024). A recent study suggested that a member of the crown group tribe Camponotini was detected in Kachin (ie mid-Cretaceous) amber (Wu et al. 2024); the provenance is uncertain until chemical methods are applied. The crown Formicidae differ from the stem lineages by morphological features summarized in Fig. 6.

The first split within the crown Formicidae is between the Leptanillomorpha and the **Euformicia** (ie "poneroformicines"). The Euformicia comprise the bulk of extant ant diversity, which is distributed in the clades Poneria (= "poneroid" clade; ~1,600 spp.) and Doryloformicia (= "formicoid" clade; ~12,600 spp.). Two synapomorphies were recently discovered for Euformicia (Richter 2022, Richter et al. 2022, Boudinot et al. 2022a) (Fig. 7): (i) masticatory margin of the female mandible is elongate (variable in

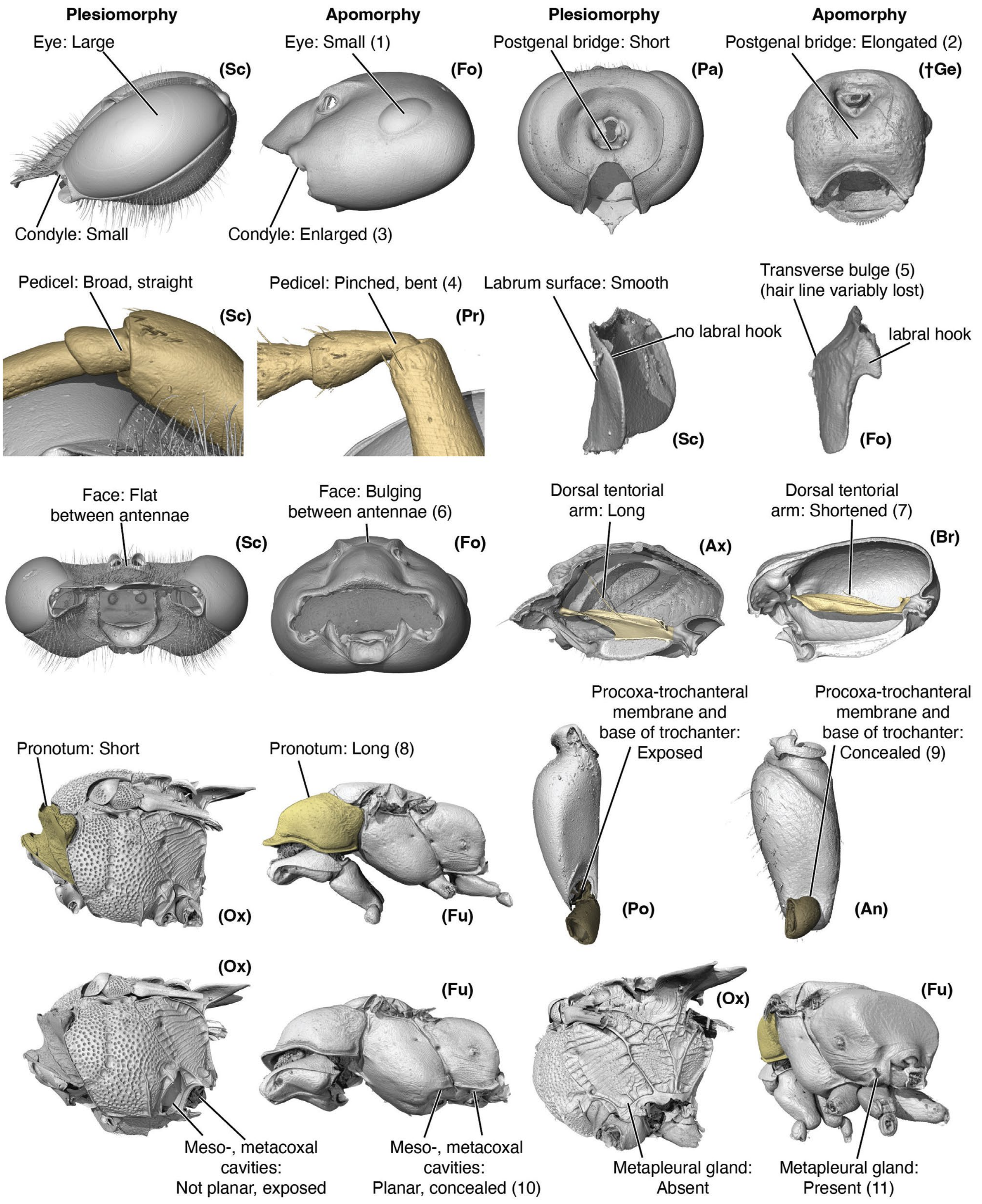


Fig. 4. Derived, diagnostic features of the Formicoidea. Outgroups are in the "Plesiomorphy" column, ingroups in the "Apomorphy" column. Numbers correspond to character state definitions in section *Summary of apomorphies of total and crown clade Formicidae*. Lettering indicates taxon names: **An** = *Amblyopone australis* (Amblyoponinae; CASENT0753222, BEB-KIT2019-08); **Ax** = *Ampulex* nr. *moebii* (Ampulicidae; SMFENT0001921, BEB-KIT033); **Br** = *Brachyponera luteipes* (Mayr 1862); **Fo** = *Formica rufa* Linnaeus 1761 (Formicinae); **Fu** = *Fulakora orizabana* (Brown 1960) (Amblyoponinae; SMFHYM0007863, BEB-KIT211); **†Ge** = †*Gerontoformica gracilis* (Barden and Grimaldi 2014) (†Sphecomyrmecinae; CASENT0741232); **Ox** = *Oxybelus rubrocaudatus* Arnold 1927 (Crabronidae; USNMENT01900491, BEB-KIT256); **Pa** = *Parischnogaster* sp. (Vespidae, USNMENT01900200, BEB-KIT066); **Po** = *Anoplius* (*Arachnophroctonus*) sp. (SMFHYM0005942, BEB-KIT2019-13); **Pr** = *Protanilla lini* Terayama 2009; **Sc** = *Sceliphron spirifex* Klug 1801 (Sphecidae); Sp = *Sphex* sp. (Sphecidae).

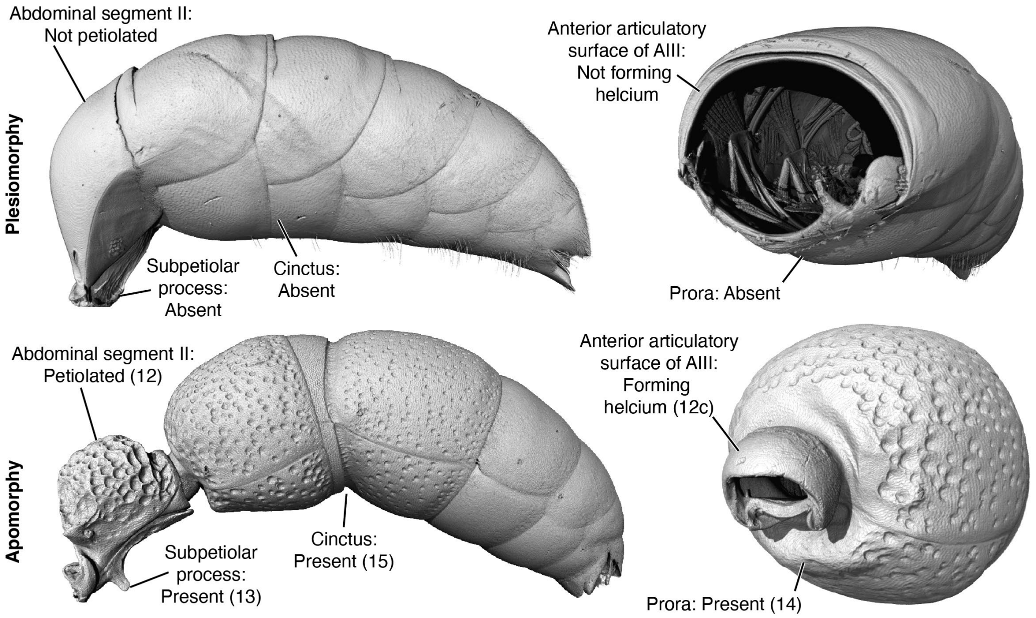


Fig. 5. Derived, diagnostic features of the Formicoidea, continued. Outgroup ("Plesiomorphy") = *Liris* (*Leptolarra*) cf. *nigricans* (Crabronidae; SMFHYM0007985, BEB-KIT241); ingroup ("Apomorphy") = *Platythyrea* cf. *schultzei* (Ponerinae; SMFHYM0007986, BEB-KIT241). Numbering corresponds to character state definitions in section *Summary of apomorphies of total and crown clade Formicidae*.

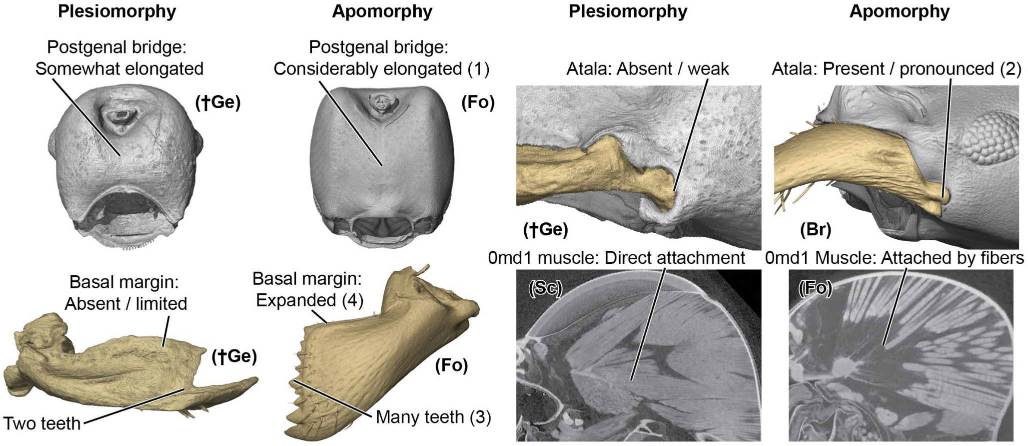


Fig. 6. Derived, diagnostic features of the crown clade Formicidae. Numbering corresponds to character state definitions in section *Summary of apomorphies of total and crown clade Formicidae*. Lettering indicates taxon names: **Br** = *Brachyponera luteipes* (Mayr 1862) (Ponerinae); **Fo** = *Formica rufa* (Formicinae); **†Ge** = †*Gerontoformica pilosa* (†Sphecomyrminae); **Sc** = *Sceliphron spirifex* (Sphecidae).

Leptanillomorpha) and (ii) the female torular apodeme (an internal feature) is present, ie there is a distinct process that projects into the head cavity from the ventral margin of the antennal torulus. While mandibular morphology is variable in both Leptanillomorpha and Euformicia, the occurrence of the torular apodeme (Fig. 7) appears to be a synapomorphy of the Euformicia (Richter et al. 2022) that is present in both sexes (Boudinot et al. 2021).

The minute **Leptanillomorpha** ("leptanilloids"; ~85 spp.; Figs. 7–10) are probably sister to the remainder of the living ants (clade Euformicia); they unfortunately lack a fossil record. Phylogenomic signal for this clade is not unanimous, but still significant (eg Borowiec et al. 2019, 2025, Romiguier et al. 2022). Many of the potential synapomorphies of the Leptanillomorpha are corollaries of subterranean habits, such as complete repression of eyes in the worker and absence of frontal carinae (Fig. 8B) (Bolton 2003); edentate mandibles (marked by arrow in Fig. 9A) and loss of the metapleural gland (Fig. 9B) are male synapomorphies (Boudinot 2015). The largely tropical **Leptanillinae** (Figs. 7–10) are confined to the Eastern Hemisphere (Griebenow 2024). These subsist on centipedes (Chilopoda) or forcepstails (Diplura: Japygidae) (Ito et al. 2022), with *Leptanilla* exhibiting the army ant syndrome and queen larval hemolymph feeding (Masuko 1990). Male genital skeletomusculature in *Leptanilla* shows extreme derivation unparalleled in ants (Griebenow et al. 2023; Fig. 10). The generic and tribal classification of the subfamily has been revised most recently by Griebenow (2024). The monotypic subfamily **Martialinae** (Fig. 11) is Neotropical, with virtually unknown biology (Rabeling et al. 2008; Boudinot 2015).

Within the Euformicia, the clade **Poneria** ("poneroids") is united by tergosternal fusion of abdominal segments III–IV, a condition that is only rarely secondarily lost (Bolton 2003, Fisher and Bolton 2016, Boudinot et al. 2022a). These ants occupy the full range of habitats

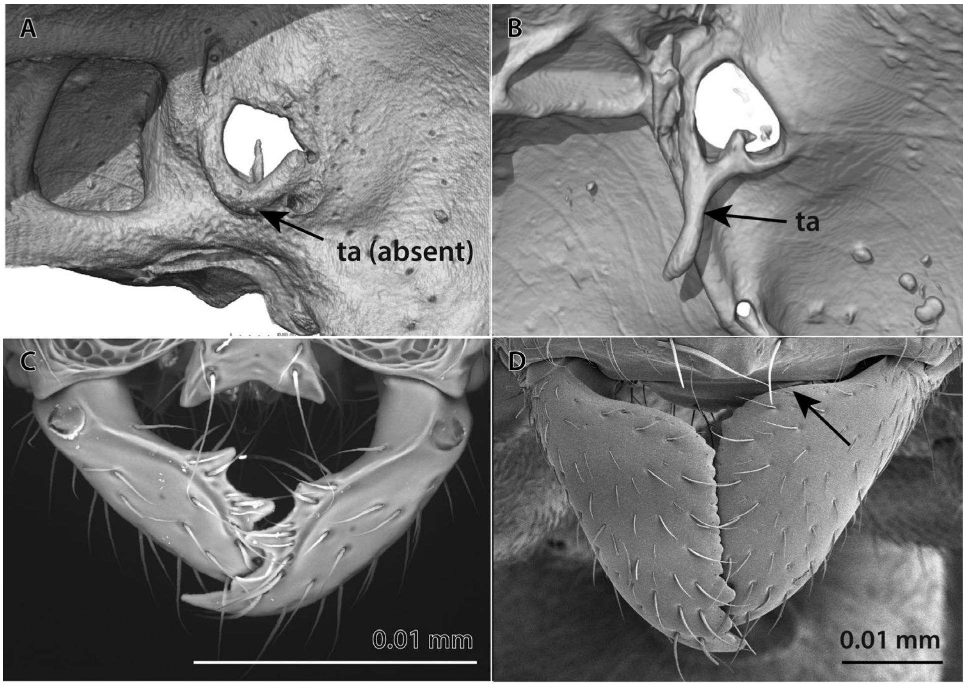


Fig. 7. Synapomorphies of Euformicia: Presence of the torular apodeme (ta) and the triangular or shovel-like shape of the mandible. A) Torular apodeme absent, *Protanilla lini*; B) Torular apodeme present, *Formica rufa* Linnaeus 1761; C) Mandibles of *Leptanilla thai* Baroni Urbani 1977 (CASENT0842784; Zachary Griebenow); D) Mandibles of *Ponera pennsylvanica* Buckley 1866 (Keller 2011), proximal mandibular margin marked with arrow.

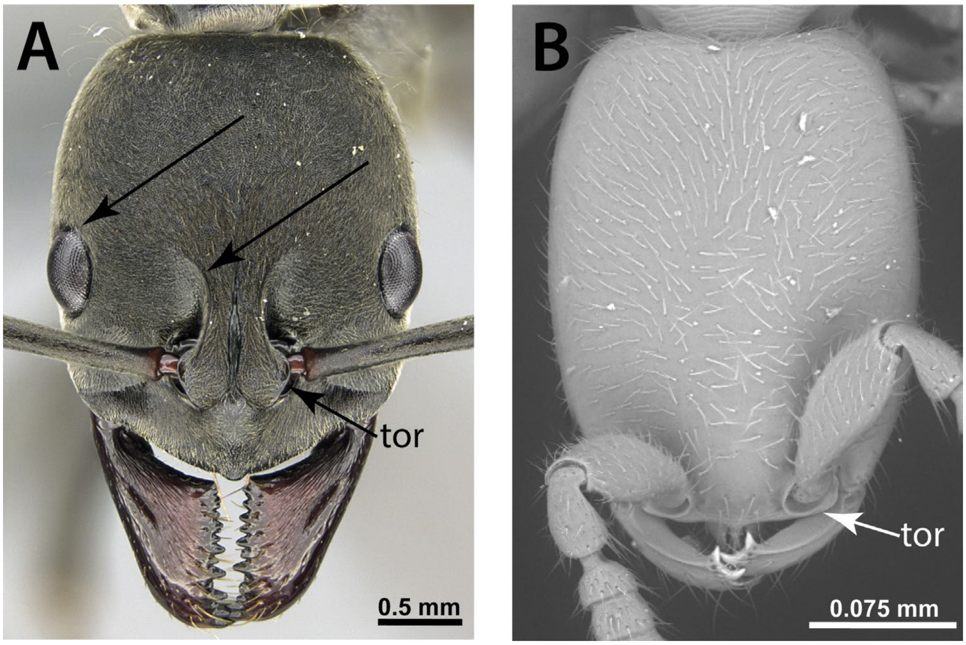


Fig. 8. Comparison of cephalic characters in the Euformicia A) and Leptanillomorpha B), frontal view. Arrows mark compound eye and frontal carina. A) *Hagensia havilandi* Forel 1901 (CASENT0888533; Michele Esposito). B) *Leptanilla phthirigyna* Griebenow et al. 2025 (CSUENT6000054; Zachary Griebenow). **tor** = torulus.

known in the Formicidae, from hypogeic to arboreal, with concealed habitats like leaf litter and soil presumably their ancestral domain. In contrast to their sister clade Doryloformicia, the Poneria are almost exclusively carnivorous. Relationships among the Poneria have been contentious, yet limited stability is emerging (Romiguier et al. 2022, Borowiec et al. 2025). The most species-rich subfamily of the Poneria is the cosmopolitan **Ponerinae** (Fig. 12), identified almost uniquely by the fusion of the torulus to the frontal lobe (Bolton 2003). No other definitive synapomorphies are yet known, meaning that the Ponerinae are currently one of the least well-defined subfamilies in morphological terms (Richter et al. 2023). Some ponerines narrowly specialize on particular prey—darkling beetles, oniscoid isopods, millipedes, earthworms, and others—while many are generalists. Colony size and reproductive strategies vary dramatically across the Ponerinae, with multiple origins of swarm-raiding (eg *Megaponera analis* [Latreille 1802]) or the army ant syndrome (eg *Simopelta*).

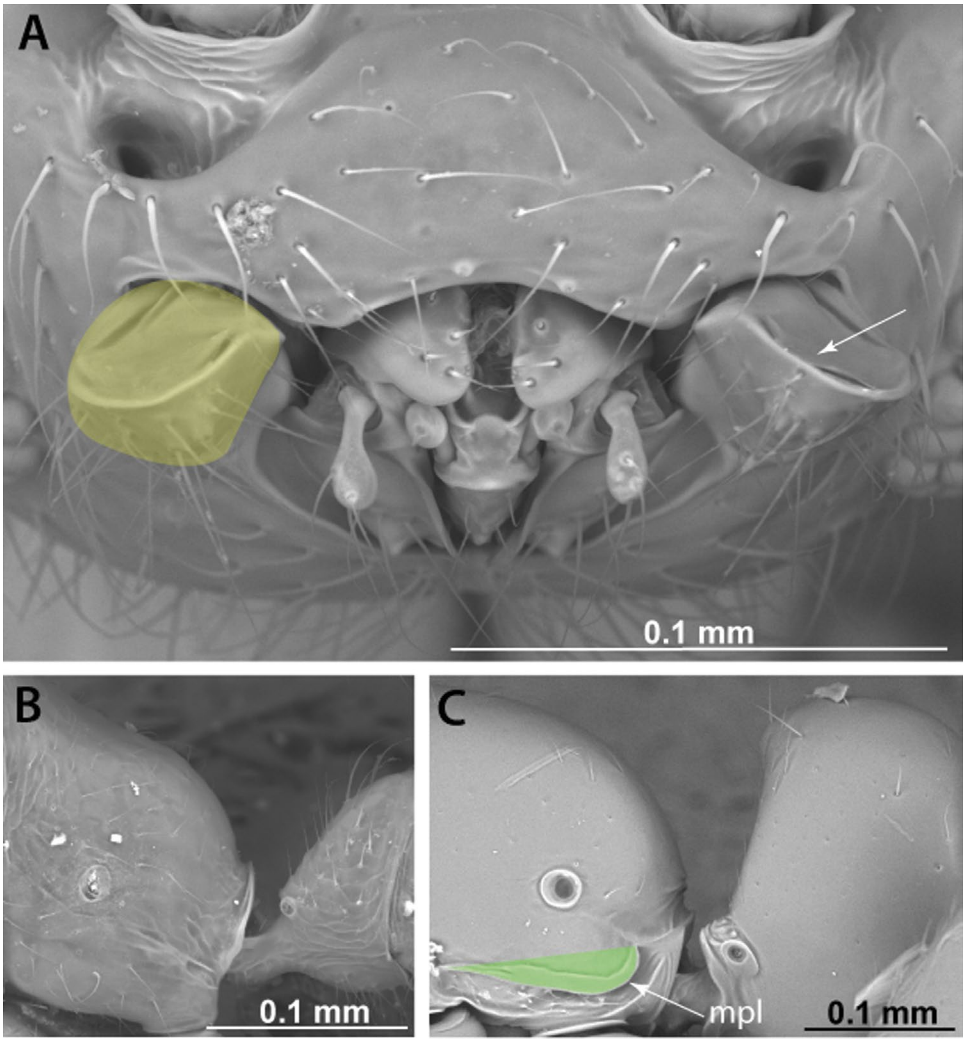


Fig. 9. Synapomorphies of the Leptanillomorpha. All images by Zachary Griebenow. A) *Leptanilla belantanoides* Griebenow et al. 2025 (CASENT0842882), male mandible (yellow) edentate. B) *Leptanilla* nr. *indica* (Kugler 1986) (CASENT0106381), male metapleural gland absent. C) *Protanilla wardi* Bharti and Akbar 2015 (CASENT0221924), cuticular flap (green; **mpl**) dorsal to metapleural gland.

Several ponerine lineages have gamergates, a distinct caste of reproductive females that is rare in other Formicidae (Peeters 2012, Boudinot et al. 2025). The generic classification was revised and natural history reviewed by Schmidt and Shattuck (2014).

The diverse Amblyoponinae and monotypic Apomyrminae are relatively well-supported by molecular data as sister groups, together forming clade **Amblyoponomorpha** (Fig. 11) (Ward and Fisher 2016, Romiguier et al. 2022, Borowiec et al. 2025). These cryptobiotic predators—usually found in humid climates—are united by compound eyes (when present) being situated posterad head midlength (Fig. 13A and C). The Amblyoponomorpha likely originated in the Afrotropics (Ward and Fisher 2016). The **Amblyoponinae** are uniquely diagnosed among Formicidae by the broad and supra-axial helcium (ie the articulation between the petiole and gaster is set above midheight of abdominal segment III; Bolton 2003, Keller 2011), while larval hemolymph feeding (Masuko 1986) is prevalent in the subfamily. Ants of the amblyoponine genus *Mystrium* Roger 1862 possess a "snap-jaw" mechanism that results in some of the fastest animal movements known on Earth (Larabee et al. 2018). The Amblyoponinae are still in need of integrative systematic revision, particularly given the paraphyly of *Stigmatomma* Roger 1859 (Ward and Fisher 2016). The **Apomyrminae** are specialized and rarely collected subterranean predators of centipedes, displaying multiple morphological convergences with the Leptanillinae (Bolton 2003, Boudinot 2015).

The relationships of the remaining Poneria (Fig. 14) are difficult to disentangle (Borowiec et al. 2025), but a candidate synapomorphy for Paraponerinae, Agroecomyrmecinae, and Proceratiinae is the fusion of the pro- and mesonotum (Richter et al. 2023) (Fig. 15). Among these subfamilies, the **Paraponerinae** are large, epigeic Neotropical ants, including the single extant species *Paraponera clavata* (Fabricius 1775). Known for outstandingly painful stings, *P. clavata* has cultural significance in the initiation rites of several Amazonian cultures (Fernandes et al. 2015). It is possible that the Paraponerinae are sister to the Agroecomyrmecinae (eg Borowiec et al. 2025) or to a clade comprising both Proceratiinae and **Agroecomyrmecinae** (Romiguier et al. 2022). The latter contains 2 extant species, *Tatuidris tatusia* Brown and Kempf 1968 and *Ankylomyrma coronacantha* Bolton 1973. The bowed mandibles and baleen-like chaetae ("thick setae"; Boudinot et al. 2021) on the mandibular under-surface of

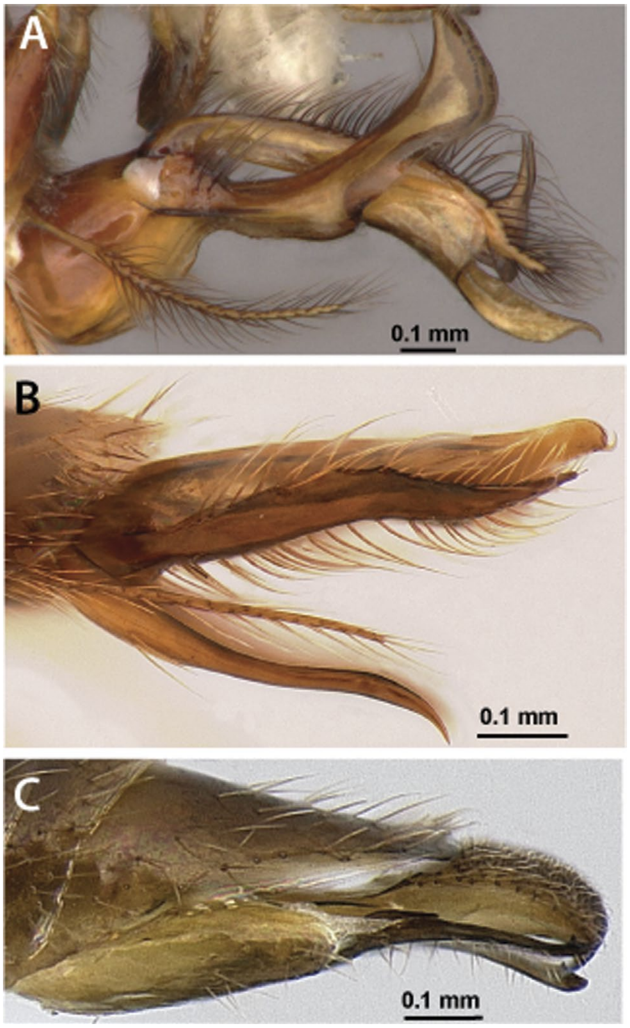


Fig. 10. Male genitalia of the Leptanillinae, profile view. All images by Zachary Griebenow. A) *Leptanilla* zhg-my06 (CASENT0106370). B) *Leptanilla* zhg-id01 (CASENT0842626). C) *Leptanilla* zhg-my10 (CASENT0842599).

the Neotropical leaf-litter-dwelling *T. tatusia* imply specialized predation, but its diet is unknown (Jacquemin et al. 2014). Even less is known of the arboreal and Afrotropical *A. coronacantha*, which has a grossly hypertrophied abdominal tergite IV (Fig. 16C). The **Proceratiinae** are diminutive pantropical ants, almost always living in concealed microhabitats. Although molecular data robustly support the monophyly of this subfamily, the only morphological synapomorphy yet known is the complete (or nearly complete) exposure of the antennal socket (Bolton 2003), which is homoplasious with Dorylinae and Leptanillinae. Proceratiines are either specialized predators on arthropod eggs (Brown 1957, Dejean et al. 1999); or, in the case of *Probolomyrmex* Mayr 1901 (Fig. 16A), polyxenid millipedes (Ito and Hosokawa 2020). Proceratiine genera are still identifiable as presented in Bolton (1994), but *Proceratium* Roger 1863 is likely paraphyletic (Borowiec et al. 2019).

Sister to the Poneria is the "formicoid clade," **Doryloformicia**, for which subfamilial relationships have been uncontroversial across molecular phylogenetic analyses. The search for synapomorphies defining this clade is ongoing and has yet to yield robust characters. One plausible synapomorphy of this clade is loss of tergosternal fusion in the abdominal postsclerites III (Boudinot et al. 2022a), although this would imply several reversals to the fused condition (eg Ectatomminae). The 2 constituent clades of Doryloformicia are the Formicia and the **Dorylinae** (Fig. 17). The latter is an exceptional radiation of subterranean predators with a pantropical to warm temperate distribution. The bulk of doryline species diversity belongs to the 2 clades that convergently acquired the suite of behavioral and morphological traits collectively termed the "army ant syndrome": one Neotropical (army ants), and the other Paleotropical (driver ants and kin). The interrelationships of genera formerly attributed to the subfamily Cerapachyinae, which was synonymized with Dorylinae by Brady et al. (2014), are statistically challenging to resolve (Borowiec 2019, Borowiec et al. 2025). The Dorylinae are well-defined morphologically (eg Bolton 1990a, 1990b, 2003, Borowiec 2016). With few exceptions (eg *Cylindromyrmex* Mayr 1870, de Andrade 1998), the Dorylinae are specialist brood predators of ants or other social insects, or are swarm-raiding generalists (Kronauer 2020). The subfamily was revised and natural history reviewed at the generic level by Borowiec (2016).

The remaining Doryloformicia, the clade **Formicia** (Figs. 16–19), are the most ecologically diverse group of ants, prevalent in the tropics and dominant among the temperate myrmecofauna. Omnivory is a reasonable synapomorphy of Formicia, as many members of this clade feed on seeds, extrafloral nectaries, or hemipteran excreta. The **Myrmeciomorpha** (Myrmeciinae and Pseudomyrmecinae; Fig. 17) are active, ground-nesting or arboreal ants with expanded compound eyes and superficially wasp-like habitus. They are united by a metabasitarsal sulcus and antennal sensilla basiconica with sockets raised above the cuticle (Bolton 2003). *Myrmecia* Fabricius 1804 and *Nothomyrmecia* Clark 1934 (**Myrmeciinae**) are restricted to Australia and New Caledonia, with Cenozoic fossil representation of the Myrmeciinae from Europe and North America (eg Archibald et al. 2006, Jouault and Nel 2022; South American representatives are debatable). These ants are primarily visual huntresses. **Pseudomyrmecinae** contrast with Myrmeciinae in the anteroposterior compression of the clypeus and short mandibles (Bolton 2003). Restricted to tropical and warm temperate climates, they are most abundant and speciose in the Americas and Madagascar. Pseudomyrmecinae is one of the principal radiations of exclusively arboreal ants, and many live in close association with plants that they protect from herbivores in exchange for domatia and nectar. The subfamily is undergoing iterative revision, and its 3 genera, *Pseudomyrmex* Lund 1831, *Tetraponera* Smith 1852, and *Myrcidris* Ward 1990, are currently identifiable using Ward (1990) and Bolton (1994).

The **Dolichoderomorpha** (Fig. 18), a clade comprising Aneuretinae and Dolichoderinae, show an array of homoplasies with the Formicinae, including a distinctive configuration of the cuticular flap dorsal to the metapleural gland orifice, described by Bolton (2003). The **Dolichoderinae** are distinctive for their rudimentary stinger and pungent chemicals produced in the pygidial glands. Dolichoderine ants are cosmopolitan, but most diverse and dominant in Australasia; they are omnivorous, and include some of the more destructive invasive species within the Formicidae worldwide. The genera of Dolichoderinae remain largely identifiable using Shattuck (1992) and Bolton (1994). Sister to the Dolichoderinae is *Aneuretus simoni* Emery 1893 (**Aneuretinae**), a relict species restricted to Sri Lanka that shares several apomorphies with Dolichoderinae but retains a well-developed sting. Together with *Nothomyrmecia macrops* Clark 1934 (Myrmeciinae: Prionomyrmecini), *A. simoni* is one of only 2 extant ants without a defined cinctus (= anterior constriction of abdominal segment IV), yet with a functional piercing stinger. While many Cretaceous-Paleogene fossils from across the world have been associated with the Aneuretinae, it is unclear

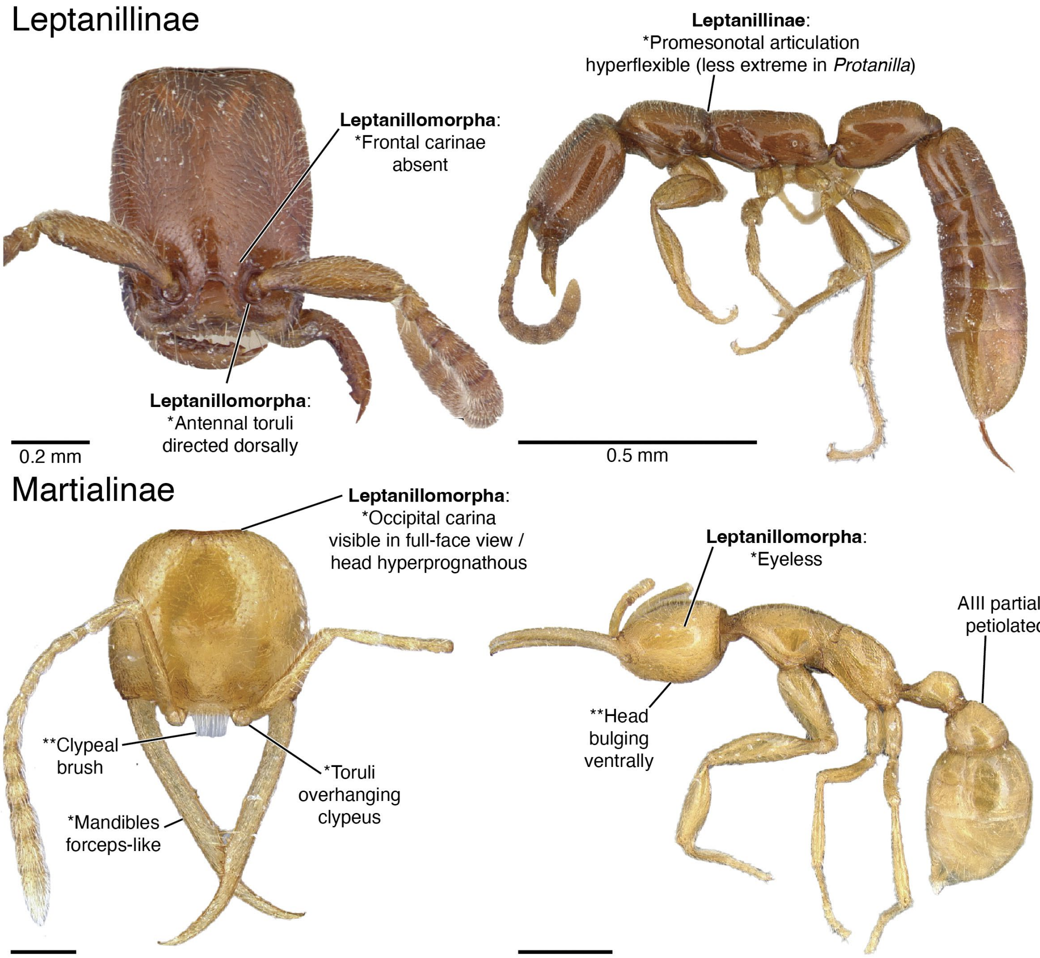


Fig. 11. Diagnostic and apomorphic characters of Leptanillomorpha. Characters from Griebenow (2024), Boudinot et al. (2022a). * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Images modified from AntWeb (Martialinae: *Martialis heureka* Rabeling and Verhaagh 2008, CASENT0106181, Michael Branstetter; Leptanillinae: *Opamyrma hungvuong* Yamane et al. 2008, CASENT0178347, April Nobile). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

which, if any, of these are closely related to *A. simoni* (Boudinot 2015, Barden 2017, Boudinot et al. 2022a, 2022c). The fossil species †*Protaneuretus succineus* Wheeler 1915 at least shares with *A. simoni* the apomorphic condition of having the posterior petiolar foramen rotated ventrad, such that the helcium is nearly perpendicular to the long axis of the petiole (Fig. 19).

Sister to Ectatomminae and Myrmicinae, the **Formicinae** (Fig. 18) is the second most diverse ant subfamily at the species level, with much of this diversity in the tribe Camponotini. Many formicines are scavengers or liquid feeders on carbohydrates, with some having established obligate mutualisms with various Sternorrhyncha (eg *Acropyga* [see LaPolla 2005]). Others are ant-plant specialists (eg *Myrmelachista* Roger 1863a, *Cladomyrma* Wheeler 1920) or acutely sighted predators (eg *Gigantiops* Roger 1863b, *Myrmoteras*). The tribal arrangement of Formicinae was substantially revised by Ward et al. (2016), following the phylogenomic results of Blaimer et al. (2015). The genera of Formicinae are identifiable using Bolton (1994), with revisions for Paleotropical taxa in Fisher and Bolton (2016).

The closest relatives of the Formicinae may be the extinct subfamily †**Formiciinae**, known only from the Paleogene of North America and Europe. All species of this extinct subfamily are only known from reproductives. These ants were gigantic, sometimes exceeding the length of the largest extant ant (Archibald et al. 2023), the queen of *Dorylus wilverthi* Emery 1899 (Raignier and van Boven 1955). Unlike this wingless form, however, formiciine queens were alate. The placement of †Formiciinae has yet to be evaluated using statistical phylogenetics; they were inferred by Lutz (1986) to be close to Formicinae due to the form of the petiole and the reduction of the stinger. Given their enlarged and exposed abdominal spiracles (Lutz 1986), it is possible that they are closely related to Dorylinae, for which this condition is synapomorphic (Bolton 1990a).

Lastly, the Ectatomminae and Myrmicinae are united as the clade **Myrmicomorpha** by a slit-shaped metapleural gland orifice (Fig. 20). The **Ectatomminae** display tergosternal fusion of abdominal segments III–IV, a character of uncertain polarity at the level of Formicia. These ants are conspicuous and abundant in the Neotropical and Indo-Australian ecoregions and absent from the Afrotropics, with the monotypic *Aulacopone* Arnol'di 1930 being endemic to Hyrcanian mixed forests (Western Palearctic). Many species are robustly built omnivores or predators that forage on the ground and vegetation, with some being specialized millipede predators (Brown 1993). The subfamily and generic boundaries therein were recently revised by Camacho et al. (2022) based

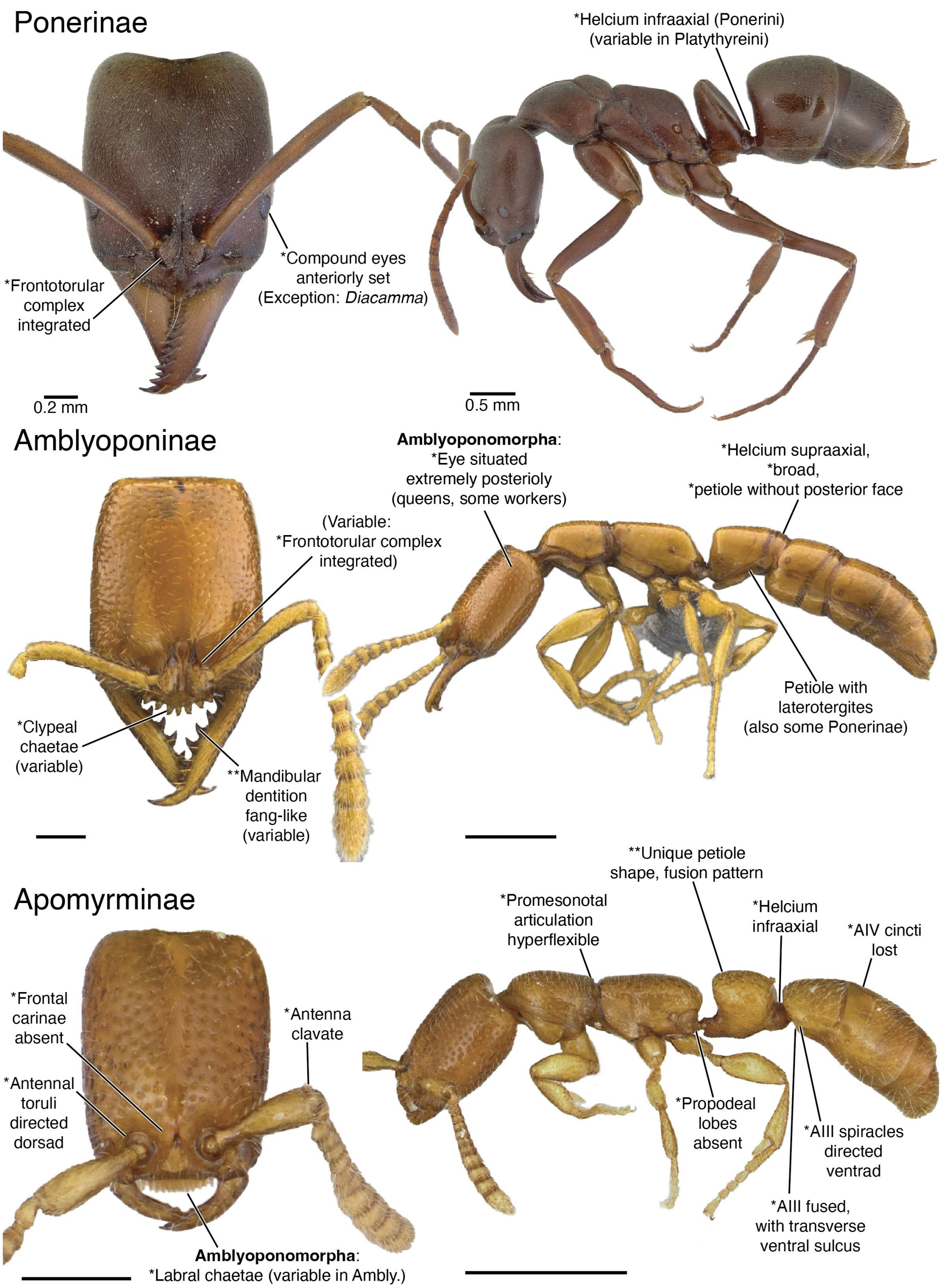


Fig. 12. Diagnostic and apomorphic characters of Ponerinae and Amblyoponomorpha (Amblyoponinae, Apomyrminae). Characters from Richter et al. (2023). * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Images modified from AntWeb (Ponerinae: *Mesoponera* anic01, CASENT0172439, April Nobile; Amblyoponinae: *Stigmatomma* afrc-za01 CASENT0813005, Peter Hawkes; Apomyrminae: *Apomyrma stygia* Brown et al. 1971, CASENT0000077, April Nobile). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

on phylogenomic analyses. The **Myrmicinae** are hyperspeciose, with nearly the full ecological and behavioral diversity of the Formicidae represented within this clade alone, in addition to such exceptional phenomena as fungus-farming (Attina). Despite this variety, myrmicines are uniquely recognizable by the circular form of their helcium, without the tergites overlapping the sternites (Bolton 1990a, 2003). Unlike the 3 next most speciose ant subfamilies, which are all attested by fossils from the beginning of the Late Cretaceous, the first definitive Myrmicinae appear in the fossil record only shortly after the K-Pg boundary (Wheeler 1915, Radchenko and Perkovsky 2016). The Myrmicinae have not been taxonomically revised at the global level since Bolton (1994), although a comprehensive phylogeny (Ward et al. 2015) and numerous regional keys have accumulated since then.

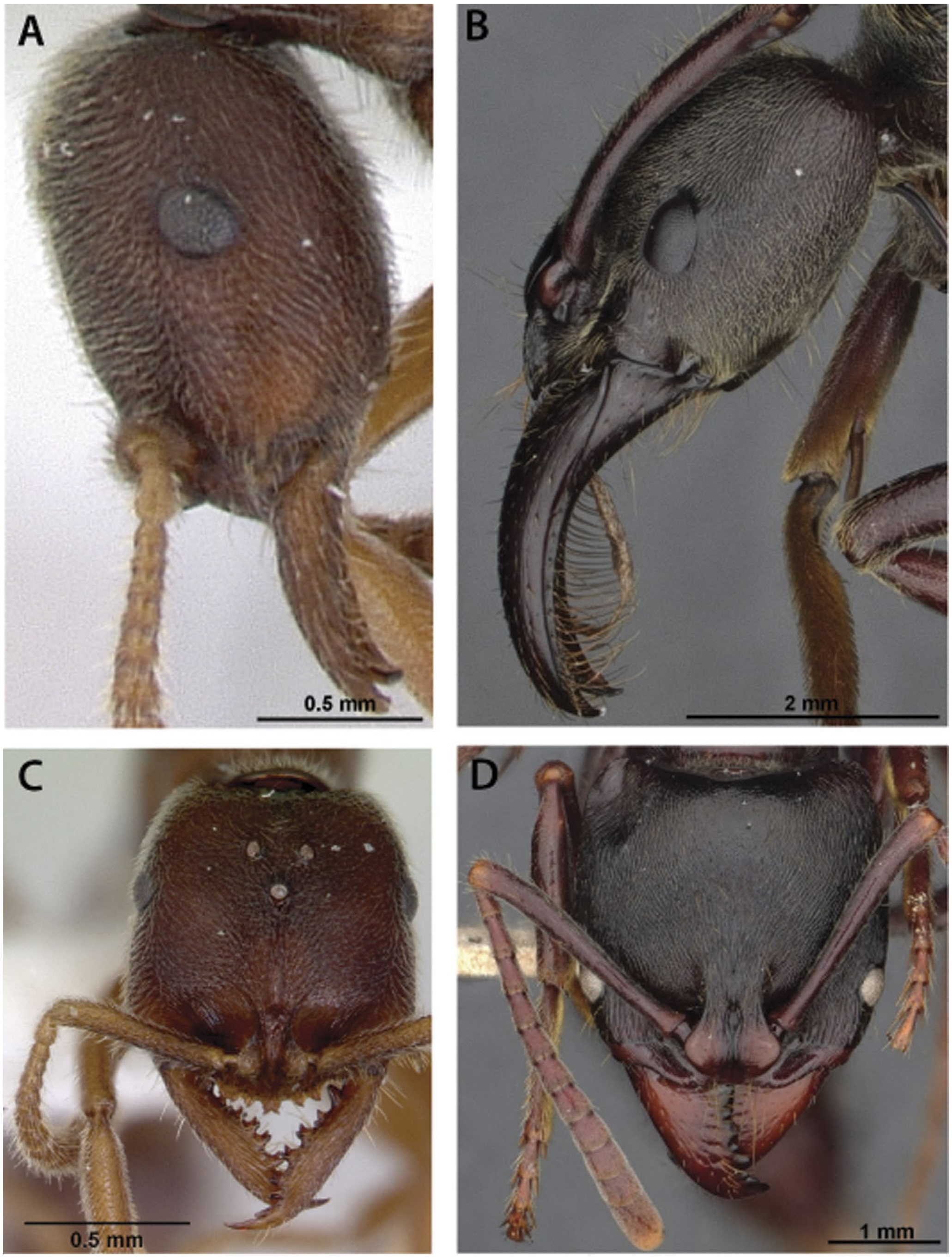


Fig. 13. Placement of compound eye in the Poneria, profile A and B) and full-face C and D) views. A, C) *Fulakora saundersi* (Forel 1892) (CASENT0172388, April Nobile). B) *Paltothyreus tarsatus* (Fabricius 1798; CASENT4034386, Brittany Kohler). D) *Pachycondyla lattkei* MacKay and MacKay 2010 (CASENT403487, Brittany Kohler).

Summary of Apomorphies of Total and Crown Clade Formicidae

The **Formicoidea** and the **crown clade Formicidae** are diagnosable by the following (variably reversed or lost) syn- and autapomorphies. For sources, see Boudinot et al. (2020, 2022a), Richter et al. (2022), and references therein. Abbreviations: F = female, W = worker, Q = queen, M = male, A = all. The strongest diagnostic conditions are underlined and characters determined since Bolton (2003, pp. 15, 288–290) are indicated with an asterisk (*). See Fig. 4, where each derived condition is numbered in parentheses.

Formicoidea or Total Clade Formicidae (ie All Ants, Living and Extinct)

Characters of the head. (**1**) F: eyes reduced in size, taking up ½ head length (note; sometimes secondarily enlarged); (**2**) F: the postgenal bridge is elongate, hence the head appears prognathous; (3*) F: the secondary (= dorsal = cranial) condyle of the mandible is conspicuously enlarged; (**4***) F (A?): the base of the pedicel is "pinched" in appearance and curved, giving the antenna a "geniculate" appearance (eg Bolton 2003) even without proportional elongation of the scape and shortening of the flagellum; (**5***) F: the labrum proximally bears

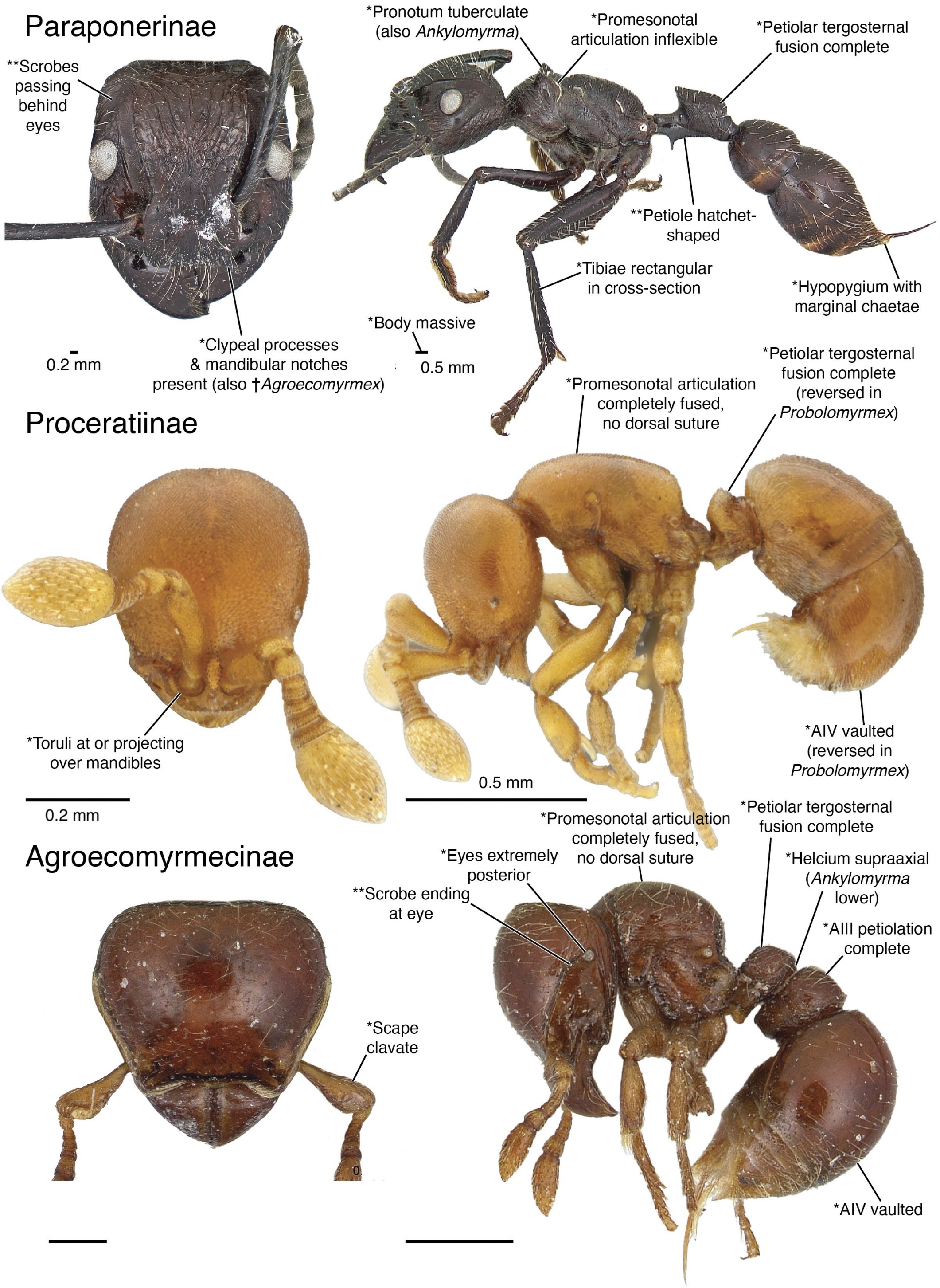


Fig. 14. Diagnostic and apomorphic characters of Paraponerinae, Proceratiinae, and Agroecomyrmecinae. Characters from Richter et al. (2023). * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Images modified from AntWeb (Paraponerinae: *Paraponera clavata*, CASENT0003165, April Nobile; Proceratiinae: *Discothyrea bobi* Chaul 2020, UFV-LABECOL000035, Júlio Chaul; Agroecomyrmecinae: *Tatuidris tatusia*, CASENT0178882, Erin Prado). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

a transverse line of chaetae, ie thickened *sensilla trichodea* (Altner and Prillinger 1980) (absent in most crown Formicidae); (6*) F: the face between the frontal carinae is bulging as seen in oral view, hence the antennal toruli are directed laterally; (7*) F: the dorsal tentorial arm is reduced, at most ⅓ the length of the anterior tentorial arms.

Characters of the mesosoma. (8*) F: the pronotum is elongate (note: secondarily shortened in various crown groups in association with claustral colony foundation, Keller et al. 2014; pronotal length variable among other Aculeata); (9*) A: the prodisticoxal foramen is closed, such that the membrane between the procoxa and

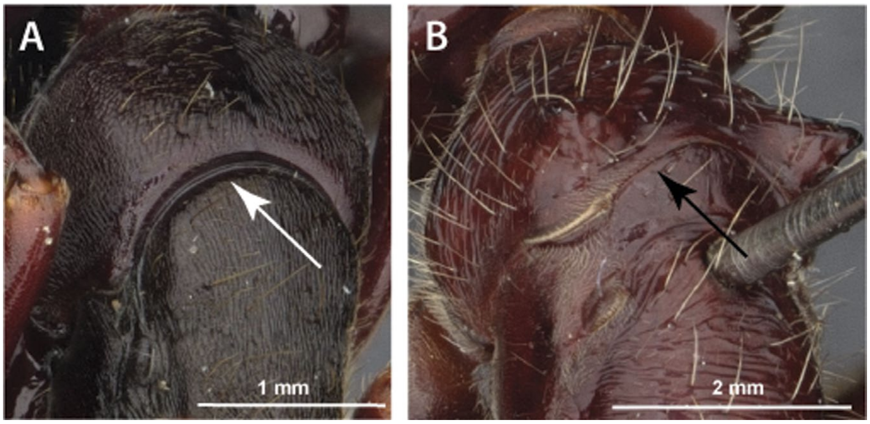


Fig. 15. Variation in the promesonotal boundary in the Poneria, marked with arrows. Images by Brittany Kohler. Fully articulate A) (*Pachycondyla lattkei*, CASENT403487). Expressed as suture B) (*Paraponera clavata*, CASENT4034385).

Fig. 16. Condition of abdominal segment IV in the Poneria. Green = tergite; pink = sternite. A) *Probolomyrmex curculiformis* Hita Garcia and Fisher 2014 (CASENT0469570, Michele Esposito). B) *Discothyrea michelae* Hita Garcia and Lieberman 2019 (CASENT0235469, Will Ericson). C) *Ankylomyrma coronacantha* Bolton 1973 (CASENT0005904, April Nobile).

protrochanter is concealed (shared among all adult ants, including social parasites; unique to the Formicidae, but approached by some female Myrmosidae); (**10***) F (A?): the meso- and metathoracic coxal cavities are set in a single plane that is parallel to the ground, hence concealed in lateral view; (11) F (A?): the metapleural gland is present.

Characters of the metasoma. (**12**) A: the second abdominal segment is petiolated, with (12a) at least some anterior elongation, (12b) indication of a node via the formation of a posterodorsal face, and (12c) formation of the helcium, ie constriction of the articulation between abdominal segments II and III (metasomal I and II) (note: occurs in some other Aculeata, such as Bradynobaenidae); (**13***) A: the "subpetiolar" process (= anteroventral process of the petiolar sternum) is present; (**14***) A: the prora is present, ie there is a transverse ridge or bulge subtending the helcium of abdominal segment II; (**15***) A: abdominal segment IV is transversely constricted, forming the cinctus.

Characters of the wings. (**16**) Q, M: forewing without 3rs-m and 2m-cu; (**17**) F: winged-wingless polyphenism present, ie morphologically distinct "Q" and "W" castes present (this excludes the †*Camelomecia* genus-group, for which wingless females are unknown, and stem taxa too poorly preserved to place with confidence; such polyphenism occurs rarely among other Hymenoptera [Hanna and Abouheif 2021]); (**18**) F: after mating, wings dehisce (ie are removed) (Bolton 2003, p. 15).

Note. Presence of the infrabuccal pouch has been thought to be a synapomorphy of the Formicidae (eg Eisner and Happ 1962, Bolton 2003); although well-developed in ants, it is also present in diverse Aculeata (Richter et al. 2022) and has not been well investigated enough to determine its polarity. Bolton (2003) also indicates the occurrence of perennial colonies and the occurrence of mass nuptial flights as synapomorphies of Formicidae. Colony lifespan in stem ants is uncertain and the polarity of mass flights within the family has yet to be tested.

Crown Clade Formicidae (ie All Living Ants and Their MRCA)

(1*) F: the postgenal bridge is considerably elongated, being >50% of the total length of the head;
(2*) F: the abductor swelling of the mandible is enlarged, hence forming a distinct atala;
(3*) F: the mandibular dentition is increased, with ≥3 teeth;
(4) F: the mandible is no longer bidentate and falciform (note: although difficult to define, the crown Formicidae do not have the "wasp-like" mandibular form of stem Formicidae);
(5*) F (A?): the fibrillar fibers of *Musculus craniomandibularis internus* (0md1) are present; and
(6) F: the propodeal spiracle is subcircular in outline.

Major Taxonomists and Pioneers

The history of ant classification can be divided into 5 eras based on the authors or publications of primary influence at the time

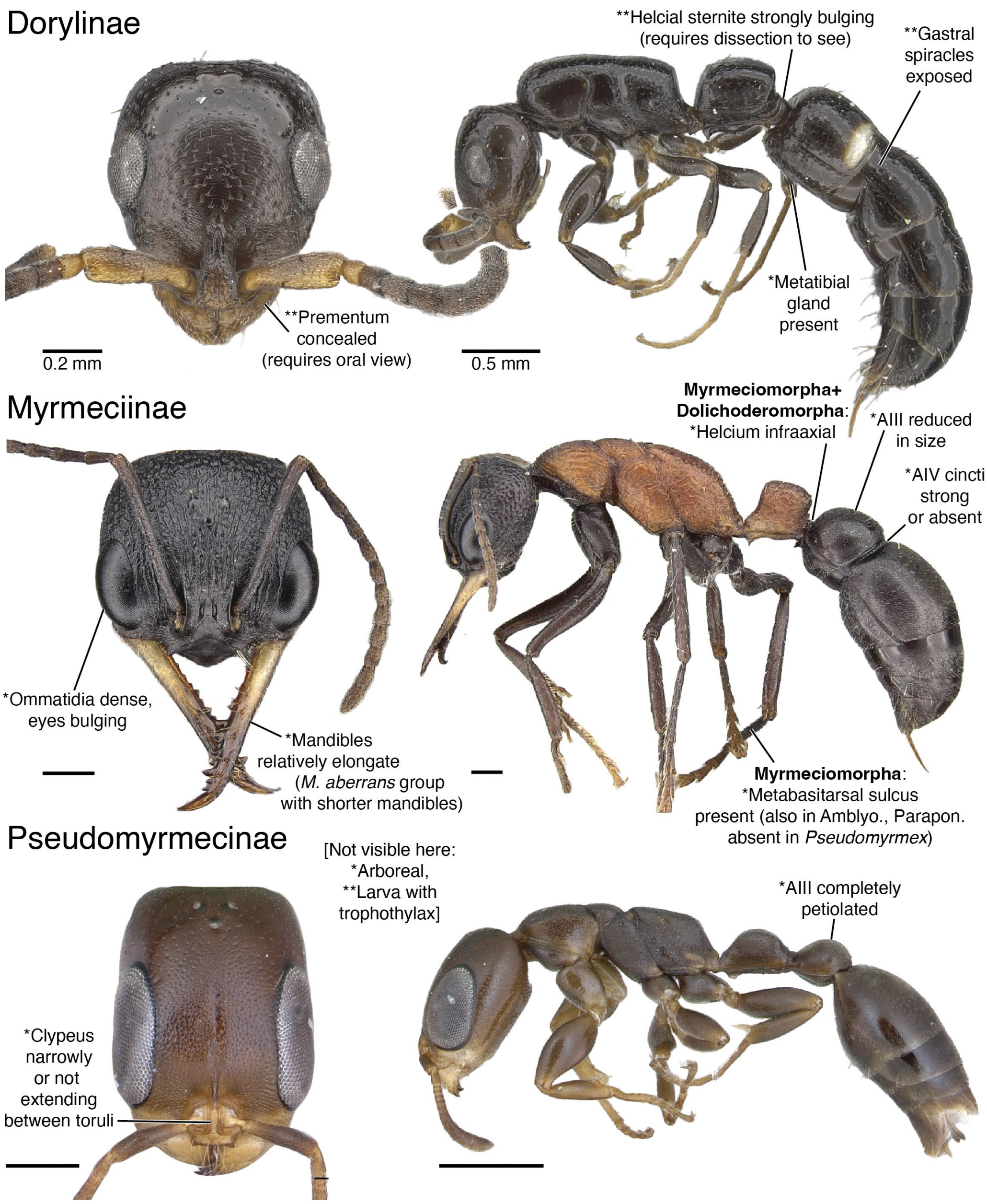


Fig. 17. Diagnostic and apomorphic characters of Dorylinae and Myrmeciomorpha (Myrmeciinae and Pseudomyrmecinae). * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Characters from Bolton (2003), Ward (1990), Brady and Ward (2005), Ward and Downie (2005). Images modified from AntWeb (Dorylinae: *Tanipone maculata* Bolton and Fisher 2012, CASENT0001335, Shannon Hartman; Myrmeciinae: *Myrmecia swalei* Crawley 1922, CASENT0914036, Ziv Lieberman; Pseudomyrmecinae: *Pseudomyrmex acanthobius* Emery 1896, CASENT0173746, April Nobile). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

(Table 2). (i) The "primordial" or earliest era of ant systematics may be construed as the prescientific writings prior to the Linnaeus (1758). Most notable among these is the 1742 to 1743 work of René Antoine Ferchault de Réaumur, rediscovered and translated by Wheeler (de Réaumur 1926). (ii) During the "classical era," Fabricius, Latreille, Lepeletier de Saint-Fargeau, and others provided the first formal definition of ants (Fabricius 1775, 1781). Names from early, preevolutionary works were adapted to meet the increasing regimentation of the taxonomic hierarchy. These works, particularly that of Lepeletier de Saint-Fargeau (1835 ("1836")), also established the early foundations of the morphological systems that were used for classifying ants until the advent of gel electrophoresis and Sanger sequencing in the late 20th century.

(iii) The "evolutionary era" (1853 to 1942) began with the first publications of Gustav Mayr (1830 to 1908; Fig. 21F), who along with Frederick Smith (1805 to 1879), William Nylander (1822 to 1899), and Julius Roger (1819 to 1865), established the foundations of the generic system for ants. Mayr's works were particularly important in this regard, as he provided "analytical tables," which we now know as keys (Mayr 1853c, d, e, 1855, 1861, 1862, 1868, 1870). Development of the subfamilial and tribal systems was spurred on

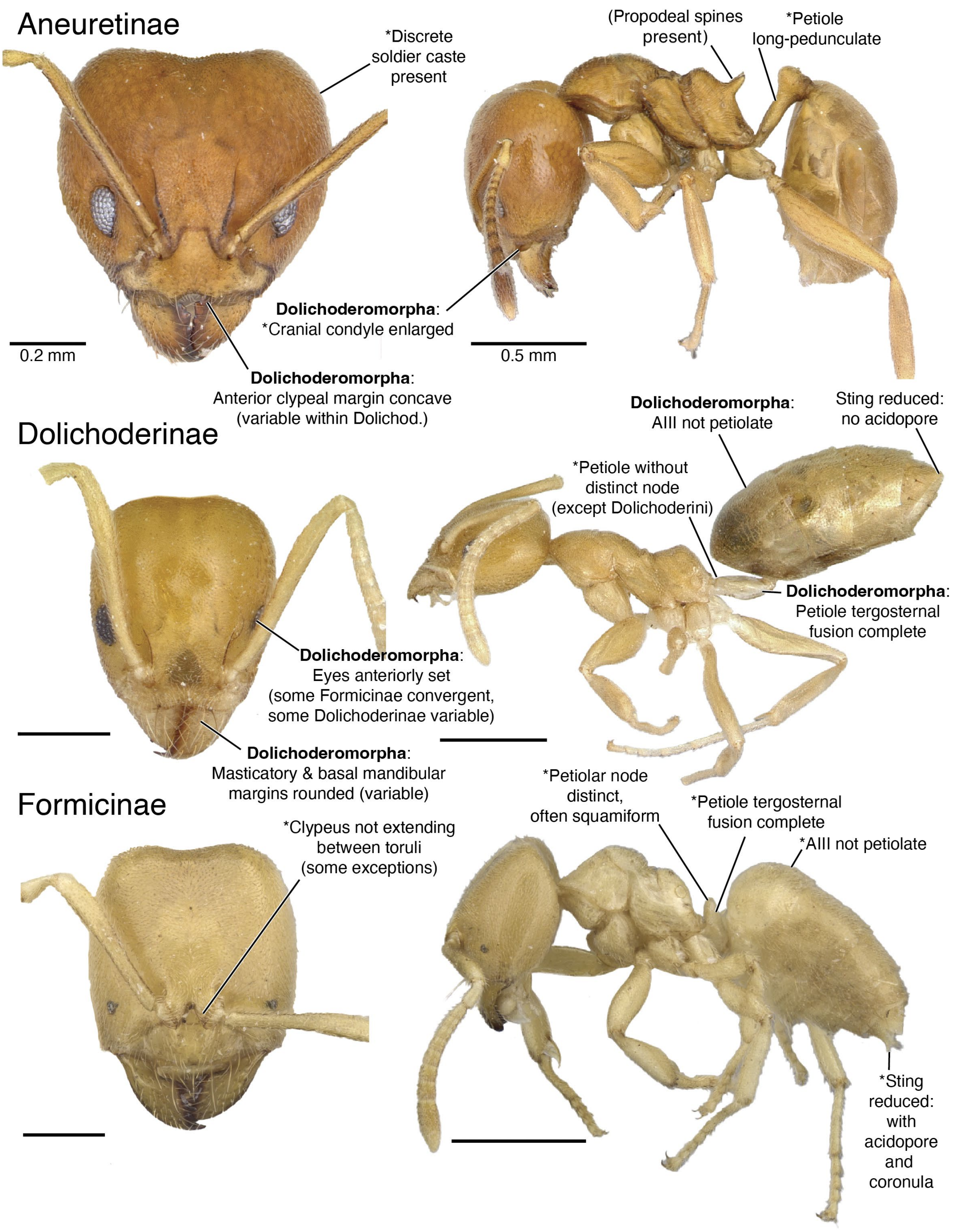


Fig. 18. Diagnostic and apomorphic characters of Dolichoderomorpha (Dolichoderinae, Aneuretinae), and Formicinae. * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Characters from Bolton (2003), Boudinot et al. (2022b, c). Images modified from AntWeb (Aneuretinae: *Aneuretus simoni*, CASENT0007014, April Nobile; Dolichoderinae: *Technomyrmex docens* Fisher and Bolton 2007, CASENT0435450, April Nobile; Formicinae: *Acropyga ambigua* Emery 1922, CASENT0249914, Will Ericson). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

by the pioneering anatomical work of Auguste-Henri Forel (1848 to 1931; Fig. 21I), particularly "*Études myrmécologiques en 1878*" (Forel 1878). Carlo Emery (1848 to 1925; Fig. 21G) produced the major framework for the subfamilial system of ants, including explicit phylogenetic hypotheses for the relationships of the higher taxa of ants, especially in his contributions to *Genera Insectorum* (1910 to 1925). William Morton Wheeler (1865 to 1937; Fig. 21H) adopted the system of Emery in *Ants of the Belgian Congo* (Wheeler 1922), and popularized myrmecology in the English language; his book, *Ants: Their Structure, Development and Behavior* (Wheeler 1910) remains a valuable reference to the present day. Collectively, Emery, Wheeler, and Forel described 7,842 original names (protonyms) (Bolton 2024), many of which represented extreme typological combinations of intraspecific categories (Brown 1950a, 1955, Wilson and Brown 1953). During this era, Felix Santschi (1872 to 1940) and Mikhail Dmitrievich Ruzsky (1846 to

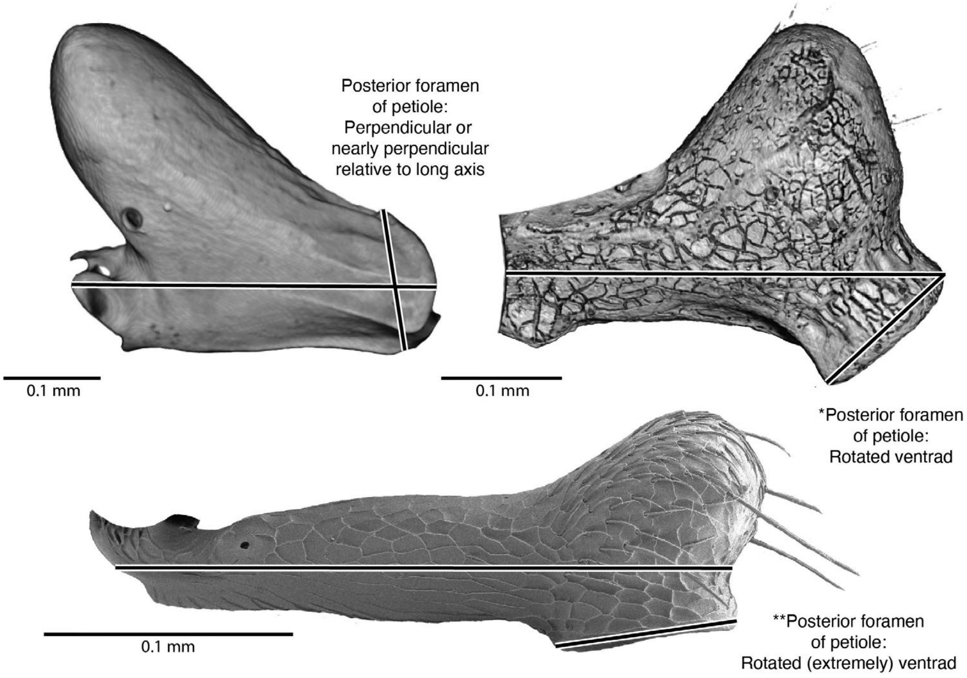


Fig. 19. A new synapomorphic condition of the Aneuretinae: ventrad rotation of the posterior petiolar foramen relative to the long axis of the petiole. Top left = *Dolichoderus thoracicus* (Smith 1860) (Dolichoderinae; BEB-KIT230, SMFHYM0007938). Top right = †*Protaneuretus succineus* Wheeler 1915 (Aneuretinae; fsu_040_desy67, CASENT0753217). Bottom = *Aneuretus simoni* (ANTWEB1008503, imaged by R. Keller).

1948) provided significant alpha taxonomic contributions, while William Harris Ashmead (1855 to 1908) attempted to classify ants in the broader context of the Hymenoptera.

(iv) The "modern era" of ant taxonomy may be marked by the first publication of William L. Brown Jr. (1922 to 1997) on ants (Brown 1943). Brown and E. O. Wilson (1929 to 2021; Fig. 21J) had an outsized influence on the development of myrmecology in this era. Besides innovative efforts to describe and catalog the ants, Brown's revisionary efforts provided the global community with a pragmatic framework for the study of ant diversity. Perhaps Brown's most notable systematic works were his hypothesized phylogeny for the Formicidae (Brown 1954) and generic revisions of the Myrmicinae (Brown 1948, 1949, 1950b, etc.) and the Ponerinae sensu lato (Brown 1952, 1965, 1975, etc.). Major contemporary contributors to the higher classification and phylogeny of ants included William Steel Creighton (1902 to 1973), Roy R. Snelling (1934 to 2008), and Robert W. Taylor. George C. and Jeanette Wheeler established the global baseline of knowledge for ant larvae (Wheeler and Wheeler 1976); Frank Morton Carpenter (1902 to 1994) and Gennady M. Dlussky (1937 to 2014), likewise, for the fossil record. The most significant single works for ant taxonomy since Mayr and Emery were no doubt those of Barry Bolton (1946 to present; Fig. 21K) (Bolton 1994, 1995, 2003) including his global *New General Catalog of the Ants of the World* (Bolton 1995).

However, smaller-scale treatments are also invaluable. During and since the aforementioned "evolutionary era," many taxonomists furthered myrmecological knowledge by cataloging and reorganizing major regional faunas. Catalogs allowed many other works to be carried out and required dedicated effort from the author(s) to gather the bibliography at the time. These taxonomists include the following: in Africa, Arnold (eg Arnold 1915), W.M. Wheeler (eg Wheeler 1922), Fisher, and Bolton (eg Fisher and Bolton 2016); in India, Bingham (eg Bingham 1903); in Southeast Asia and Indomalaya, Chapman, Capco (eg Chapman and Capco 1951), Viehmeyer, Wheeler, Yamane, Terayama, Wang, and others; in Australia, Crawley and Taylor (eg Taylor and Brown 1985); in Palearctic Asia, Ruzsky, Dlussky, Karawaiew, Radchenko, and Pisarski; in Central and South America, Kusnezov, Bruch, Borgmeier, Mann, Kempf (eg Kempf 1972), and Brandão (eg Brandão 1991); and in North America, Creighton (eg Creighton 1950), Snelling, and G. C. and J. Wheeler. A more detailed, comprehensive, and up-to-date list of catalogs and synoptic classifications can be found on AntCat (www.antcat.org).

The "modern era" also saw women become professional ant systematists for the first time—Jeanette Wheeler (first publication: 1951) and Maria Lourdes de Andrade (first publication: 1992). Prior to this point, only 5 pioneer female myrmecologists were recognized with species names designated arising from their collections and study (Table 1). Despite exclusion from the sciences, these women made their mark on the study of ants. They were naturalists who corresponded with Mayr, Forel, and Darwin (Mary Treat, 1830 to 1923; Fig. 21A) (Bonta 1991, Carruso and Kohn 1997, Creese 2000) and explorers who published species descriptions (Princess Therese von Bayern, 1850 to 1925; Fig. 21B) (von Bayern 1897, Creese 2000) and contributed new species to the London Museum (Lucy Cheesman, 1881 to 1969; Fig. 21C) (Hugh 2013). In the 20th century, Elizabeth Skwarra (1886 to 1961; Fig. 21D) published zoological studies and collected Neotropical ant-plants that informed 2 studies by Wheeler (1931, 1934), and Mary Talbot (1903 to 1990; Fig. 21E) established the field of physiological ecology with her rigorous experimental work on ants (Kannowski 2012). Talbot was recognized by 2 patronyms, of which one represents a key taxon for the study of social parasitism (Borowiec et al. 2021).

(v) Lastly, the end of the "modern era" and the beginning of the "contemporary era" is marked by the near-simultaneous publication

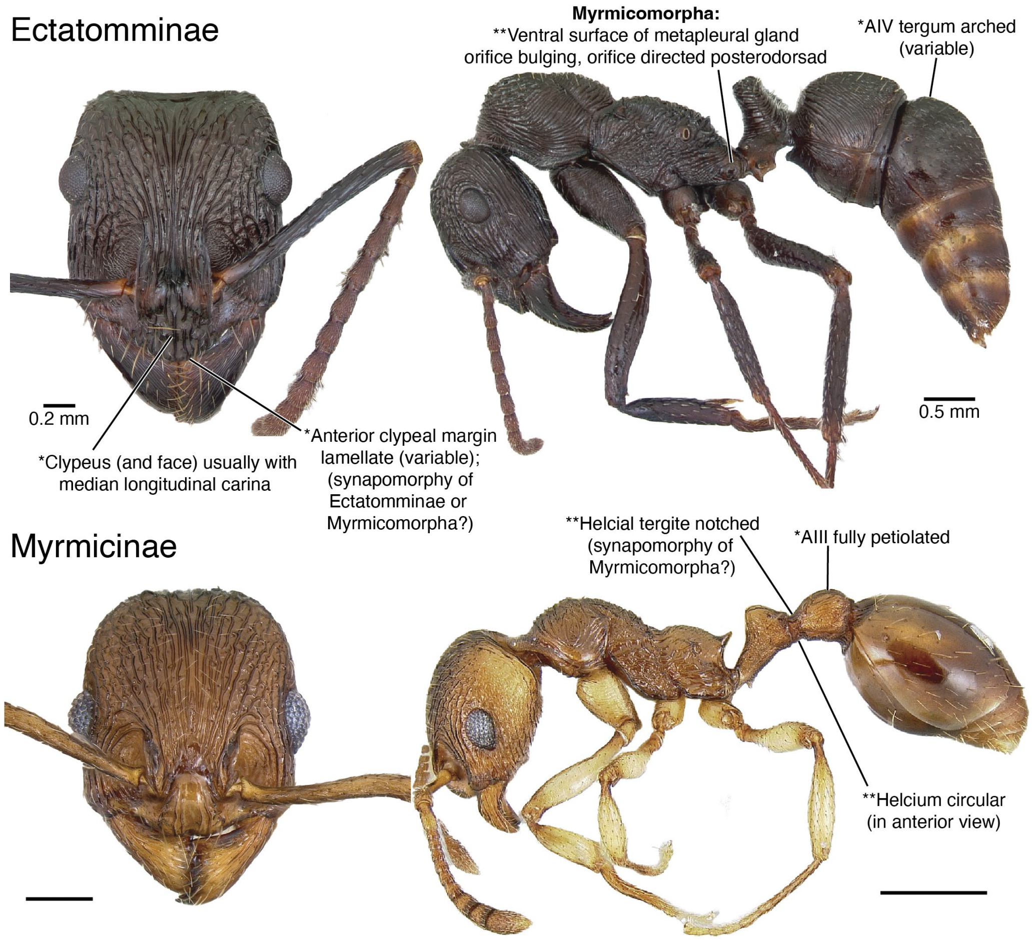


Fig. 20. Diagnostic and apomorphic characters of Myrmicomorpha (Ectatomminae and Myrmicinae). * = synapomorphies; ** = autapomorphies; absence of asterisks = diagnostic plesiomorphies. Characters from Bolton (2003), Keller (2011), Boudinot et al. (2022a), and Camacho et al. (2022). Images modified from AntWeb (Ectatomminae: *Ectatomma edentatum* Roger 1863a, CASENT0173376, April Nobile; Myrmicinae: *Huberia brounii* Forel 1895, CASENT0106136, Michael Branstetter). Scale bars for all: 0.2 mm (head); 0.5 mm (profile).

of the multilocus Sanger sequencing phylogenetic studies of Moreau et al. (2006) and Brady et al. (2006).

To summarize these periods, a compendium of the most prolific ant taxonomists is presented in Table 2, notably including a relatively small number of women. It is also striking how few of those authors were based in equatorial regions, despite an enormous diversity of ants in tropical South America, sub-Saharan Africa, Indomalaya, and the Global South generally. Nonetheless, in recent years the contributions made by women in taxonomy and other fields in myrmecology have increased (Lucky et al. 2020), as has taxonomic work conducted in South America, Africa, and Asia. These developments show that myrmecologists are indeed slowly dismantling unjust barriers and improving minority representation among future generations of ant researchers. This growth can be seen in Supplementary Appendix IV, where we present a comprehensive list of notable and major taxonomists across all eras.

Modern Phylogenetic Studies

The internal topology of the Formicidae has received substantial attention over the past 2 centuries. The first explicitly evolutionary classification of ants was proposed by Emery (1877a; Fig. 22A). Much later, Brown (1954) eschewed the popular Emery-Wheeler system (eg Emery 1910, Wheeler 1920), recognizing one main bipartition and 9 subfamilies, some of which he recognized as paraphyletic (Fig. 22B). Brown (1954) inferred several relationships supported by more recent evidence, notably his “myrmecioids,” which, minus the Formicinae, are now supported by phylogenomic inference. Taylor (1978) rearranged the phylogeny proposed by Brown into an alternative bipartition (see Keller 2011 for details). Brown’s classification of Formicidae was evolutionary-taxonomic, allowing for the recognition of paraphyletic groups, which formed grades from which derived lineages arose. In contrast, Bolton (2003) strove for reciprocal monophyly in all higher ant taxa, recognizing 21 extant subfamilies in 6 putative clades based on putative apomorphies (Fig. 22C). This classification relied on cladistic reasoning, previously published analyses, and an intuitive reconstruction of the ground plan of the crown clade Formicidae (Appendix 3 of Bolton 2003).

Several studies contemporaneous with Bolton (2003) applied maximum parsimony to morphological data to infer the phylogeny of higher-level ant taxa (eg Lattke 1994, Ward and Brady 2003), or morphology plus limited sequence data (Brady and Ward 2005, Ward and Downie 2005). These early morphology-based studies met little success in resolving the phylogeny of the Formicidae: the results of Baroni Urbani et al. (1992) and Grimaldi et al. (1997) were poorly supported and concurred only on the monophyly of the dorylomorphs. The use of supraspecific terminals rather than single specimens for each terminal (Prendini 2001) in these studies

Fig. 21. Pioneer women myrmecologists and collectors and the major ant taxonomists of the 19th and 20th centuries. (From top left to bottom right): A) Mary Treat in 1920 (from the Darwin Correspondence Project); B) Therese von Bayern in 1911; C) Lucy Evelyn Cheesman (copyright Trustees of the NHM London Library and Archives); D) Elizabeth Skwarra 1928 (copyright Senckenberg Deutsches Entomologisches Institut); E) Mary Talbot circa 1935 (source unknown); F) Gustav Mayr; G) Carlo Emery; H) William Morton Wheeler (1910, public domain); I) Auguste Forel; J) Bill Brown and E. O. Wilson (courtesy T. Schultz); K) Barry Bolton (from the subject himself).

further obscured the phylogeny of the Formicidae: later research demonstrated that some of these terminals were not monophyletic. The exemplar-based, poneromorph-focused study of Keller (2011) described 139 anatomical characters in detail, many novel, in a digital atlas of 5,250 SEM images. Most subfamilies were recovered as monophyletic, but several conclusions were later refuted, eg Formicinae + Dolichoderinae as sister to all other Formicidae (eg Brady et al. 2006, Moreau et al. 2006). Despite this, Keller (2011) remains an invaluable compendium of morphological variation across ants.

Initial efforts at phylogenetic inference from molecular data provided little resolution (eg Ohnishi et al. 2003, Astruc et al. 2004, Saux et al. 2004, Ouellette et al. 2006). However, even the earliest maximum likelihood (ML) analyses of 18S and 28S rRNA (Sullender and Johnson 1998; Fig. 23) revealed a clade never before proposed—the Doryloformicia ("formicoid clade"), which has remained unchallenged by all subsequent analyses. The twenty-first century saw a new consensus on ant phylogeny emerge from molecular data, contrasting with the multivocal hypotheses premised on morphology alone. Model-based phylogenetic inference from several nuclear loci recovered the Poneria as a clade sister to the Doryloformicia (except Rabeling et al. 2008), but with less robust support (eg Brady et al. 2006, Moreau et al. 2006, Schmidt 2013, Ward and Fisher 2016) (Fig. 22D). The internal phylogeny of the Doryloformicia proved

Table 1. Species names recognizing pioneering women in the field of myrmecology

Pioneer	Species
Mary Treat (1830–1923)	*Aphaenogaster mariae* Forel 1886 *Aphaenogaster treatae* Forel 1886 *Dolichoderus mariae* Forel 1885
Therese von Bayern (1850–1925)	*Azteca theresiae* Forel 1899b *Neoponera theresiae* (Forel 1899a) *Odontomachus chelifer theresiae* Forel 1895 *Pogonomyrmex theresiae* Forel 1899b
Lucy Evelyn Cheesman (1881–1969)	*Camponotus cheesmanae* Donisthorpe 1932 *Pheidole cheesmanae* Donisthorpe 1941 *Polyrhachis (Evelyna) cheesmanae* Donisthorpe 1937 *Polyrhachis (Campomyrma) cheesmanae* Donisthorpe 1943 *Technomyrmex cheesmanae* Donisthorpe 1945
Elizabeth Skwarra (1886–1961)	*Acanthostichus skwarrae* Wheeler 1934 *Macromischa skwarrae* Wheeler 1931 *Myrmelachista skwarrae* Wheeler 1934 *Pheidole skwarrae* Wheeler 1934 *Strumigenys skwarrae* Wheeler 1934 *Temnothorax skwarrae* (Wheeler 1931)
Mary Talbot (1903–1990)	*Formica talbotae* Wilson 1977 *Monomorium talbotae* DuBois 1981

Colors indicate species status at time of writing: red = valid; black = invalid (synonym); green = original combination; purple = junior homonym.

robust and well-supported, whereas there was only weak support for the internal phylogeny of the Poneria. The discovery of *Martialis heureka* Rabeling and Verhaagh 2008 introduced the hypothesis that *M. heureka* was sister to all other crown ants (Rabeling et al. 2008), and thus inspired expeditions to collect more of these ants, spurred ongoing debate about the placement of this species (eg Kück et al. 2011, Borowiec et al. 2019, 2025, Romiguier et al. 2022, Cai 2024), and renewed interest in deep morphological patterns among ants.

The model-based molecular revolution revealed multiple instances of striking homoplasy across the Formicidae. A notable case of reciprocal illumination was the splitting of the tribe Agroecomyrmecini from the Myrmicinae by Bolton (2003) based on details of the petiole and postpetiole, an action later justified by the multi-locus phylogenetic study of Ward et al. (2015). The latter study discovered that the sole extant representative of the Agroecomyrmecini (*Tatuidris)* not only belongs to the Poneria, but is sister to *Ankylomyrma*, previously regarded as an unrelated myrmicine. The genetic and morphological implications of this discovery are still open questions (eg Romiguier et al. 2022, Richter et al. 2023), given the remaining phylogenetic uncertainty of relationships among the major lineages of Poneria. Another morphology-based hypothesis overturned by sequence data was the leptanillomorph grouping of Bolton (2003), in which Apomyrminae and Leptanillinae were postulated as sister taxa. In other instances, morphological intuition was vindicated: the Ectatomminae were shown to be sister to the Myrmicinae (Moreau et al. 2006, Ouellette et al. 2006), as proposed by Brown (Keller 2011: Fig. 4), and most of the subfamilies delimited by Bolton (2003) were found to be monophyletic—save for Cerapachyinae, which was synonymized under Dorylinae by Borowiec (2016).

The application of high-throughput sequencing to ant phylogenetics began in the 2010s, which reinforced the internal phylogeny of the Doryloformicia (Fig. 22D) (Branstetter et al. 2017c) and contributed greatly to the stabilization of higher ant classification. To date, most phylogenomic studies of ants rely on ultraconserved elements (UCEs) (McCormack et al. 2012, Faircloth et al. 2014; Branstetter et al. 2017c) to explore relationships within and among subfamilies (Blaimer et al. 2015, 2018, Branstetter et al. 2017c, 2022, Borowiec 2019, Griebenow 2020, Camacho et al. 2022). Romiguier et al. (2022) instead generated low-coverage whole genome data, with >4,000 protein-coding loci representing all subfamilies and 63 genera. Restriction site-associated DNA sequencing (RADseq) has also served species-level taxonomy well (Zhang et al. 2019). Together, these studies led to a significantly refined classification, ensuring that all subfamilies and most recognized genera are monophyletic, and improved resolution for many nodes. Before the advent of high-throughput next-generation sequencing technologies, conventional Sanger sequencing of selected genes helped catalyze early major systematic revisions at genus and tribe levels for some clades in the Formicidae (eg Myrmicinae: Ward et al. 2015, Dolichoderinae: Ward et al. 2010, Ponerinae: Schmidt 2013), while others remain to be revisited using genomic data.

Nonetheless, certain nodes in the ant phylogeny have proven difficult to resolve via phylogenomic inference, at least given the current reliance on UCE sequence data. ML inference from UCEs originally showed sensitivity of the topology of the Poneria to coding scheme, compositional heterogeneity, and consideration of gene-tree discordance (Branstetter et al. 2017c) (Fig. 24C–E). Subsequent ML phylogenomic inference was robust to analytical perturbations, plus outgroup sampling (Romiguier et al. 2022). Recently, despite several rounds of data reduction and supposed accommodation of compositional heterogeneity, Cai (2024) recovered the same internal relationships of the Poneria as did Romiguier et al. (2022). This phylogenomic hypothesis (Fig. 24F) is strongly discordant with most previous ones (Fig. 24A–C, and E), differing markedly in its implications for anatomical and behavioral evolution within the Poneria (Richter et al. 2023).

The root of the Formicidae also remains contentious. Only Rabeling et al. (2008) and Schmidt (2013) supported the Leptanillinae + Euformicia. Other studies favored the Leptanillomorpha (Borowiec et al. 2019, 2025, Romiguier et al. 2022), Martialinae + Euformicia (Kück et al. 2011, Cai 2024), or were indecisive between these (Moreau and Bell 2013, Branstetter et

Table 2. Most prolific taxonomists of ants, based on alpha taxonomic contributions

Era	Taxonomist	Total taxa (Protonyms)	Valid taxa (incl. combs.)	Publication dates	Region or taxon
Classical (1758–1851)	**Linnaeus, C.**	**24**	**18**	**1758–1771**	**World**
	Fabricius, J. C.	**95**	**56**	**1775–1804**	**World**
	Christ, J. L.	15	0	1791	W. Palearctic
	Olivier, A. G.	13	8	1792	World
	Latreille, P. A.	**73**	**53**	**1798–1818**	**World**
	Spinola, M.	20	11	1806–1853	World
	Leach, W.E.	15	2	1815–1825	W. Palearctic
	Westwood, J. O.	29	18	1829–1854	Dorylinae
	Lund, P. W.	13	4	1831	Brazil
	Guérin-Méneville, F. E.	28	15	1831–1857	World
	Lepeletier de Saint-Fargeau, A. L. M.	2	4	1835	World
	Shuckard, W. E.	32	20	1838–1841	Dorylinae
	Foerster, A.	24	9	1850	W. Palearctic
	Jerdon, T. C.	42	28	1851 (1865)	World
Evolutionary (*Precladistic*) (1853–1942)	Nylander, W.	53	33	1846–1857	W. Palearctic
	Heer, O.	101	58	1849–1879	Fossil
	Smith, F.	**736**	**499**	**1851–1879**	**World**
	Mayr, G.	**793**	**641**	**1853–1908**	**World, Fossil**
	Roger, J.	226	173	1857–1863	World
	Emery, C.	**2127**	**1471**	**1869–1926**	**World**
	Forel, A.	**4166**	**2556**	**1869–1948**	**World**
	André, Ern.	125	101	1874–1913	World
	Ruzsky, M. D.	179	56	1894–1946	Palearctic
	Wheeler, W. M.	**1549**	**789**	**1900–1942**	**World**
	Viehmeyer, H.	244	161	1904–1925	World
	Arnold, G.	218	147	1905–1962 (1994)	Afrotropical
	Karawaiew, J.	279	115	1906–1937	World
	Santschi, F.	**2417**	**1261**	**1906–1941**	**World**
	Donisthorpe, H.	392	205	1908–1950	World + Fossil
	Stitz, H.	262	132	1909–1940	World
	Crawley, W. C.	107	57	1911–1928	Australasia
	Mann, W. M.	347 (295)	226 (221)	1911–1948	Neotropical
	Menozzi, C.	212	116	1918–1952	World
	Clark, J.	228	143	1924–1951	Australasia
Modern (1942–2006)	Smith, M. R.	99	62	1916–1969	World
	Borgmeier, T.	161	98	1920–1971	Neotropical
	Kusnezov, N.	161	66	1923–1978	Neotropical
	Arnol'di, K. V.	132	59	1926–1978	Palearctic
	Weber, N. A.	270	115	1934–1982	World
	Bernard, F.	128	50	1935–1985	Palearctic, Afrotropical
	Brown, W. L., Jr.	**294 (262)**	**250**	**1943–2002**	**World**
	Kempf, W. W.	**157 (135)**	**143**	**1949–1978**	**Neotropical**
	Collingwood, C. A.	102 (90)	80	1950–2017	Palearctic

Table 2. Continued

Era	Taxonomist	Total taxa (Protonyms)	Valid taxa (incl. combs.)	Publication dates	Region or taxon
	Wilson, E. O.	**438 (430)**	**395 (393)**	**1951–2021**	**World**
	Taylor, R. W.	132 (114)	130	1958–2017	Australasia
	Baroni Urbani, C.	113 (110)	81	1962–2008	World
	Dlussky, G. M.	342 (314)	299	1962–2020	Fossil + Palearctic
	Snelling, R. R.	94 (89)	86	1963–2008	World
	Bolton, B.	**995 (991)**	**968**	**1969–2016**	**World**
	Elmes, G. W.	55 (10)	52 (10)	1971–2010	*Myrmica*
	Hong, Y.-C.	71	70*	1974–2002	Fossil
	Brandão, C. R. F.	71 (35)	69 (34)	1982–	Brazil
	Radchenko, A. G.	205 (145)	164 (145)	1983–	Palearctic + Fossil
	Agosti, D.	102 (31)	86 (31)	1983–2012	World
	De Andrade, M. L.	130 (118)	128 (116)	1992–2007	World, Fossil
	Xu, Z.-H.	119 (69)	111 (61)	1994–	China
	Zhou, S.-Y.	105 (69)	95 (59)	1997–2019	China
Contemporary (*Phylogenetic*) (2006–)	Yamane, Sk.	109 (18)	108 (18)	1978–	Indomalaya
	MacKay, W. P. and MacKay, E. E.	155 (131)	142 (118)	1980–2020	World
	Ward, P. S.	120 (118)	119 (117)	1980–	World
	Terayama, M.	156 (149)	146 (139)	1981–2020	Indomalaya
	Ogata, K.	80 (17)	79 (17)	1982–2021	*Myrmecia*, *Strumigenys*
	Seifert, B.	136 (119)	116 (107)	1982–	W.Palearctic + *Cardiocondyla*
	Shattuck, S. O.	269 (145)	261 (137)	1985–	World
	Lattke, J. E.	280 (260)	179 (159)	1987–	*Leptogenys*, Ectatomminae
	Kohout, R.	173 (172)	173 (172)	1987–2015	*Polyrhachis*
	Longino, J. T.	234 (219)	234 (219)	1988–	Central America
	Férnandez, F.	93 (74)	89 (70)	1989–	Colombia, Neotropical
	Fisher, B. L.	617 (81)	615 (81)	1995–	World
	Heterick, B. E.	170 (166)	169 (165)	1997–2021	Australasia
	Csősz, S.	73 (44)	70 (42)	1998–	World
	Eguchi, K.	67 (51)	64 (48)	1998–	Indomalaya
	LaPolla, J. S.	95 (80)	93 (78)	1999–	Formicinae, Fossil
	Bharti, H.	107 (83)	104 (80)	2001–	India
	Perfilieva, K. S.	53 (11)	52 (11)	2002–	Fossil
	Feitosa, R. M.	51 (16)	50 (15)	2005–	Neotropical
	Jaitrong, W.	99 (71)	99 (71)	2005–	Indomalaya
	Zettel, H.	71 (57)	70 (56)	2006–	Indomalaya
	Hosoishi, S.	72 (29)	72 (29)	2008–	Indomalaya
	Branstetter, M. G.	89 (37)	89 (37)	2009–	Neotropical/World
	Hita Garcia, F.	136 (99)	136 (99)	2009–	*Tetramorium*
	Rakotonirina, J. C.	97 (97)	97 (97)	2013–	Madagascar
	Prebus, M. M.	62 (41)	62 (41)	2014–	*Temnothorax*

Table 2. Continued

Era	Taxonomist	Total taxa (Protonyms)	Valid taxa (incl. combs.)	Publication dates	Region or taxon
	Salata, S.	174 (158)	174 (158)	2014–	Palearctic, Malagasy
	Borowiec, L.	69 (8)	69 (8)	2014–	Palearctic

We considered ant taxonomists those who have published taxa as first authors, or who have ant taxonomy as their major line of research. Minimum cutoff for inclusion of modern and contemporary authors in this table is ≥50 valid taxa since the modern era. The cutoff was implemented as there were far fewer systematists earlier than later, and alpha taxonomic contribution was chosen as a convenient metric. Some active dates are added in parentheses when a long diastema preceded a final publication. Authors spanning more than one period are partitioned based on the date range in which the majority of their works were published. Systematists defining the earlier periods are bolded. Women are underlined. For a more comprehensive list, see Supplementary Appendix IV.

al. 2017c). Correction for both compositional (across alignment) and site (within-sequence) heterogeneity recovers the Leptanillomorpha irrespective of dataset (Borowiec et al. 2019, Romiguier et al. 2022), while the site-heterogeneous CAT-GTR substitution model is claimed to favor Martialinae + Euformicia (Cai 2024, but see Boudinot and Lieberman, 2025, and Cai, forthcoming). In order for these controversies to be resolved, future work must accommodate the sources of bias and scrutinize effects of discordant phylogenetic signals inherent in high-throughput sequence data for ants (Borowiec et al. 2025).

Databases

Behind the recent advances in understanding global patterns of ant diversity and evolution is a growing backbone of online systems and protocols to curate and share global taxonomic and informational infrastructure (Soberón and Peterson 2004). Here, we focus on a few major milestones in the effort to capture key elements of the taxonomic infrastructure of ants, particularly ant taxonomic literature, taxonomy, classification, specimens, and traits (Dunn et al. 2007).

Having quality information available in real-time is central to scientific quality and productivity. From obtaining scientific articles to accessing specimen information available in museum collections or DNA sequences, modern science requires globalized data. Making such data freely accessible to anyone with an internet connection promises equal access to participate in the scientific endeavor. It is especially important to make such resources available to researchers in species-rich tropical countries. Meanwhile, the need for global datasets will certainly grow as new artificial intelligence systems are integrated into taxonomy production lines.

Several efforts have sought to provide reliable public data about ant taxonomy. The first initiatives endeavored to gather all the available literature, as in William L. Brown, Jr.'s 1961 proposal to develop an "International Taxonomic Register" to facilitate the publication of species descriptions. To address the same problem, ANTBIB, a reference compilation of all the available literature, was published as a book in 1996 (Ward et al. 1996). At the same time, Barry Bolton published his monumental catalog (Bolton 1995) covering the taxonomic history of every extinct and extant ant species. These publications were limited by their printed form. Advances in information technology would continue to change the landscape in ensuing decades. For example, around the turn of the millennium, Ted Schultz and Donat Agosti digitized Brown's extensive library of reprints and shared it via the Memorial Digital Library with the help of Dan Kjar (Schultz and Kjar 1999), and additionally on Plazi. Bolton's catalog was updated and published in CD-ROM in 2007, containing information up to the year 2005 (Bolton et al. 2007).

The advent of the Internet profoundly affected databasing. Modern technologies offer global reach, enable community science efforts, and make updates and treatments of information easy to facilitate. In 2002, Brian Fisher at the California Academy of Sciences (CAS) started **AntWeb** to make accessible the world's ant collections, in particular type collections. The database includes specimen records and images submitted from collections around the world. Currently, 869,900 specimens, 61,225 of them imaged (with more than a quarter million images) are available on the AntWeb platform. A sister project, **AntCat**, was developed in 2010 by the Fisher-Esteves lab at CAS to provide nomenclatural support for AntWeb but also to establish a community management system for ant taxonomic literature and taxonomic history, to help maintain the taxonomic infrastructure around species names. AntCat started by merging references from Ward's ANTBIB and Bolton's 1995 catalog. The platform is maintained by a community of taxonomists and has become the standard taxonomic reference for ants, and whenever possible provides free and universal access to the literature itself.

AntWiki offers updated information on several topics, with its main goal being "to provide a home page for every ant" (AntWiki 2024). It uses the "wiki" concept and technology to collect and combine information from several sources. It also compiles information on different topics such as species accounts, identification keys, and morphology. As stated on AntWiki, "AntWiki does not manage specimens or detailed nomenclatural data (catalogs), but rather summarizes and reports them." **AntMaps** has been maintained by the Okinawa Institute of Science and Technology Graduate University (AntMaps 2024). It tracks the published records and specimens available in several databases, combining them in the Global Ant Biodiversity Informatics (GABI) (Guénard et al. 2017) to offer the most current data about the distribution of every valid ant species. Ant databases can also be found in global fauna aggregators, such as the Global Biodiversity Information Facility (GBIF; GBIF.org 2025) and Specify Collections Consortium (Specify Collections Consortium and Contributors 2025) for distribution data, or GenBank (GenBank 2004) or Barcode of Life Data Systems (BOLD) (Ratnasingham et al. 2024) for DNA. These larger aggregators also play a significant role for ant taxonomy, as several collections are maintained locally but not uploaded into AntWeb or AntMaps. It should be noted, however, that all online ant databases require quality control by the end user. There are inevitably misidentifications, which are caught and corrected slowly by taxon specialists or museum curators with the authority to change the records, so data users should exercise caution rather than trusting records blindly.

Apart from the previously mentioned sites offering global coverage, a number of local websites seek to keep track of local faunas. These sites include the Ants of Costa Rica (Longino 2010a), the Japanese Ant Image Database (Japanese Ant Database Group 2008), AntArea (France) (AntArea Association 2010), FORMIDABEL (Belgium) (Brosens et al. 2013), Ants of New Guinea (New Guinea and adjacent archipelagos) (Ants of New Guinea 2014), Hormigas

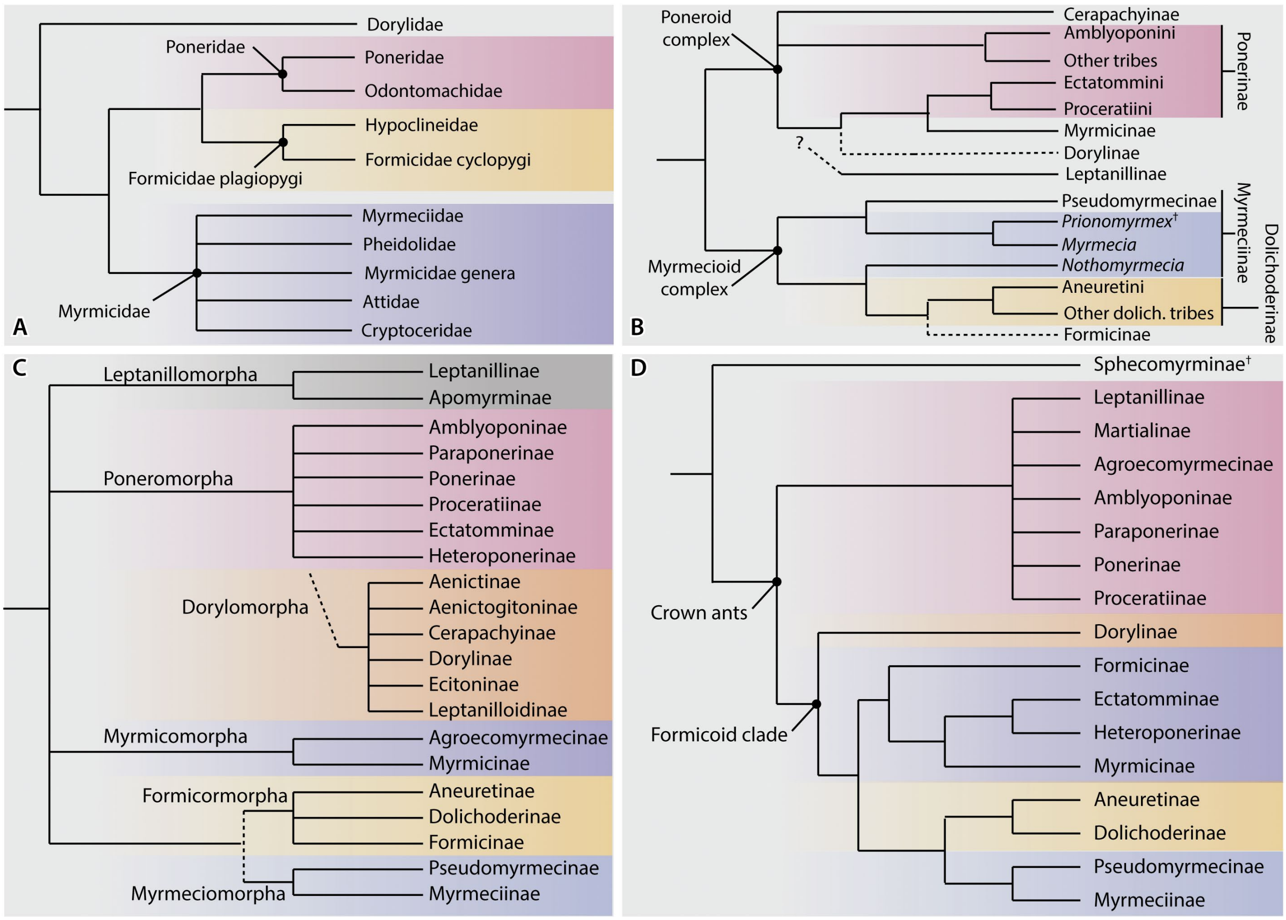


Fig. 22. Historical to more recent phylogenetic hypotheses concerning the Formicidae. A) Emery (1877a). B) Brown (1954). C) Bolton (2003). D) Ward (2007).

Ibéricas / Formicidae.es (Iberian Peninsula) (Alarcón 2024, 2025), and Ants of Cyprus (Demetriou et al. 2025). SCIANTS Amazonia (SCIANTS 2025), based at Museu Paraense Emílio Goeldi, Pará, Brazil, focuses on the ants of the Brazilian Amazon (eg Albuquerque et al. 2021), while the ATLANTIC ANTS initiative collates ant records from across the Atlantic Rainforest domain (Silva et al. 2022). Some institutions keep their own database collections but may not load this information into any global aggregator (Los Angeles Natural History Museum [LACM]), or may simply have few ant records digitized or widely available at this time (Smithsonian National Museum of Natural History [USNM], Muséum d'histoire naturelle de Genève [MHNG; but see Landry 2024], Museu de Zoologia da Universidade de São Paulo [MZSP]). Other major institutions do not keep a digitized collection (Muséum national d'Histoire naturelle [MNHN], Natural History Museum UK [NHMUK], Musee Royal de l'Afrique Centrale [MRAC], Royal Belgian Institute of Natural Sciences [RBINS], etc.). Even worse, some hyperdiverse regions host no collections whatsoever (most of the Afrotropics, Papua New Guinea, Central America).

Future developments should integrate all of these efforts into one global resource. That would involve drawing systematics from AntCat, advanced mapping from AntMaps, imaging and collections from AntWeb, comprehensive information from AntWiki, and other information (eg 3D models, behavioral, ecological, and DNA data) from additional sources. One goal should be to create cloud tools to maintain collections. Such tools should enable institutions with few or no resources to keep collections updated and their data available. Additional goals range from advanced taxonomy to interactions with community science platforms (eg iNaturalist) (iNaturalist 2025).

Integration of ant information is beginning. AntWeb fuses data from AntCat to show taxonomic information by species, but also goes one step further by linking information about type specimens. AntWiki also shares information from AntMaps. Most public ant databases each share links to the other sites listed above, but these connections also reflect an enduring problem. Funding is scarce and decentralized, and most of the initiatives are isolated and lacking in both material and human resources. Conversely, at least some tools seem to be going in the right direction. One of the most promising is Taxonworks (Trivellone et al. 2018), a project still in development but which has support from several taxonomists in different fields located around the world.

Regions in Need of Biodiversity Exploration

Several key regions for ant diversity worldwide have been highlighted in recent research. Kass et al. (2022) presented a high-resolution global diversity map for ants based on described species, showing richness peaks in tropical regions (Fig. 25). Most studies of insect distribution and demography are focused on the Western Palearctic and Nearctic, covering less than 20% of global insect diversity—increased data collection from tropical regions is greatly needed (Wagner et al. 2021). Studies of ants are no exception; one macrotaxonomic evaluation of global ant distributions recommends that

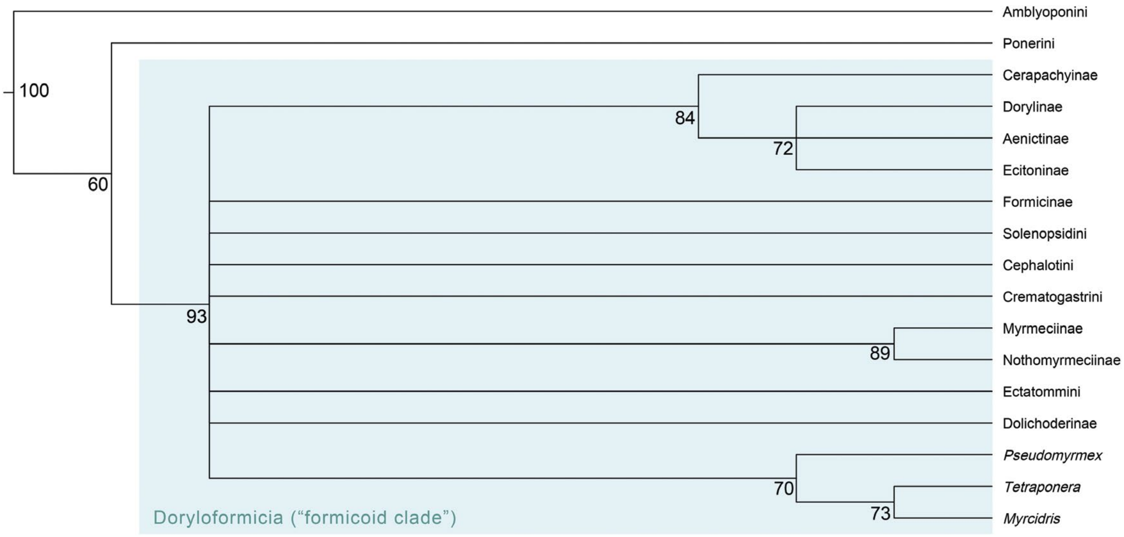


Fig. 23. Earliest molecular phylogeny of the Formicidae (Sullender and Johnson 1998) based on 18S and 28S rRNA.

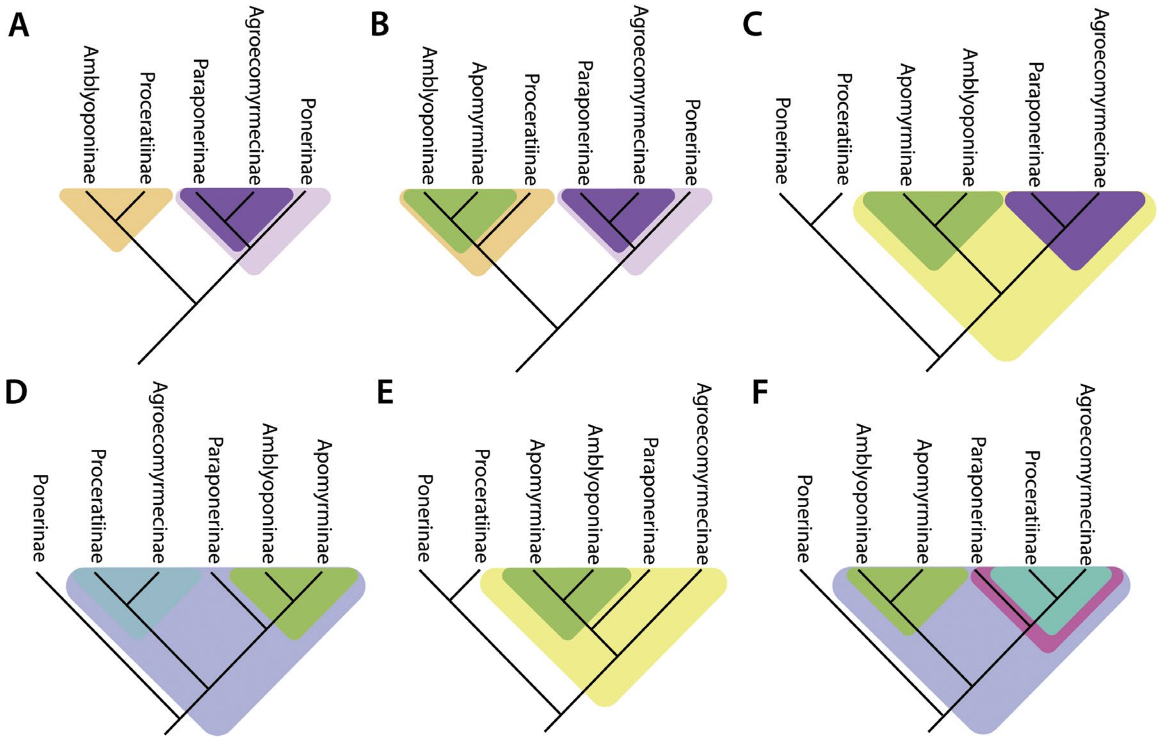
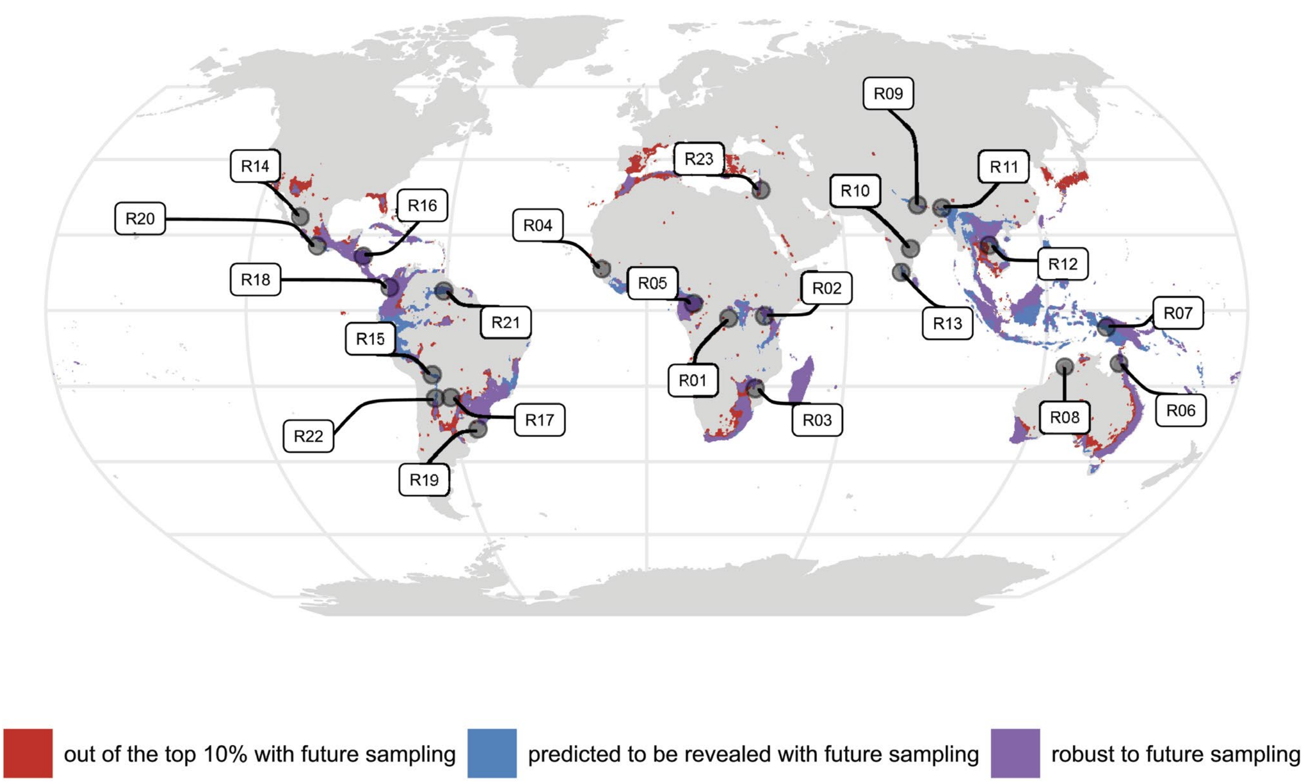


Fig. 24. Topology of the Poneria according to several molecular studies. A) Moreau et al. (2006), Brady et al. (2006), Schmidt (2013), Moreau and Bell (2013). B) Ward and Fisher (2016). C) Branstetter et al. (2017: fig. 1A). D) Branstetter et al. (2017: fig. 1B). E) Branstetter et al. (2017: fig. 1C). F) Romiguier et al. (2022), Cai (2024), Borowiec et al. (2025).

"inventory efforts need to be pursued for at least another generation" before large-scale biogeographic patterns of ants can be considered settled (Economo et al. 2018).

The European ant fauna, excluding the Mediterranean, is well-resolved taxonomically (Seifert 2018). Gaps exist elsewhere in the Palearctic, like Jordan and Kuwait, where predicted biodiversity far exceeds observed values, likely due to insufficient fieldwork (Chen and Ding 2022), while some Mediterranean areas are within the top 10% of regions with undiscovered species (Kass et al. 2022), despite extensive sampling. The Iberian Peninsula owes its diversity to convoluted orography (Tinaut and Ruano 2021).

Critical tropical regions needing exploration (Fig. 25) include Australia, central Africa, Indonesia, southern China, New Guinea, the Central Andes, and the Western Ghats (Kass et al. 2022, Guénard et al. 2010, Fernández et al. 2021, Jenkins et al. 2011, Andersen et al. 2023, Chen and Ding 2022). While some ant-rich regions overlap with vertebrate diversity centers (Kass et al. 2022, Dantas and Fonseca 2023), there are mismatches, particularly in Central



Ant rarity centers adapted from Kass et al. 2022. Science, 8(31):eabp9908

Fig. 25. Global regions in need of ant biodiversity exploration. Colored areas correspond to the distribution of ant rarity centers predicted using a random forest model by Kass et al. (2022, Figs. 4–6): in red, the empirical ant center predicted to fall out of the top 10% with future sampling, in purple, the empirical ant centers robust to future sampling, in blue, the "missing" ant centers predicted to be revealed with future sampling, and in gray, the ant centers not currently or not predicted to be present. Gray dots correspond to the specific regions that have been identified as the highest priority regions that could harbor hidden ant diversity, either due to lack of exploration or due to lack of knowledge. Labels refer to: Afrotropical: R01, Chad, Central Africa (Chen and Ding 2022). R02, Eastern Central Africa (Kass et al. 2022). R03, South and Southeastern Africa (Kass et al. 2022). R04, Guinea-Bissau, Mali, Mauritania, Niger, Burkina Faso, West Africa (Chen and Ding 2022). R05, Western Central Africa (Kass et al. 2022). Australasia: R06, Australian Monsoonal (seasonal) Tropics (Andersen et al. 2023). R07, Melanesia (Kass et al. 2022). R08, Australia, North Kimberley bioregion (Cross et al. 2016). Indomalayan: R09, Himalaya, Nepal and Northeast India (Kass et al. 2022). R10, Indian States of Andhra Pradesh and Chhattisgarh (Bharti et al. 2016). R11, Bhutan, South Asia (Chen and Ding 2022). R12, Southeast Asia (Kass et al. 2022). R13, The Western Ghats and Sri Lanka (Kass et al. 2022). Nearctic: R14, México (northwestern), Sierra Madre Occidental (Kass et al. 2022). Neotropic: R15, Bolivia (Fernández et al. 2021). R16, Central America (Fernández et al. 2021). R17, Chaco, Chaco region (Fernández et al. 2021). R18, Colombia, Chocó-Darién moist forest (Fernández et al. 2021). R19, northwestern Brazil and portions of the Cerrado savanna (Fernández et al. 2021). R20, Mexico, Sierra Madre Oriental and Sur and Trans-Mexican Volcanic regions (Kass et al. 2022, Rocha-Ortega et al. 2023). R21, The Guiana Shield (Kass et al. 2022). R22, Yungas Rainforest (Fernández et al. 2021). Palearctic: R23, Jordan, Kuwait, West Asia (Chen and Ding 2022).

Africa and Southeast Asia (Kass et al. 2022). The need for additional research in Asia was underscored by Guénard et al. (2010) who noted that, despite recent efforts, the distribution of ants in the region remains poorly understood: the Himalayas, northeastern Indian subcontinent, Burma, Andhra Pradesh, and Chhattisgarh all exhibit collection gaps (Bharti et al. 2016, Chen and Ding 2022, Kass et al. 2022, Subedi 2022), and large areas of Thailand, Vietnam, and many Philippine and Indonesian islands are rarity hotspots (Kass et al. 2022). In the Afrotropical region, the relative paucity of ants compared to vertebrates is likely due to limited sampling (Chen and Ding 2022, Kass et al. 2022). Despite increased sampling over the past 30 yr, most of Africa remains unsampled. Based on intensive sampling in South Africa and Tanzania, Robertson (2000) predicted a 2.4-fold potential increase in Afrotropical ant diversity. Recent revisions using collections at Pretoria (AFRC), Barcelona (KGAC), Tervuren (MRAC), and Brussels (RBINS) have revealed many undescribed Afrotropical species in limited areas. Overall, >60% of African ant species are likely undescribed, with higher proportions in under-collected regions such as the Congo rainforest, mountains of Angola, the Eastern Arc, Albertine Rift, and Central Africa, and northern Mozambique and Zambia. For example, Zambia has 142 described ant species compared to 475 in Zimbabwe, which is only half the size of Zambia but more extensively surveyed (Janicki et al. 2016).

The Neotropics likewise lack the standardized data collection and coordinated monitoring essential for effective conservation outcomes (Montgomery et al. 2021). Lack of data availability or identification resources hinders comprehensive understanding of ant biodiversity in the ecoregion: for instance, only 63 ant species are recorded from the Brazilian state of Rio Grande do Norte (Janicki et al. 2016), which is surely an extreme underestimate. In Central America, Rocha-Ortega et al. (2023) pinpoint myrmecological sampling gaps in regions like the Sierra Madre Oriental, Occidental, and Sur; the Trans-Mexican Volcanic Belt; and El Salvador. Approximately 52% of the Brazilian Amazon remains unsampled, with significant gaps in its northern, southeastern, and western regions (Andrade-Silva et al.

2022). The "Arc of Deforestation," known for severe biodiversity loss due to anthropogenic activities, stands out as an area with expected high ant diversity. In the Atlantic Forest, Silva et al. (2022) identified substantial knowledge gaps in deciduous forests, semideciduous forests, and highlands of the Serra do Mar. Humid forests in Petén-Veracruz (Mexico, Guatemala, Belize), the Caribbean, and western Ecuador are comparatively less studied, while all arid biomes receive less attention than forests: xeric shrublands, grasslands and wetlands in Brazil and dry forests across Mexico, Mesoamerica, South America, and the Caribbean Islands remain poorly sampled (Divieso et al. 2020, Feitosa et al. 2022). Fernández et al. (2021) stress the urgency of research in the Chaco, Inter-Andean valleys, Chocó-Darién humid forests, Guiana shield, and Yungas rainforest, given ongoing habitat destruction. Disproportionate sampling near research centers, roads, and rivers is evident throughout, exacerbating lack of data (Andrade-Silva et al. 2022, Silva et al. 2022).

Meanwhile, Australasia, encompassing tropical rainforests in New Guinea and adjacent islands, subtropical and cool-temperate forests in Australia, and arid zones in the Australian interior, harbors a diverse ant fauna. The diversity of New Guinea, where 60% of known species are endemic, is likely underestimated due to remote and poorly surveyed areas. Australia is recognized as a global ant hotspot with ~1,300 described species, but some estimates suggest >8,200 species, with many undescribed species within *Anonychomyrma* Donisthorpe 1947, *Meranoplus* Smith 1853, and others (Andersen 2016, Leahy et al. 2020, Andersen et al. 2024).

Addressing these global knowledge gaps poses significant challenges, requiring substantial efforts in detection alongside essential infrastructure, collections, and human and financial resources (Cardoso et al. 2011). Still, while regions in need of further biodiversity exploration represent critical gaps in our understanding of ant diversity, we acknowledge that prioritizing systematic study of existing collections is equally vital for advancing ant systematics. Major collections (eg ANIC, INPA, LACM, MCZC, MZSP, USNM) house a wealth of poorly identified material, and addressing this backlog is essential to unlocking the potential of these specimens for clade-based, phylogenetic, and biogeographic ant studies of global scope. Expeditions to under-sampled regions, while invaluable for documenting previously unknown diversity, risk compounding this backlog if not accompanied by investments in efficient specimen processing, digitization, and integration with existing datasets. Additionally, obstacles to improving sampling include limited local expertise, insufficient funding, inadequate infrastructure for remote access locations, and security concerns in regions like the Congo basin, Sri Lanka (Dias et al. 2020), and Burma. Moreover, navigating varying and often burdensome permitting requirements presents additional hurdles (Britz et al. 2020).

To balance these needs, ongoing initiatives like Ants of Colombia, SCIANTS Amazonia, Formigas do Brasil, and TAOCA (Carvalho et al. 2023) aim to not only fill geographic gaps but also adopt strategies that mitigate the challenges posed by limited expertise, inadequate infrastructure, and complex permitting requirements. By combining targeted fieldwork with robust infrastructure development, these programs ensure that newly collected materials contribute meaningfully to global ant systematics. Moreover, they seek to bridge the gap between local taxonomy and broader phylogenetic frameworks by fostering collaboration among researchers, enhancing accessibility of collections, and prioritizing analyses that integrate regional discoveries into a global context. This dual approach aligns with long-lasting improvements, ensuring that exploration efforts complement rather than detract from systematic advances.

Challenges in Advancing Ant Systematics

Taxonomy is crucial for comprehending ants and other organisms, including their ecology, distribution patterns, developmental pathways, and behavioral responses. Accurate species identification enables scientific communication and ensures the transferability of research findings. Support for accurate taxonomy continues to be foundational to ongoing biodiversity conservation efforts, management of invasive species, and basic biological discovery (Britz et al 2020). Conversely, inaccurate taxonomy can lead to error cascades (Bortolus 2008) that may result in severe ecological and economic consequences. Success stories in support of advancing taxonomy include training programs such as the US National Science Foundation's partnership for enhancing expertise in taxonomy programs (PEET) (Boero 2001, Rodman and Cody 2003) and Accelerating Research Translation program (ART), the Brazilian National Council for Scientific and Technological Development (CNPq) Programme to Support Research Projects for the Training and Qualification of Human Resources in Biological Taxonomy ("Protax"), and the Distributed European School of Taxonomy.

An extensively documented "taxonomic impediment" prevents timely documentation of life on Earth, including ants. Taxonomists and nontaxonomists perceive the taxonomic impediment differently. Taxonomists view it as obstacles to biodiversity classification and description, such as training gaps, funding shortages, and restrictive or excessive specimen use regulations (Britz et al. 2020). Substantial evidence points toward a lack of expert personnel, rather than a lack of technical approaches, as the main reason for slow taxonomic progress (Engel et al. 2021). Opportunities for taxonomic training are few and far between; even if interested, most people would struggle to gain this knowledge because of the long, highly specific apprenticeship usually required to understand ant taxonomy. Conversely, nontaxonomists focus on practical challenges faced by users of taxonomic tools, including species identification difficulties and inadequate access to comprehensive species information like biology, distribution, and conservation status. Bridging this gap is crucial for advancing the role of taxonomy in biodiversity prediction and enhancing its contributions to fields like conservation and biosecurity. This disconnect between theory and practice only further divides scientific communities, discredits taxonomy as a respected science worth supporting, and impedes the progress that would lead to dissemination of more effective materials and information for identifying and understanding organisms.

Understanding and overcoming taxonomic impediments in all senses is necessary to improve taxonomic preparedness (Wheeler and Cracraft 1996)—a predictive understanding of biodiversity. The rapid and accurate identification of invasive species is crucial for agriculture, the economy, and native biodiversity conservation. However, understudied taxa can evade detection, making eradication or quarantine efforts impractical, as seen with ants in Hawaii (Krushelnycky et al. 2005). Effective preventative measures rely on thorough taxonomic research encompassing both potentially destructive pest species and natives. Native and endemic species can resemble invasive species, complicating pest control efforts and risking unintended threats to endemic species. For instance, *Nylanderia* Emery 1906, known for global spread through human transport, is frequently intercepted at ports but often misidentified (Williams et al. 2022). In the Caribbean, several adventive *Nylanderia* species resemble endemics, potentially disguising invasions (Williams et al. 2020). Similarly, the tropical fire ant, *Solenopsis geminata* (Fabricius 1804), was first misidentified as the red imported fire ant (*Solenopsis invicta* Buren 1972) in southern Asia (Wetterer 2011, 2013). Cryptic invasions, such as those involving *Nylanderia fulva* (Mayr 1862) and *S. geminata*, can remain undetected for decades, delaying effective management (Wetterer 2011, 2013).

Despite its crucial role in biodiversity conservation, taxonomy suffers from low prestige and insufficient resources and is often derided as intellectually undemanding (Werner 2009, Haszprunar 2011, Wägele et al. 2011, Feitosa et al. 2023). Moreover, despite the scientific rigor of taxonomic revisions, these works are systemically undervalued by traditional recognition systems such as citation indices (Agnarsson and Kuntner 2007). This devaluation of taxonomy limits funds and cultivates reluctance from high-impact journals to publish taxonomic research (Godfray et al. 2002, Wägele et al. 2011), with particular bias against noncharismatic invertebrate taxa. As a result, arthropod taxonomy suffers from lack of visibility—not only to prospective scientists, who face few opportunities for employment and career advancement, but also to funding agencies and university administrations, who do not view systematics as an impactful science with tangible returns. There is an urgent need for increasing recognition of taxonomy within scientific discourse (Haszprunar 2011) to advance biodiversity science, eg cataloging and conservation. Such recognition must include full citation of species authors in scientific publications (Feitosa et al. 2023), and explicit guidelines for citing foundational taxonomic works; these norms are essential for fair attribution of intellectual effort and the integrity of scientific progress (Meier 2016). Until these practices become standard across all disciplines, the career outlook for taxonomists will continue to be challenging, limiting new entrants and hindering biodiversity conservation efforts.

Additionally, as the "publish-or-perish" regime in academia disincentivizes expansive taxonomic revisions, new ways of recognizing the value of monographs are urgently needed. Without a doubt, most long-lasting improvements to ant systematics are those that are clade-based and global in scope or, at the very least, cover entire biogeographic regions—but many years of taxonomic work often culminate in a single publication that is unlikely to be cited often in future research. This, understandably, is unappealing to career scientists when the number of a researcher's publications matter for professional advancement (Löbl et al. 2023). Consequently, many of the largest ant genera have never received comprehensive revision(s), including the Afrotropical faunas of *Camponotus, Pheidole*, and *Crematogaster*, and the global faunas of *Hypoponera* Santschi 1938 and *Solenopsis* Westwood 1840. Meanwhile, several widespread genera definitively revealed as nonmonophyletic through phylogenomics (eg *Lordomyrma* Emery 1897 [Lucky and Sarnat 2010]; *Proceratium* [Borowiec et al. 2019]; and *Stigmatomma* [Ward and Fisher 2016]) have not yet been accordingly split. An exception that proves this rule is the case of *Pheidole* in the Americas, which was the subject of a monumental revisionary monograph by Wilson (2003). The sheer size of this particular work, however, makes the identification keys somewhat difficult to use in practice. It is an unfortunate fact that large monographic treatments are usually infeasible in the contemporary academic environment, especially for emerging taxonomists.

Beyond institutional neglect, practical geopolitical realities also obstruct taxonomy. Following globalization of the world's economies, global resources should in theory become more accessible and less restricted to a privileged few. However, new impediments continue to emerge, including restrictive border controls, localized conflicts and warfare, and long-drawn bureaucratic paperwork requirements for access permissions (Mc Kay et al. 2023). Originally intended to guard wildlife from overexploitation, these regulations now purportedly safeguard the rights of nation-states to commercial benefits from scientific discoveries within their borders. This is compounded by the Nagoya Protocol, which was developed to prevent biodiversity exploitation in the Global South but has had a negative impact on noncommercial activities like scientific research (Deplazes-Zemp et al. 2018, Colella et al. 2023). Studies are therefore often geographically limited in access to specimens necessary for comprehensive revisions.

Systematic myrmecology also faces limitations inherent to the study system per se, beyond obstructions to the field of taxonomy in general. The small size of most ants led to mounting techniques prior to the mid-1900s which often rendered type specimens unusable: card-mounting obscured ventral features with glue, or left the specimen wholly embedded therein. Fortunately, technological solutions abound addressing these problems today. For example, morphometric use for these specimens could be restored by µ-CT, which can sometimes visualize glue-marred types in situ.

Sexual dimorphism in the Formicidae is extreme with few exceptions (*Cataulacus* Smith 1853, some *Cephalotes* spp.), ergatoid males notwithstanding. This presents a pervasive methodological challenge: if male descriptions are disconnected from those of conspecific females, "dual taxonomy" is the result, with conspecific sexes described as separate taxa. This quandary is inevitable for clades in which males are more easily collected than workers, like the Dorylinae (Borowiec 2016) and Leptanillinae (Bolton 1990b). In most ants, workers form the basis for classification by default since males are seasonal and short-lived in their occurrence (Smith 2023). Nonetheless, male phenotype often contains critical phylogenetic information unavailable from the female castes (eg LaPolla et al. 2012, Boudinot 2013, Griebenow et al. 2023). Resolution of dual taxonomies once necessitated intensive collecting to obtain males in the nest, which is not always practicable. Again, technology today offers solutions to once intractable problems: dissociated, disparate castes can now be connected with genetic sequencing (Ward and Brady 2009, Griebenow et al. 2022). Historic undersampling of males may have resulted in underestimation of intraspecific morphological variation (Lim et al. 2012) and thus oversplitting; future focus on sampling males will help resolve this problem, as will development of a system for the identification and classification of males, even if it requires the recognition of morphotaxa that may or may not be associated with this time.

The oft-declared objective to document every species on Earth is asymptotically challenging. We must therefore consider whether the goal of describing all extant ants is realistic. More than 18,000 ant taxa have been described, of which >14,000 are valid (Bolton 2024), and it is inferred that 2 or 3 times more ant species inhabit the Earth (Ward 2014). In the last 24 years (from 2000 to 2024), 4,324 ant taxa have been described (AntWiki), or 180 annually. If we accept the estimation of Ward (2014), the total number of extant ant species is between approximately 26,000 to 39,000. If new species description continues at its current pace, then describing all extant ant species will take between 80 and 160 yr.

It is possible that within this timeframe, an untold portion of ant diversity may be extinguished by anthropic pressures. However, the myrmecological community today is much larger and more productive than it was at the turn of the millennium. If we even double the rate of species description, ie to 360 new species per year, an incredible 9,000 ant species could be introduced to science by the year 2050.

The Future of Ant Taxonomy

In the coming years, ant taxonomy will certainly continue the trend of collecting more morphological and genetic data, enhanced by technological advances. This will be combined with deeper integration of disparate information types to shift the field towards explicit, quantifiable hypothesis testing, spearheaded by molecular phylogenetics, morphometrics, and population genetics, among other techniques. Exacting approaches can address ever-growing concerns with reproducibility and repeatability, but importantly, they also directly link historical ant systematics research with the present and future—for example, the deposition of voucher specimens with unique identifiers in perennial collections has become the norm, rather than the exception. To ensure sustainability of the field, it will be crucial to recruit new systematists through initiatives such as field courses and undergraduate research experiences.

Quantitative morphological studies facilitate the comparison of results from independent datasets of multiple modes, which can enhance accuracy and simplify taxonomic decision-making. Automation of morphometric measurement will help acquire the scale of data required for statistical rigor (Baur and Leuenberger 2011, Seifert et al. 2014, Csősz and Fisher 2016), although automation is vulnerable to inaccurate data and analytical misspecification (Csősz et al. 2023). 3D volumes reconstructed from µ-CT image stacks provide an alternative source of replicable morphometrics (Hita Garcia et al. 2017, 2019), although widespread and high-throughput adoption of this approach is so far limited by cost. Nonetheless, the advent of cybertaxonomy (Sarnat et al. 2019) and turbotaxonomy (Riedel et al. 2013), coupled with progress in machine learning algorithms (Pyron 2023), holds immense potential for accelerating biodiversity assessments in the near future.

The future of ant systematics will be best served by an integrative taxonomic approach (Schlick-Steiner 2010, Yeates et al. 2011), encompassing molecular phylogenetics, morphology, and distributional data, or even bioacoustics, cuticular hydrocarbons, and venomics. Even in light of cutting-edge technology, the continued importance of voucher specimens cannot be understated—these specimens are the critical link between molecular data and morphology. Moreover, the integrative template for taxonomy produces multiple types of data relevant to researchers across various disciplines and drives modern taxonomists to develop collaborative networks, interdisciplinary expertise, and intellectual curiosity. One recent sign of a shift towards this multidisciplinary mentality is a major trend towards multiauthorship in ant systematics. This partly reflects greater recognition of the work of specimen collectors, who are now often engaged more actively in taxonomic revisions in which they participated with a significant number of samples.

Beyond technical innovations, sustainability of the field requires recruitment of new systematists through initiatives such as field courses and undergraduate research experiences. Despite the importance of descriptive taxonomy, descriptive taxonomists themselves are an ever-diminishing resource (Wheeler 2008). Meanwhile, courses focused on taxonomy and organismal biology are being discarded from university curricula, leaving natural history museums as refugia for taxonomic research (Britz et al. 2020). In part, this is because taxonomy has historically been characterized as a cottage industry of individuals working in isolation (Wheeler 2008), with an aspiring student being trained by a “master” taxonomist, comparable to an apprenticeship. This paradigm—unchanged since the preindustrial era—presupposes that students are interested in taxonomy as a career choice, and so does nothing towards recruitment.

An effective method for returning taxonomy to curricula, boosting recruitment, and enhancing training is through the Course-Based Undergraduate Research Experiences (CURE) model. CUREs are laboratory courses that challenge students to address authentic research problems with unknown answers broadly relevant to stakeholders outside the classroom (Shortlidge et al. 2017). By conducting research within the classroom setting, these opportunities reach a significantly broader student audience compared to traditional volunteer-based lab work, thereby providing invaluable research exposure to students who might otherwise never be given such opportunities. CUREs grant students opportunities to learn about taxonomy as a career choice, train in the discipline, and consider its relevance to their professional interests.

In closing, the coming years of systematic myrmecology will see an increased emphasis on integrating disparate data sources when formulating taxonomic hypotheses, and additionally introduce active, innovative efforts to recruit the next generation of systematists. If the needed resources are provided—namely, those perennial limiting factors of funding, training, and permits (Britz et al. 2020)—the future of ant systematics will be bright.

Conclusion

From the earliest typification to the contemporary moment, ant systematics has embraced natural history, phylogenetics, and large-scale, quantitative approaches to resolve questions of species identity, ecology, and relationships through time. International collaboration is now commonplace and there is a broad growth of the field with respect to young systematists, with a trend toward gender balance, although retention remains a key issue. In addition to field growth through training, which establishes continuity of knowledge and skill, there is an appreciation for and investment in shared resources, benefitting all researchers in the field regardless of seniority or position.

The tools and methods of molecular biology have provided fertile ground for systematists, resolving many longstanding questions of ant evolutionary history insoluble from morphological evidence alone, while yielding many new pathways of inquiry. The potential of genomics still expands, with several untapped avenues of exploration, eg chromosomal rearrangement and long-read sequencing. Likewise, the systematic study of ant morphology has been revolutionized by the application of µ-CT, revealing the fine structural form of living and extinct ants in 3D as well as their internal anatomy in a visually understandable and comprehensive manner for the first time. Full linkage of sequencing and imaging technologies has not yet been realized, but will profoundly influence the trajectory of systematic myrmecology, as will the development of AI.

The tasks of ant systematics are far from over. It is necessary for the current and future community of myrmecologists to continue collecting, sorting, labeling, identifying, and preserving specimens, whether fossil or extant, as these specimens and their associated metadata (locality information, sequences, images, etc.) will live as long as we continue to pursue our curiosity about nature.

Acknowledgements

We are grateful to Alex Wild for photographs of ant natural history; Barry Sullender, for granting permission to reproduce research findings and for providing context; Barry Bolton, for sharing his new New General Catalog and his historical photograph (Fig. 21K); Brittany Kohler, for several photomicrographs; and Kass et al. (2022), for permission to adapt their map of ant biodiversity rarity centers. We extend additional thanks to the Editors in Chief of *ISD*, Hojun Song and Jason Bond, for inviting this review, and to Phil Ward and Bonnie Blaimer, whose comments improved the text. We acknowledge provision of beamtime, related to the proposal BAG-20210019 at beamline P05 at PETRA III at DESY, a member of the Helmholtz Association (HGF). We appreciate support during the beam times by Fabian Wilde, Julian Moosmann, and Felix Beckmann. This research was supported in part through the Maxwell computational resources operated at Deutsches Elektronen-Synchrotron DESY, Hamburg, Germany. We thank Tomáš

Faragó for tomographic reconstruction of the datasets acquired at KIT and Angelica Cecilia and Marcus Zuber for the assistance at the beamline. We acknowledge the KIT Light Source for the provision of instruments at their beamlines, and we would like to thank the Institute for Beam Physics and Technology (IBPT) for the operation of the storage ring, the Karlsruhe Research Accelerator (KARA).

Supplementary material

Supplementary material is available at *Insect Systematics and Diversity* online.

Funding

This research has received funding from the Fundação de Apoio à Pesquisa do Estado de São Paulo (FAPESP) grant 2023/12809-0 (to GPC), National Science Foundation (NSF) grants DEB-1754242 (to SGB), DEB-2026772 (to AL, incl. JSW and AP), DEB-1927161 (to TRS and JS-C), DEB-2144915 (to PB), and DEB-2146104 and IOS-2127521 (to RMMA); Hungarian Research Network (HUN-REN) co-financed by the National Research, Development, and Innovation Fund (Hungary) under Grant No. K 147781 (to SC); The National Council for Scientific and Technological Development (CNPq)—Grants 304012/2023-8 (to RMF), 382108/2024-8 (to LPP), 172721/2023-7 (to MAU); The Japan Society for the Promotion of Science (JSPS) Grants-in-Aid for Scientific Research (KAKENHI) 22F22761 (to AK); Ministerio de Ciencia, Innovación e Universidades (MICIU), Agencia Estatal de Investigacíon (AEI), Project PID2022-139689NBI00 (MICIU/AEI/10.13039/501100011033) and the European Regional Development Fund (ERDF), European Union (to MM); RSP acknowledges support for publication fees from the Science Research Initiative (SRI) Program; and the JSPS International Postdoctoral Fellowship (to AR). Support for micro-computed tomographic work at the Senckenberg Gesellschaft für Naturforschung was provided by the Senckenberg DigiUnit initiative (to BEB).

Conflicts of interest. None declared.

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