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Poneroid Ants



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Poneroid ants are a clade composed of six well-defined subfamilies that are morphologically heterogeneous (Agroecomyrmecinae, Amblyoponinae, Apomyrminae, Paraponerinae, Ponerinae and Proceratiinae) (Fig. 1). Poneroids include just 11% of extant ant species, and molecular data [4] recognize it as the sister group of the formicoids [12], the clade with the bulk of species diversity (Fig. 2). Not included in either of the poneroids or formicoids are ► *Leptanillinae* and *Martialinae*, two diminutive subfamilies composed of highly specialized tiny subterranean workers. Their relationship to other extant ants remains inconclusive. The now obsolete term “poneromorph” [2] should not be confused with “poneroid.” The various “-morphs” were tentative groups of similar-looking subfamilies without any claim of phylogenetic relationships or formal taxonomic status.

Prior to quantitative phylogenetic analyses, there was a long taxonomic history of treating ants that are superficially similar to wasp ancestors as a large and heterogeneous subfamily

Ponerinae, which included the current poneroid subfamilies as well as *Leptanillinae*, the formicoid subfamilies *Ectatomminae* and *Heteroponerinae*, and all the ► *Dorylinae* that do not display army-ant behavior (formerly included in the now obsolete subfamily *Cerapachyinae*). Ponerinae *sensu lato* was defined by putative ancestral traits exhibited by its members rather than the existence of shared derived characteristics. William Morton Wheeler remarked that “the Ponerinae comprises unmistakably primitive and generalized forms and therefore constitutes a group of twofold interest, first, as the ancestral stock of the higher subfamilies, and second, as the oldest existing expression of social life among the Formicidae” [13]. Wheeler’s view persisted for a century, with subsequent authors explicitly treating Ponerinae *sensu lato* as an all-encompassing taxon from which the other subfamilies arose [5].

The twenty-first century has already brought major changes to the higher classification as subfamilies were redefined [2], morphological characters were formalized in a phylogenetic framework [5], and internal phylogeny was revealed by DNA data ([4] and included references). The current scheme (Fig. 2) recognizes poneroids not as a collection of primitive or ancestral ants, but as an evolutionary radiation that occurred independent from and simultaneous to formicoids [4].

The poneroid radiation resulted in a set of morphologically distinct subfamilies, several of which have only one or two extant species, suggesting a high degree of past extinction events.



Poneroid Ants, Fig. 1 Poneroid ants are almost all ground predators (solitary or in a group; generalists or highly prey-specific), with colonies seldom reaching more than hundreds of workers: (a) *Adetomyrma goblin* (subfamily Amblyoponinae) workers are minute and blind cooperative hunters of linear arthropods; (b) *Discothyrea*

mixta (Proceratiinae) predate specifically on spider eggs (yellowish, mixed with white ant eggs); (c) *Bothroponera soror* (Ponerinae) shows the archetypal limited size divergence between queens (dealate queen is bottom left) and workers (male is top left); (d) *Neoponera commutata* (Ponerinae) colonies have a few thousand workers that

Amblyoponinae is peculiar because most of its species lack the diagnostic petiole of ants (Fig. 1a). This alone led to the idea that amblyoponines represented the transition between wasps and “higher” ants, strengthening the view that poneroids as a whole were ancestral, but this atypical petiole is better considered a reversal. Apomyrminae (one species) was initially placed within Amblyoponinae, then Leptanillinae due to its similar underground habitus, and is now the sister clade to Amblyoponinae (Fig. 2). Proceratiinae (Fig. 1b) and ► Paraponerinae (Fig. 1e) were historically associated with Ectatomminae as a tribe within Ponerinae *sensu lato* and considered the link to subfamily Myrmicinae. Indeed, their morphology includes a mixture of primitive traits shared with other poneroids and derived traits common among formicoids. The poorly-known Agroecomymecinae has two extant monotypic genera previously placed in Myrmicinae. Amid these clades sits Ponerinae *sensu stricto* (Fig. 1c, d), containing the bulk of the poneroid species and exhibiting a broad range of morphologies, particularly in their mandibles that reflect diverse feeding habits [11]: generalist to highly specialist predators, hunting exclusively underground or above ground.

The impact from the shift of viewing poneroids as an ancestral stock to recognizing them as one of two main independent ant radiations cannot be overstated. Because ponerines-as-basal ants was the dominant paradigm, authors turned to poneroids for clues about putative ancestral states for everything from morphology to behavior, while formicoids were held as the “higher” ants and their traits considered advanced. Poneroids as an independent parallel radiation to formicoids, however, require reassessment of social complexity across different lineages. Traits uniquely present among poneroids might not represent examples of early stages in ant evolution, but rather advanced states. Likewise, the formicoids as a whole exhibit a mix of ancestral and advanced traits, and it is important to carefully discern

between the two to understand the possible causes of their greater ecological success.

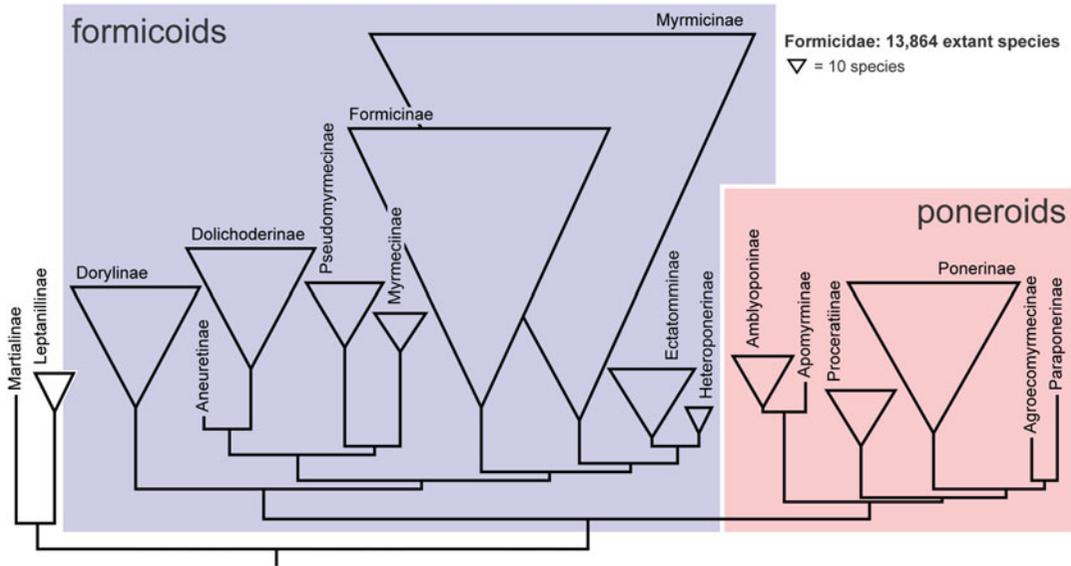
In light of the current phylogeny, it is tempting to focus on Leptanillinae and Martialinae for clues about early stages in ant evolution, as this clade lies outside the formicoids and poneroids (Fig. 2). However, we cannot assume that, relative to a sister clade that is morphologically diverse and highly speciose, a small clade (69 species) represents the ancestral condition [6]. Rather, lone branches are often evolutionary “experiments” in adaptation for a particular niche that were not very successful and an evolutionary dead end due to morphological specialization. A better interpretation is that the larger sister clade is a lineage that remained generalized, thus giving rise to greater diversity in the long run but also retaining species that more likely reflect ancestral conditions. Not only is it unlikely that ants radiated from a highly specialized subterranean clade with reduced morphology [7], but the Cretaceous fossil record is rich with unspecialized forms that lived above ground [1].

How to Assess Social Complexity in Ants?

Sociality is always a composite of interconnecting traits including age structure, genetic composition, group size, communication mechanisms, division of labor, and degree of task specificity. In ants these interacting traits can be magnified by marked morphological differences among adult nestmates (queens and workers) and often supplemented by enduring mutualisms with plants, bacteria, fungi, or sap-sucking insects. The diversity in ant diets and ecology is unparalleled among insects, but commonalities across lineages are easier to grasp by focusing on the fundamental dichotomy in colony characteristics (modified from Ref. [3]): (A) foraging strategies, i.e., how resources are *acquired*, and (B) how

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Poneroid Ants, Fig. 1 (continued) are column raiders on termites; (e) *Paraponera clavata* (Paraponerinae) are one

of the very few arboreal hunters (solitary generalists). Body sizes range from 3 to 25 mm. (Photos © Alex Wild)



Poneroid Ants, Fig. 2 Evolutionary relationships among extant subfamilies of ants. Area of triangles represents relative numbers of species (phylogeny after Ref. [4]; species count after AntCat.org [March 2020])

resources are *allocated* to produce new adults, i.e., body size of queens and workers, their degree of dimorphism, and the number of workers (colony size) and gynes reared annually. Both worker morphology (including body size) and colony size have likely coevolved with foraging strategies across ants, while queen morphology (including body size and ovariole numbers) has coevolved with the hazards of colony foundation and selection for optimal size and longevity of colonies. Hence, social complexity in an organizational sense can be assessed by comparing degrees of dimorphism between workers and queens. Unlike social wasps and bees that are constrained by the need to fly for both castes, ant workers can evolve to be 10–20 times as small as queens [9]. In addition, various ant species show strong morphological specialization within the worker caste (e.g., minors and majors) or a soldier caste with unique traits absent in workers. Hence the behavioral intricacies inherent to social life are amplified in the large proportion of ant species showing pronounced morphological differences within colonies.

Colony size is an essential attribute of ant species, because evolutionary increases in foraging force allowed new lifestyles, i.e., group

hunting, mass raiding, scavenging dispersed carcasses, collection of honeydew, or assembly-line tasks like fungus-farming. Mature colony size is determined by queen fecundity (queen number also), the degree of caste dimorphism, and the amount of resources extracted from the environment. An increased dimorphism is mostly linked to a reduction in size of the workers, with the consequence that more individuals can be manufactured with finite colony resources (= food intake) [9]. Increased caste dimorphism also allows “claustral” ► [colony foundation](#), i.e., founding queens are able to raise the first workers using internal metabolic reserves only if the queen-worker size difference is sufficient. Because claustrality requires gynes that are costly relative to workers, only populous colonies have enough resources to produce them in sufficient numbers every year.

Social Complexity in Poneroid vs. Formicoid Ants

The close phylogenetic relationship between ants and spheciform Apoidea [12] suggests that the ancestor of ants was a solitary winged ground-

hunting parasitoid wasp. We can thus expect that early ants expressed transition states including (i) slight divergence in the body size of queens and wingless workers, (ii) “non-claustral” independent colony foundation (founding queens must forage to feed the first brood), and (iii) small colony size. These expectations are supported by the biology of various extant ants, both poneroid and formicoid, e.g., *Euponera sikorae*, *Harpegnathos* and *Odontoponera* (all Ponerinae), *Myrmecia* (Myrmeciinae) and *Rhytidoponera* (Ectatomminae). In these, besides the presence/absence of wings, queens and workers are highly similar in size and have the same ovariole numbers (Fig. 1c). Non-claustral ICF is the rule across Amblyoponinae and Ponerinae, and also in the formicoid subfamilies Ectatomminae, ► *Myrmeciinae*, and ► *Pseudomyrmecinae* [8]. Similarly, many species in all these subfamilies have colonies with just a few dozens of workers or less [8, 11]. Therefore, many poneroids and a minority of formicoids share these three ancestral traits. Even more, sporadic shifts to “gamergate” (mated egg-laying workers) reproduction (list of species at the end) are restricted to these subfamilies (except *Pseudomyrmecinae*).

Importantly, the occurrence of trophallaxis differs sharply between poneroids and formicoids. Trophallaxis underlies trophic exchanges and storage within colonies, and anatomical adaptations in the digestive track (e.g., crop, proventriculus) seem crucial for this. Trophallaxis (excluding “pseudotrophallaxis”, where sweet liquid food is carried between the mandibles) is absent in poneroids (*Diacamma* is an exception), and this may have constrained larger colony sizes. In contrast, trophallaxis is found throughout the formicoids, including the lineages that otherwise show primitive traits. This unequivocal difference may reflect a fundamental shift in diets that characterize formicoids: almost all poneroids are strict predators, while many of the Ectatomminae, Myrmeciinae, and Pseudomyrmecinae collect nectar or honeydew in addition to live or dead arthropods. This shift is associated with the evolution of arboreal lifestyles that characterize many Dolichoderinae and Formicinae.

The vast majority (90%) of formicoid species belong to subfamilies Dolichoderinae, Formicinae, and Myrmicinae (Fig. 2) that often show a high degree of queen-worker dimorphism. Claustral colony foundation is strictly restricted to these three large subfamilies [9], even though shifts to dependent foundation evolved frequently, often accompanied by the evolution of ► *non-flying queens* (ergatoid queens or short-winged queens). These formicoid subfamilies can also show huge increases in colony size, often resulting from the evolution of minute workers [9]. Moreover, novelties in reproductive structure such as polyandry, biased sex allocation ratios, and thelytoky combined with or instead of sexual reproduction are concentrated in these three clades. Similarly, ► *social-parasitic* queens are unknown in poneroids, but ubiquitous within the large formicoid subfamilies (and just a couple species of *Ectatomma* and *Myrmecia*). Unlike Formicinae or Myrmicinae, the Dorylinae include taxa at both extremes of a gradient in queen-worker divergence and social complexity (e.g., monomorphic workers in *Lioponera* vs. highly polymorphic workers and huge queens in *Dorylus*).

In formicoid lineages, larger colonies can be associated with striking variations in body size among workers, underlying an increased efficiency in division of labor. However, a few poneroids show the developmental ability to produce pronounced worker polymorphism as well as strong queen-worker dimorphism, e.g., *Amblyopone australis*, and termite specialists such as *Centromyrmex bequaerti*, *Megaponera analis*, and the *Neoponera laevigata* species-group [10, 11]. Others such as *Brachyponera lutea*, *Myopopone castanea*, *Paltothyreus tarsatus*, and *Simopelta pergandei* show strong queen-worker dimorphism only [10, 11]. Intracolony body size variability appears restricted to species with larger colonies, but both these traits never reach the magnitude characteristic of many formicoids.

In summary, poneroid taxa radiated within the narrow confines of predation involving individuals or small groups (Fig. 1). In contrast, formicoid subfamilies radiated in very distinct ways linked with a highly diversified diet together with trophallaxis: some kept their social traits

unchanged (and resemble poneroids), while others innovated with exaggerated queen-worker dimorphism and its numerous consequences on colony structure. Rather than a sequential series of radiations, the four dominant ant subfamilies (Ponerinae, Myrmicinae, Formicinae, and Dolichoderinae) diversified together [11]. “List of gamergate species <https://antwiki.org/wiki/Category:Gamergate>” “List of species with ergatoid queens https://antwiki.org/wiki/Category:Ergatoid_queen”

References

1. Barden, P., & Grimaldi, D. A. (2016). Adaptive radiation in socially advanced stem-group ants from the cretaceous. *Current Biology*, *26*, 515–521. <https://doi.org/10.1016/j.cub.2015.12.060>.
2. Bolton, B. (2003). Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute*, *71*, 1–370.
3. Boomsma, J. J., & Gawne, R. (2018). Super-organismality and caste differentiation as points of no return: How the major evolutionary transitions were lost in translation. *Biological Reviews*, *93*, 28–54. <https://doi.org/10.1111/brv.12330>.
4. Borowiec, M. L., Rabeling, C., Brady, S. G., Fisher, B. L., Schultz, T. R., & Ward, P. S. (2019). Compositional heterogeneity and outgroup choice influence the internal phylogeny of the ants. *Molecular Phylogenetics and Evolution*, *134*, 111–121.
5. Keller, R. A. (2011). A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the Poneromorph subfamilies. *Bulletin of the American Museum of Natural History*, *355*, 1–90.
6. Linksvayer, T. A., & Johnson, B. R. (2019). Re-thinking the social ladder approach for elucidating the evolution and molecular basis of insect societies. *Current Opinion in Insect Science*, *34*, 123–129.
7. Lucky, A., Trautwein, M. D., Guénard, B. S., Weiser, M. D., & Dunn, R. R. (2013). Tracing the rise of ants – Out of the ground. *PLoS One*, *8*(12), e84012.
8. Peeters, C. (1997). Morphologically “primitive” ants: Comparative review of social characters, and the importance of queen-worker dimorphism. In B. Crespi & J. C. Choe (Eds.), *The evolution of social behaviour in insects and arachnids* (pp. 372–391). Cambridge: Cambridge University Press. p. 552.
9. Peeters, C., & Ito, F. (2015). Wingless and dwarf workers underlie the ecological success of ants (Hymenoptera: Formicidae). *Myrmecological News*, *21*, 117–130.
10. Peeters, C., & Molet, M. (2010). Evolution of advanced social traits in phylogenetically basal ants: Striking worker polymorphism and large queens in *Amblyopone australis*. *Insectes Sociaux*, *57*, 177–183.
11. Schmidt, C. (2013). Molecular phylogenetics of ponerine ants (Hymenoptera: Formicidae: Ponerinae). *Zootaxa*, *3647*, 201–250.
12. Ward, P. S. (2014). The phylogeny and evolution of ants. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 23–43.
13. Wheeler, W. M. (1910). *Ants. Their structure, development, and behavior*. New York: Columbia University Press.