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Pheidole



Alexandre Casadei Ferreira
Departamento de Zoologia (DZOO), Laboratório de Sistemática e Biologia de Formigas (LSBF), Universidade Federal do Paraná (UFPR), Curitiba, PR, Brazil

Among the ants, the genus *Pheidole* stands out for its great diversity, morphological variation, and behavioral complexity. Since its description 180 years ago, information on the diversity, ecology, and evolution of the genus has steadily accumulated. It has a very wide geographic distribution, occupies a diversity of habitats, and has a broad range of feeding behaviors.

Phylogeny and Systematics

The genus *Pheidole* is the most diverse among myrmicine ants, with 1,047 valid species, 134 valid subspecies, and 6 known fossils. Estimates suggest the existence of about 1,500 *Pheidole* species [5]. Among ant genera as a whole, only the formicine genus *Camponotus*, with 1,041 valid species, rivals *Pheidole* in diversity.

Pheidole has a cosmopolitan distribution, occurring in the New World from New England to the cold temperate regions of Argentina and throughout the continents of the Old World [5]. Species diversity is positively related to

temperature and precipitation, with higher richness in the New World compared to regions of similar environmental conditions in the Old World [1].

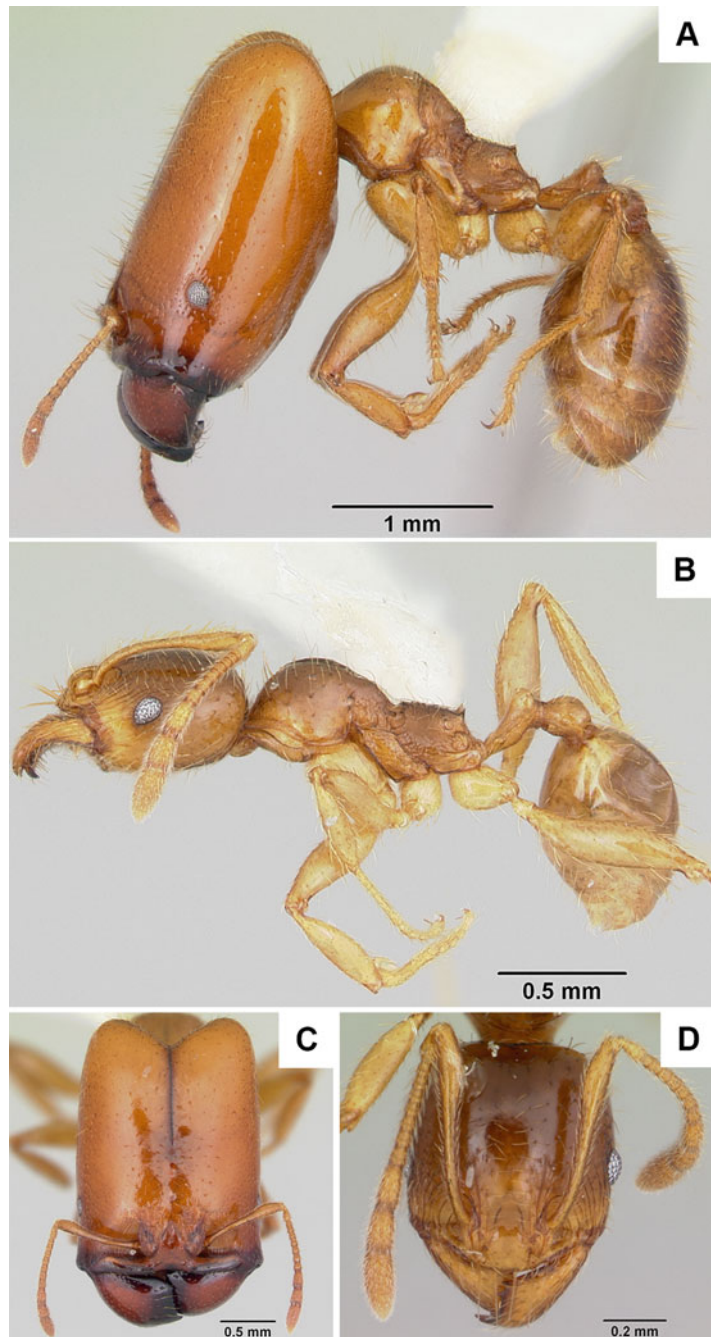
The sister group of *Pheidole* is a clade containing *Cephalotes* and *Procryptocerus*. The divergence time among *Pheidole* and these two other genera is estimated at 58 mya. *Pheidole* diversification began in the New World and was restricted to this region until approximately 13 mya when a single lineage colonized the Old World and began to diversify there [1, 2].

Most species of *Pheidole* have at least some development of simple spines on the propodeum, but spines are typically absent elsewhere on the body. In a few cases, spines may occur elsewhere and may be branched. These exceptions include some Dominican amber fossils and extant radiation of highly spinescent forms in Fiji and New Guinea.

Caste

A key feature of *Pheidole* is the conspicuous worker dimorphism (Fig. 1). The great majority of species have two sharply differentiated worker castes – minor workers (Fig. 1b, d) and major workers (Fig. 1a, c) – without intermediates. Major workers (sometimes referred to as “soldiers”) differ from minor workers by their proportionally larger heads. Both major and minor workers have a reduced ► **venom apparatus** and

Pheidole, Fig. 1 *Pheidole absurda* showing the dimorphism between workers. Major in lateral (a) and frontal (c) view. Minor in lateral (b) and frontal (d) view. (Source: AntWeb.org (CASENT0103138 and CASENT0103139))



no functional ovaries. The venom apparatus is often characterized as nonfunctional, although it is associated with ► [exocrine glands](#) that aid in trail demarcation.

Some *Pheidole* majors have highly modified heads. Species of the lamia group have the mandibles, clypeus, and frons forming a flat surface

used to obstruct the close nest entrance, a phenomenon known as phragmosis. This morphology is very similar in function to that occurring in some species of *Cephalotes*, *Colobopsis*, queens of *Blepharidatta conops*, and other groups. An as yet unexplained modification can be found in members of the *distorta* group,

Pheidole, Fig. 2 Pheidole recruitment. (a) Major and minors on a dead bee. (b) A sardine bait with recruitment of majors and minors. (Photos by Dr. Sebastian Sendoya)



in which the head in lateral view has a bizarre, deeply semicircular concave margin, a remarkable feature not seen in other species groups.

The morphological differences between majors and minors reflect a division of labor in the colony [4]. Minors are primarily responsible for the care of the queen and brood, nest maintenance, and foraging. Foraging minors lay odor trails that direct other workers to food resources (Fig. 2) [3]. Minors defend food from intruders and commonly cooperate to carry large food items. Majors are primarily responsible for defense, both in the nest and at resources. They also process and in some cases transport food [3]. The large, muscle-filled heads of majors are associated with tasks requiring strength such as defense against intruders or cracking seeds. In some majors can assume functions typical of the minors, such as

nest maintenance and brood care [4]. Majors usually have a very restricted behavioral repertory but can expand it in response to a decrease in the number of minors. However, majors are somewhat inefficient in carrying out these activities because of morphological limitations and inexperience [4].

Morphological differentiation related to feeding can be extreme. In some species of the *pilifera* group, there is a third caste of workers with extremely large heads, the “supermajors,” assumed to specialize in milling seeds. These species are found in arid regions of the Southern United States and Northern Mexico (e.g., *P. pilifera* and *P. rhea*).

The division of tasks is not only related to morphological differences. As found in other groups of social insects, a worker’s behavior

changes with age [4]. A worker engaged in caring for the queen and brood and in nest maintenance early in adult life may later leave the nest to forage and also provide nest defense. This pattern is seen in a great many social insects, as younger workers with a greater life expectancy are engaged in relatively safe in-nest tasks, while the older, more experienced individuals, are exposed to higher-risk tasks outside the nest.

Ecology

Pheidole can be found in a variety of microhabitats, especially soil and litter. In tropical forests they commonly nest at ground level, from the deepest soil layers to decomposing wood on the surface. A few species are entirely arboreal, nesting in stems, under epiphytes, or in carton nests. In the Neotropics a few species are specialized to occupy ► [ant-plants](#). Examples include the highly specialized associations of *P. bicornis* with *Piper* and *P. tachigaliae* with *Tachigali* and less specialized associations such as *P. cramptoni* with *Cordia* and *Piper* [5]. A few of the small species can be also found living inside the nests of other ants and, less commonly, with termites. In Brazil *P. dinophila* and *P. calens* have only been found in nests of the large ponerine ant ► [Dinoponera](#). *P. termitobia*, *P. mittermeieri*, and *P. perpusilla* are commonly found inside termite mounds.

This genus also displays a wide range of feeding strategies and habits. Even though many species are predators and/or scavengers, the majority have a generalized diet. An example of this pattern is the Neotropical *P. biconstricta*, typically found in the Amazon rainforest. The workers are extremely aggressive and forage for live insects in large groups with a behavior similar to army ants. However, this species can also be associated with sap-sucking insects and extrafloral nectars. Among the numerous nutritional components explored by *Pheidole*, seeds represent a significant fraction of the diet, usually associated with species that inhabit open areas (e.g., the *pilifera* group) and less commonly with forest species (e.g., some members of the *tristis* group).

Another important feature usually seen in *Pheidole* is the foraging strategy used in the

exploitation of resources. The workers forage in large groups generated through mass recruitment, wherein thousands of individuals collaborate to monopolize food supplies. This results in extensive trails along which workers quickly remove and transport the provisions to the colony.

Social Parasitism

A few *Pheidole* species are workerless social parasites, invading nests of other *Pheidole* species and producing only reproductive individuals. Nine cases of social parasitism are known in the genus, some with marked morphological modifications. The most extreme morphological changes are present in *P. neokohli* and *P. acutidens*. These have highly unusual pupa-like males that are brachypterous and physogastric. The queens have small heads with delicate sickle-shaped mandibles, no wing venation, and an unusual distended gaster. Curiously, the queen of *P. acutidens* has lost the second pair of wings but maintains the external mesosomal morphology typical of a fully alate species, a very peculiar and unique feature in Hymenoptera.

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