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Spiny Ants (*Polyrhachis*)

Simon Robson
School of Life & Environmental Sciences, The University of Sydney, Sydney, NSW, Australia

Diversity, Distribution, and Evolutionary History

With over 700 described species divided into 13 subgenera and numerous species groups, the formicine ant genus *Polyrhachis* represents one of the most morphologically and behaviorally diverse genus of ants. These medium-sized ants are often recognizable by the presence of spines, their colorful integument, the lack of a meta pleural gland, and the enlarged first segment of the gaster, which can be as long as ½ to ¾ of the length of the gaster as a whole. Restricted to Old-World biogeographic regions, the genus achieves its greatest diversity in the Indo-Malayan, Oriental and Australasian regions [2]. Molecular evidence suggests the group originated in SE Asia approx. 58 million years ago, dispersing once to Africa and several times to Australia [8].

With the exception of the polyphyletic subgenus *Myrmhopla* (a recognized "waste basket group" [2]), each of the remaining 12 subgenera are morphologically distinct and easily recognizable, a consistency at the subgeneric level that is closely matched by their related ecology and nesting habits.

Morphological Diversity

Petiolar spines are present in the workers of most species, accounting for the genus name (Greek: *poly* = many, *rhachis* = ridge or spine). The position and size of the spines, however, varies widely within the genus. Most *Polyrhachis* possess spines on either part or all of the mesosoma (on either the first or last segments: the pronotum and propodeum) as well as the gaster. Within the *Cyrtomyrma* subgenus, spines are predominantly found on the last segment of the mesosoma (the propodeum) and the gaster, while *Chariomyrma* always possess spines on the first and last segments of the mesosoma (pronotum and propodeum) as well as the gaster. The subgenus *Polyrhachis* is unique in also possessing mesonotal spines, as well as petiolar spines of such extraordinary length that can be as long as the entire gaster of the ant itself (Fig. 1).

The color of the *Polyrhachis* integument is highly variable. Many are covered with a metallic gold or silver pubescence but there are spectacular examples of gold, silver, black, red, green, and even blue workers (Fig. 2). The diversity of worker coloration is expanded even further with variation in the actual region of the worker body that is colored. Even for species with similar coloration, the actual region of the body color can

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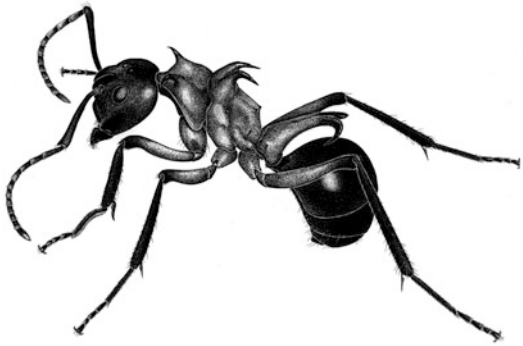
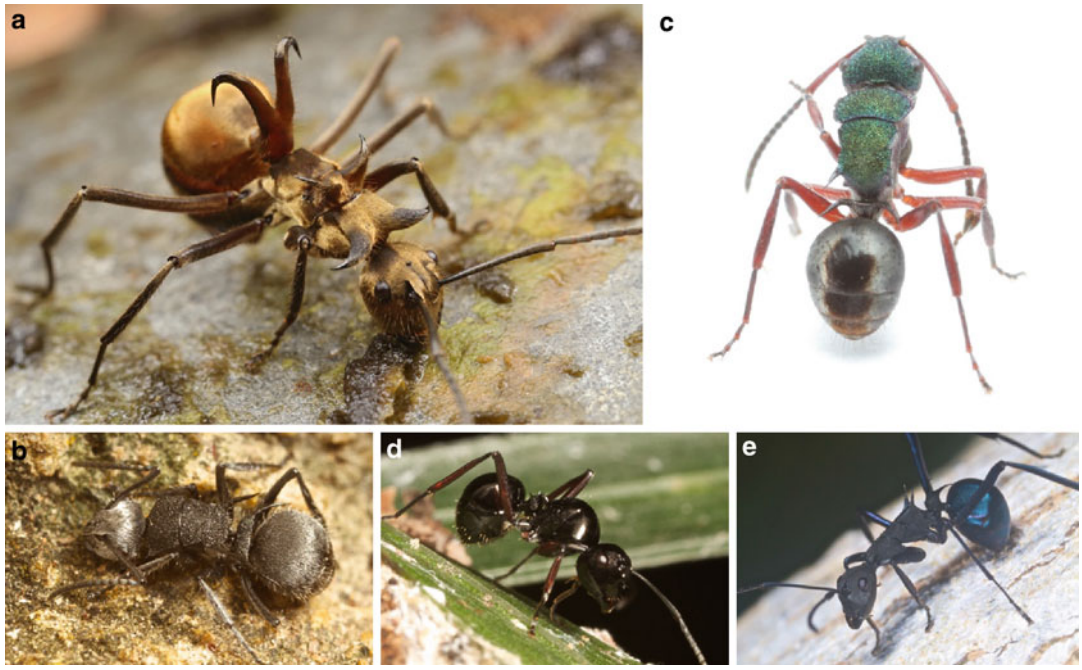
vary from the head, the mesosoma, the petiole, or various combinations of the three (Fig. 3). It is no wonder that Edward O. Wilson refers to *Polyrhachis* as "the birds of paradise of the ant world."



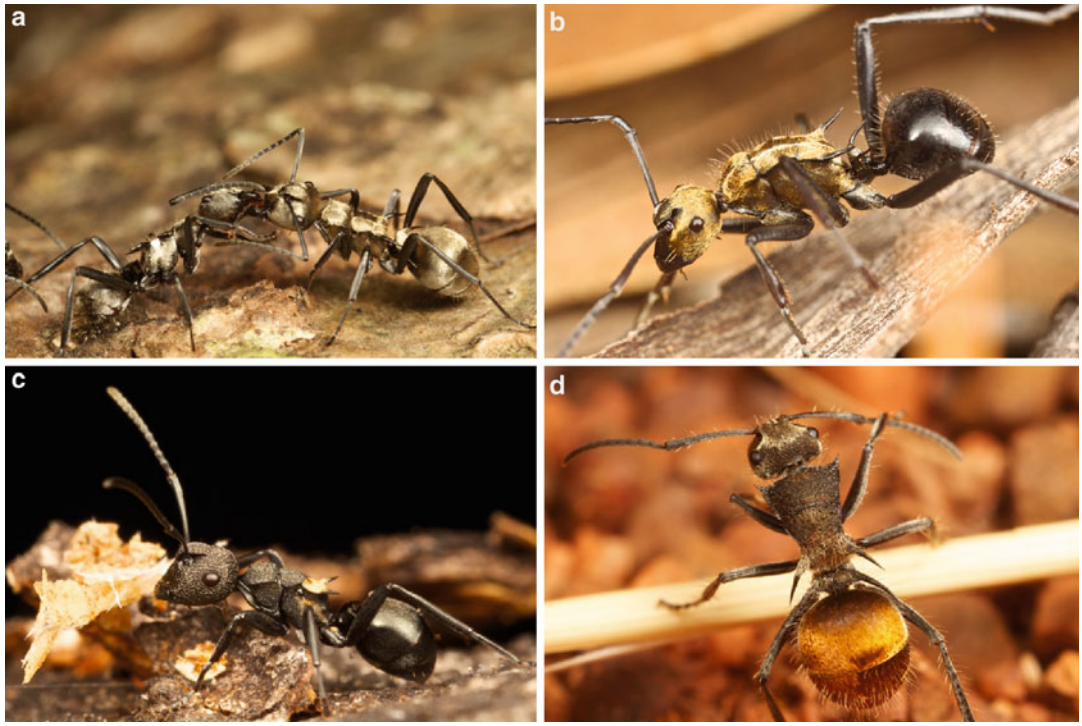
Spiny Ants (*Polyrhachis*), Fig. 1 *P.* (*Polyrhachis*) sp. with extensive pronotal, mesonotal, and petiolar spines. (Drawing by Rudolf J. Kohout)

Nesting Sites and Structural Diversity

Nesting habits and nest material are highly diverse, ranging from subterranean ant nests in the soil to lignicolous, lithocolous, and arboreal nests. The diversity of nesting locations is matched with a similar diversity of nesting material, with many species, even terrestrial nesting ones, including additional material into the nest itself [10]. *Polyrhachis* just seem to like building! Species within the *Campomyrma, Chariomyrma*, and *Hagiomyrma* subgenera typically nest within the soil but often include plant material around the nest. The mulga ant *P. (Campomyrma) macropa* decorates the crater entrance to its nest with a very distinctive layer of phyllodes from the mulga plant *Acacia aneura* (Fig. 4a). Species within the *Cyrtomyrma* subgenus appear to nest exclusively in arboreal habits with nests made from plant material lined with silk. This silk is produced predominantly by their own larvae (Fig. 4b), but some species are known to also include spider silk in their nests [3]. *P. (Myrmhopla) dives* can form



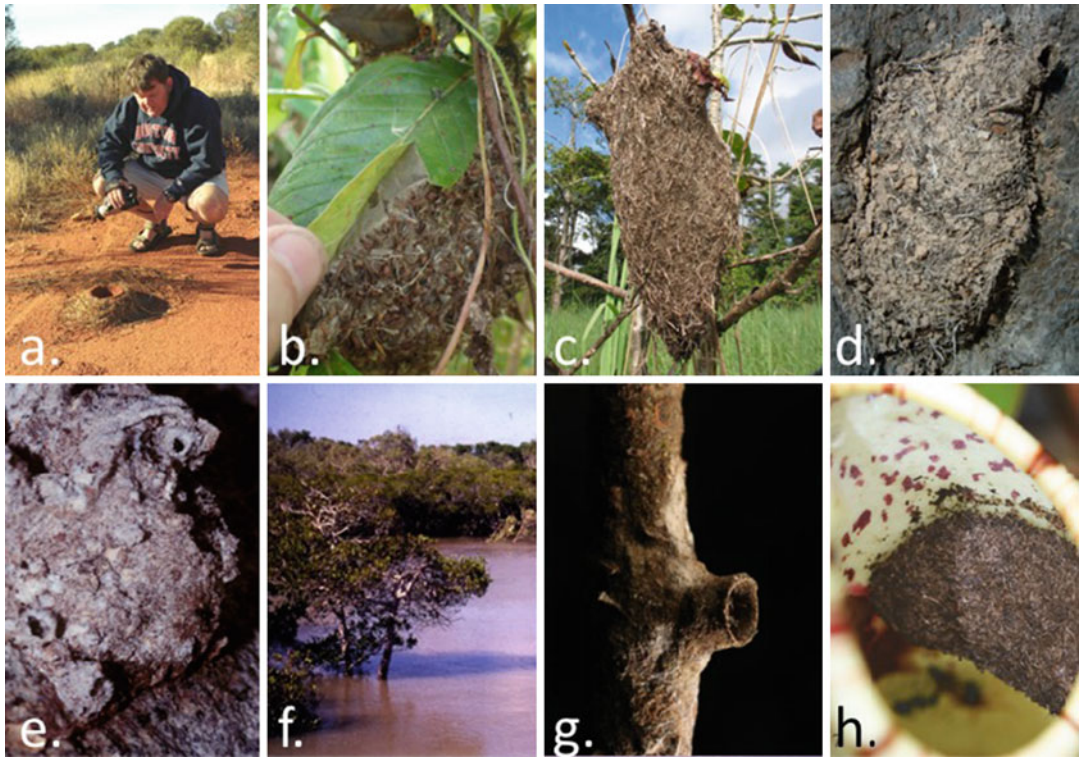
Spiny Ants (*Polyrhachis*), Fig. 2 Color variation in *Polyrhachis.* (**a**) *P.* (*Polyrhachis*) sp., (**b**) Appropriately named *P.* (*Chariomyrma*) *senilis* with a silver head, (**c**) *P.* (*Chariomyrma*) *hookeri*, (**d**) *P.* (*Cyrtomyrma*) *australis*, (**e**) *P.* (*Myrmhopla*) *tubifex*. (Photos (**a**) by Steve Shattuck, (**b**–**e**) by Ajay Narendra)



Spiny Ants (*Polyrhachis*), Fig. 3 Variation in which body segments are colored. (**a**) *P.* (*Hedomyrma*) *cupreata* with an entirely gold body, (**b**) *P.* (*Hagiomyrma*) *semiaurata*, with gold head and mesosoma, (**c**) *P.* (*Hedomyrma*) *machaon* with gold on the rear segment of the mesosoma only, (**d**) *P.*(*Chariomyrma*) nr. *aurea* with only a golden gaster. (Photos by Ajay Narendra)

► supercolonies with multiple large arboreal nests often constructed from plant material only (Fig. 4c). The formation of nests within hollow twigs and under bark is common in the *Hedomyrma* subgenus, but a single species within the typically ground-nesting *Hagiomyrma*, *P. thusnelda*, form nests on the sides of rock walls comprised of such diverse material as fresh kangaroo dung or even the mud from wasp nests (Fig. 4d). Neighboring rock-wall nests of *P. (Hedomyrma) turneri* are comprised of silk, but rather than using their own larvae as a resource the silk is stolen from the egg cases of spiders (Fig. 4e) [9]. This mass of silk in turn appears to become a resource for a wider community of spiders who then chose to inhabit and deposit their own egg sacs in the walls of the ant's nest. Unlike the ► weaver ants *Oecophylla*, no *Polyrhachis* species are known to form chains to manipulate the nest substrate [5].

Perhaps the most unusual nesting habits are displayed by *P. (Chariomyrma)* so*kolova* who form subterranean nests in mangroves which can be inundated by high tides (Fig. 4f) [11], an undescribed species of *Polyrhachis* from Borneo which constructs arboreal silk nests that perfectly mimic hollow twigs (Fig. 4g), and the formation by *P. (Myrmothrinax) nepenthicola* of nests within the pitcher of carnivorous pitcher plants. Nests are constructed on the inner wall of the pitcher, above the level of the liquid, with a hole in the wall of the pitcher providing access to the nest from the external foraging areas (Fig. 4h) [7]. Unlike the ► carpenter ant *Camponotus schmitzi* [1], there is no suggestion that *P. nepenthicola* actually swims and forages in the digestive liquid of the pitcher plant.



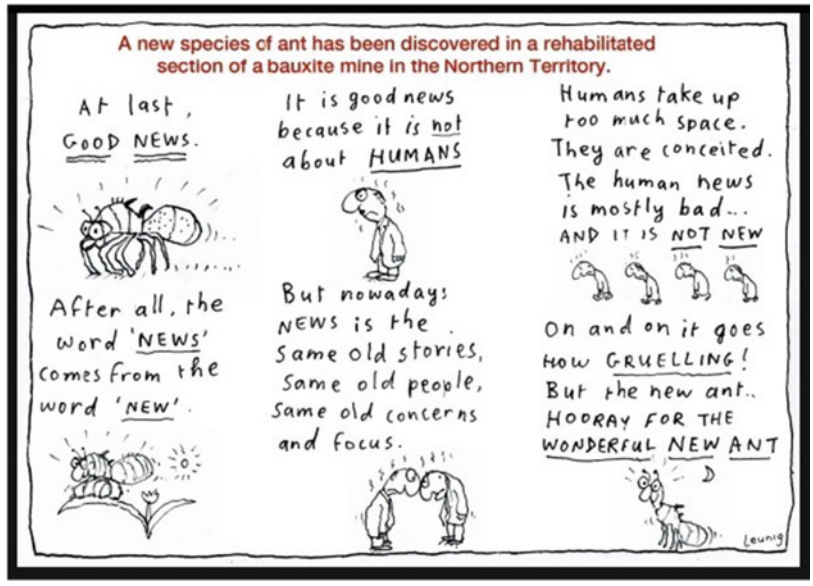
Spiny Ants (*Polyrhachis*), Fig. 4 Variation in the nesting habits of *Polyrhachis*. (**a**) Crater-like nest entrance of the subterranean-nesting mulga ant *P.* (*Campomyrma*) *macropa*, decorated with the phyllodes of the mulga, (**b**) A typical arboreal *Polyrhachis* nest, showing the outer layer of plant material and the inner layer of larval silk (subgenera *Cyrtomyrma* and many *Myrmhopla*), (**c**) A large arboreal nest (approximately 1 m in length) of the supercolonial *P* (*Myrmhopla*) *dives* often composed of only plant material, (**d**) *P.* (*Hagiomyrma*) *thusnelda* nest on the side of a rock wall constructed almost entirely of mud from a wasp's nest, (**e**) A soft *P.* (*Hedomyrma*) *turneri* nest on the side of a rock wall constructed from the silk of spider egg cases, (**f**) Nests of the mangrove nesting *P.* (*Chariomyrma*) *sokolova* submerged 1 m under spring tides, (**g**) Camouflaged "twig" nest of *Polyrhachis* (*Myrmhopla*) sp. constructed from larval silk, (**h**) Carton nest of *P.* (*Myrmothrinax*) *nepenthicola* inside a pitcher plant; the ants exit the nest via a hole in the wall of the pitcher. (Photos (**a**) and (**h**) by Rudolf J. Kohout, (**b**–**f**) by Simon Robson, (**g**) by Steve Shattuck)

The Evolution of Nest-Weaving Behavior

The diversity of nesting habits and the degree to which larval silk is (or is not) incorporated into the nests is similar to that of ants as a whole, providing a valuable opportunity to examine the evolution of these behaviors within a single genus.

Phylogenetic studies suggest that despite earlier predictions relating the evolution of arboreality with the use of larval silk in nests and the loss of pupal cocoons, arboreality and larval silk use appear to be the ancestral state for the genus [12]. Basal *Polyrhachis* were arboreal nest weaving species that used larval silk in nest production, with the transition to subterranean nesting and the loss of nest-weaving occurring in the more derived species. However, arboreality and nest-weaving has been partially regained on at least two occasions. Two nonweaving subterranean species have reverted to arboreal nesting habits (without regaining the use of silk in their nests), while a third subterranean species (*P. thurneri*) constructs silk nests on the sides of rocks (using silk from spiders and not from its own larvae). While *Polyrhachis* appear to have "come down from the trees" and abandoned the use of larval silk, in an evolutionary sense later species appear to have decided that it wasn't

Spiny Ants (*Polyrhachis*), Fig. 5 The swimming ant *P.* (*Chariomyrma*) *sokolova*. (Photo © Mark Moffat)



Spiny Ants (*Polyrhachis*), Fig. 6 Ant taxonomy is a good thing

worth the effort and subsequently returned to an arboreal life-style, albeit with the loss of larval silk nest walls.

Behavioral and Ecological Diversity

The morphological and behavioral diversity of the genus is matched by the diversity of sociobiology and ecology and the genus as a whole represents a rich source of studies in social insect biology. Larvae pupate without cocoons in *Cyrtomyrma* and *Myrmatopa* but cocoons are produced in the remainder of subgenera [11]. Polydomous colonies of the arboreal nesting and silk-weaving *Polyrhachis (Cyrtomyrma) robsoni* contain numerous dimorphic queens [13], workers of the mangrove nesting *P. (Chariomyrma) sokolova* readily swim across the surface of water left behind by receding tides (Fig. 5) [11] and species of the arboreal-nesting subgenera *Myrmatopa* and *Myrmathrinax* make a loud highly synchronized

rattling noise when disturbed by striking their gasters against the hard nest substrate when disturbed. Unlike other arboreal species, the nest walls of *Myrmathrinax* and *Myrmatopa* are typically quite hard and constructed of extremely fine plant material, which may predispose their use of substrate-based sound as some form of alarm communication or response. All species of the *Hirtomyrma* subgenus appear to have adopted a parasitic lifestyle, occupying the nests of other subterranean ants. Is it possible they have given up nest construction entirely?

Broad ecological characteristics can vary across the range of the genus. *Polyrhachis (Campomyrma)* species are nocturnal in Australia, for example, but seem to be diurnal in south east Asia [2]. The distinctive morphology, color, and arboreal habits of the genus may explain why they have become the targets of many mimics in tropical ecosystems, especially spiders [4], as well as other nest-inhabiting inquilines.

Historical Note

Behavioral, evolutionary, and socioecological studies of *Polyrhachis* have benefited tremendously from the extensive taxonomic studies of Rudolf J. Kohout (1933–2016 [6, 7] and many other papers). Unfortunately, Rudy was unable to complete his work on the subgenera *Campomyrma* and *Hedomyrma*, but his colleagues are working to bring his revisions of these two subgenera to completion. Ant taxonomists are not often mentioned in the public media, so it seems fitting that the description of *Polyrhachis kohouti* in 2015 in his honor resulted in a wonderful cartoon that appeared in Australia's national newspaper the same year (Fig. 6).

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