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Monomorium

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Monomorium, with 383 described species and subspecies, is one of the most speciose genera of ants in the hyperdiverse subfamily Myrmicinae [1]. However, a recent molecular phylogenetic review of the subfamily shows that the genus as presently defined is not monophyletic, with species scattered across the Solenopsidini clade and several even positioned outside it [2]. Accordingly, further studies are expected to move species outside the genus, as it already happened for the widespread pest species *Monomorium destructor* (now *Trichomyrmex destructor*) and several others.

Nonetheless, the number of described species is likely a gross underestimate of the genus's true diversity. Some zones, such as arid Australia, may harbor up to 750 species [3]. *M. fieldi* and *M. rothsteini*, found in mainland Australia, are fine examples of this overlooked species richness, as recent DNA barcoding, morphological, and behavioral studies suggest that these two, formerly recognized as single species, may in fact be a complex of tens of different taxa.

The vast majority of described *Monomorium* species inhabit the Old World tropics. About half of them occur in the Afrotropical zoogeographic region, considered the radiation center of the genus, although Australia might have the highest species richness. Relatively very few endemic species occur in North America (all in the *M. minimum* group) and even fewer in the Neotropical region.

Considering the cosmopolitan distribution and species richness, it is not surprising that *Monomorium* species are found in many terrestrial habitats and microhabitats. Despite their ubiquity, most described species have not been studied, so that very little is known of their natural history. Most species seem to have a rather generalized diet, but entire species groups, such as *M. rothsteini*, are granivorous. Workers show striking morphological diversity across the genus, but within species-groups, they tend to be relatively uniform. Queens, likewise, display an exceptional degree of polymorphism, with some species having ergatoid and brachypterous (short, nonfunctional wings) queens, along with or instead of fully winged reproductive females [4].

Some species are among the most successful and widely distributed tramp ants, such as the flower ant *Monomorium floricola*, *Monomorium salomonis*, and the pharaoh ant *Monomorium pharaonis*. The latter, in particular, deserves a more thoroughly description not only because of its worldwide distribution [5] and pest status but also because it is one of the better studied ant

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species on a range of topics [6], being relatively easy to maintain in the laboratory for many generations. As a result, *M. pharaonis* has strong potential as model organism to investigate a wide array of question related to ant sociobiology, sociogenomics, development, collective behavior, etc. The remainder of this entry is mostly devoted to this one species.

Distribution

The tropical pharaoh ant, *Monomorium pharaonis* (Fig. 1), has long been considered the world's most persistent and difficult to eradicate household [5]. It is probably the most widely distributed ant species on the planet, with published and unpublished specimen records covering more than 1200 sites across every inhabitable continent [5] (Fig. 2). It is the only ant recorded from Aves Island, a remote, uninhabited islet in the central Caribbean.

Its worldwide distribution is the result of hundreds of years of human-mediated introduction and dispersal through commerce and trade, and there are reasons to consider it the tramp ant with the longest invasion history. A first indication might come from the story of how this ant acquired its species name. Linnaeus named the species *pharaonis* (referring to the ancient Egyptian king's palace) in 1758 because the type specimen came from Egypt. However, Egypt has very few records of this species, suggesting that the type specimen came from an invasive population. *M. pharaonis* was already been reported worldwide by the 1890s at a time when most of the world's ant fauna was poorly documented.

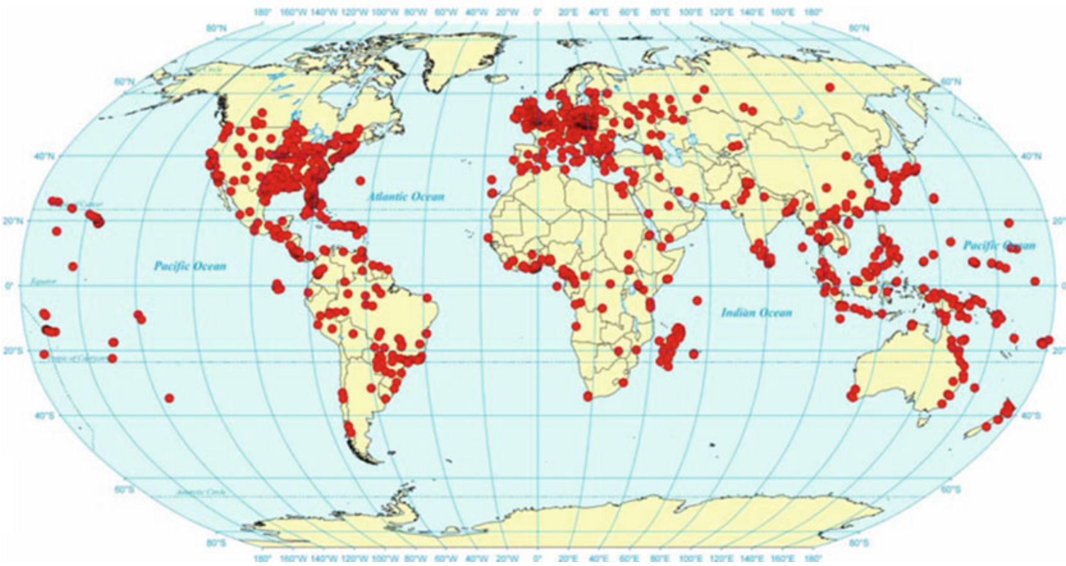
It seems likely that *M. pharaonis* started its worldwide dispersal mainly through introduction into large cities of commercial importance as a stowaway on. This is illustrated by the previous common name "ship ant." By the start of the twentieth century, it was present in every large city of commercial importance in the USA and likely around the world. Since then, with the increase in global trades and air travel, *M. pharaonis* has spread virtually anywhere.

The native range of this species remains unclear, but the tropical regions of Asia appear to be most likely, as outdoor records are much more common there than elsewhere [5]. In most of its present range, and especially in temperate regions, *M. pharaonis* is present almost exclusively inside human-built structures, and it is by far the commonest tropical ant in heated buildings of Europe and North America.

Life History

Like many tramp ants, *M. pharaonis* has a suite of traits collectively termed an "invasive ant syndrome" [7] that have facilitated its establishment and spread in exotic localities. For example, as detailed below, they have very broad nutritional and nesting requirements; they practice intranidal mating, have short generation times, and can produce new sexuals at any time of the year; and colonies are highly polygynous and reproduce by budding.

Monomorium, Fig. 1 Worker (left) and queen (right) of *M. pharaonis*



Monomorium, Fig. 2 Records distribution of *M. pharaonis*. (From [5])

Foraging

M. pharaonis is an opportunistic scavenger, making conspicuous foraging trail networks to feed on a variety of food materials, particularly dead insects. This allows it to thrive in unstable, highly variable environments. The foraging trails have been extensively studied [8]. They are structured in a way that prioritizes recruitment at the food source and maximizes the number of food items that can be rapidly discovered and exploited. In this, the ants use at least three types of pheromones: (1) a long-lasting attractant, which builds the trail network and can still be detected after several days without reapplication, (2) a short-term attractant, which decays faster and is used to mark the food sources, and (3) a repellent that marks an unprofitable or hazardous area. *M. pharaonis* was the first social insect species found to use a negative pheromone [9]. Moreover, recruitment operates from existing trails, rather than from the nest.

Such decentralized recruitment, along with the use of different pheromones, ensures prompt regulation of the trails and a rapid response to newly discovered opportunities. The mode of trail formation and regulation adapt *M. pharaonis* exceptionally well to exploit patchy resources, typical of the unstable environments where the ant lives. The efficiency of the entire process is further enhanced by the presence of a behaviorally distinct class of workers specialized in the perception of the long-lasting attractant pheromone. These “pathfinders” can relocate and re-establish old foraging trails [10].

Colony Structure

Due to *M. pharaonis*’s presence almost exclusively inside heated buildings in temperate regions, the species is notorious as a pest in hospitals, where it is known as a vector for diseases [11]. Nests found in and around household items are ephemeral and subject to frequent disturbance. This factor, along with overcrowding, results in budding, in which a part of the colony leaves the natal nest on foot to form a new colony nearby. New and old colonies remain connected through trail networks, which favors rapid expansion into new habitats. As a result, colonies commonly inhabit many nests (polydomy), each with many queens (polygyny).

No field data are available for the distribution of colony size in nature. In the laboratory a typical mature colony may contain around 2000 workers and 200 queens, but relatively large colonies can contain many thousands of workers and many hundreds of queens. It has also been shown that, in response to budding, the preferred minimum group size is around 470 individuals, with a 10:1 ratio of workers to queens [12].

Development and Division of Labor

M. pharaonis has three larval instars, with differences between worker-destined and sexual larvae apparent as early as the second instar. While worker second and third instar larvae are covered in various types of hairs, sexual larvae are larger and almost naked. Larvae have a crucial role in processing and distributing protein resources to the rest of the colony. In particular, third instar larvae have been shown to boost the egg-laying rate of queens [13] and to affect the production of new queens and males [14].

As in many social insects, workers are monomorphic but go through a behavioral shift as they age (age polyethism) [15]. Young workers perform tasks inside the nest, such as brood tending and cleaning, while the darker older workers perform outside tasks such as foraging. Additional specialization seems to occur within the worker caste, as some individuals appear to serve as repletes [16], and some nurse workers specialize on feeding young versus old larvae [17]. Worker life-span is around 10 weeks, but queens live much longer, usually about 6–8 months.

Production of Sexuals

Under laboratory conditions, colonies go through a reproductive cycle, with new queens and males produced about every 6 months. However, the production of new sexuals is initiated as soon as the existing queens senesce, die, or are experimentally removed from the colony.

Sexual production appears to be regulated by the ratio of adult workers to eggs [18]. When this ratio is low, no sexuals are produced, as a high number of eggs presumably signals the presence of many fertile queens. In all studied *Monomorium* species, workers lack reproductive organs, and all brood comes from queen-laid eggs. Males are probably produced year-round but are only allowed to fully develop when queen brood is developing. Workers are believed either to cannibalize or starve male and queen larvae when fecund queens are present [19].

However, newly mated queens can produce new queens soon after mating, so that minimum generation time can be as short as 6 weeks, much less than in most ants.

Mating

Although queens and males have fully formed wings, they do not engage in mating flights. Rather, they mate within the natal nest. Queens are single-mated, but each male can inseminate up to four queens [20]. Long-term intranidal mating is expected to lead to high levels of inbreeding and hence to increased homozygosity, but *M. pharaonis* appears to be quite resilient to inbreeding depression, as colonies can be maintained in the laboratory for many generations. This mating behavior also means that each colony effectively constitutes its own breeding population, which in turn may help to explain the extreme genetic differentiation observed across colonies around the world [$F_{ST} = 0.751$], the largest value for genetic differentiation at nuclear loci reported for any non-selfing sexually reproducing organism [21]. This F_{ST} value far exceeds the values reported for other invasive ants with a similar pattern of dispersal, such as the Argentine ant *Linepithema humile* ($F_{ST} = 0.419$) and the invasive garden ant *Lasius neglectus* ($F_{ST} = 0.334$). Despite such a degree of genetic differentiation among colonies, nestmate recognition in *M. pharaonis* is almost nonexistent, with workers displaying only transient aggression. This ensures that at least under laboratory conditions, different colony lineages can be merged.

The Pharaoh Ant as a Model System

In recent years *M. pharaonis* has become a model organism in research that could not be conducted with other ant species. Colonies can be maintained across many generations due to intranidal mating, resilience to inbreeding, short generation time, and a generalized diet. The availability of genetically divergent colony lineages, the possibility of triggering sexual production at any time by removing the queens, and the fact that sexuals readily mate regardless of relatedness allow for controlled breeding experiments and artificial selection on quantitative traits, both at the individual and the colony level [22]. Examples include the genetic basis of cuticular hydrocarbon profiles, individual-level behavior, and colony-level traits like collective behavior or caste and sex ratio. Furthermore, because of the availability of *Wolbachia*-infected and uninfected colonies, it is possible to investigate the effects of this endosymbiont on a variety of traits [22].

Finally, *M. pharaonis* and other *Monomorium* species likely possess blastogenic caste determination, in which female caste is determined in the embryo. In worker-destined embryos of *M. emersoni*, the germ cells responsible for the formation of the adult gametes degenerate early in development [23]. This will enable research into which factors (genotype of embryo, genotype of queen and worker nestmates, maternal environmental effects, nutrition and pheromone environmental effects, etc.) influence the developmental processes of caste determination and differentiation, as well as the evolutionary genetic underpinnings of the caste system [24].

Cross-References

▶ Argentine Ant
▶ Caste Determination
▶ Cuticular Hydrocarbon
▶ Ergatoid
▶ Introduction
▶ Nestmate Recognition
▶ Pheromones
▶ Polydomy
▶ Polyethism
▶ Recruitment at the Food Source
▶ Tramp Ants

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