A Comparative Study of the Nests, Gardens and Fungi of the Fungus-growing Ants, Attini.

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The Attini or fungus-growing ants are exclusively New World in distribution and are found approximately from 40° N. Latitude to 44° S. Latitude. Their sole food source are fungi, which they grow on substrate brought into the nest. The fungus grows as a vegetative mycelium planted by the ants. First the substrate (leaves or flowers in the higher attines) is prepared by the ants cutting it into small pieces. Then it is pressed by the mandibles so that it becomes a pulpy mass to which saliva has been added. Liquid fecal droplets are either added during the preparation or at some time soon afterwards. The substrate is subsequently forced into the garden with the aid of the fore feet and mandibles. Finally, the ant picks up pieces of the adjacent mycelium and dots the particle with them. These become islands of growth and the garden may grow rapidly under this treatment. When the ants are actively bringing in substrate small gardens may double in weight or bulk in several weeks.

This involved behavioral pattern is repeated by the several hundred species of the entire range of some 12 genera.

External appearance of the nest

The external appearance of the nest tends to be different according to the species. The smallest and most primitive species, such as *Cyphomyrmex* and *Apterostigma*, have only a bare hole as an entrance and this could be a crack in rotted wood. Such cracks are partially blocked to leave a small entrance. The tropical *Myrmicocrypta* and *Mycocepurus* species pile up the fine grains of soil to make irregular and sometimes furrowed heaps on the soil surface.

The most characteristic entrance to the nest of most species (Fig. 1) is in the form of a symmetrical low crater. The craters may be suggestive of a coral atoll, flat in the center and with a low rim. The hole is usually in the middle. The ants march out from this with their burden of excavated soil to a distance, short in the smallest ants and longer in larger ants, before dumping the soil. The northernmost species (Fig. 1) creates a rim to the crater that is higher in one direction than in the others and it is lunate. The crater of *Mycetophylax conformis* (Mayr) of the Caribbean seashore is in the form of a circular crater with no part particularly higher than another. The form and size are repeated after the winds and rain destroy it, sometimes a dozen times in a day of showers. This form and size appears to be a generic character since other species in the interior of semi-desert Argentina are similar to conformis.

The craters of Sericomyrmex urichi Forel of Trinidad are regularly flat and unusually large for the size of the ants. The ants tend to use one part of the crater rim at a time for dumping the soil grains from excavating. If there is a time lag between excavations, one part of the rim may have a bleached color of tropical red clay compared with the brighter red color of freshly excavated soil.

The genus Apterostigma is not ordinarily a crater-former but a nest of mayri Forel formed a lunate crater of 75 mm diameter in Panama. Nearby, a nest of dentigerum Wheeler formed a 50 mm mound of soil at the entrance of the nest.

The grassland species of the subgenus Moellerius of Acromyrmex characteristically have a turret entrance to their nest in the form of grass or grass and soil particles. The ants march out from the entrance for several centimeters before depositing their soil burdens in the form of a more or less lunate crater. This may be concealed in a tuft of grass and the nest is therefore particularly inconspicuous.

The species of Atta retain the general crater-forming habit of more primitive attines but form craters of the largest sizes which more or less coalesce together. Commonly one part of the crater will be highest and this is usually the part on the down slope if the nest is not on level ground.

General nest architecture

The large surface area covered with craters and the great volume of sub-surface soil occupied by the cells of the mature Atta colony obscure the general plan of attine nests. These are much simpler, as the smaller populations of ants would necessitate.

The simplest of all is the irregular, pre-formed cavities occupied by the yeast-culturer, Cyphomyrmex rimosus (Spinola). The nests may be in the soil, under bark of rotted wood, in humus about roots of epiphytes (once observed as high as 30 meters in a 60-meter tree in rain forest), or in a dead snail shell on the ground.

Other species of the genus also nest in the soil or in humus among roots of epiphytes. The type nest of longiscapus Weber in Colombia was unusual in being in the form of a sack of agglutinated humus suspended from rootlets in a densely forested steep ravine. The sack was 2-7 mm thick and surrounded a single garden 40 mm high and 30 mm wide.

The ants of such genera of small ants as Mycocepurus, Mycetophylax and Myrmicocrypta form one or several chambers in the soil. The tunnel entrance of one Mycocepurus tardus Weber nest was less than 1 mm in diameter and led irregularly to a 20 mm cell at a depth of 205 mm. That of *Mycetophylax conformis* was similarly tenuous and led by a tortuous route to a total depth of 650 mm, having several small cells branching off enroute. The nests of *Myrmicocrypta buenzlii* Borgmeier consisted of one or several chambers of comparatively large size, some 100 mm in diameter, and at depths of 25 to 90 mm. A nest of the common *Apterostigma mayri* had the single cell about 7 cm in diameter at a depth of 45 mm. Other *Apterostigma* nests were barely beneath the hard shell of rotted wood. Common sites include the humus at the base of epiphytic plants.

The nests of *Sericomyrmex* generally resemble those of *Trachymyrmex*, sometimes having a single cell or two or three. One of *harekulli* Weber had the first cell 85 mm high by 95 mm broad at a depth of 200 mm. The next was at a depth of 380 mm and the third was 500 mm underground. A nest of *urichi* had seven gardens at depths from 10 to 22 cm. The cells containing the garden varied from 3 cm to 12 cm in height and from 5 to 9 cm in diameter.

The nests of the small species of *Trachymyrmex* such as *bugnioni* Forel have correspondingly small cells, one colony having a 20 mm single chamber at a depth of 200 mm. Slightly larger species, such as the widespread *cornetzi* Forel, may have a turret entrance and a main cell some 45 mm in diameter at a depth of 70 mm. More shallow is the cell made initially by the new queen. The larger species, such as the widespread *urichi* Forel, will have multiple chambers in a vertical series. One of *urichi* had five, one above the other to a depth of 30 cm; another had six cells at depths from 2.5 to 27 cm. They were from 3 to 12 cm in diameter. One of *zeteki* Weber had a single chamber at a depth of 80 mm that was 80 mm broad and 60 mm high. Such rather shallow nests of a single large cell may occur in other large species but more commonly as the colony grows more cells will be added at greater depths. In some cases of the northern *septentrionalis* they are in a vertical series while in others they branch off at several levels. (Fig. 2).

In general, the size of the nest itself is indicated by the size of the external craters or turret. Most species have only one crater or turret but the nest may consist of 1-7 or more chambers. The most shallow chamber is regularly at the site which the female first excavated when she dug into the ground after her nuptial flight. This is enlarged by her first broods. Chambers are added later as the colony grows, both deeper and laterally.

The mature nests of *Acromyrmex* often differ markedly from those of *Atta* despite the general similarity in habits of the ants. Quite commonly those of *octospinosus* (Reich) and *hystrix* Latr. nest above soil level in trash at the base of trees. One of the former occurred at a height of 5 meters in the crown of a large palm, where dead fronds accumulated. One of hystrix was in the mass of aerial roots at the base of a tree in rain forest, the mass being some 174 cm high and 150 cm broad. Several score fungus gardens were scattered in this well-aerated pile of humus and roots. Other nests in the soil are much smaller and simpler and appear to lack the organization of Atta. That of lundi Guérin is noteworthy in having a large cell one-half meter or more in diameter. The mound builders have a large central chamber under a few centimeters of thatch cover.

The nest of the ants of the subgenus Moellerius of grasslands is more like that of a large Trachymyrmex but has larger cells. Bruch figures one of silvestrii Emery that consists of three vertical tunnels (converging at the top), one with three cells in vertical series and the other two with 11-15 cells, some of them forming opposite pairs. The widespread landolti Forel nest may have three or more cells in a vertical series.

The Atta nest

Excellent diagrams of the mature Atta nest, both in surface view and in section, have been published by South American authorities. Brazilian investigators have examined Atta sexdens L. particularly, and those of this species and cephalotes L. have been the general subjects of economic investigations. Amante (1967) compares the nest architecture of capyguara Gonçalves with other species in the same area. Bucher and Zuccardi (1967) have correlated the nest of vollenweideri Forel with the calcium carbonate layer of the soil and shown general effects on soil of this ant (see also Weber 1966a, b). In recent years nests of the United States species have been described by Moser.

The fungus garden

The fungus garden is the distinctive feature of the life of attine ants. It is the source of food and the place where the brood is kept. The queen resides here and the garden is the focus of the activities of the ants. As the queen lays eggs, the workers take them and distribute them to adjacent cells of the garden.

The garden is the creation of the workers and does not last long if they are removed. Their salivary and anal secretions, added to the garden, are necessary. The contribution of these excretions is being elucidated by current biochemical research.

Whatever the fungus will grow on is called substrate. This, however, is not a simple matter of the ants bringing in anything to the garden. Whatever is brought has to be rigorously treated, as described earlier.

While vegetal substrate is generally used, some of the smaller ants use insect excrement, especially of caterpillars (Lepidoptera) or wood-boring beetles (Coleoptera). In addition, smaller ants may regularly use carcasses of insects, often of ants. These seem to be insects that have died and fallen to the forest floor, since arboreal ant carcasses may be found in terrestrial fungus gardens of species not known to climb trees. As good a growth of fungus may be found on shiny, hard pieces of insect chitin as on succulent substrate, indicating the ability of the fungus to grow for some time on ant excretions when the mycelium is not in contact with nutritive substrate.

An odd situation is the fact that the ants treat their own brood at times like pieces of substrate, similarly embedded in the walls of the garden cells. This is particularly the case with young pupae, which need no care until ready to emerge as callows (young adults). Larvae, when embedded, have the head capsule out so that they can easily be fed.

There is an extensive list of plants known to be harvested by *Atta* and *Acromyrmex*. Moeller in 1893 concluded that in South Brazil the ants would take almost any plant. Cherrett (1968) lists 36 species of Guyana plants exploited by *Atta cephalotes* at one site.

The garden of *Cyphomyrmex rimosus minutus*, Mayr and its close allies consists of cheese-like masses about 1/4 to 1/2 mm in diameter that are placed on pellets of insect excrement brought into the nest by the ants. These masses consist of tightly packed cells that look like ordinary yeast. The garden of other species of *Cyphomyrmex* and of other genera of similarly small ants consist of fine filaments or hyphae growing from small pieces of substrate. This could be insect excrement, small fragments of rotted wood or insect carcasses, or pieces of leaves and flowers. Such gardens in *Cyphomyrmex*, *Mycocepurus* and many *Trachymyrmex* are from 3-8 cm in diameter. In *Apterostigma* the entire garden is enclosed in an extremely thin and fragile veil of hyphae.

Despite the general similarity, generic differences may be recognized. The gardens of *Cyphomyrmex* often are 20-50 mm in diameter, corresponding to the 2-3 mm size of the ants. Those of *Mycocepurus* are also small but looser. The gardens of *Myrmicocrypta* are large (50-80 mm) compared with the small size of the ants. All three genera have cells (using the word to mean a hollow compartment as in a sponge) a few mm in diameter. The ants of *Apterostigma* use insect excrement and the particles of substrate are correspondingly rounded. The gardens of *Trachymyrmex* tend to have a laminated structure, the septa being hung from rootlets entering the ceiling of the chamber. In other cases the fragile garden may consist of masses suspended independently from rootlets and loosely held together by mycelial threads. Some gardens rest completely on stones on the floor of the excavation. The gardens of *Sericomyrmex* are disproportionately large and the substrate is often pale golden brown, fruity and succulent.

The most fragile gardens are those of species like *Mycetophylax conformis* and *Acromyrmex* (*Moellerius*) *landolti* *balzani* Emery which use grass for substrate. Such material is relatively long and narrow, creating an irregular mesh of cells, and the mycelium is scanty.

The largest gardens are those of the largest ants, *Acromyrmex* and *Atta*. The former may have a single very large garden or may have a number in the 8-12 cm range. Those of *Atta* appear to be more consistently globular, except where flattened at the base, and 10-13 cm.

Many species of various genera show versatility in suspending the garden from the flat underside of partially buried rocks.

The Fungus

The only true fungi considered here are those that are actually cultured by ants in their normal nests in nature. This rules out all those fungi reported from abandoned substrate, which would be of great variety.

Aside from the yeast-like form of the fungus of *Cyphomyrmex rimosus minutus* and its allies, all attines culture fungi in the form of a mycelium consisting of hyphae or filaments. Current research is showing the variety and nature of these ant fungi from cultures which I have supplied to mycologists.

The forms taken by the ant fungi have been given various names. The name, Kohlrabi clusters, was early applied to the fungus of *Acromyrmex* and other ants that was in the form of clusters of inflated hyphae. The term, staphyla, from the Greek for a cluster of grapes, was suggested as more appropriate. A gongylidium is an individual hyphal swelling. The term bromatium was early used for the mass of yeast-like cells and is retained for the *Cyphomyrmex* that has this type.

The terms used in these studies, then, are: *gongylidium* for the individual swollen hypha characteristic of nearly all ant fungi, *staphyla* for the naturally occurring cluster of gongylidia and *bromatia* for the fungus of *Cyphomyrmex rimosus* type.

The identity of the ant fungi is currently being investigated and *Lepiota* sp. appears to be the valid name for the fungus grown by ants of at least two genera.

Fig. 1. External indication of the same nest of _Trachymyrmex septentrionalis_ McCook being excavated in sand by a young colony after winds and rain removed the crater (10-12 cm in diameter) during a week in July in Florida.

A - July 1 B - July 3 C - July 7 D - July 8

Craters of these shapes are commonly formed by species of the genera _Sericomyrmex_, _Trachymyrmex_, _Acromyrmex_ and _Atta_, the size varying according to the species.

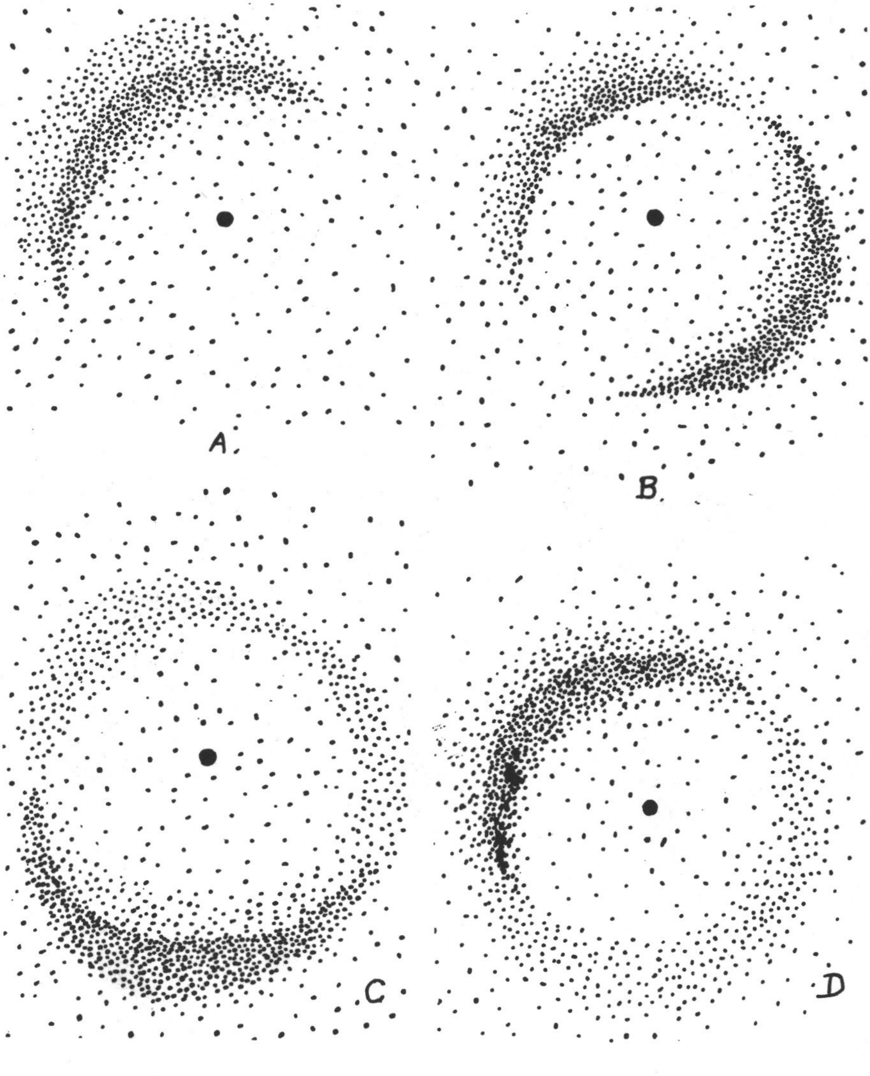
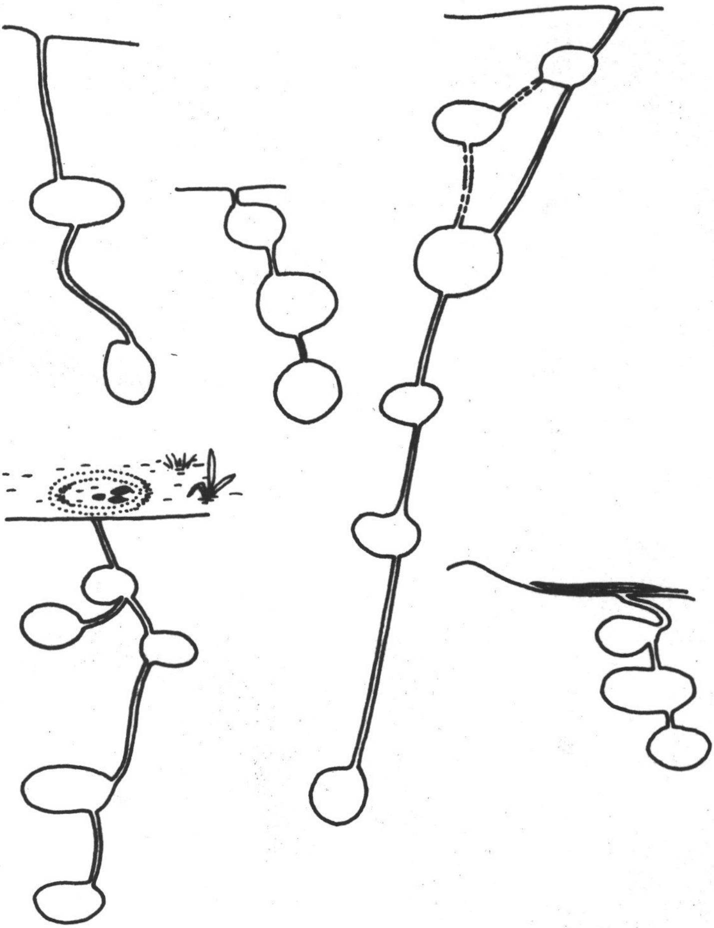


Fig. 2. Some of the chambers and their relationships in Trachymyrmex septentrionalis (after Wheeler 1911). Such multiple chambers are found in many attines. In Atta there may be several hundred and with more than one entrance to the surface. Externally the most common indication is some variation of the craters shown in Fig. 1.



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