VOL. XXIII, NO. 8 WASHINGTON AUGUST, 1912

THE NATIONAL GEOGRAPHIC MAGAZINE

NOTES ABOUT ANTS AND THEIR RESEMBLANCE TO MAN

BY WILLIAM MORTON WHEELER, PH. D.

PROFESSOR OF ECONOMIC ENTOMOLOGY IN HARVARD UNIVERSITY

Dr. Wheeler is the author of an unusually entertaining book, "Ants, Their Structure, Development, and Behavior," published by the Columbia University Press. The volume contains 650 pages and several hundred illustrations, and is probably the most scholarly and suggestive work on the subject that has been published. The pictures illustrating this article are from the above book.

IT IS sometimes profitable to turn away from the consideration of the social and economic problems, which so constantly beset us, to a study of the social insects and their methods of solving the problems which they, too, have had to face during their long and strenuous evolution.

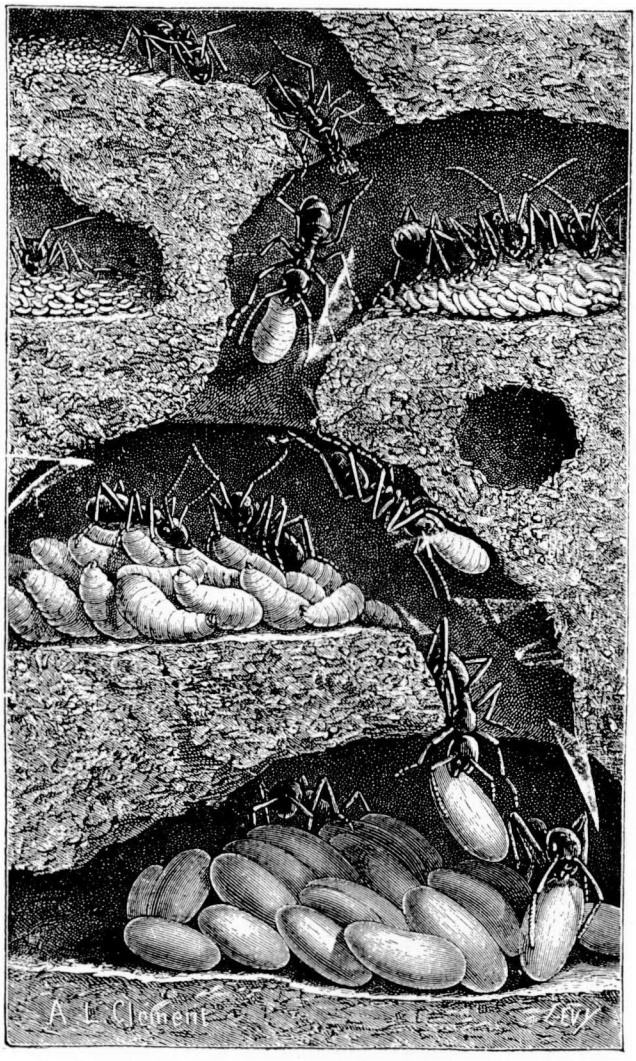
Though in most respects man and the insect differ enormously, both nevertheless display some remarkable convergent similarities. They are the only two successful and dominant animal types of the present age, and, so far as they are social, not only have had to encounter the same obstacles, but have learned to overcome many of them in the same manner.

The social insects, however, have been more successful than man in organizing stable communities, because they have frankly trusted and followed their instincts and have therefore carried their social organization to its logical, or perhaps we had better say instinctive, conclusion, whereas man's intellectual processes and the ideals and dissentions to which they give birth forever prevent a definitive solution of economic problems and keep him in a state of active and ceaseless evolution.

We naturally find, therefore, that the stable and well-regulated insect societies, which have "neither guide, overseer, nor ruler," have always aroused the admiration of those who long for a rigid communistic control of human society, while the individualist turns away from them with a feeling akin to horror.

THREE GREAT PROBLEMS OF EXISTENCE

It is well known that three great problems must be solved by every organism that would survive in the struggle for existence; first, how to obtain a sufficient quantity of the right kind of food; second, how to reproduce its kind and bring up its offspring, and, third, how to protect itself and its offspring from the injurious effects of both the lifeless and the living environment. And although all animals are constantly impelled to the solution of these problems by the primal instincts of hunger, love, and fear, the solution is often extremely difficult. And it is especially difficult in the social and colonial animals, because these must en-



INTERIOR OF AN ANT NEST OR FORMICARY (AFTER ERNEST ANDRÉ)

Showing the arrangement of the chambers and galleries and the ants' method of classifying the brood according to stages. The lowermost chamber contains only cocoons (pupæ), the next above mature larvæ, while the young larvæ and eggs are in the superficial chambers.

ter into severe competition not only with other organisms, but also with the members of their own species, to whom they are, moreover, bound by indissoluble ties.

There are two main groups of social insects, the termites and the social Hymenoptera, the latter embracing three minor groups, the social wasps, the social bees, and the ants. It is more than probable that social habits were developed independently in all four of these groups, and that such resemblances as they exhibit are due more to what biologists call convergence than to blood relationship.

Ants are to be found everywhere, from the arctic regions to the tropics, from timberline on the loftiest mountains to the shifting sands of the dunes and seashores, and from the dampest forests to the driest deserts. Not only do they outnumber in individuals all other terrestrial animals, but their colonies even in very circumscribed localities often defy enumeration. Their colonies are, moreover, remarkably stable, sometimes outlasting a generation of men. Such stability is, of course, due to the longevity of the individual ants, since worker ants are known to live from four to seven and queens from 13 to 15 years. In all these respects the other social insects are decidedly inferior.

A GREAT PRODUCER OF SPECIES

Not only are the colonies of the wasps and bumblebees of rather rare occurrence, but they are merely annual growths. The honey-bees, too, are very short-lived, the workers living only a few weeks or months, the queens but a few years. The termites, though perhaps longer-lived than the bees and wasps, are practically confined to very definite localities in the tropics. Only a few of the species have been able to extend their range into temperate regions.

Thus unquestionably the most successful and dominant of all these groups is the ants, for these have produced the greatest number of species, have occupied all parts of the earth, except the very tops of the high mountains and the cold arctic and antarctic regions, with untold multitudes of individuals, and have developed the most intimate and complicated rela-

tionships to other insects and the vegetation of the planet. It is therefore particularly instructive to study the methods whereby the ants as social insects have solved the problems of nutrition, reproduction, and protection.

The ant colony or society may be regarded as an organism which, like the individual insects of which it consists, grows and develops to a fixed adult size, and the size to which it grows is characteristic of the species, just as is the size of any individual. Some ants always form diminutive colonies of only a few dozen individuals, whereas the colonies of other species, when mature, may comprise thousands or hundreds of thousands. The growth of these colonies obviously depends on the quantity and quality of the available food supply and on its distribution for immediate consumption, or its storage for the future use of the colony.

THE INTRICATE PROCESS OF FOOD CONSERVATION

Ants feed on a great variety of substances, but in all cases only the liquid portions of the food are taken into the alimentary tract. If the food is solid, minute particles of it are rasped off by means of the tongue and pressed into a small pocket in the floor of the mouth. The juices expressed from the mass are then sucked back through the gullet into a dilated portion of the alimentary tract, the crop, and the useless pellet is spit out.

The crop is very distensible, but thin-walled and lined with a layer of chitin, which is impenetrable to the liquid contents, so that none of the food, so long as it is stored in this receptacle, can be absorbed or digested. The crop is closed behind by a complicated valve, which separates it from a short, bag-like stomach, the walls of which have a permeable lining, so that it and the succeeding portions of the alimentary tract, the intestine, are able to digest and absorb any food which may be permitted to enter them through the valve.

The crop and true stomach have been called respectively the "social" and "individual" stomachs, because the liquid food stored in the former is in great part distributed by regurgitation to other ants, whenever they signify their hunger by protruding their tongues and making supplicatory gestures with their feelers, and because none of the food in this receptacle can be used by the individual unless it passes back through the valve into the true stomach.

The crop is thus a storage reservoir from which both the individual and the colony can be supplied with nutriment. Other older and cruder methods of the distribution and storage of food coexist among ants with this more modern and more efficient method.

Thus solid foods may be carried into the nest entire and then dismembered and the pieces distributed to different parts of the nest to be still further comminuted and sucked dry by groups of ants, or the solid food may be carefully stored in special chambers.

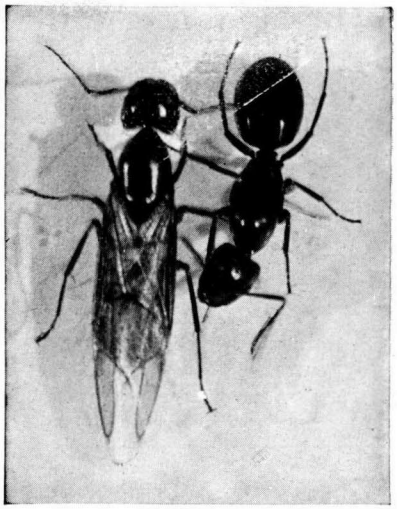


Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

QUEENS OF A COMMON ANT (*Camponotus americanus*)

One of the queens is fecundated and has lost her wings and is thus prepared to start a colony. Ant societies are societies of females. The males really take no part in the colonial activities, and, in most species, are present in the nest only for the brief period requisite to insure the impregnation of the young queens. The males take no part in building, provisioning, or guarding the nest, or in feeding the workers or the brood. They are in every sense the *sexus sequior*. Hence the ants resemble certain mythical human societies like the Amazons, but, unlike these, all their activities center in the multiplication and care of the coming generations.

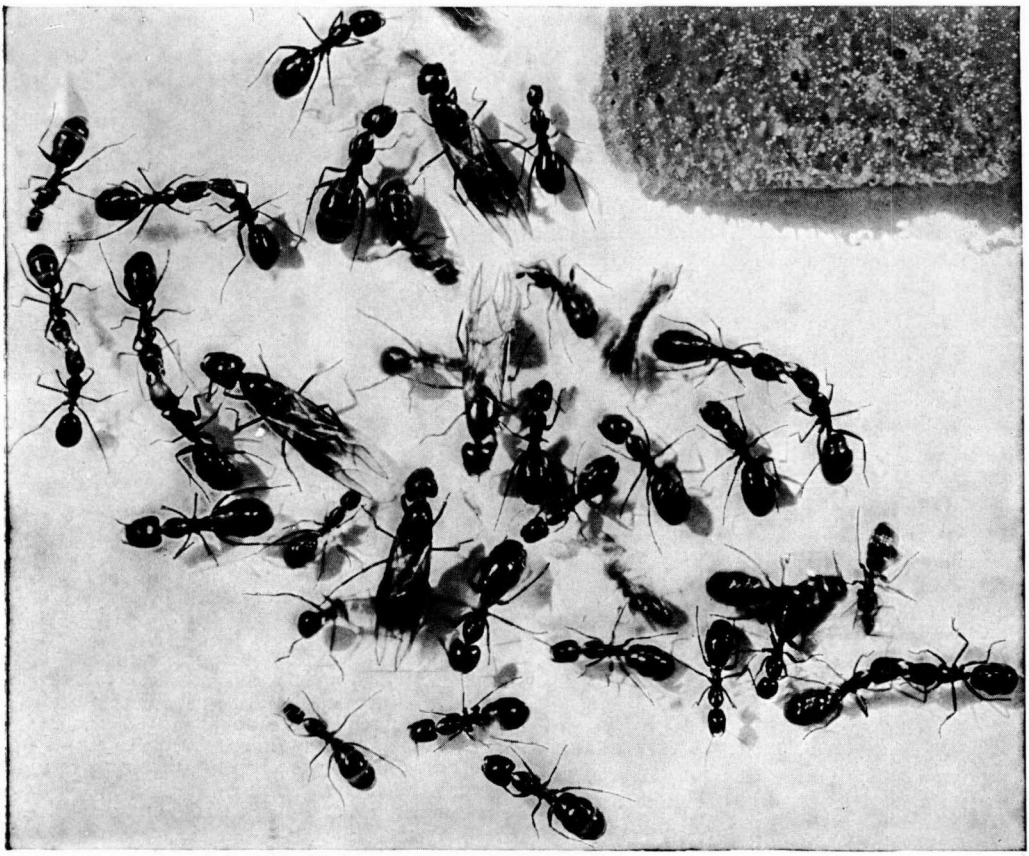


Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

PORTION OF A *Camponotus americanus* COLONY WITH WORKERS AND VIRGIN QUEENS

Five pairs of workers are seen in the act of feeding one another by regurgitating liquid food from the social stomach or crop. Many observers, especially McCook, have dwelt on the exquisite care bestowed by ants on their own bodies and those of their comrades. Much of the time spent by these insects in the dark recesses of their nests is devoted to cleansing the surfaces of their bodies with their tongues and strigils. This process is not only necessary for removing all particles of the earth in which the ants work so much of their lives, but it also invests their bodies with a coating of slightly oleaginous saliva, which probably protects them from moisture and may be sufficiently antiseptic to prevent the growth of lethal moulds and bacteria.

A DETERMINED ATTEMPT AT SELF CIVILIZATION

As ants were primitively carnivorous or predacious insects, it is rather difficult to understand how they could have developed societies at all, for as a general rule we find that predacious animals, which have to hunt their prey or to lie in wait for it, like the spiders, hawks, and tigers, live solitary lives, and that only vegetarians like the caterpillars, sparrows, rodents, and ruminants, which have easy access to a large amount of food, develop gregarious or social habits.

There can be no doubt that the ants have found it difficult to reconcile their carnivorous appetites with their social proclivities, for we find that they have attempted this reconciliation in diverse ways.

Most of the species of the oldest, most primitive, and most conservative subfamily, the Ponerinæ, have not been able to relinquish their carnivorous habits, and have therefore been prevented from forming large colonies. Most of the species of this subfamily, in fact, form colonies of only a few dozen individuals, and these colonies are, moreover, rare and depauperate in appearance.

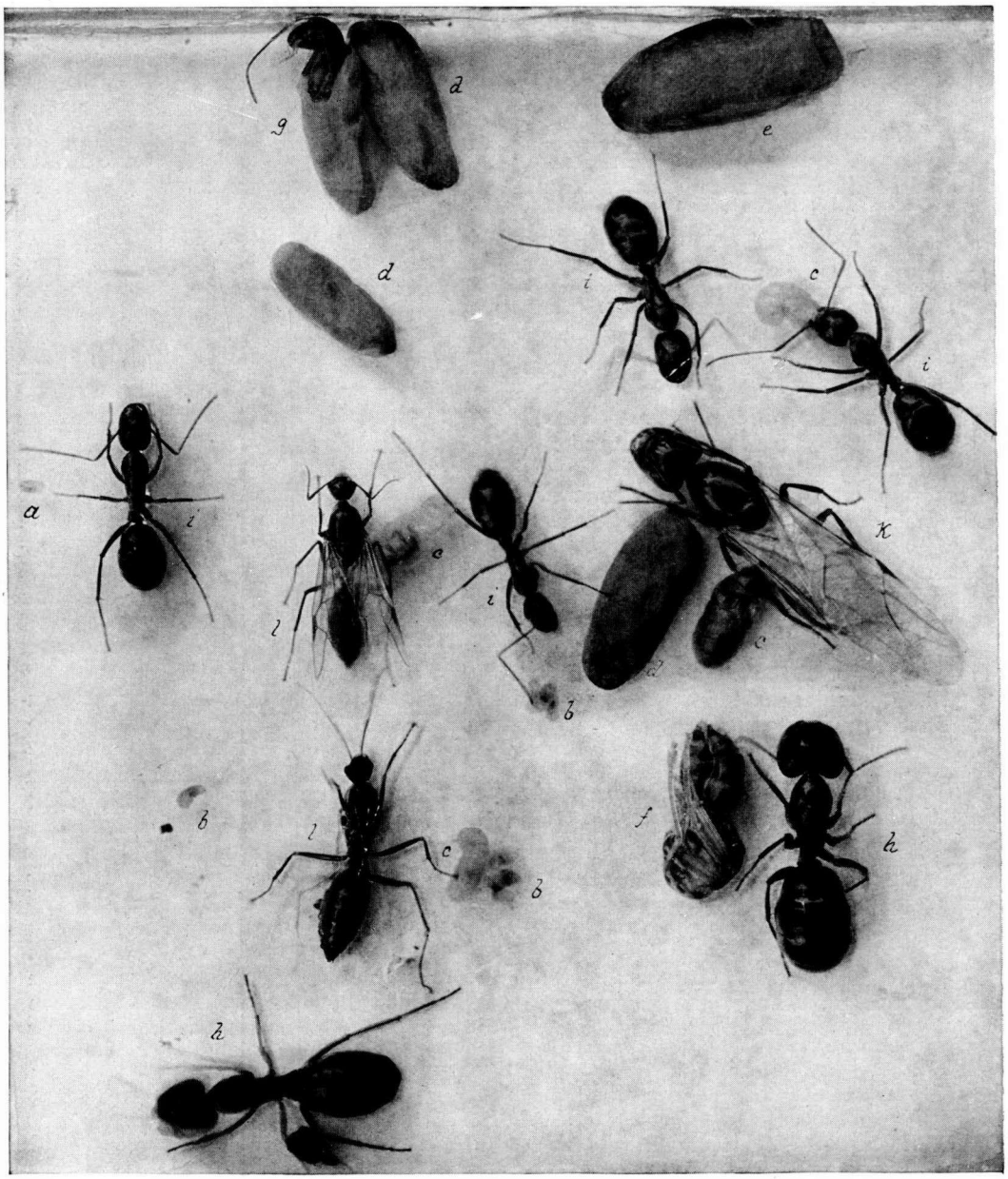


Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

PORTION OF A COLONY OF *Camponotus americanus* AT THE HEIGHT OF THE BREEDING SEASON

a, egg; *b*, young larvæ; *c*, older larvæ; *d*, worker cocoons; *e*, queen cocoon; *f*, worker major pupa removed from cocoon; *g*, worker media, in the act of hatching; *h*, major workers; *i*, minor workers; *k*, virgin female, or queen; *l*, males. Magnification about two diameters.

Another subfamily, the Dorylinæ, embracing the wonderful driver ants of Africa and the legionary ants of the American tropics, are also highly carnivorous, but nevertheless succeed in forming immense colonies, often of hundreds of thousands of individuals. This they accomplish by relinquishing the sedentary habits so characteristic of the great majority of ants. They keep moving in long files through the jungles, capturing or killing all the insects they encounter, and even overrunning dwellings, and, in their search for cockroaches and other vermin, driving out the human inhabitants. From time to time these strange ants bivouac for the night or for a few days in some hole in the ground, or under a tree, but soon continue their predatory march. Evidently they are able to remain carnivorous, and at the same time to develop large colonies, only because they are nomadic and can thus draw their food supply from a large area.

The Ponerinæ and Dorylinæ ants have thus adopted the only modes of life which will permit a union of predatism and sociability.

Their colonies must either remain small and rare, or, if populous, must keep moving from place to place. As each of these conditions has serious disadvantages, we find that the majority of ants have preferred to become more and more vegetarian, though, like man, usually without completely abandoning their carnivorous appetites.

A FAVORITE FOOD

One of the earliest departures from an exclusively animal diet is seen among the ants which attend plant-lice, scale insects, and leaf-hoppers and feed on their saccharine excrement. This excrement is, of course, merely plant sap slightly altered in its chemical constitution by passing through the digestive tract of the insects, and containing much water, some sugar, and a little nitrogenous matter.

Many ants are so inordinately fond of this food that they not only acquire an intimate acquaintance with the habits of the adult plant-lice and scale insects, but actually collect and store their eggs in the nests during winter in order that they may during the ensuing spring distribute the hatching young over the roots or foliage of the plants. This is a well-developed habit among the species of *Lasius* throughout temperate North America and Eurasia (see pictures, pages 743, 744).

Other plant juices, such as the nectar of flowers and the similar liquid secreted by the glands on the petioles of leaves and by green galls, are also assiduously collected by ants. There is, moreover, a singular tendency for some ants which are engaged in this collection of nectar and plant-lice excrement to become "honey-ants" through an extraordinary exaggeration of the instinct to store liquid food in the crop or social stomach.

LIVING STOREHOUSES FOR FOOD

Certain individuals, the "repletes," of the colony refrain from leaving the nest and foraging for food and become converted into flagons by distending the crop to such enormous dimensions that the abdomen looks like a transparent bead (see pictures, pages 747, 748). In this condition they hang by their claws from the roof of the nest chamber and thenceforth spend all their lives receiving liquid food from the tongues of the foraging ants, storing it in their crops, and regurgitating it to hungry individuals when the liquid food supply outside the nest becomes inadequate. This is, of course, apt to be the case periodically in dry regions, so that we find the true honey-ants only in deserts like those of the southwestern states, northern Mexico, South Africa, and central Australia.

In such localities also a further adaptation to vegetarianism may be frequently observed in many species of ants which take to harvesting and eating the seeds of the small herbaceous plants. This harvesting habit is evidently a last resort in regions where insect food is very scarce or confined to a brief season.

There are several dozen species of harvesting ants in North America alone, the most conspicuous being those of the genus *Pogonomyrmex*, the species of which range all the way from Montana to the Argentine through the dry western portions of two continents. It was for-

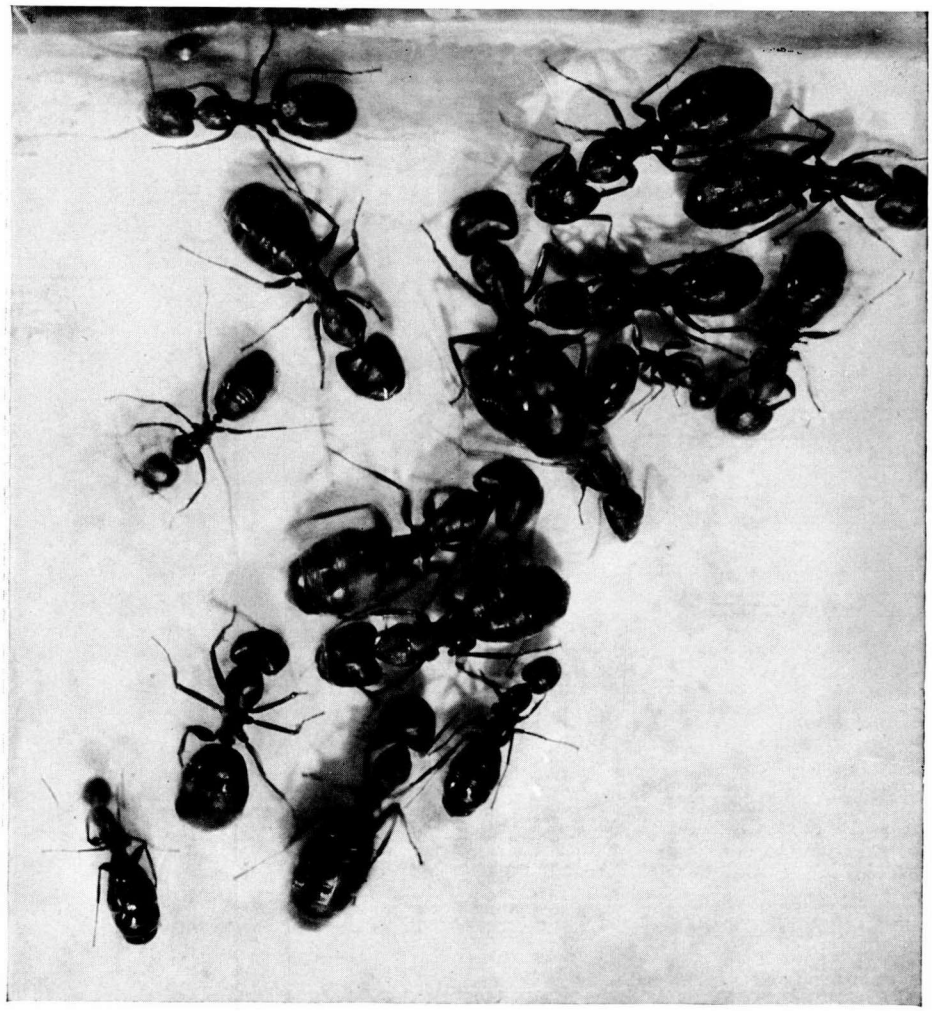


Photo by the Author

MAJOR AND MINOR WORKERS OF *Camponotus americanus*

The worker is produced by inadequate nourishment; is "a hunger form." Magnification about two diameters (see text, page 742)

merly supposed that these ants intentionally sowed seeds in the ground in order that they might later harvest the crop, but this supposition has been shown to be erroneous. The ants merely visit the plants, which are often at some distance from the nest, and carry the seeds home over well-beaten paths.

FARMER ANTS

That ants can carry on agricultural or horticultural pursuits has, however, been proved by a study of the peculiar Attii, a tribe comprising more than a hundred species, all confined to America and nearly all to the tropics. These ants live on fungi which they cultivate on beds of triturated leaves, or insect excrement in specially excavated chambers.

The large species of the genus *Atta* cut pieces of leaves from trees, carry them into the nest in great numbers, cut them into smaller fragments, and build them up on the floors of the chambers into sponge-like masses, over the surface of which a delicate white fungus rapidly proliferates. This fungus, which is constantly weeded by the smallest ants in the colony, is prevented from fruiting and constrained to produce peculiar clus-

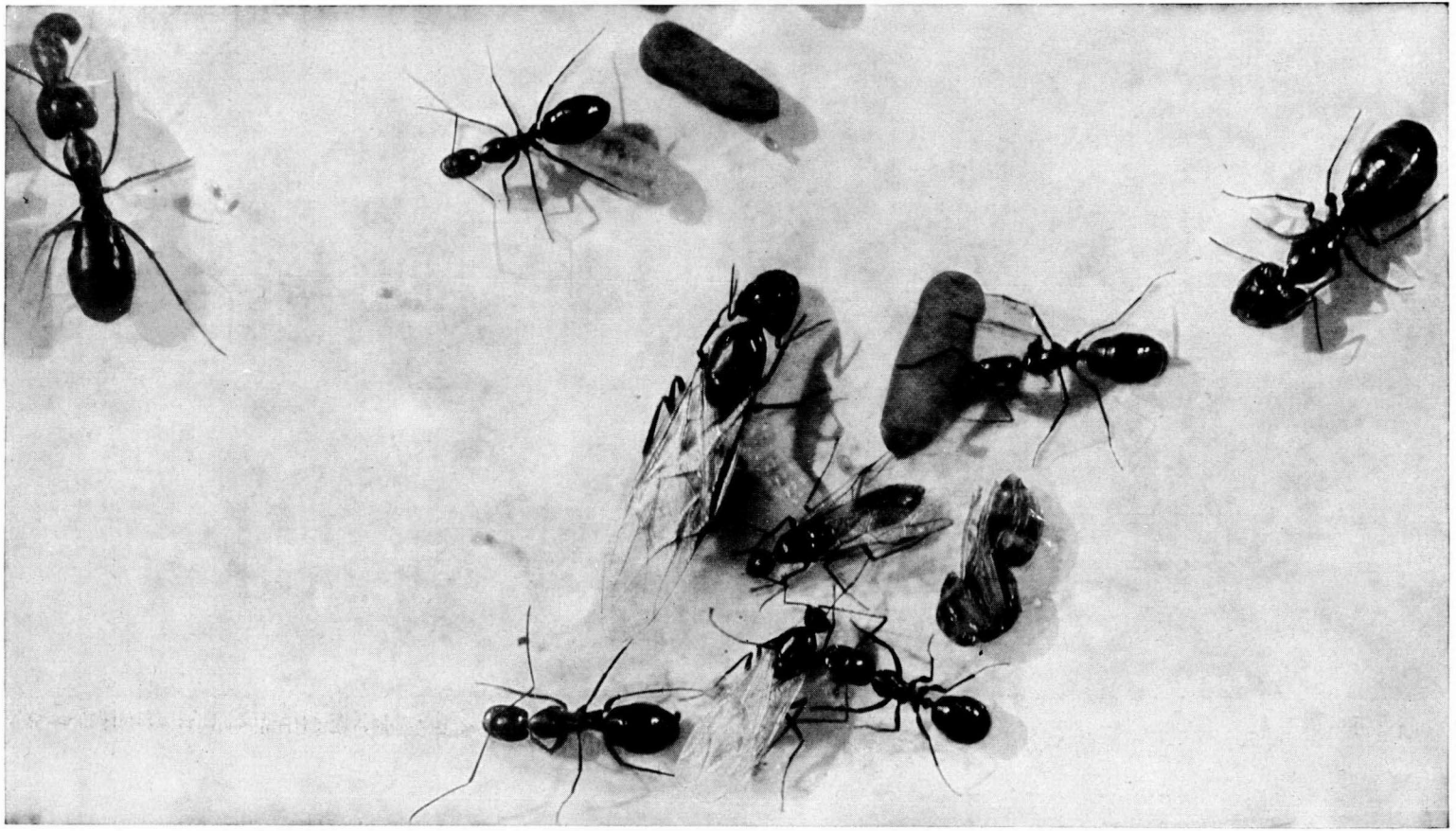


Photo by Mr. J. C. Hubbard and Dr. O. S. Strong

PORTION OF COLONY OF *Camponotus americanus*

The large, winged individual is a virgin queen; the two smaller ones are males; the large-headed wingless individuals are major, the small-headed ones minor workers. A major worker, in the left-hand upper corner, is carrying a half-grown larva in its mandibles. Eggs, very young larvæ, cocoons, and one pupa removed from its cocoon are also shown. Magnification about two diameters.

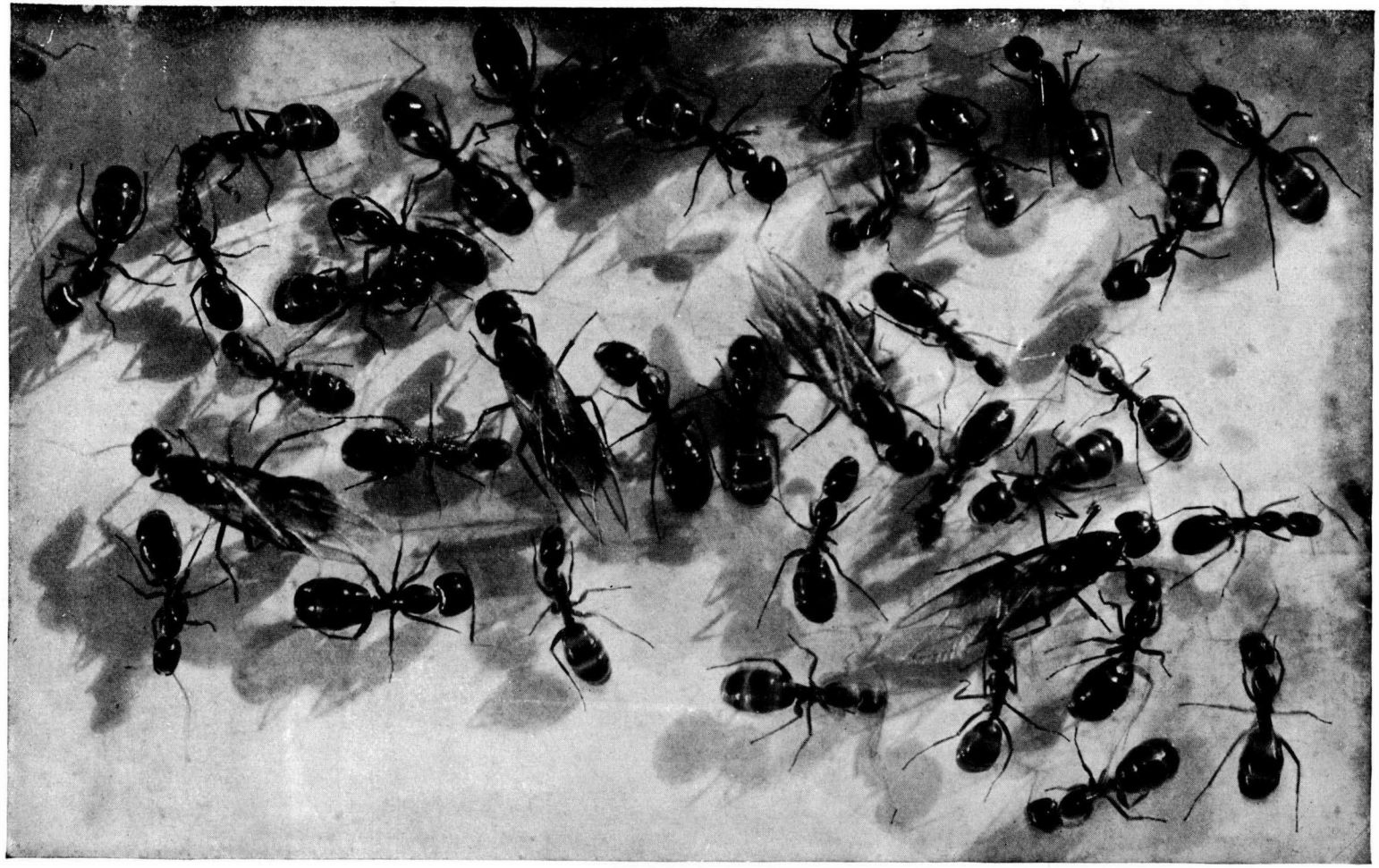


Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

PORTION OF COLONY OF *Camponotus americanus*

Four virgin queens and numerous workers. In the upper left-hand corner one of the workers is seen in the act of receiving food from another by regurgitation. Magnification about two diameters

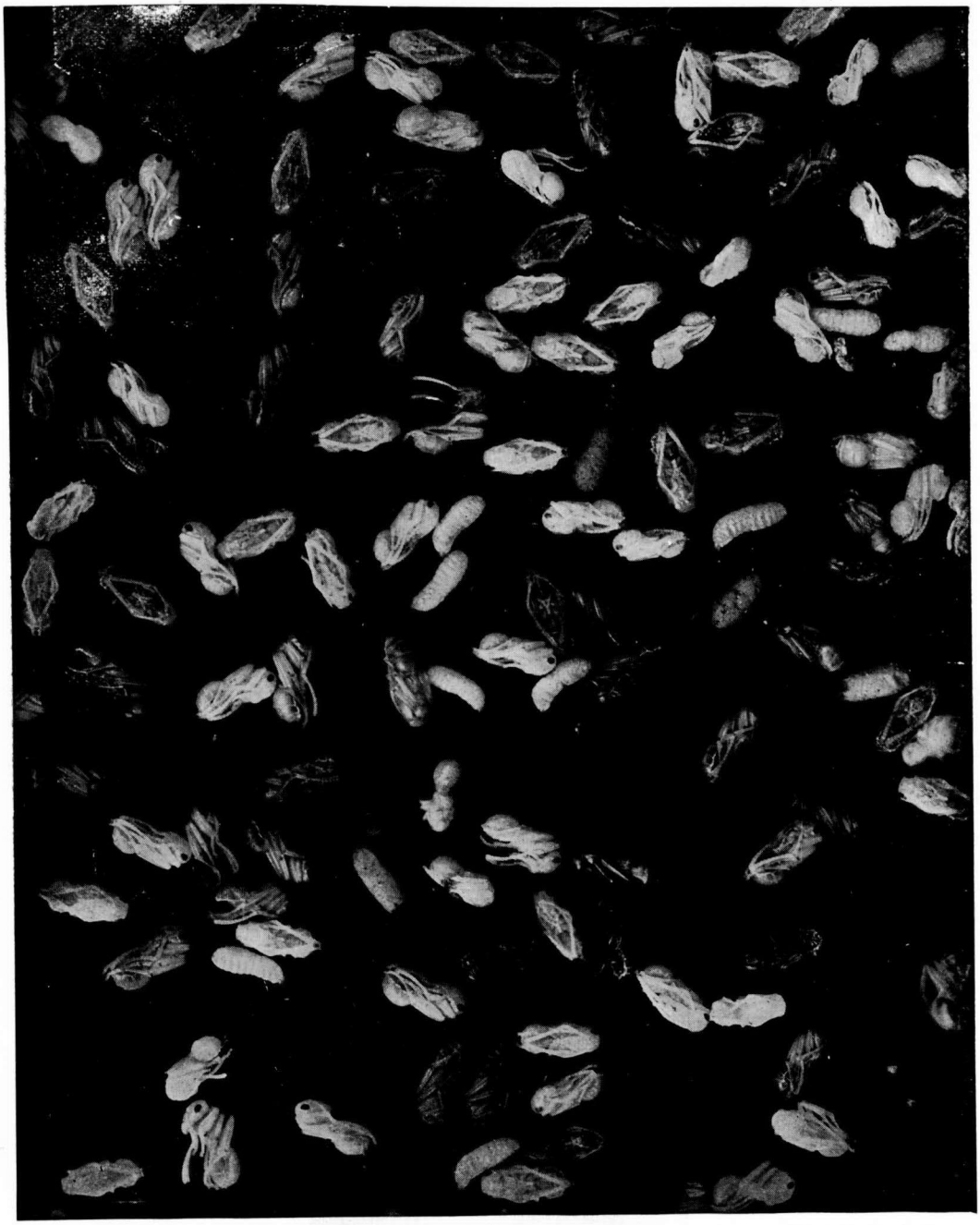


Photo by the Author

ADULT WORKER LARVÆ, SEMI-PUPÆ, AND NUDE AND COVERED PUPÆ IN VARIOUS STAGES OF PIGMENTATION OF *Formica subsericea*

Magnification two diameters

ters of small, glistening food-bodies called "ambrosia" (see pictures, pages 750-754).

Some of the small Attii, instead of building their fungus-gardens on the floors, suspend them from the ceiling of the chambers, so that the masses of substratum clothed with fungus filaments hang down like white velvet curtains. This habit is beautifully developed in several species of *Trachymyrmex* and *Mycetosoritis*. One of these, *Trachymyrmex septentrionalis*, ranges as far north as the pine-barrens of New Jersey.

None of the Attii or their larvæ, so far as known, can eat anything except the particular kind of fungus which they cultivate. To appreciate the advantages to which these completely vegetarian ants have attained in thus substituting an easily controllable and abundant food-supply for the scarce and precarious insect diet of their predatory ancestors, one must observe these wonderful ants in Brazil or Central America, moving over their long trails in interminable processions, defoliating whole trees and carrying their leafy burdens like banners to their huge nest craters, which often spread over a quarter of an acre or more.

The foregoing remarks show that the ethnic history of ants parallels that of man to the extent that these insects were originally flesh-eating hunters, then shepherds of food-producing herds, and finally agriculturists, and that they have been compelled to pass through these stages or forfeit the advantages of living in populous and stationary communities. It is evident, furthermore, that the social needs of ants, like those of man, have been even more exigent than hunger.

SOCIAL DIETITIANS

The skill and success with which the higher ants have thus adapted their diet to the requirements of sociability contrasts markedly with the conditions in the other social insects. The social wasps are carnivorous, to be sure, but their colonies are small and rare like those of the Ponerinæ, and in temperate regions merely annual growths. The social bees have retained the exclusively vegetarian diet of their solitary ancestors, but, as they have greatly specialized by restricting this diet to nectar and pollen, they have become dangerously dependent on the evanescent flowers. And though they have learned to construct a wonderful system of cells for food storage, they are quite unable to control the food supply. Finally, the termites, though completely vegetarian, have also become too specialized by restricting their diet to wood, or cellulose, a hard and innutritious substance, which, though abundant, can be assimilated only with great difficulty.

It is significant, therefore, that the termites of Africa and the Indomalayan region, which form the largest and most aggressive colonies, have become fungus-growers. But even these have not yet learned, like the Attiine ants, to grow "ambrosia" for all the members of the colony. The working population of the nests still has to live on wood in order to produce the excrement which is used in the construction of the gardens. The fungus itself is fed only to the young and to the sexual individuals.

It is a biological axiom that all organisms tend to propagate so rapidly that they are continually in danger of outrunning their food supply. This danger is even greater in the social or colonial than in the solitary organism, because the former is necessarily much hampered in its movements, and if every individual of which the colony consists be permitted to reproduce the food supply would very soon become so inadequate as seriously to impair the functions of the community as a whole. Hence it is not surprising that all social or colonial organisms are bound to restrict the reproductive function of their component individuals. This is true even of the individual organism itself regarded as a colony of cells.

REGULATING THE GROWTH OF FAMILIES

The four groups of social insects have, therefore, had to face a very difficult problem, and it is interesting to note that they have solved it in essentially the same manner as other social aggregates, the cell-aggregate, or individual organism included, namely, by restricting the reproductive function to a very few of the component individuals and by reducing

Photo by the Author

NEST OF A VERY COMMON ANT: *Lasius (Acanthomyops) latipes*

Only the irregular superficial galleries and chambers are shown as they appear when the stone covering the nest is removed. The care of the nest is an important matter with all ants, for convenience, no less than sanitation, requires that the galleries and chambers be kept scrupulously clean. All species, therefore, remove any refuse food, empty cocoons, pupal exuviæ, meconial pellets, dead members of the colony, etc., to a proper distance from the living apartments. Veritable kitchen middens are established for this purpose, either in the open air or, if the colony is nesting under a large stone, in one of the deserted surface galleries.

the great majority to sterility and endowing them with a purely nutritive or protective function.

Nevertheless there are some interesting minor differences in the solutions of the problem of reproduction as exhibited by the termites on the one hand and the social Hymenoptera on the other. Although both of these groups bring up their brood in such a manner that the majority of individuals in the colony are sterile and only a few normally capable of reproduction, the termites make sterile or worker forms out of both male and female individuals, whereas the wasps, bees, and ants produce sterile forms only among the females and merely reduce the number of males and permit them to develop only at certain seasons.

Hence among the social Hymenoptera we have three castes: males, fertile females, or queens and sterile females, or workers. The workers among ants and termites, however, may be still further differentiated into workers proper and soldiers, the former having a nutritive, the latter a protective, function.

This remarkable method of reducing the reproductivity of a society, whilst insuring its nutritive success, is of no little interest at the present time. It is probably not a mere coincidence that we

Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

WORKERS AND COCOONS OF THE ANT WHICH PASTURES AND GUARDS PLANT-LICE: *Lasius* (*Acanthomyops*) *claviger* (SEE TEXT, PAGES 735, 736)

This is a common herder of root-lice in the northern States. From the small cocoons males and workers will hatch; from the two large ones queens. The pale individuals at *a* are just-hatched callows. Magnification about two diameters.

should be most diligently discussing eugenics, or the restriction of reproduction to the sane in mind and body, at a time when we are also most exercised by the high cost of living. Did space permit, it could be shown that man, like other social organisms, has for ages sought and is still seeking means of regulating the reproductivity of his race to prevent its exceeding its food supply, and that the expedients on which he has relied in the past, such as monasticism, wars, and the adoption of religious, property, and caste restrictions to marriage, have been only partially successful.

In termites, both sexes, as we have seen, coöperate equally in the activities of the colony, so that each nest contains, besides a king and queen, a host of workers and soldiers of both sexes. The colonies of ants and the other social Hymenoptera, however, are essentially feminine, since they contain one or more queens and a great number of workers, which are all sterile females, and only at certain times of the year contain any males. These, moreover, take no part in the colonial activities, but live only to mate with the queens of other colonies during the annual marriage flight.

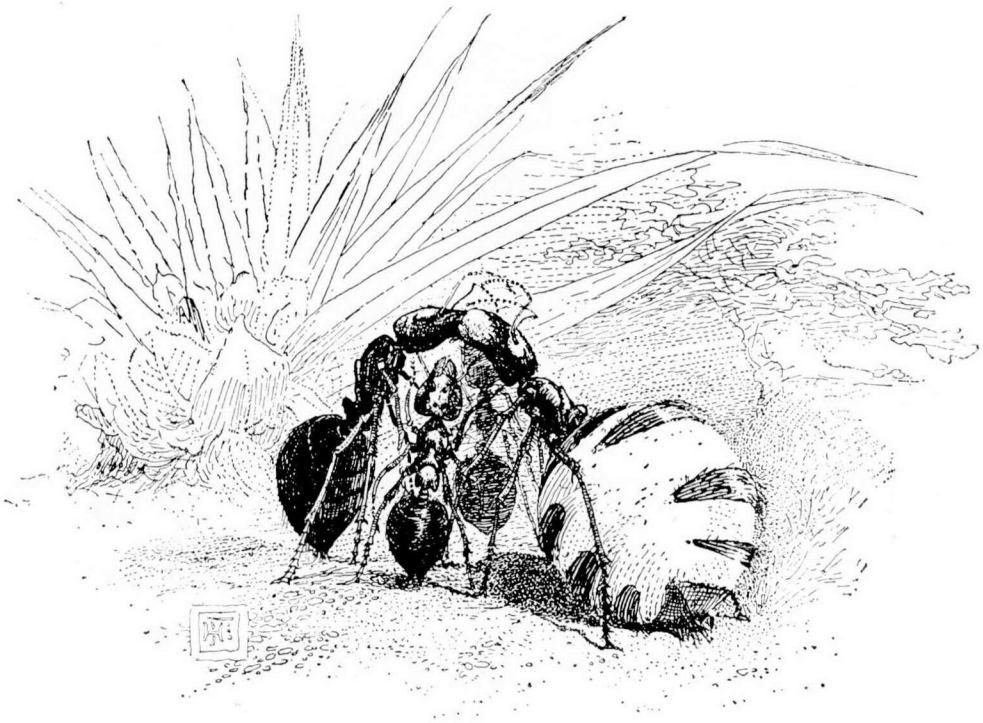
We are therefore prepared to find that maternity is the pivotal instinct about which all the activities of the ant colony revolve. Not only the queen, the repro-

A COLONY OF THE ANT WHICH HOARDS THE EGGS OF THE CORN-ROOT LOUSE IN ITS NESTS OVER WINTER AND DISTRIBUTES THE JUST-HATCHED YOUNG IN THE SPRING ALONG THE ROOTS OF THE MAIZE

Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

COLONY OF *Lasius* (*Acanthomyops*) *claviger*, A COMMON SUBTERRANEAN ANT IN THE WOODS OF THE EASTERN STATES, WHICH NURSES THE ROOT LICE

Two mother queens, without wings, several winged or virgin queens, and males are scattered through the throng of workers. Three queen cocoons and numerous worker cocoons are also shown. Magnification about two diameters (see pages 735, 736).



THE HONEY ANT, WHOSE STOMACH IS DEVELOPED INTO A FOOD RESERVOIR FOR THE REST OF THE ANT COLONY

The picture shows the honey ant (*Myrmecocystus hortideorum*) in the act of regurgitating food to workers of the ordinary form. (After H. McCook.) (See text, page 736.)

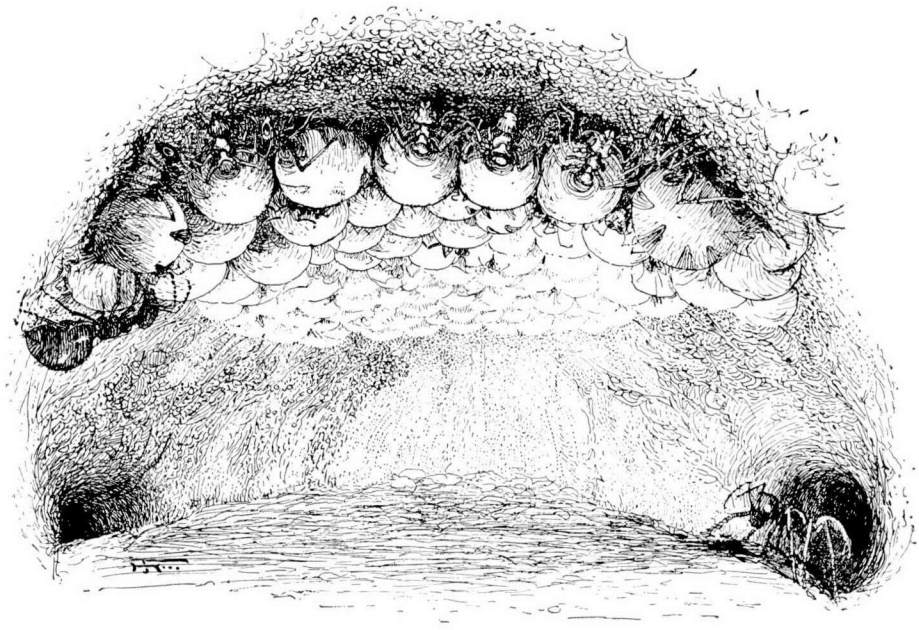
ductive center of the colony, but all the workers act as though they were obsessed with a perfect mania of reproduction and nursing. Unless this fact is clearly appreciated, much of the behavior of ants will remain enigmatic, meaningless, or absurd.

Nothing shows more clearly the strength of the maternal instincts in ants than the development of the colony from its inception till it becomes in turn the mother of other colonies. After mating with the male high in the air, the queen descends to earth and loses her wings, either by breaking them off at the base against the stones or blades of grass or by tearing them away with her mandibles, for they are to be of no further use to her. She then seeks some small cavity under a stone or piece of bark, or digs one in the ground, and closes it after her, so that she is completely shut off from the world (see picture, page 763).

In this little cell she passes days, weeks, or even months without food while waiting for the eggs in her ovaries to mature. The now useless wing-muscles, which fill her large thorax, dissolve in the blood and go to build up the yolk of the eggs, and a similar fate overtakes the great masses of fat which she stored away in her abdomen during her larval life in the maternal nest.

THE INFANT OFFSPRING FEED THE STARVING MOTHER

Eventually she lays a small batch of eggs and cares for them till they hatch as helpless grub-like larvæ. These she feeds with her saliva, but as the supply of this is meager, the larvæ grow slowly, pupate prematurely, and emerge as very small and feeble workers. They nevertheless at once set to work to expand the colony by opening up a gallery to the outside world and go forth to forage. They bring in food to their starving mother and henceforth spend their days in foraging, enlarging the nest by excavating additional galleries and chambers, and in



The "replete" workers, with their social stomachs distended with the sweet exudations of oak galls, hang from the vaulted roof of the chamber in a cluster and function as so many food reservoirs. (After H. McCook.) (See text, page 736).

rearing the successive broods of larvæ from the eggs which the queen is now able to produce in quantities.

The larvæ are fed more abundantly as the number of workers increases, and therefore develop into larger and more vigorous individuals. As time goes on and at the proper season, male larvæ appear and develop, and the female larvæ are so well fed that they can develop beyond the worker stage and become queens.

With the appearance of these sexual forms the colony has reached maturity, and although it may persist for many years, it merely repeats each year this same cycle of feeding and rearing as great a number of individuals as possible on the amount of food which the workers can secure.

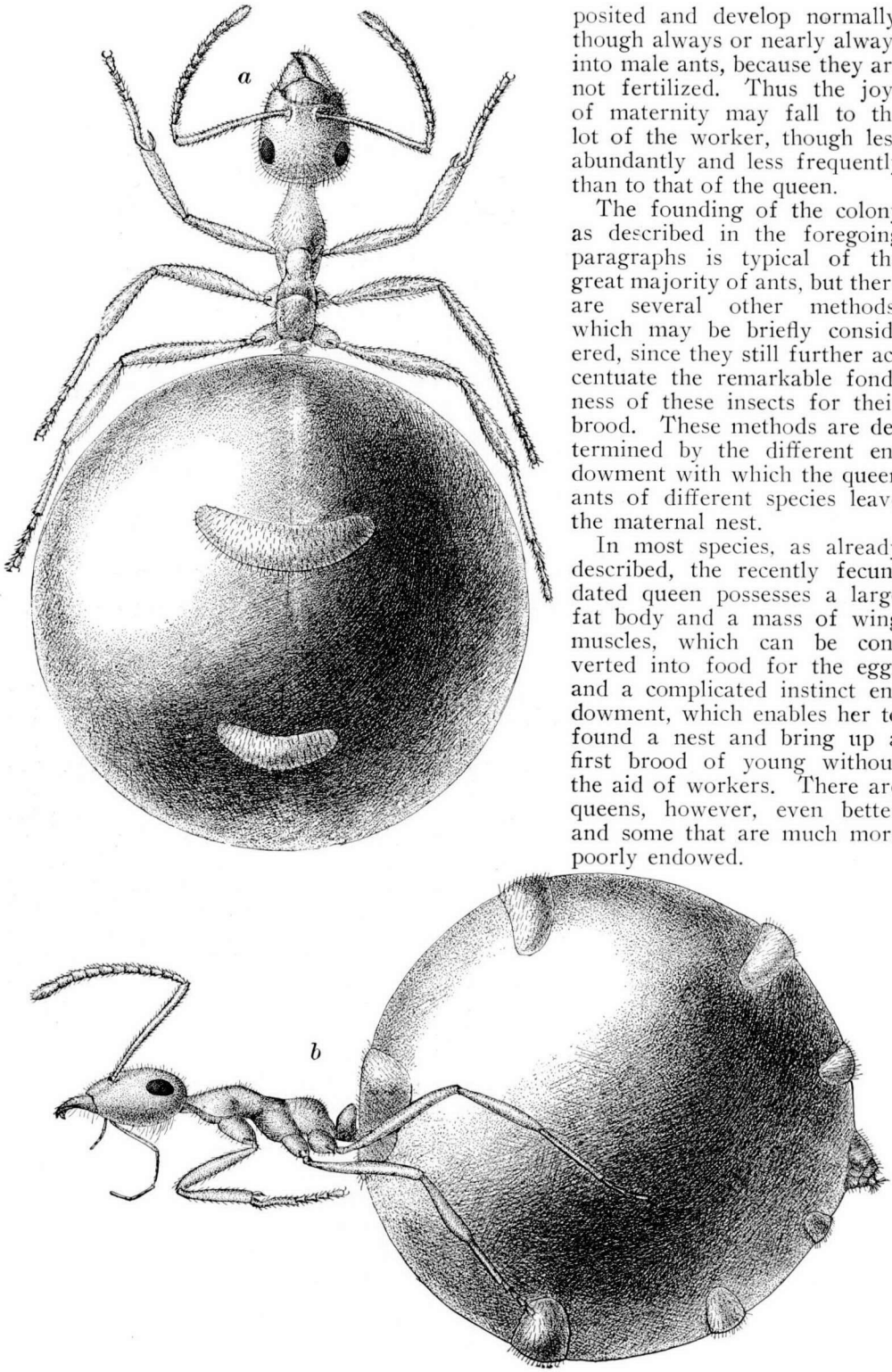
The queen may live a dozen years or more, and each worker may live three to four years, but the males usually live only a few weeks and die after the nuptial flight, being exhausted and knowing neither how to feed themselves nor how to return to the nest.

THE HIGHEST DEGREE OF SELF-SACRIFICE

Most extraordinary during the development of the ant colony is the behavior of the workers, for though sterile and, under ordinary circumstances, unable to lay eggs, they nevertheless exhibit all the other maternal instincts in an exaggerated degree. The worker, as we have seen, is a form produced by inadequate nourishment. It is a hunger form, so inured to long fasting during its larval life that even when it reaches maturity it seems to prefer to starve, for though greedy to fill its social stomach with liquid food whenever there is an opportunity, it dispenses this store most generously to the larvæ and its sister ants and permits very little of it to pass the valve into the individual stomach, only enough, in fact, to maintain healthful activity.

Ants are, therefore, the most thoroughgoing of communists, to whom individual possession as such has no meaning beyond its benefit to the community as a whole.

But even the worker's sterility, which has given certain individualistic thinkers such bad dreams, is neither fixed nor irrevocable. If the colony has a very abundant food supply, or if its queen dies, the small, undeveloped eggs, which are always present in the ovaries of the workers, may grow to full size, be de-



posited and develop normally, though always or nearly always into male ants, because they are not fertilized. Thus the joys of maternity may fall to the lot of the worker, though less abundantly and less frequently than to that of the queen.

The founding of the colony as described in the foregoing paragraphs is typical of the great majority of ants, but there are several other methods, which may be briefly considered, since they still further accentuate the remarkable fondness of these insects for their brood. These methods are determined by the different endowment with which the queen ants of different species leave the maternal nest.

In most species, as already described, the recently fecundated queen possesses a large fat body and a mass of wing muscles, which can be converted into food for the eggs and a complicated instinct endowment, which enables her to found a nest and bring up a first brood of young without the aid of workers. There are queens, however, even better and some that are much more poorly endowed.

THE FAMILY STOMACH OR REPLETES OF THE HONEY ANT OF THE GARDEN OF THE GODS (*Myrmecocystus hortideorum*)

a shows the insects as seen from above; *b* in profile. In both the segments of the abdomen are widely separated by the thin intersegmental membrane, which is greatly stretched by the distended crop, or social stomach. (Author's illustration.) (See text, page 736.)

BORN WITH A WELL-STOCKED LARDER

To the former class belongs the queen of the fungus-growing ants, which not only leaves the maternal nest with the mental and bodily endowment of the ordinary queen, but also inherits some property in the form of a bundle of fungus filaments from the gardens of the maternal nest, tucked away in the little pocket in the floor of her mouth. After she has excavated her chamber in the soil and closed its entrance, she is thus in a position not only to bring up a first brood without extraneous aid, but to start the gardens with the fungus pellet, which she spits out, and keeps growing by careful weeding and by manuring it from time to time with her excrement, or even with her own broken eggs, till the first-ling workers hatch and begin to bring in the leaf material or caterpillar excrement, which is henceforth used as the only substratum for the gardens.

Very different is the endowment of the queens of a number of parasitic ants. These queens are either very small and feeble or lack the instincts and initiative that would enable them to found a colony independently. They are therefore compelled to seek assistance in this arduous task, and they succeed in securing it in one of the three following ways:

The young queens of some parasitic ants enter the colonies of an allied species, the workers of which then either kill their own queen and adopt the parasite in her stead or permit the latter to kill their queen. After the reproductive center of the host colony has been thus destroyed, the intrusive queen lays her eggs and permits her young to be brought up by the alien workers. These die off in the course of a few years, but by that time they have reared at least one brood of the parasitic species and the colony, now consisting exclusively of the queen and workers of this species, is sufficiently vigorous to lead an independent existence. This method of colony formation, in which the queen is relieved from the difficult task of feeding and rearing a first brood, has been called temporary social parasitism. It is characteristic of many of the largest and most prosperous ants of the north temperate zone—*e. g.*, of the mound-building ant of the Alleghanies (*Formica exsectoides*) and the fallow ant of Europe (*F. rufa*).

THE KIDNAPPERS

A different method is adopted by the slave-making ant *Formica sanguinea* and many of its subspecies (see picture, page 755). The young queen enters a nest of the common black *Formica fusca* or of some one of its many varieties, kills or drives away any of the workers when, irritated by her odor, they rush forth to attack her, then hastily collects a lot of the worker pupæ of the *fusca* and stands guard over and defends them till they hatch. These workers at once affiliate themselves with the queen as intimately as if she were their own mother and bring up her brood for her as soon as it appears.

The *sanguinea* young inherit their mother's peculiar instinct to attack the *fusca* colonies in the neighborhood and to kidnap the worker pupæ. They bring these pupæ back to the maternal nest and eat some of them, but permit others to hatch and become "auxiliaries," or "slaves." Thus what has been called slavery among ants is merely a form of parasitism, in which the "slave" species is really the host. In old colonies the *sanguinea* workers often lose the slave-making habit, and as the *fusca* workers then completely die out, there ensues an emancipation of the *sanguinea* colony from the host like that observed in the temporary social parasites.

THE SLAVERS

A third method is adopted by the young queens of the permanent social parasites. These queens enter the colonies of an alien species and are adopted like the queens of the temporary social parasites, after the enforced death of the host queen, but the worker offspring of the parasite are destined always to live with the host species. There are really two methods of insuring this result. One is by slavery, as in the case of the amazon ants (*Polyergus*), the workers of which are unable to feed themselves, to care for

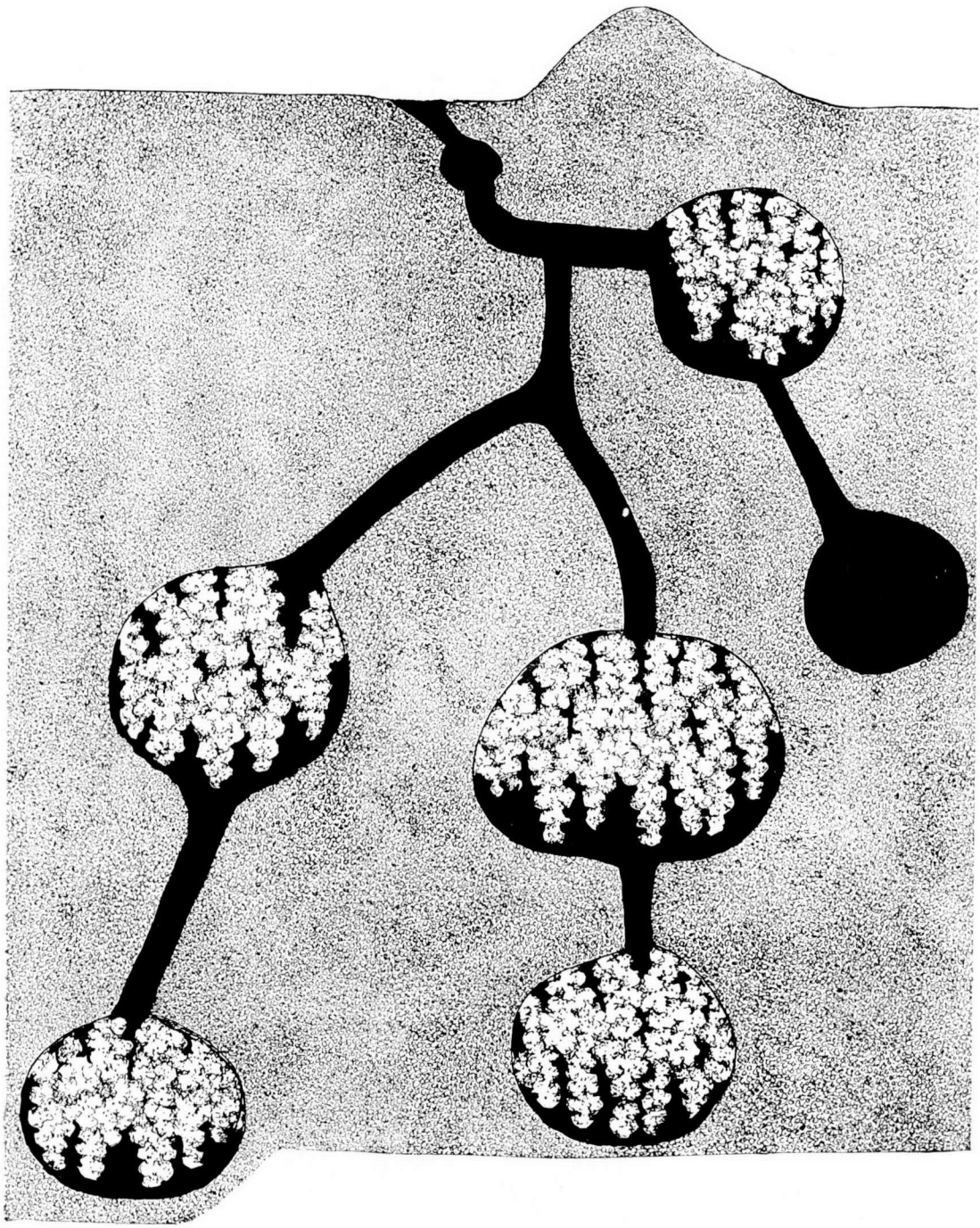
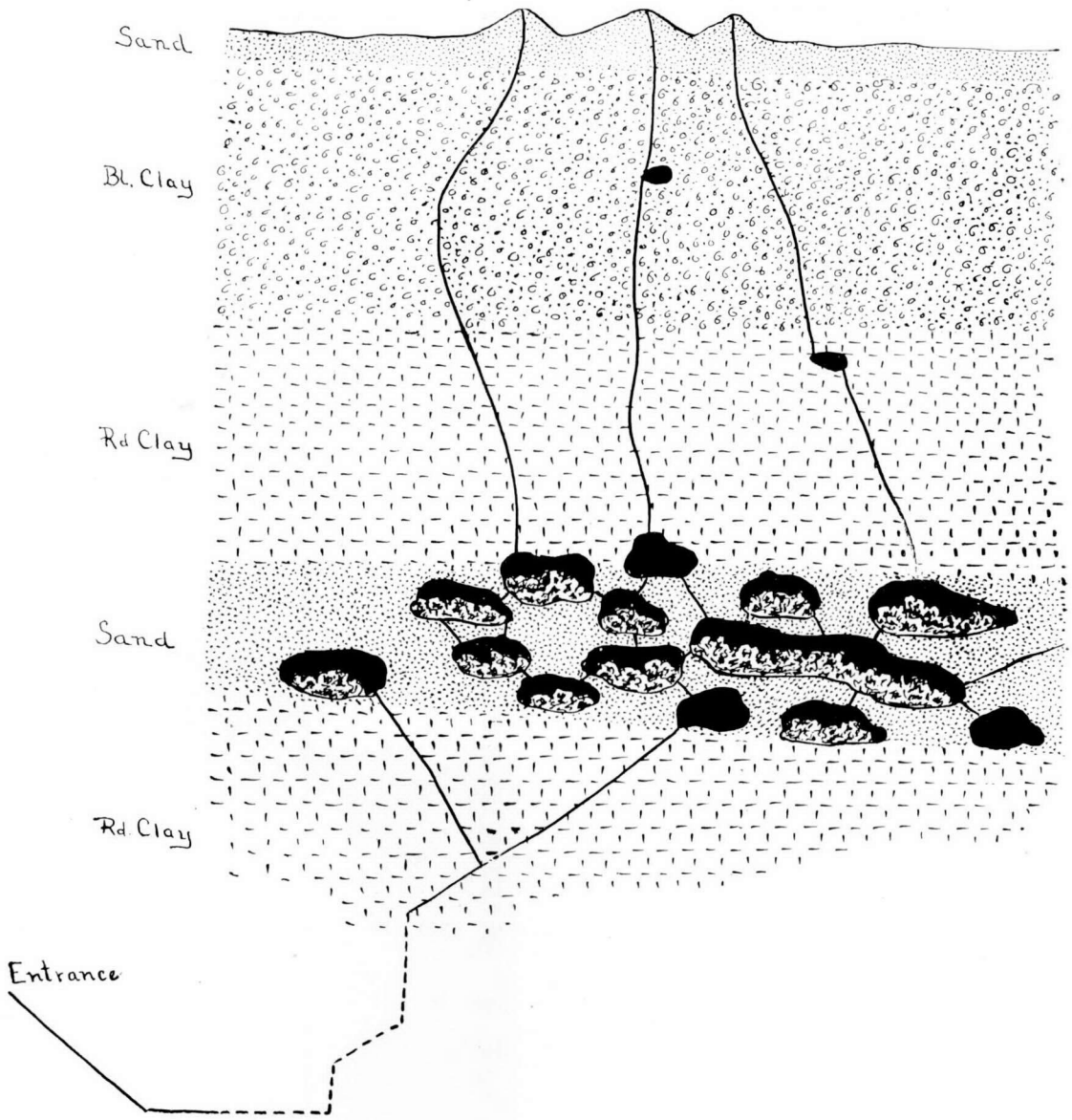


ILLUSTRATION OF THE GARDENS OF A FUNGUS-GROWING ANT (*Trachymyrmex obscurior*) OF THE SOUTHERN STATES

The figure shows near the surface the small original chamber formed by the queen, five chambers, with pendent fungus gardens, and a newly excavated chamber, in which the garden has not yet been started (see text, pages 737 and 738).



From a sketch by Messrs. A. L. Melander and C. T. Brues

NEST DIAGRAM OF THE TEXAN LEAF-CUTTING ANT (*Atta texana*).

The large chambers, with sponge-like fungus gardens on their floors, are situated in a stratum of sand under layers of red and blue clay and several feet below the surface, on which the nest craters have their openings (see text, pages 737 and 738).

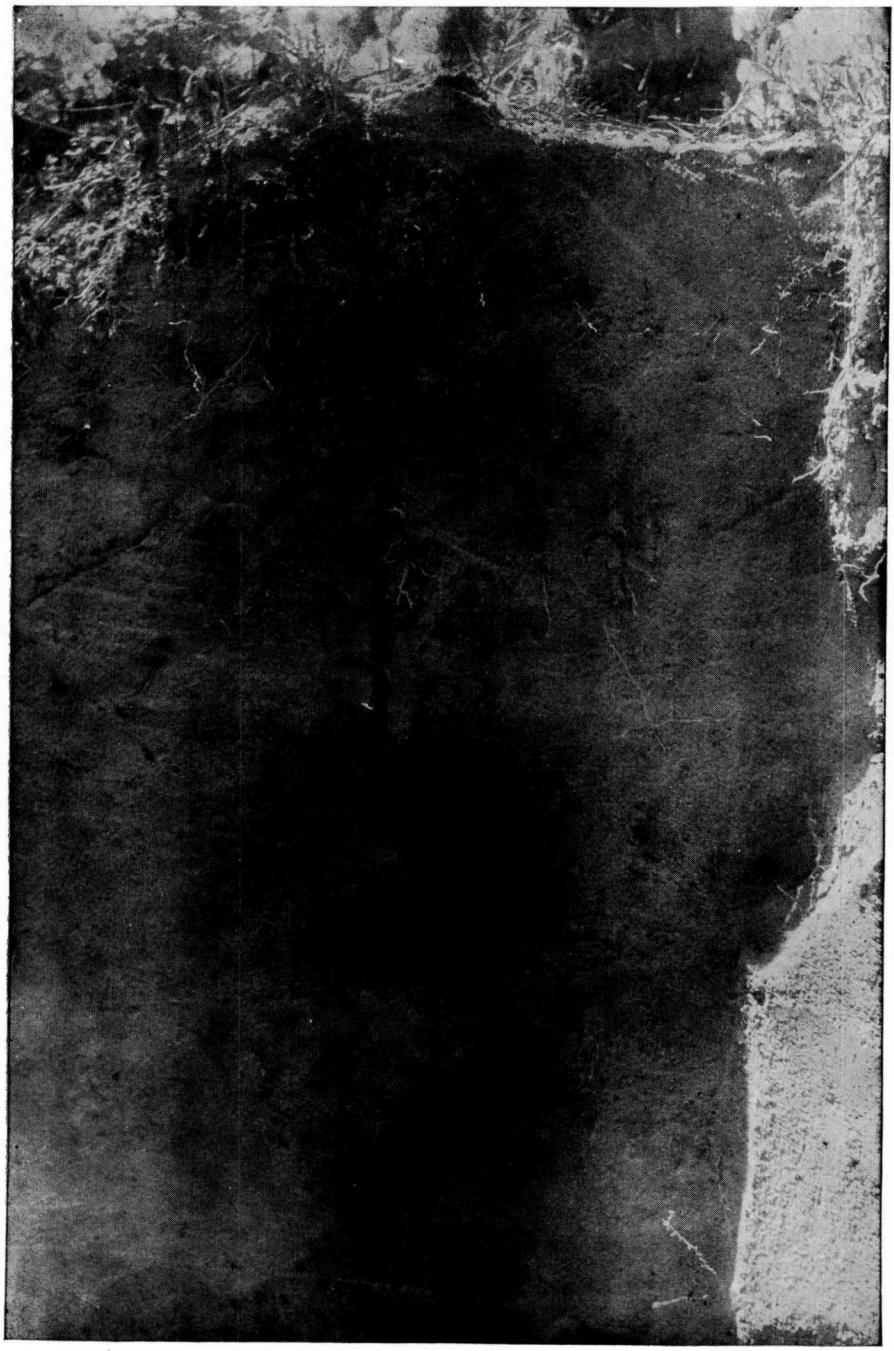


Photo by C. G. Hartman

A PHOTOGRAPH OF A SECTION OF THE NEST OF A SMALL TEXAN FUNGUS-GROWING ANT (*Mycetosoritis hartmani*)

Two of the three chambers of the nest, which is excavated in pure sand, contain pendent fungus-gardens. About one-fourth the natural size

Photo by C. G. Hartman

NEST CHAMBER OF A SMALL TEXAN FUNGUS-GROWING ANT (*Mycetosoritis hartmani*)

The middle chamber of the preceding figure one-fourth larger than natural size, showing in the upper right-hand corner some of the rootlets to which the garden is suspended

their brood, or to excavate the nest, and are therefore compelled to keep kidnapping the young of the host species in order to secure the performance of these tasks. The other method is by completely suppressing the worker caste in the parasitic species, so that the queen after her adoption in the nest of the alien species can at once produce males and females within the host colony's lifetime, which is very short because the host queen has been eliminated.

These various methods of colony formation show that among ants the extreme adaptations of parasitism have for their sole object the securing of better opportunities of reproduction.

The restriction of reproduction to a few members of the colony brought with it, among other advantages, the usurpation of the nutritive and protective functions by a special caste, the workers, which, moreover, comprised the majority of the personnel of the colony. Later these functions were delegated to two subdivisions of this caste, the workers proper and the soldiers.

Among the special adaptations for the protection of the colony we may cite the development of the sting and of the various poisonous or malodorous secretions with which the workers spray or smear the bodies of their enemies, the enlarged mandibles of the soldiers, and above all the excavation or construction of the nest, which protects the colony both from its enemies and from excessive drought, cold, and heat.

Photo by the Author

LARVÆ OF THE TEXAN AGRICULTURAL ANT (*Pogonomyrmex molefaciens*)

The brilliant white color and tensity of the skin in these grub-like creatures is due to the great accumulations of fat, which will be used, in part at least, during pupation in building up the body of the adult ant. Magnification about five diameters.

ANTS THAT BUILD INCUBATORS

Ants no doubt originally nested in the earth, and the majority of species still prefer this habitat. It was while living in this plastic material that they learned to prefer irregular galleries and chambers and to become great opportunists, in marked contrast with the social wasps and bees, which have never been able to depart from their habit of rearing their young in combs made of a refractory substance like paper or of an expensive secretion like wax.

The ants early discovered the great advantages of being able to carry their brood from place to place when danger threatened.

In connection with this free method of dealing with the brood, they were also led to add to the original subterranean nest a kind of tepidarium or incubator, in which the young could be placed during the warmest hours of the day for the purpose of hastening their development (see pictures, page 759). This incubator is the mound or dome of pebbles or vegetable detritus, which surmounts the subterranean nest of many of the more conspicuous species of North America and Eurasia, especially in mountain regions, where the summers are so short that the ants have to utilize every bit of mid-day heat in order to bring their young to maturity.

The mound is riddled with chambers and galleries and is not only fully exposed to the sun, so that its temperature is several degrees higher than that of the surrounding soil, but its slopes are often constructed in such a manner to catch the heat rays perpendicularly and form the most effective regions of the heavens. This orientation of the nests is indeed often so conspicuous and definite that they can be used as compasses (see pictures, pages 742, 759).

In the tropics where the soil is often saturated or flooded with water during the rainy season, and where devices for conserving the heat are quite unnecessary, many ants have learned to construct paper nests on the trees. Such nests superficially resemble the nests of wasps. They contain no combs, however, but only a maze of irregular, intercommunicating galleries and chambers. A few tropical species belonging to three different genera (*Œcophylla, Myrma,* and *Camponotus*) inhabit nests consisting in part at least of a fine silken web.

REPAIRING THE NEST WITH SILK

It was long a mystery how ants could manufacture silk, but it has been recently shown that the ants themselves do not spin the silk, but use their larvæ for this purpose. The process can be actually observed by making a rent in the wall of the nest and then following the movements of the ants under a magnifying glass. They separate into two brigades, one of which stations itself on the outside of the nest and draws the edges of the rent as close together as possible by pulling with claws and mandibles, while the other, inside the nest, moves the spinning larvæ back and forth across the gap till it is filled out with a dense felt-work of extremely fine silken threads (see picture, page 764).

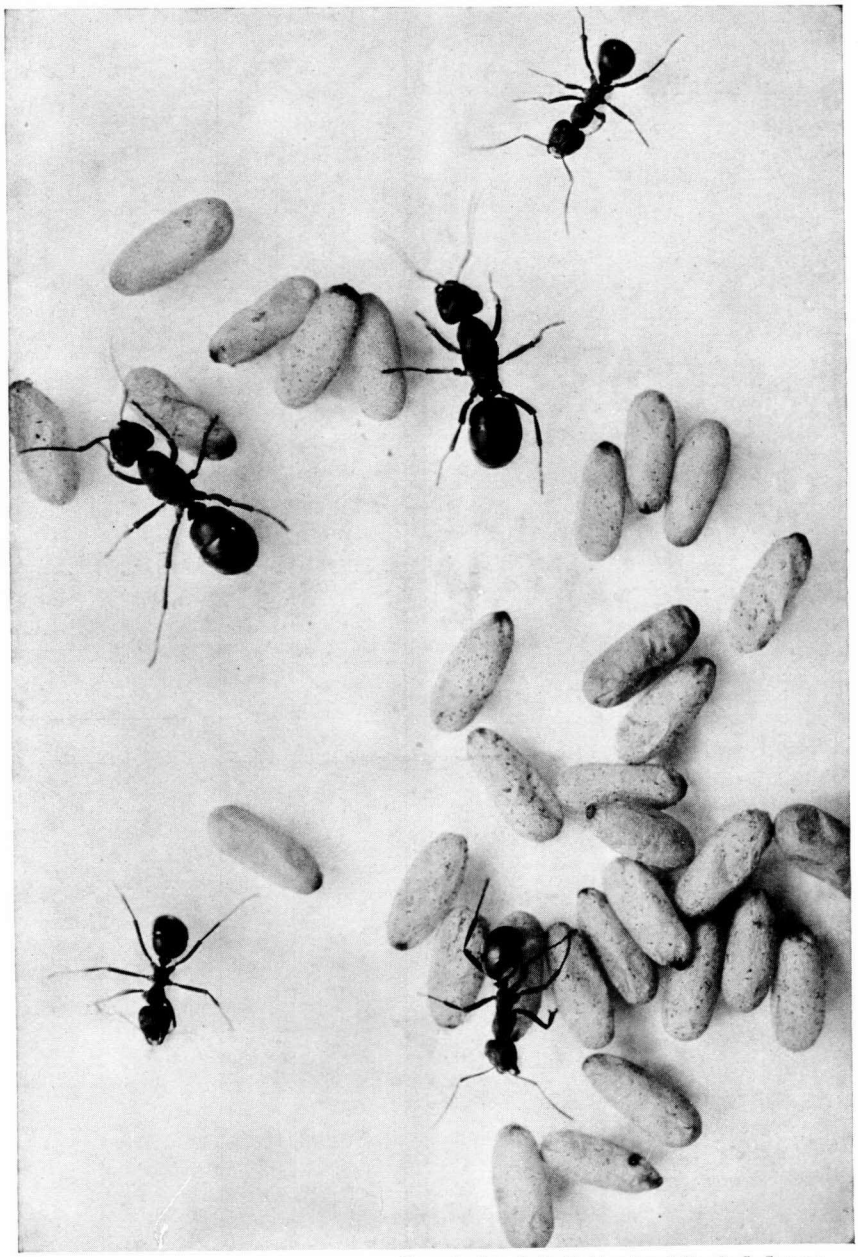


Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

PORTION OF A COLONY OF AN AMERICAN SLAVE-MAKING ANT (*Formica sanguinea subintegra*) (SEE TEXT, PAGE 748)

Two females after the removal of the wings, three workers, and a number of worker cocoons, nearly twice the natural size

Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

COLONY OF *Aphœnogaster picea*, A COMMON ANT IN THE WOODS OF THE EASTERN STATES

The mother queen of the colony is seen at *a* in the lower right-hand corner of the photograph, a male at *b* in the upper left-hand corner

Photo by Mr. J. G. Hubbard and Dr. O. S. Strong

WORKERS OF THE COLONY OF *Aphœnogaster picea*, SHOWN IN THE PRECEDING PICTURE

In this rather primitive ant the workers are all of the same size and shape, not polymorphic as in *Camponotus americanus* (see pages 735, 737, and 738) and many other species. Magnification about twice the natural size.

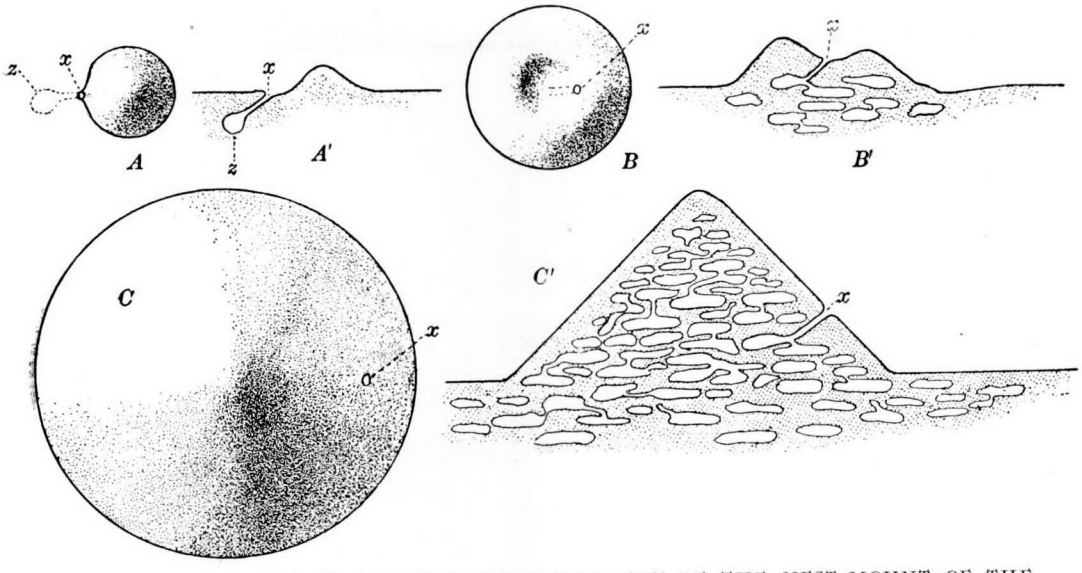
LARGE NEST OF THE MOUND-BUILDING ANT (*Formica exsectoides*)

This nest, located at Scotch Plains, N. J., is 1 meter high, has a basal diameter of 3.25 meters, and a circumference of 10.21 meters

Photo by the Author

NEST OF THE OCCIDENT ANT (*Pogonomyrmex occidentalis*) WHICH BUILDS INCUBATORS FOR ITS YOUNG

On the Dry Plains at Las Vegas, New Mexico. The nest cone has its entrance near the base and nearly always on the east or south side. It is closed at night by the workers, and the advantage of having it in this position is to insure its being opened earlier in the morning when the warmth of the sun awakens the workers (see text, pages 746 and 747).



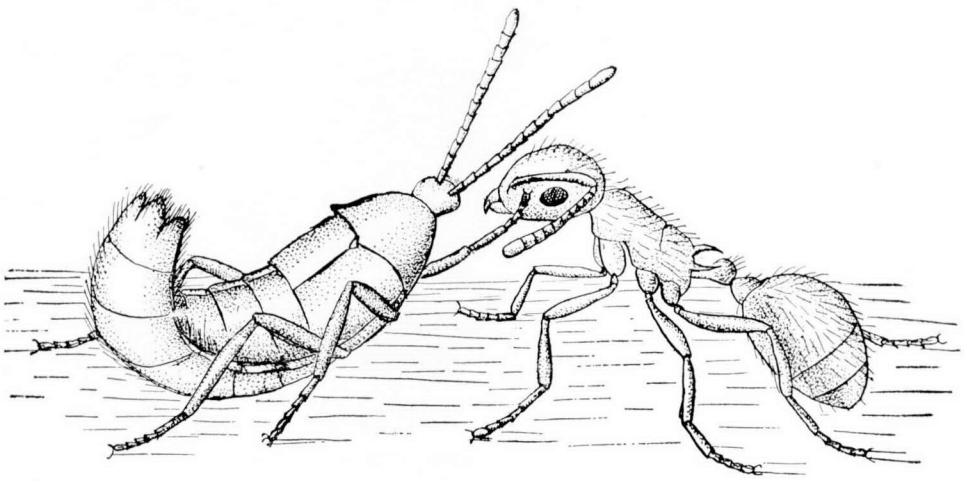
DIAGRAMS OF THREE STAGES IN THE DEVELOPMENT OF THE NEST-MOUNT OF THE OCCIDENT ANT (*Pogonomyrmex occidentalis*) WHICH BUILDS INCUBATORS FOR ITS YOUNG

A, small mound of earth thrown up by the queen when starting her formicary; *x*, entrance; *z*, first chamber; *A'*, same nest in section; *B*, crater nest (second year) formed by incipient colony; *B'*, section of same; *C*, dome of adult colony; *C'*, section of same showing galleries and chambers used for incubation of the young (see text, pages 746 and 747).

Photo by the Author

MOUND OF THE THATCHING ANT (*Formica rubiginosa*) OF COLORADO

The mound, which is made of coarse twigs and grass-blades, may be two or three feet **in** diameter



ANT GUEST OR PARASITE (*Atemeles*) SOLICITING FOOD FROM A WORKER *Myrmica* (AFTER E. WASMANN)

The beetle strokes the cheeks of the ant in order to induce her to regurgitate a drop of liquid food from her social stomach. Any insect which by means of its shape, odor, or behavior can delude the ants into feeling that it may be another out or one of their larvæ can secure free board and lodging in their nests (see text, page 748).

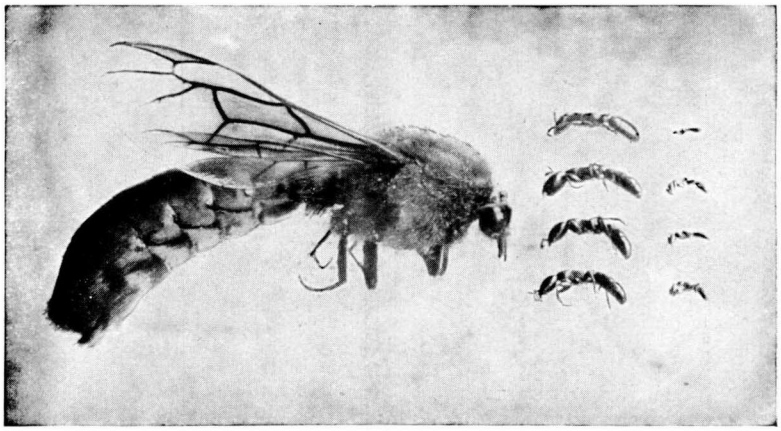


Photo by the Author

MALE AND WORKERS OF A SOUTH AFRICAN DRIVER ANT (*Dorylus fimbriatus*)

The male is a very large, hairy insect with large eyes; the workers are small and blind, but vary greatly in size.

The driver ants (Dorylii) in the tropics of the Old World and the allied legionary ants (Ecitonii) in the corresponding regions of America do not confine themselves to collecting dead or disabled insects. They move in long files over or immediately beneath the surface of the ground and capture myriads of living insects and their larvæ. So efficient are they in exterminating all kinds of vermin, including rats and mice, that they are welcomed into the houses, even if their owners are obliged to vacate for the time being.

In some countries the ants are regarded as useful allies in destroying the insect pests of plantations. According to Magowan, quoted by McCook (1882): "In many parts of the province of Canton, where, says a Chinese writer, cereals cannot be profitably cultivated, the land is devoted to the cultivation of orange trees, which, being subject to devastation from worms, require to be protected in a peculiar manner, that is, by importing ants from the neighboring hills for the destruction of the dreaded parasite. The orangeries themselves supply ants which prey upon the enemy of the orange, but not in sufficient numbers; and resort is had to hill people, who, throughout the summer and winter, find the nests suspended from branches of bamboo and various trees. There are two varieties of ants, red and yellow, whose nests resemble cotton bags.

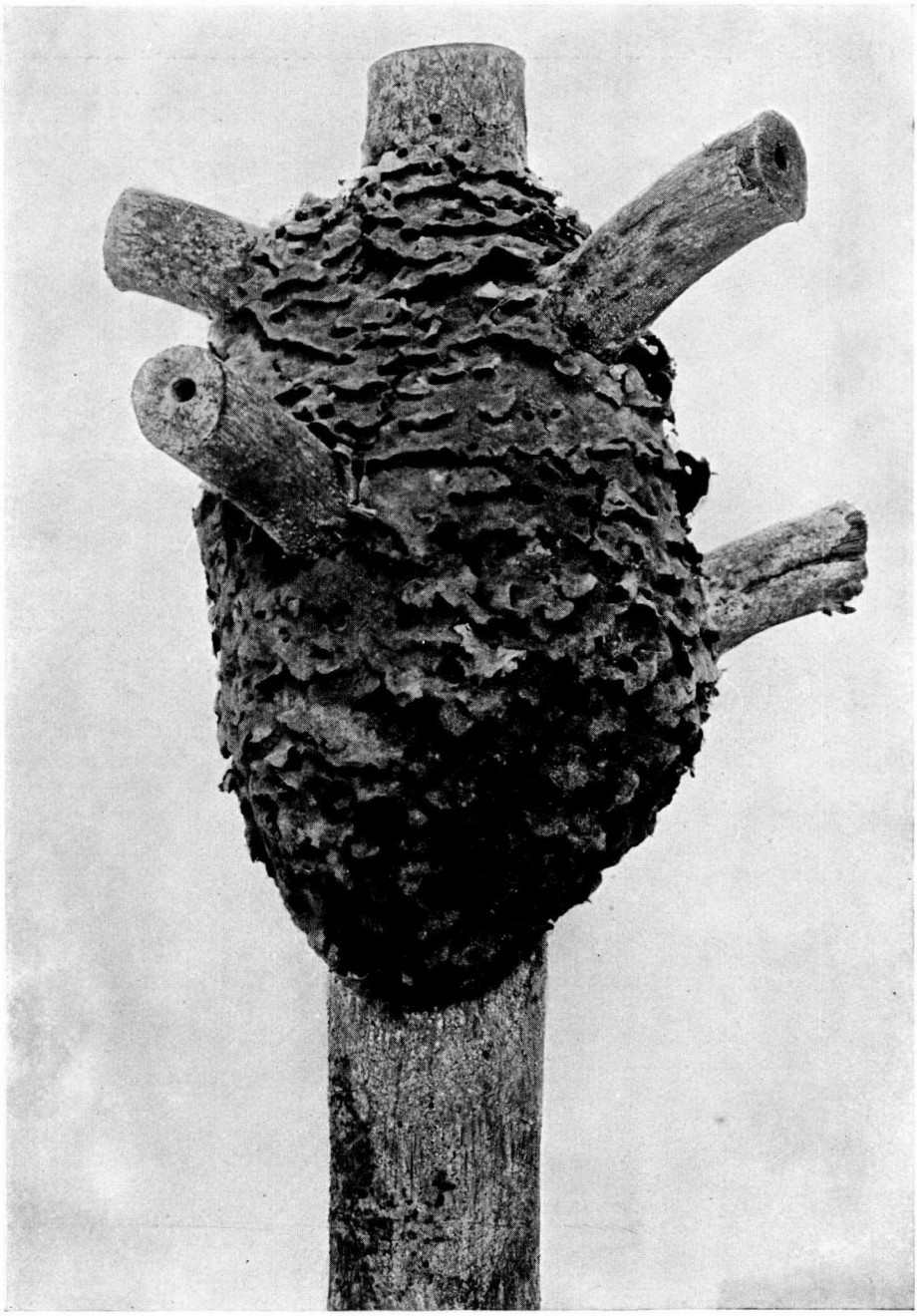
"The orange-ant feeders are provided with pig or goat bladders, which are baited inside with lard. The orifices they apply to the entrance of the nests, when the ants enter the bag and become a marketable commodity at the orangeries. Orange trees are colonized by depositing the ants on their upper branches, and to enable them to pass from tree to tree, all the trees of an orchard are connected by a bamboo rod."

An interesting side-light is thrown on the various nutritive, reproductive, and protective devices in ants by the behavior of the insects that live as guests or parasites in their nests. Of these insects, called myrmecophiles, some 1,500 species have been described, a wonderful assemblage of creatures whose sole aim in life is to exploit the ants. They stay in the nests because these afford warmth, food, and protection. Some myrmecophiles feed on the larvæ and pupæ, or even on the adult ants, and some, known as true guests or symphiles, have developed glands that emit a redolent secretion which seems to fascinate the ants much as a catnip fascinates cats. The more highly developed of these true guests are fed and reared by the ants as if they were ant larvæ.

EVER READY HOSPITALITY

The only explanation of such extraordinary behavior towards parasites which eventually injure or destroy the colonies they infest must be sought in the inordinate fondness of the ants for their own brood and for one another. Observation and experiment have shown that any insect which, by means of its shape, odor, or behavior can delude the ants into feeling that it may be another ant or one of their larvæ, can secure free board and lodging in their nests (see picture, page 760).

Having discussed some of the more



NEST OF AN ARBOREAL BRAZILIAN ANT (*Azteca trigona*)

This nest consists of paper (carton) and is built around a branch of the trumpet tree (*Cecropia adenopus*). (Photograph from a specimen in the American Museum of Natural History.)

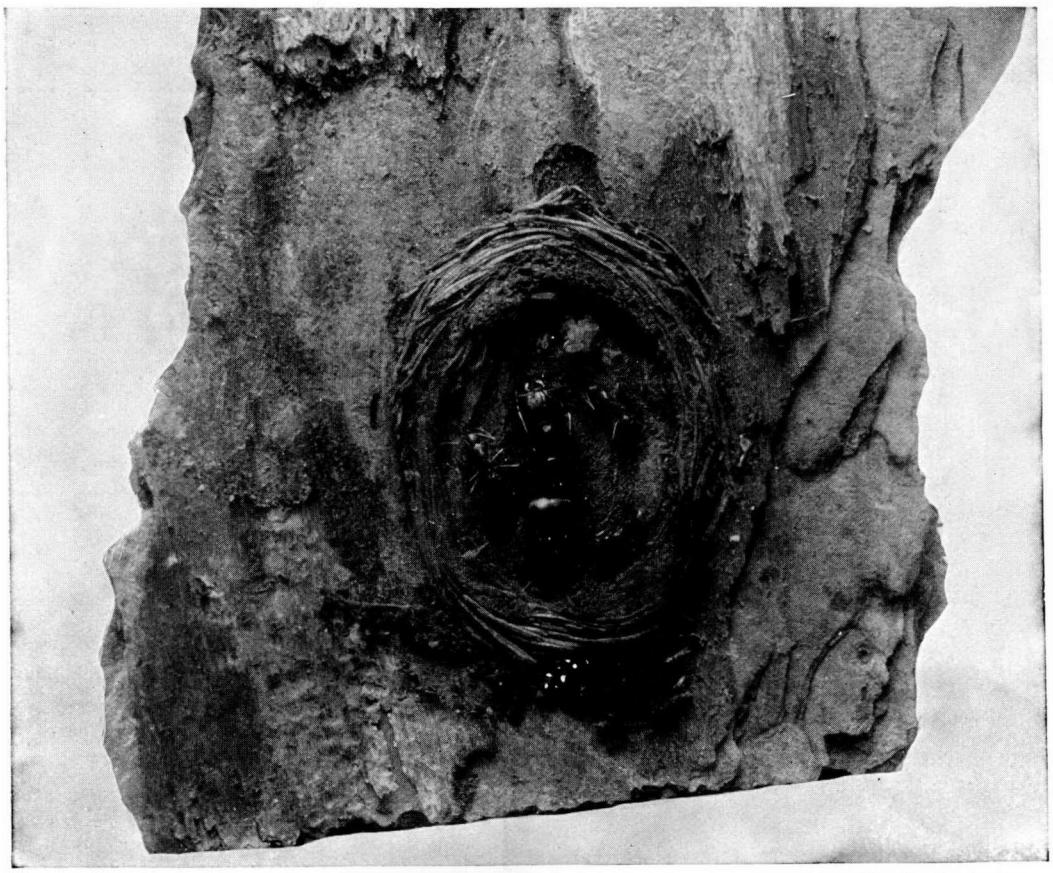


Photo by the Author

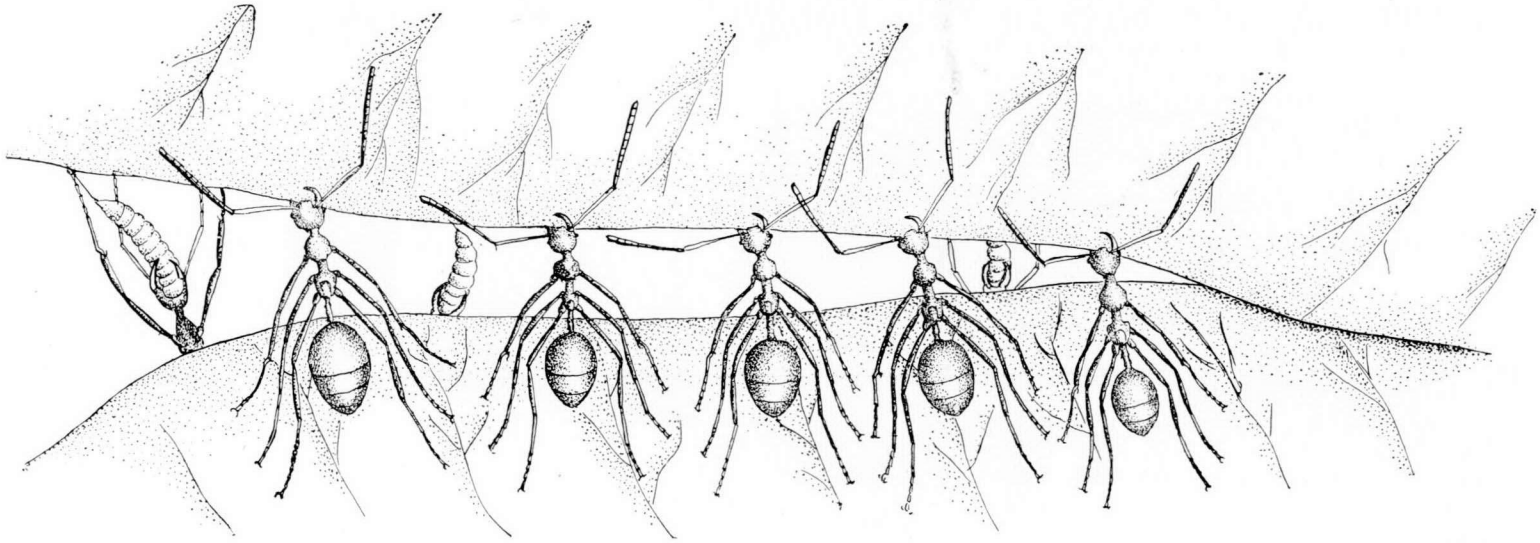
INCIPIENT COLONY OF CARPENTER ANT (*Camponotus pennsylvanicus*)

The queen has established her colony in the abandoned cocoon of a beetle (*Rhagium lineatum*) under pine bark, has reared a few small workers, and has started a second brood, represented by a small cluster of larvæ in the upper part of the chamber (see text, pages 741-742). In incipient ant colonies the queen mother takes no food often for as long a period as 8 or 9 months, and during all this time is compelled to feed her first brood of larvæ exclusively on the secretion of her salivary glands.

striking peculiarities which the ants have developed during the long course of their evolution, a word may be added in conclusion on the prospects of future developments. It must be confessed that these prospects are not very bright, for, strange as it may seem, there are no indications that these insects have made any considerable evolutionary progress since early Tertiary times.

The exquisitely preserved ants of the Baltic amber, belonging to the Lower Oligocene formation, are in all respects like existing ants. All of them belong to existing subfamilies, most of them even to existing genera, and a few of them are practically indistinguishable from species inhabiting Europe today. That some of them were herders of plant-lice is proved by blocks of amber containing masses of ants mingled with the plant-lice which they were attending when the liquid resin of the Oligocene pines flowed over and embedded them. Possibly the soldier caste is a recent innovation, but the differentiation of the males, queens, and workers was as extreme and precisely of the same character then as now.

This seems to force us to the conclusion that all the great features of ant-life must have been established during the Mesozoic Age, and although many spe-

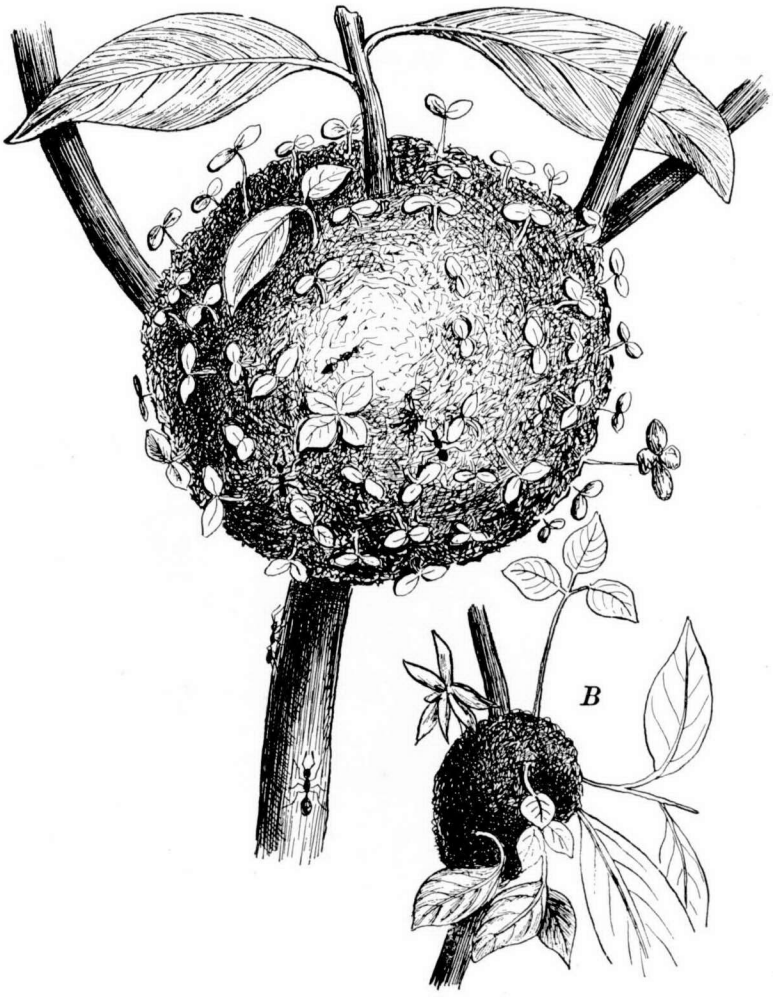


THE REPAIRING OF A RENT IN THE NEST OF THE RED TREE ANT (*Œcophylla smaragdina*) (AFTER F. DOFLEIN)

The nest is made of leaves, held together with a silken web. The figure shows the workers repairing a rent, one brigade of them being occupied in drawing the edges of the leaves together, while the others on the inside of the nest move the spinning larvæ back and forth across the gap (see text, pages 747 and 748).

AN EPIPHYTIC ANT PLANT (*Myrmecodia pentasperma*) OF THE BISMARCK ARCHIPELAGO (AFTER F. DAHL)

The large pseudobulb is filled with cavities, which are nearly always tenanted by ants (*Iridomyrmex cordatus*)



ANT GARDENS OF THE AMAZON (AFTER E. ULE)

A a large, *B* a small spherical, sponge-like mass of earth which is built around the axils of the branches of trees in the tropical forests and, according to Ule, is seeded by the ants with parasitic plants.

cies, subspecies, and varieties have since arisen and may yet arise, we must nevertheless admit that the future development of the group will probably be limited very largely or exclusively to a more minute differentiation of existing forms and a greater refinement of existing modes of behavior.