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SOCIAL LIFE AMONG THE INSECTS[1]

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LECTURE IV—ANTS, THEIR DEVELOPMENT, CASTES, NESTING AND FEEDING HABITS

ON one occasion several years ago when I was about to lecture on ants in Brooklyn, a gentleman introduced me to the audience by quoting the sixth to eighth verses of the sixth chapter of Proverbs, and then proceeded in utter seriousness to give an intimate account of their author. He said that Solomon was the greatest biologist the Hebrews had produced, that he had several large and completely equipped laboratories in which he busied himself throughout his reign with intricate researches on ant behavior and that the 700 wives and 300 concubines mentioned in the Bible were really devoted graduate students, who collaborated with the king in his myrmecological investigations. The gentleman deplored the fact that the thousand and one monographs embodying their researches had been lost, and concluded by saying that he was delighted to introduce one who could supply the missing information. As he had consumed just forty-three minutes with his account of Solomon and his collaboratrices, I had to confess my inability to "deliver the goods" in the remaining seventeen. From what recondite sources of biblical exegesis the Brooklyn gentleman drew his information I have never been able to ascertain, but I am sure that Solomon's few myrmecological comments, which have come down to us from about 970 B. C., are very accurate—far more accurate than that story of Herodotus, written some 500 years later, of the gold-digging ants of India, which were as large as leopards, and whose hides were seen by Nearchus in the camp of Alexander the Great, and whose horns were mentioned by Pliny as hanging, even in his time, in the temple of Hercules at Erythræ.

[1] Lowell Lectures.

This and the many other ant stories invented or disseminated by ancient and modern writers are certainly not devoid of interest, but the actual behavior of the insect is so much more fascinating that you will pardon me for not dwelling on them.

The Formicidæ constitute the culminating group of the stinging Hymenoptera and have attracted many investigators for more than a century and especially during the past thirty years. Unlike the honeybee these insects make no appeal to our appetites nor even to that vague affection which we feel for most of the common denizens of our forests, fields and gardens, but only to our inquisitiveness and anxiety. Hence the vast literature which has been written on the ants may be said to have been prompted by scientific, philosophic or mere idle curiosity or by our instinct of self-preservation. In the presence of the ant we experience most vividly those peculiar feelings which are aroused also by many other insects, feelings of perplexity and apprehension, which Maeterlinck has endeavored to express in the following words: "The insect does not belong to our world. Other animals and even the plants, despite their mute lives and the great secrets they enfold, seem not to be such total strangers, for we still feel in them, notwithstanding all their peculiarities, a certain terrestrial fraternity. They may astonish or even amaze us at times, but they do not completely upset our calculations. Something in the insects, however, seems to be alien to the habits, morals and psychology of our globe, as if it had come from some other planet, more monstrous, more energetic, more insensate, more atrocious, more infernal than our own. With whatever authority, with whatever fecundity, unequalled here below, the insect seizes on life, we fail to accustom ourselves to the thought that it is an expression of that Nature whose privileged offspring we claim to be. . . . No doubt, in this astonishment and failure to comprehend, we are beset with an indefinable, profound and instinctive uneasiness, inspired by beings so incomparably better armed and endowed than ourselves, concentrations of energy and activity in which we divine our most mysterious foes, the rivals of our last hours and perhaps our successors. "

The similarities which the ants, as one of several families of aculeate or stinging Hymenoptera, necessarily bear to the wasps and bees, are so overlaid by elaborate specialization and idiosyncrasies that their primitive vespine characters are not very easily detected. I wish to dwell on some of these specializations, but before doing so, it will be advisable to give under separate captions a brief summary of what I conceive to be the fundamental peculiarities of the ants:

(1) The whole family Formicidæ consists of social insects, that is, it includes no solitary nor subsocial forms such as we found among the beetles, wasps and bees. We are therefore unable to point to any existing insects that might represent stages leading up to the social life of the ants. Within the family, nevertheless, we can distinguish quite a number of stages in a gradual evolution of social conditions from very simple, primitive forms, whose colonies consist of only a few dozen individuals, with a comparatively feeble caste development, to highly specialized forms with huge colonies, comprising hundreds of thousands of individuals and an elaborate differentiation of castes.

(2) The number of described species of ants is approximately 3,500, but if we include their subspecies and varieties, many of which will probably be raised to specific rank by future, less conservative generations of entomologists, we shall have more than double the number. This is far in excess of the number of all other social insects, including both the groups I have already considered and the termites. The ants are therefore the dominant social insects.

(3) This dominance is shown also by their geographical distribution, which is world-wide. There are ants everywhere on the land-masses of the globe, except in high arctic and antarctic latitudes and on the summits of the higher mountains. The number of individual ants is probably greater than that of all other insects. With few exceptions, the termites are all confined to tropical or subtropical countries, and the number of social wasps and bees in temperate regions is very small.

(4) We found that the social wasps arose from the Eumenine solitary wasps and the bees from the solitary Sphecoids. All the authorities agree that the ants had their origin in neither of these ancestral stocks, but among the Scolioids, a distinct offshoot of the primitive Vespoids. Of the four modern families of the Scolioids, the Psammocharidæ, Thynnidæ, Mutillidæ and Scoliidæ, the last seems to be most closely related to the ants. Since they must be traced to ancestors which were winged in both sexes, the Thynnids and Mutillids, which have wingless females, are excluded, and the family Psammocharidæ is not very closely allied to the Formicidæ.

(5) The ants, unlike the social wasps and bees, are eminently terrestrial insects. They inherited and seem very early to have exaggerated the terrestrial habits of their primitive Scolioid ancestors. The majority of the species in all parts of the world still nest in the soil. Many of them later took to nesting in dead or decaying wood, and more recently a number of species, especially in the rain-forests of the tropics, have become arboreal and nest by preference in the twigs of trees and bushes or construct paper or

silken nests among the leaves and branches. The terrestrial habit led to a permanent phylogenetic suppression of the wings in the workers, an ontogenetic loss of the wings in the queens and a diminution of the eyes in both of these castes. A few very archaic ants still possess large eyes like the wasps and bees, but in the great majority of species, which are more or less subterranean, and therefore practically cave-animals during much of their lives, the eyes have dwindled, and in many species have almost or completely disappeared. The great abundance of ants in the desert, savanna and prairie regions of the globe indicates that they arose during some period of the Mesozoic, perhaps during the Triassic or Liassic, when the climate was warm but arid. Their extensive adaptation to low, damp jungles, with their rank vegetation, seems to have developed during the Cretaceous or early Tertiary. The ants therefore resemble the solitary wasps, which are still conspicuously abundant in hot, arid regions. Both groups are represented by only a small number of species in cool, moist regions, like New Zealand, the British Isles and certain mountain ranges, like the Selkirks of British America.

(6) In the social wasps and bees we found that the worker,

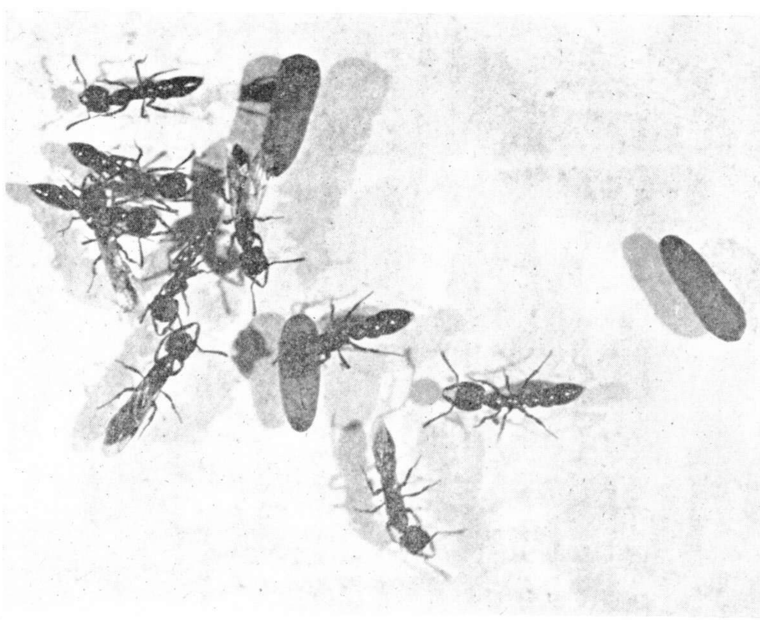

FIG. 54

Stigmatomma pallipes, a primitive, subterranean Ponerine ant of the United States. The winged individuals are virgin queens and are very similar to the workers. Nearly twice natural size. (Photograph by J. G. Hubbard and O. S. Strong.)

or sterile caste, though distinctly differentiated, is, nevertheless, very much like the queen, or fertile female. In ants the differences are much greater. Even when, as in many primitive ants (Fig. 54), the worker resembles the queen in size and form, it never possesses wings, and in most ants the two castes are so dissimilar that they have often been described as separate species. The male ant, too, is much less like the queen than is the corresponding sex among the social wasps and bees (Fig. 57). It is evident, therefore, that all three castes are more highly specialized. In many ants, as we shall see, the worker, queen and male may each become differentiated into two or more castes, a phenomenon which is nowhere even suggested among the wasps and bees.

(7) Very long and intimate contact with the soil has made the ants singularly plastic in their nesting habits. While most social wasps and bees construct elaborate combs with very regular, hexagonal cells of such expensive substances as paper and wax, the ants merely make more or less irregular galleries or chambers in the soil or dead wood or if they construct paper or silken nests avoid a rigid type of architecture. Hence the great variability of nesting habit in the same species. This plasticity and saving of time and labor are very advantageous, because they enable the insects, when conditions of temperature or moisture become unfavorable or when bothersome enemies settle too near the nest, to change their habitation readily and without serious loss to the colony. Espinas long ago noticed the importance of the terrestrial habits of ants. He says: "Ants owe their superiority to their terrestrial life. This assertion may seem paradoxical, but consider the exceptional advantages afforded by a terrestrial compared with an aërial medium in the development of their intellectual faculties! In the air there are the long flights without obstacles, the vertiginous journeys far from real bodies, the instability, the wandering about, the endless forgetfulness of things and of oneself. On the earth, on the contrary, there is not a movement that is not a contact and does not yield precise information, not a journey that fails to leave some reminiscence; and as these journeys are determinate, it is inevitable that a portion of the ground incessantly traversed should be registered, together with its resources and its dangers, in the animal's imagination. Thus there results a closer and much more direct communication with the external world. To employ matter, moreover, is easier for a terrestrial than an aërial animal. When it is necessary to build, the latter must, like the bee, either secrete the substance of its nest or seek it at a distance, as does the bee when she collects propolis, or the wasp when she gathers material for her paper. The terrestrial animal has its building materials close at hand, and its architecture may be as

varied as these materials. Ants, therefore, probably owe their social and industrial superiority to their habitat.''

(8) The plasticity of ants is shown even more clearly in their care of their young, which are not reared in separate cells but in clusters and lie freely in the chambers and galleries of the nest where they can be moved about and easily carried away or hidden when the colony is disturbed or the moisture and temperature conditions are unfavorable. Like their continual contact with their physical environment, their intimate acquaintance with their young in all their stages has been an important factor in the high psychological development of the Formicidæ.

(9) A similar plasticity characterizes their feeding habits. As a group they feed on an extraordinary range of substances: the bodies and secretions of other insects, seeds, delicate fungi, nectar, the saccharine excreta of plant-lice, scale insects, etc. Some species seem to be almost omnivorous.

(10) All this adaptability, or plasticity in nesting and feeding habits is, of course, an expression of a very active and enterprising disposition and has resulted in the formation of a vast and intricate series of relationships between ants and other organisms, including man. These restless, indefatigable, inquisitive busybodies, forever patrolling the soil and the vegetation in search of food, poke their noses, so to speak, into the private affairs of every living thing in their environment. Nor do they stop at this; they actually draw many organisms, by domesticating them or at any rate attaching them to their nests or bodies, into the vortex of their ceaseless, impudent activities. Nearly every week during the past twenty years I have received from some entomologist somewhere on our planet one or more vials of ants with a request for their identification, often because they had been found associated with some insect or plant which the sender happened to be investigating. In the next lecture I shall describe a number of the strange partnerships into which ants have entered as a result of their inordinate and unappeasable appetites.

As my time is limited I shall select for discussion only a few of the topics suggested in the foregoing summary, namely, the main taxonomic divisions of the family Formicidæ, polymorphism, or the development of castes, the origin and growth of colonies, the structure of the alimentary canal in adult and larval ants and the evolution of the feeding habits.

In their main outlines, at least, the phylogenetic relationships of the various subdivisions or subfamilies of the Formicidæ have been clearly established. There are seven of them: the Ponerinæ, Cerapachyinæ, Dorylinæ, Pseudomyrminæ, Myrmicinæ, Dolicho-

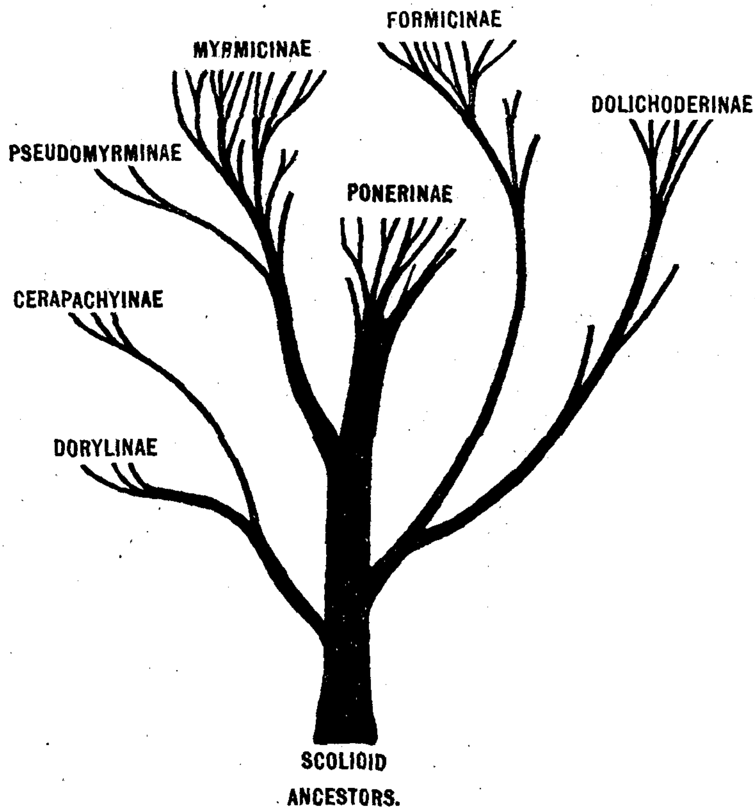

FIG. 55
Ancestral tree showing the putative phylogenetic relations of the family Formicidæ as a whole and of its subfamilies to one another.

derinæ and Formicinæ. The Ponerinæ constitute the primitive, basic stock of the family and have given rise to the six other subfamilies, which are represented in the ancestral tree (Fig. 55) as so many branches. Their thickness roughly indicates their vigor or comparative development and their height their degree of specialization and dominance in the existing fauna. All the subfamilies are well represented in the tropics of both hemispheres, but in the north temperate region nearly all the species belong to the two largest and highest subfamilies, the Myrmicinæ and Formicinæ. In temperate North America and Eurasia there are very few Dolichoderinæ and Ponerinæ and no Cerapachyinæ nor Pseudomyrminæ. A small number of Dorylinæ extend as far north as Colorado, Missouri and North Carolina (35° to 40°) and to about the same latitude on the southern shores of the Mediterranean.

With the exception of a series of peculiar parasitic genera, which are represented only by males and females, all ants possess a sharply defined worker caste. In primitive groups, like the

Ponerinæ, Cerapachyinæ and Pseudomyrminæ, the worker is nearly as large as the queen but lacks the wings and has therefore a more simply constructed thorax, the compound eyes are smaller and the simple eyes or ocelli are minute or absent. In the three subfamilies mentioned the worker is monomorphic, that is, it always has the same form though it may vary somewhat in size. In the four remaining subfamilies (Dorylinæ, Myrmicinæ, Dolichoderinæ and Formicinæ) we find the same uniformity of the worker in many species, but in a considerable number it has become highly variable, or polymorphic, as a result of agencies which have acted independently in each subfamily or even within the limits of a single genus (Figs. 57 and 58). In such cases the workers can be arranged in a graduated series, beginning with large, huge-headed individuals more like the queen in stature, and ending with minute, small-headed individuals, which may be very much smaller than the queen. Such a series exhibits not only great morpholog-

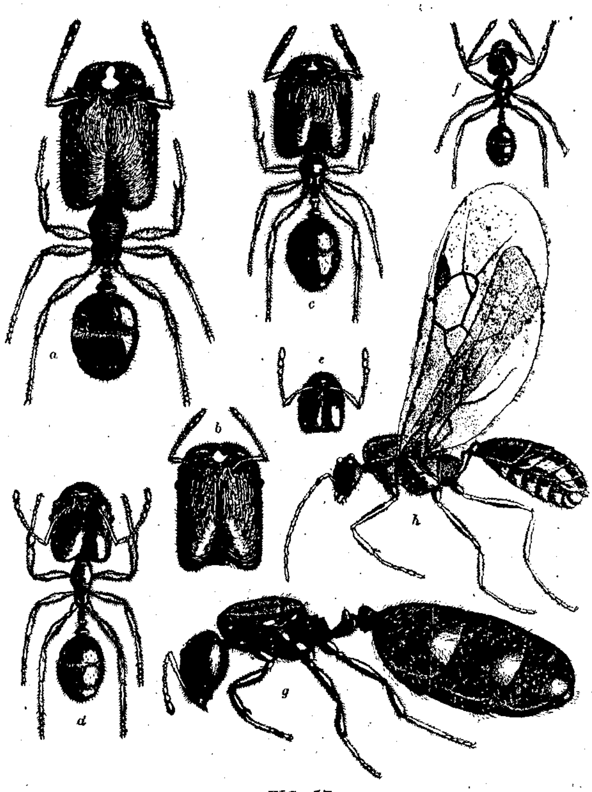

FIG. 57

A small Myrmicine harvesting ant of Texas, *Pheidole instabilis,* with polymorphic worker caste. *a,* soldier; *f,* worker; *b* to *e,* forms intermediate between the soldier and worker (lacking in most other species of the huge genus Pheidole); *g,* queen (deälated); *h,* male. The figures are all drawn to the same scale.

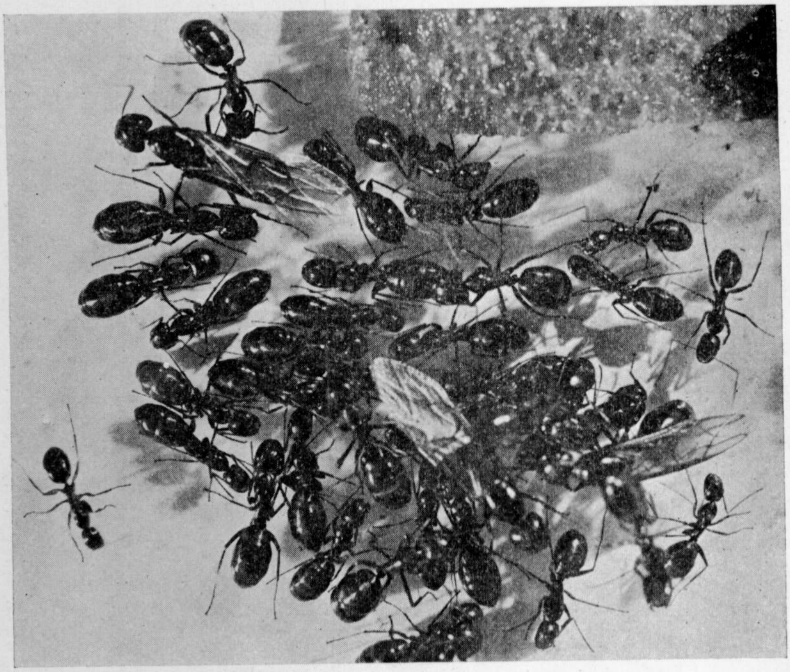

FIG. 58
Portion of a colony of a common Formicine ant (*Camponotus americanus*), comprising virgin, winged queens and workers, the latter showing the unstable polymorphism in stature and size of head, characteristic of most species of the genus. (Photograph by J. G. Hubbard and O. S. Strong.)

ical but also great functional differences among its members. The largest individuals commonly act as policemen or defenders of the colony, but in some species their powerful jaws enable them to crush seeds or the hard parts of insects, so that the softer parts may be exposed and eaten by the smaller individuals (Fig. 57). The latter excavate the nest, forage for food, nurse the young and in some species devote all their energies to the cultivation of the fungus gardens. In a graduated series like the one described we usually call the largest workers "maximæ," the smallest "minimæ" and the intermediate forms "mediæ," the word "operariæ" (workers) being understood in each case. Now in some ants only the two extremes, the maximæ and the minimæ, of the polymorphic series proved to be serviceable to the colony, so that all the intermediate forms (mediæ) have been eliminated, leaving the worker caste distinctly dimorphic. In such ants we call the maximæ "soldiers" (*milites*) and the minimæ "workers" (*operariæ*). This condition has been attained in several genera and subgenera among the Myrmicinæ and Formicinæ (Pheidole (Fig. 57), Oligomyrmex, Colobopsis, etc.). In still other genera, where soldiers were not needed or were too expensive to rear and maintain, on account of their great size and appetites, they too have been eliminated and the worker caste is represented only by the tiniest individuals of the originally polymorphic series (Carebara, Tranopelta, Pædalgus, Solenopsis, etc.). There is therefore an enormous difference in these ants in size and structure between the queen and the only surviving worker form of the species. In Carebara, *e. g.*, the queen is several thousand times as large as the worker! Nevertheless, both are merely extreme female forms of the same species and may, of course, develop from the eggs of the same mother.

But the worker is not the only caste that has become dimorphic. In some species there are two distinct forms of queen, in others two distinct forms of male. In these cases one of the forms is winged, the other usually apterous. And here again, by suppression of the winged female or winged male, the wingless form may become the only surviving fertile form of its sex in the species. All these developments are interesting because they indicate that the distinctions among the various castes have arisen gradually by continuous or fluctuating variations and that the survival and persistence of some of them and the elimination of others have led to the sharply discontinuous series of castes which we find in many ants.

It is obvious that some of the differences between the various castes, especially those in size, are due to differences in the amount of food consumed during the larval stages, but the profounder morphological differences which separate the queens, soldiers and workers, must be due to other causes. We must suppose either that the food administered to the larvæ differs in quality or that there are several different kinds of eggs, some of which develop into fertile, other into sterile forms. In a sense the latter would be mutations, like the various sterile forms of the evening primrose, which make their appearance generation after generation from some of the seeds of the fertile forms. In the case of the ants, however, we find that the workers not infrequently lay viable eggs, and though they are never fertilized and generally develop into males, the latter may mate with queens and thus be a means of establishing a representation of the characters of their worker mothers in the germ-plasm of the species. The peculiar anomalies known as gynandromorphs, that is, individuals partly male and partly female, which occasionally occur among ants, also indicate that the queens, soldiers and workers arise from as many different kinds of eggs, since there are three different kinds of gynandromorphs, exhibiting respectively combinations or mosaics of male and queen, male and soldier and male and worker characters. It is difficult to see how such perfectly definite combinations could be produced by larval feeding, and it is equally difficult to account for them as the results of internal secretions. In the present state of our knowledge we can only surmise that the differences between the queen and worker castes were originally ontogenetic and determined by feeding, as they still are in the social wasps and bees, but that in the ants the germ-plasm has somehow been reached and modified, so that an hereditary basis for caste differentiation has been established.

The ant colony may be initiated and developed by one of two different methods which I shall call the independent and the dependent. The former is peculiar to the nonparasitic, the latter to the parasitic species. Leaving an account of the ants which employ the dependent method for the next lecture, I would say that the great majority of ants establish their colonies in essentially the same manner as Vespa and the bumble-bees. The winged, virgin queen, after fecundation during her nuptial flight, descends to the ground, rids herself of her wings and seeks out some small cavity under a stone or piece of bark, or excavates a small cell in the soil. She then closes the opening of the cell and remains a voluntary prisoner for weeks or even months while the eggs are growing in her ovaries. The loss of the wings has a peculiar effect on the voluminous wing-muscles in her thorax, causing them to break down and dissolve in the blood plasma. Their substance is carried by the circulation to the ovaries and utilized in building up the yolk of the eggs. As soon as the eggs mature, they are laid and the queen nurses the hatching larvæ and feeds them with her saliva till they pupate. Since she never leaves the cell during all this time and has access to no food, except the fat she stored in her abdomen during her larval life and her dissolved wing-muscles, the workers that emerge from the pupæ are all abnormally small. They are, in fact, always minimæ in species which have a polymorphic worker caste. They dig their way out through the soil, thus establishing a communication between the cell and the outside world, collect food for themselves and their mother and thus enable her to lay more eggs. They take charge of the second brood of eggs and larvæ, which, being more abundantly fed, develop into larger workers. The population of the colony now increases rapidly, new chambers and galleries are added to the nest and the queen devotes herself to digesting the food received from the workers and to laying more eggs. In the course of a few years numerous males and queens are reared and on some meteorologically favorable day the fertile forms from all the nests of the same species over a wide expanse of country escape simultaneously into the air and celebrate their marriage flight. This flight provides not only for the mating of the sexes but also for the dissemination of the species, since the daughter queens, on descending to the ground, usually establish their nests at some distance from the parental colony.

It will be seen that the queen ant, like the queen wasp and bumble-bee, but unlike the queen honeybee, is the perfect female of her species, possessing not only great fecundity but in addition all the worker propensities, as shown by her ability to make a nest and bring up her young. But as soon as the first brood of workers appears, these propensities are no longer manifested. That they are not lost is shown by the simple experiment of removing the queen's first brood of workers. Then, provided she be fed or have a sufficient store of food in her body, she will at once proceed to bring up another brood in the same manner as the first, although she would have manifested no such behavior under normal conditions.

As already stated, this independent method of colony formation is the most universal and is followed alike by tropical and extratropical ants. It is undoubtedly the primitive method and, as we shall see, the one from which the dependent method has been derived. It differs from that of Vespa and Bombus, nevertheless, in leading to the formation of perennial colonies even in temperate and boreal regions. The queen ant may, in fact, live from 12 to 17 years and although, like other aculeates, she is fecundated only once, may produce offspring up to the time of her death. Unlike the queen honeybee she is never hostile to her own queen daughters, and in many species of ants some of these daughters may return after their marriage flight to the maternal colony and take a very active part in increasing its population. In this manner the colony may become polygynic or pleometrotic, and in some instances may contain a large number of fertile queens. When such a colony grows too large it may separate into several, the queens emigrating singly or in small companies, each accompanied by a detachment of workers, to form a new nest near the parental formicary. This behavior is exhibited by the well-known mound-building ant (*Formica exsectoides*) of our New England hills. You will notice that its mounds usually occur in loose groups or clusters and that the workers of the different nests are on friendly terms with one another and sometimes visit back and forth. We may, of course, call the whole cluster a single (polydomous) colony, but it really differs from a number of colonies only in the absence of hostility between the inhabitants of the different mounds. In certain tropical ants, like the Dorylinæ (Figs. 59 and 60), however, I am inclined to believe that the only method of colony formation is by a splitting of the original colony into as many parts as it con-

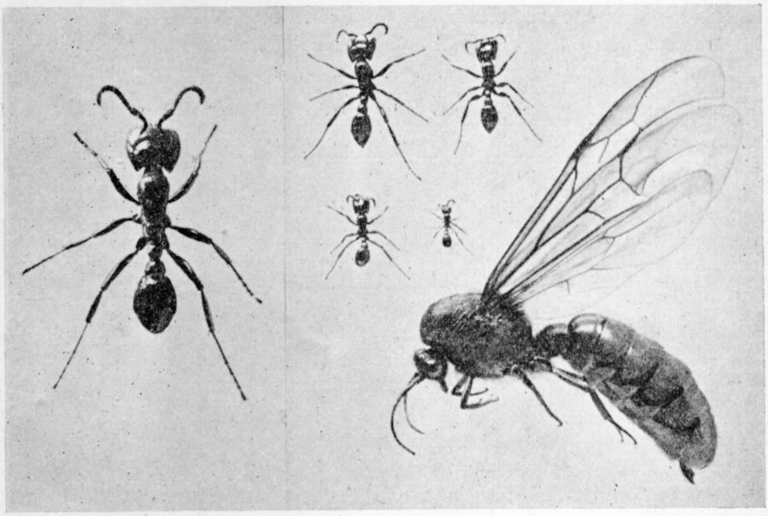

FIG. 59

Argentinian legionary (Doryline) ant *Eciton* (*Acamatus*) *strobeli*. Workers showing polymorphism and male, photographed to the same scale as the four smaller workers. (Photograph by Dr. Carlos Bruch.)

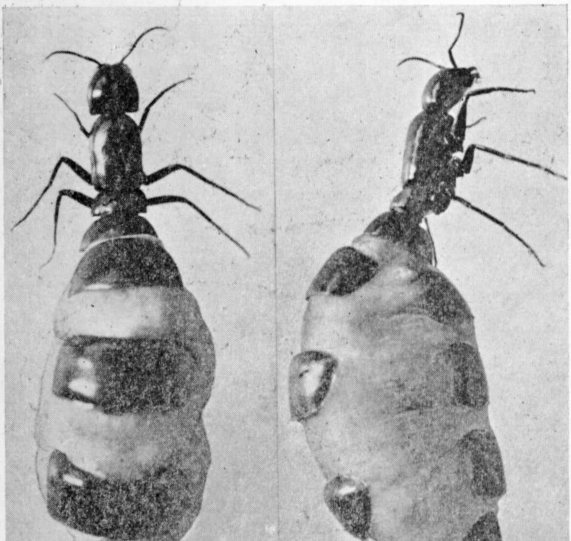

FIG. 60

Dorsal and lateral view of the wingless queen (dichthadiigyne) of *Eciton* (*Acamatus*) *strobeli*. Same scale as Fig. 59. (Photograph by Dr. Carlos Bruch.)

tains young queens. These huge, clumsy creatures (Fig. 60) are always wingless and must therefore be fecundated in the nest, and since the colonies, which comprise hundreds of thousands of workers, are nomadic and keep wandering from place to place, they must become independent entities as soon as they are formed.

We possess no accurate data on the age that ant colonies may attain. Some of them certainly persist for 30 or 40 years and probably even longer. In such old colonies the original queen has, of course, been replaced by successive generations of queens, that is, by her fertile daughters, grand-daughters and great-grand-daughters, and the worker personnel has been replaced at a more rapid rate, because the individual worker does not live more, and in most instances lives considerably less, than three or four years.

The feeding habits of ants are so varied and complicated that it will be advisable before considering them to describe the structure of the alimentary canal in both adult and larva. The mouth-parts of the adult are of the generalized vespine type and consist

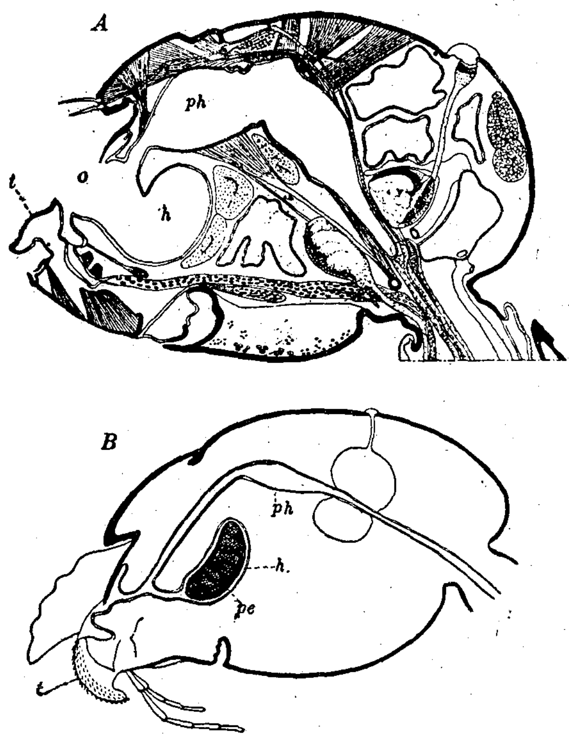

FIG. 61

Sagittal sections through the heads of ants. A, of queen *Lasius niger* with the mouth open (After Janet). B, of queen *Camponotus brutus* with the mouth closed. *t*, tongue; *o*, oral orifice; *ph*, pharynx; *h*, infrabuccal pocket; *pe*, pellet *in situ*, made up of solid particles of food refuse and strigil sweepings. Note stratification in the substance of the pellet, indicating successive meals or toilet operations.

of a small, flap-like upper lip, or labrum, a pair of strong, usually toothed mandibles, a pair of small maxillæ and a broad lower lip, or labium. The maxillæ and labium are each provided with a pair of jointed, sensory appendages, the palpi. The mandibles, which are really the ant's hands, vary greatly in shape in different genera and are used not only in securing the food but also in many other activities, such as digging in the earth or wood, transporting other ants or the young, fighting, leaping, etc. Liquids are, of course, merely imbibed and swallowed, but solid food is seized and crushed with the mandibles and the juices or smaller particles licked up with the tongue, which is a roughened pad at the tip of the lower lip (Fig. 61*t*) just anterior to the opening of the duct of the salivary glands. The small particles thus collected are carried back into a small chamber or sac, the infrabuccal pocket (Fig. 61*h*), which lies immediately below and anteriorly to the mouth-opening (*o*). This pocket is an important structure since it serves as a receptacle not only for the more solid particles of food but also for the dirt, fungus-spores, etc., which the ant collects during her toilet operations, for the ant is an exquisitely cleanly insect and devotes much of her leisure to licking and burnishing her own smooth or finely chiseled armor and that of her nest-mates. Moreover, the tip of the fore tibia is furnished with a beautiful comb or strigil which can be opposed to another comb on the concave inner surface of the fore metatarsus. The ant cleans her legs and antennæ by drawing them between these combs, which are then drawn across the mouth, with the result that any adhering dirt is carried off into the infrabuccal pocket. In this manner the dirt and the solid or semisolid food particles are combined and the whole mass moulded in the infrabuccal pocket into the form of a roundish oblong pellet (Fig. 61*B pe*). After any liquid which it may contain has been dissolved out and sucked back into the mouth, the pellet is cast out, so that no solid food actually enters the alimentary canal. All adult ants therefore subsist entirely on liquids.

The alimentary canal proper is a long tube extending through the body and divided into sections, each with its special function. The more anterior sections are the mouth cavity, the pharynx (Fig. 61 *ph*), which receives the ducts of certain glands, and the very long, slender gullet, which traverses the posterior part of the head, the whole thorax and the narrow waist, or pedicel of the abdomen as far as the base of its large, swollen portion, the gaster. Here the gullet expands into a thin-walled, distensible sac, the crop, which is used for the storage of the imbibed liquids. At its posterior end the crop is separated from the ellipsoidal stomach by a peculiar valvular constriction, the proventriculus. The hindermost sections of the alimentary tract are the intestine and the large, pear-shaped rectum. The crop, proventriculus and stomach are the most interesting of these various organs. Forel calls the crop the "social stomach," because its liquid contents are in great part distributed by regurgitation to the other members of the colony and because only a small portion, which is permitted to pass back through the proventricular valve and enter the stomach, is absorbed and utilized by the individual ant. That the crop functions in the manner described can be readily demonstrated by permitting some pale yellow worker ant to gorge herself with syrup stained blue or red with an aniline dye. The ant's gaster will gradually become vividly colored as the crop expands. Now if the insect be allowed to return to the nest, other workers will come up to it, beg for food with rapidly vibrating antennæ and protrude their tongues, and very soon their crops, too, will become visible through the translucent gastric integument as they fill with the stained syrup. Then these workers in turn will distribute the food by regurgitation in the same manner till every member of the colony has at least a minute share of the blue or red cropful of the first worker.

The alimentary tract of the helpless, legless, soft-bodied ant grub or larva is much simpler than that of the adult. The mouthparts are similar but more rudimentary. As a rule, the mandibles are less developed but in some larvæ they are strong, dentate and very sharp. The lower lip is fleshy and protrusible and provided with sensory papillæ instead of palpi, and the unpaired duct of the long, tubular and more or less branched salivary glands opens near its tip. The mouth-opening is broad and its lining in many species is provided with numerous transverse ridges beset with very minutes spinules (Fig. 62*C*). Larger, pointed projections or imbrications may also cover the basal portions of the mandibles. All these spinules and projections are probably used in triturating the food but perhaps when rubbed on one another they may also produce shrill sounds for the purpose of apprising the worker nurses of the hunger or discomfort of their charges. The gullet is long and very slender and opens directly into the large stomach, which throughout larval life is closed behind, that is, does not open into the intestine. A communication with the more posterior portion of the alimentary tract is not established till the larva is about to pupate. Then all the undigested food which has accumulated in the stomach since the very beginning of larval life is voided as a large black pellet, the meconium.

In the larvæ of the Pseudomyrminæ (Figs. 62, 63 and 64) there are certain very peculiar additional structures which may be briefly described. The head is not at the anterior end of the body as in other ant larvæ but pushed far back on the ventral surface so that it is surrounded by a great hood formed from the three thoracic

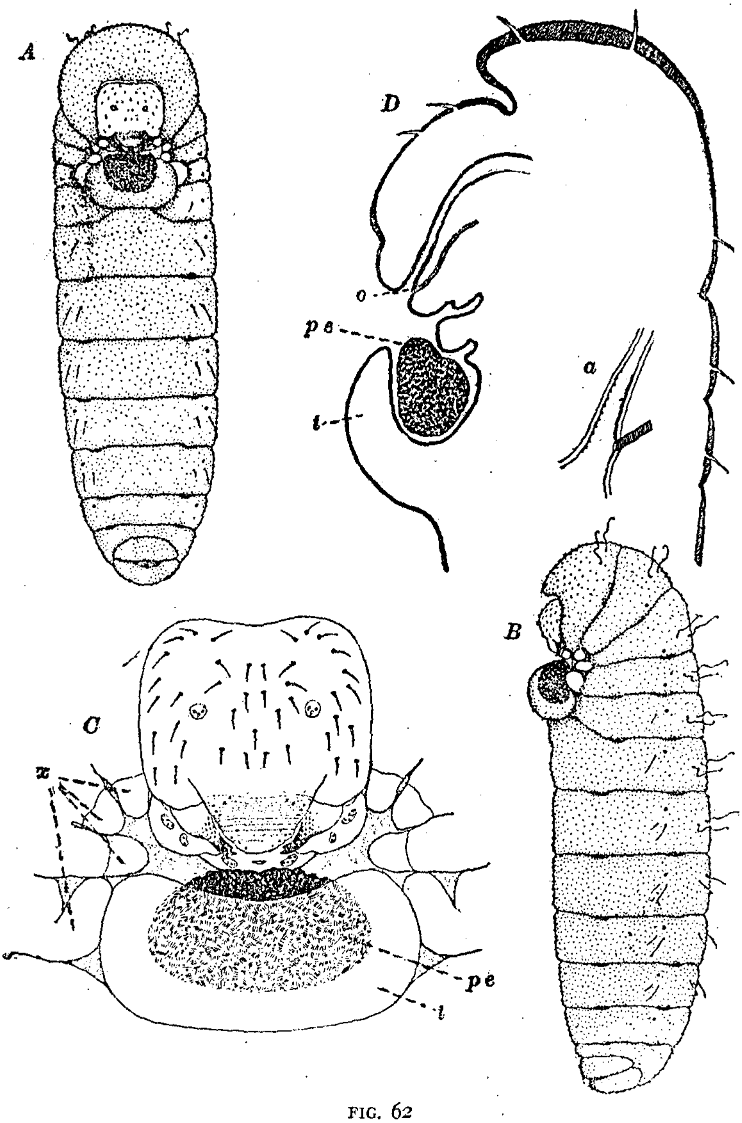

FIG. 62
Larva of *Pseudomyrma gracilis*. *A*, ventral; *B*, lateral view; *C*, head and adjacent portions of same enlarged; *D*, sagittal section through anterior portion of larva. *o*, oral orifice; *x*, exudatoria; *t*, trophothylax, or pocket, which holds the pellet; (*pe*), deposited by the worker nurses and which is eaten by the larva. Note the hooked dorsal hairs of the larva, which serve to suspend it from the walls of the nest. *a*, mouth cavity, more enlarged to show the fine spinules (also seen in *C*), which serve to triturate the pellet and probably also as a stridulatory organ.

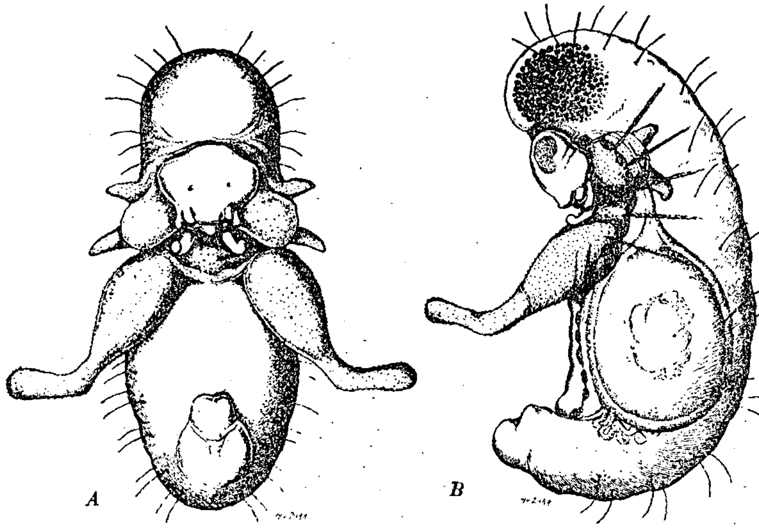

FIG. 63
A, ventral; *B*, lateral view of the first larval stage ("trophidium") of the Ethiopian *Pachysima latifrons*, showing the peculiar appendages ("exudatoria") surrounding the head. These belong to the three thoracic and the first abdominal segments.

segments, and the first abdominal segment, which lies immediately behind the head, has in the midventral line a singular pocket, the trophothylax (*t*). Furthermore, each side of this segment and each ventrolateral portion of the several thoracic segments is developed as a peculiar protuberance or appendage, which functions as a blood-gland, or exudatorium (*x*).

Unlike the adult ants the larvæ can devour solid food, though they are often fed, at least in their youngest stages, with liquids regurgitated on their mouths by the worker nurses. The larvæ of the Pseudomyrminæ are fed with the pellets (*pe*) from the infrabuccal pocket, which are placed by the workers in the trophothylax where they are within easy reach of the mandibles and can be gradually drawn into the mouth, triturated and swallowed. Some primitive ants (Ponerinæ, some Myrmicinæ, etc.) actually feed their young with pieces of insects or entire small insects, which are simply placed on the ventral surface of the larva within reach of its mouth-parts.

In a former lecture I referred to the fact that the larvæ of the social wasps, either before or after feeding, produce droplets of a sweet salivary secretion, which are eagerly imbibed by the adult wasps, and I designated this interchange of food between adult and larva as trophallaxis. I have recently made some observations which show that the ant larvæ also produce secretions which appeal to the appetites of their nurses. These secretions are more varied than in the wasps. Certain ant larvæ undoubtedly supply their nurses with saliva, but many or all sweat a fatty secretion through the delicate general integument of the body, and the larval Pseudomyrminæ produce similar exudates from the papillæ or appendages above described. Although these various substances are produced in very small quantities they are of such qualities that they are eagerly sought by the adult ants. This explains much of the behavior which has been attributed to maternal affection on the part of the queen and the workers, such as the continual licking and fondling of the larvæ, the ferocity with which they are defended and the solicitude with which they are removed when the nest is disturbed. In other words, a decidedly egoistic appetite, and not a purely altruistic maternal anxiety for the welfare of the young constitutes the potent "drive" that initiates and sustains the intimate relations of the adult ants to the larvæ, just as the mutual regurgitation of food initiates and sustains the similar relations among the adult workers themselves.

I am convinced that trophallaxis will prove to be the key to an understanding not only of the behavior I have briefly outlined

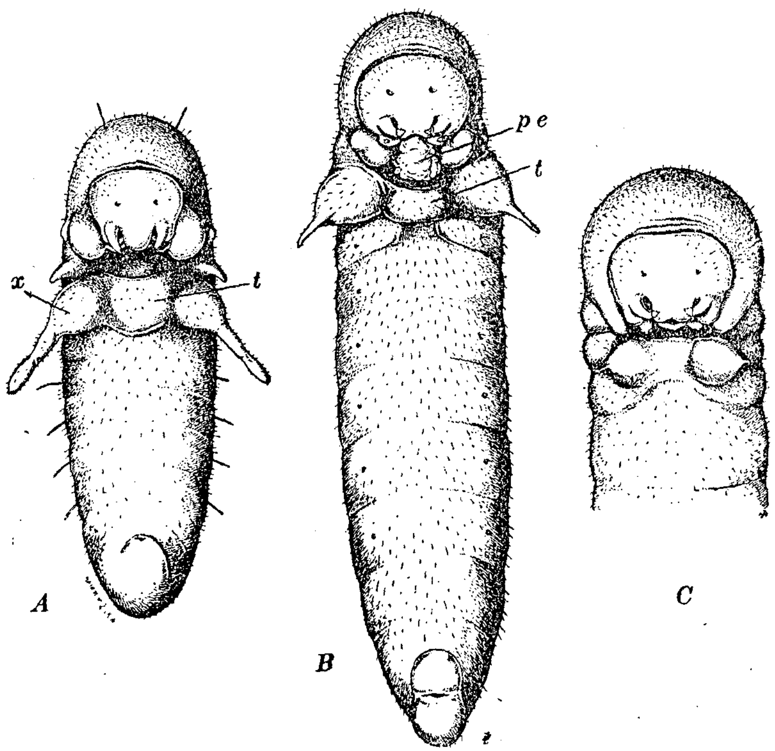

FIG. 64

Second, third and fourth (adult) larval stages of Pachysima latifrons, showing the gradual dwindling of the exudatoria. *A* and *B* show the trophothylax (*t*); and *B* also shows the food pellet *pe*; which is the pellet formed in the infrabuccal pocket of the worker nurse; *x*, exudatorium. See Figs. 62 and 63.

but also of the relations which ants have acquired to many kinds of alien organisms. In the accompanying diagram (Fig. 65) I have endeavored to indicate how trophallaxis, originally developed as a mutual trophic relation between the queen ant and her brood, has expanded with the growth of the colony, like an ever-widening vortex, till it involves, first, all the adults as well as the brood

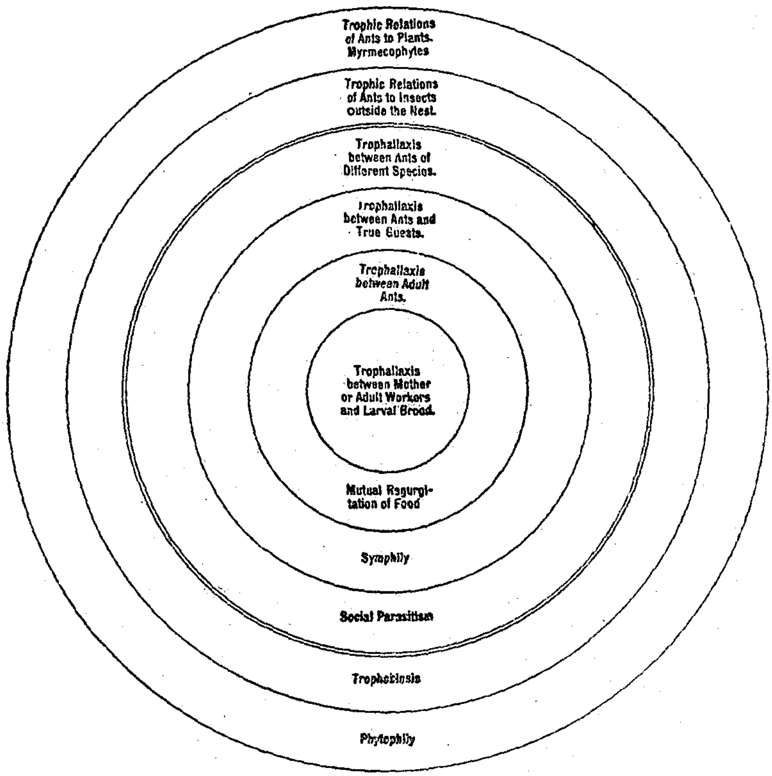

FIG. 65
See text for explanation.

and therefore the entire colony; second, a great number of alien insects that have managed to get a foot-hold in the nest as scavengers, predators and parasites (symphiles); third, alien social insects, that is, other species of ants (social parasites); fourth alien insects that live outside the nest and are "milked" by the ants (trophobionts), and fifth, certain plants that are regularly visited or even inhabited by the ants (myrmecophytes). These extranidal relationships, represented by the two outer rings in the diagram are, of course, incomplete or one-sided, since the organisms which they represent are not fed but merely cared for or protected by the ants. In my next lecture I shall have more to say about some of these relationships.

(To be continued)