THE SCIENTIFIC MONTHLY

JANUARY, 1923

SOCIAL LIFE AMONG THE INSECTS[1]

By Professor WILLIAM MORTON WHEELER

BUSSEY INSTITUTION, HARVARD UNIVERSITY

LECTURE V. PARASITIC ANTS AND ANT GUESTS

THE ants are so favorable for the study of certain phenomena which I have been unable to more than touch on in the preceding lectures that I have set this lecture apart for their fuller consideration. I allude to the phenomena which biologists embrace under the terms "symbiosis" or "mutualism" and "parasitism." Social life may, indeed, be regarded merely as a special form of symbiosis. This term, which signifies the living together of organisms in a balanced, cooperative, reciprocally helpful manner, is commonly applied interspecifically, that is, to partners thus related but belonging to different species, but there is no reason why it should not be applied to the same kind of relations between individuals of the same species, that is intraspecifically. Symbiosis is probably never realized in its ideal form, which would require that each of the partner organisms should render to the other in food or services an exact equivalent of what it receives. So great is the greed of organisms that one member of the partnership usually tends to snatch more than its share of the profits accruing from the association. One member is therefore exploited, while the other becomes correspondingly dependent, that is, parasitic. In some groups of animals symbiotic, or mutualistic relations may thus lapse into parasitism, but it seems to me improbable that parasitism among insects has had such an origin. The common and perhaps exclusive source of the phenomenon among these highly specialized organisms is predatism. In fact, the most typical of parasitic insects are really refined predators, which usually, on growing to their full stature, kill the hosts they have been carefully sparing and, one might say, using as food-getting instruments.

[1] Lowell Lectures.

Since this is not exactly the form of parasitism exhibited by other organisms, such as the tape-worms, certain barnacles and bacteria, I prefer to call it "parasitoidism."

Yet even among the insects there are so many kinds and degrees of dependence on other insects that a concise classification is impossible. The phenomena are extremely diverse and protean, merging and melting into one another in the most bewildering manner. My limited time and the exigencies of exposition therefore compel me to condense and schematize. I am, moreover, dealing with a small fragment of a vast subject. The whole organic world is burdened with parasitism, so shackled and impeded by it that progressive evolution becomes inhibited in every group in which it appears, and the classes that have escaped its paralyzing touch are very few. Professor J. M. Clarke has shown that parasitism made its appearance in marine animals as early as the Cambrian and that it has kept recurring ever since, specializing and leading to "degeneration" and thus robbing group after group of species of all hope of further progress. Although they may persist for ages they are doomed to extinction, and only the independent forms, those that neither lapse into parasitic habits nor waste their vitality in nourishing parasites, stand any chance of becoming the ancestors of future types. We therefore belong to a lineage which, by some rare good fortune, escaped all the culs-de-sac of parasitism—till we became social.

The very conditions of social life tend to facilitate the development of the host and parasite relations. Not only do the members of a society become more tolerant of alien organisms in their midst and even domesticate and breed them, but the nests and domiciles because of the protection they afford, their higher temperature, the stores of food, the refuse even, the helpless young and infirm old they contain—all representing so much nourishment—attract hordes of predators, scavengers, inquilines, guests and parasites in the strict sense of the word. And the crowding together of the social organisms greatly facilitates the interchange of all kinds of small parasites, such as mites, moulds and bacteria from host to host. On the other hand, the members of a society are themselves normally temporary parasites of one another, the young of the adults, the old of the young, and even the whole colony, as a unit, may become a temporary or permanent parasite on the colony of some other species. We noticed cases of this kind among the social wasps and bees, namely, *Vespa arctica* and *austriaca* and the various species of Psithyrus, and we shall find more numerous examples among the ants. I did not have time even to enumerate the alien beetles, flies, etc., that live in the nests

of the social wasps and bees, but they are numerous, and we shall find that the termites are surpassed only by the ants in the number of their parasites.

Although man furnishes the most striking illustrations of the ease with which both the parasitic and host rôles may be assumed by a social animal, his capacities in these directions have been little appreciated by the sociologists. Massart and Vandervelde seem to be the only authors who have attempted to do justice to the matter. Our bodies, our domestic animals and food plants, dwellings, stored foods, clothing and refuse support such numbers of greedy organisms, and we parasitize on one another to such an extent that the biologist marvels how the race can survive. We not only tolerate but even foster in our midst whole parasitic trades, institutions, castes and nations, hordes of bureaucrats, grafting politicians, middlemen, profiteers and usurers, a vast and varied assortment of criminals, hoboes, defectives, prostitutes, white- slavers and other purveyors to antisocial proclivities, in a word so many non-productive, food-consuming and space-occupying parasites that their support absorbs nearly all the energy of the independent members of society. This condition is, of course, responsible for the small amount of free creative activity in many nations. Biology has only one great categorical imperative to offer us and that is: Be neither a parasite nor a host, and try to dissuade others from being parasites or hosts. Of course, this injunction is no more easily obeyed than Kant's famous imperative, of which it embodies the biological meaning, for a parasite always treats its host as a means and not as an end, and the thoroughly parasitized host must abandon all hope of being an end in itself.

I have expressed myself somewhat drastically on human parasitism. If I attempted to utter all my opinions on the subject I should probably not be permitted to survive till the next lecture, even in so tolerant a community as Boston. But so vividly are the development and consequences of biological dependence illustrated by the ants that by confining myself to them, and possibly allowing a hint to escape here and there, you will be able to construct your own analogies. The more striking relations of ants to other organisms are enumerated in the accompanying list. I considered the relations to the Phytophthora (Fig. 78) in the preceding lecture, and our knowledge of the relations to the higher plants is in a state too controversial to admit of satisfactory exposition within the limits of this lecture. We may therefore confine our attention to social parasitism, or the behavior of ants as parasites and hosts of one another and to the myrmecophiles, or animals that use the ants as hosts. Social parasitism is exhibited by two

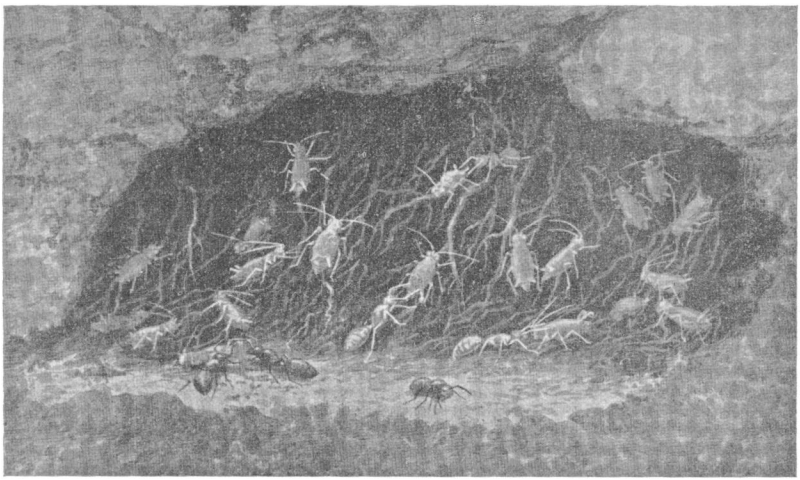

FIG. 78

Ants attending aphids on the roots of grasses and other herbs. (From a drawing by T. Carreras, after E. Step.)

series of species, one in which the parasitic and host colonies occupy separate though contiguous nests and therefore rear their broods in separate chambers, or nurseries, the other in which the two colonies have become so intimately united that they occupy a single nest and bring up their young in common. It will be seen that not only each of these series, but also that of the myrmecophiles begins in predatory (indicated by asterisks) and terminates in definitively parasitic relations.

RELATIONS OF ANTS TO OTHER ORGANISMS

I. SOCIAL PARASITISM (Ants as Parasites)
  A. *Compound Nests* (Broods reared separately)
    *1. Brigandage (Cleptobiosis)
    *2. Thievery (Lestobiosis)
    3. Neighborliness (Plesiobiosis)
    4. Tutelage (Parabiosis, Phylacobiosis)
    5. Hospitality (Xenobiosis)
  B. *Mixed Colonies* (Broods reared together)
    *1. "Slavery" (Dulosis)
    2. Temporary Social Parasitism
    3. Permanent Social Parasitism
II. MYRMECOPHILY (Ants as Hosts)
    *1. Persecuted Intruders (Synechthrans)
    2. Indifferently Tolerated Guests (Synoeketes)
    3. Mess-mates (Commensals)
    4. True Guests (Symphiles)
    5. External Parasites (Ectoparasites)
    6. Internal Parasites (Entoparasites)
III. TROPHOBIOSIS (Relations of Ants to Phytophthora, etc.)
IV. PHYTOPHILY (Relations of Ants to Plants)

The great armies of the nomadic legionary ants to which I alluded in my previous lecture often attack the nests of other ants and carry away and devour all their larvæ and pupæ. This is, of course, pure predatism and is not included in the list because it is hardly a true interspecific association. This is obviously prevented by the itinerant and highly carnivorous behavior of the plunderers. In the compound nests, however, the colonies of the two species occupy stationary nests which are so close together that their galleries may interdigitate or intercommunicate and permit one of the species to enter the nest of the other. Different ant colonies even of the same species are so hostile that their mere existence in such contiguity implies that one of the species is to some extent exploiting the other. That the manner of exploitation differs in different ants will be seen from the following brief account of the various known types of compound nests:

(1) Certain small but aggressive ants, which secure at least a portion of their sustenance by waylaying the foraging workers of another species and snatching away their food, deserve the name of brigands. Such ants naturally make their nests near those of the species they plunder. Thus *Dorymyrmex pyramicus* in our southwestern states often constructs its nests in the clearing surrounding or even on the large mounds of harvesting ants of the genus Pogonomyrmex (Fig. 79).

(2) In cases of what I call "thievery" the exploitation is more

FIG. 79

Mound of agricultural ant (*Pogonomyrmex occidentalis*) bearing a crater (at *a*) of a small brigand ant (*Dorymyrmex pyramicus*).

subtle and efficient. The thief-ants, all of which are subterranean and have very small workers, nest in the earthen walls of populous ant or termite nests, much as the little red house ant (*Monomorium pharaonis*) nests in the walls of our dwellings. The chambers of the two nests are connected by extremely tenuous galleries, excavated, of course, by the thief-ants and permitting them to invade the nests and feed on the brood of their large neighbors, but preventing the latter from entering the nests of the robbers, who are either ignored or overlooked on account of their diminutive size, and therefore carry on their depredations unhindered. The abundance of food which they thus secure enables them to rear very large queens and males, but the workers themselves are condemned to perpetual dwarfishness by their criminal mode of life. The most remarkable thief-ants are found in the large termite nests of the tropics, and the conditions described attain their most extreme expression in the genus Carebara. The workers are minute, pale yellow and blind, the queens and males deeply colored and several thousand times as large as the workers. Arnold has recently suggested that these extraordinary differences in size must make it impossible for the young queen to feed her first brood of workers and hence to establish her formicary in the typical independent manner of other ants. For this reason, when she leaves the parental nest to take her nuptial flight, she carries, attached by their mandibles to the tufted hairs on her feet, several workers, which thus accompany her till she has made her cell in some termite mound, and then take charge of rearing her first brood. On reading Arnold's account I examined a number of females and males of the Ethiopian *Carebara vidua* in my collection and at once found the minute workers attached as he describes. The accompanying sketch (Fig. 80) shows one of the queens carrying two workers. These, of course, also attach themselves to the males that leave the nest at the same time, but as they do not accompany the nest-founding queens and die just after mating, the workers that happen to choose air-planes of the wrong sex also perish.

(3) What, for lack of a better term, I have called "neighborliness," is a very common relationship between two, or more rarely three or even four species of ants living in nests, often with interdigitating but never with intercommunicating galleries, under the same stone or in the same log. Usually the ants of the different colonies, when they happen to meet, are more or less hostile. If one of the species is small and weak it undoubtedly derives some protection from merely living near a large and powerful neighbor, or the feebler may feed to some extent on the refuse of the larger

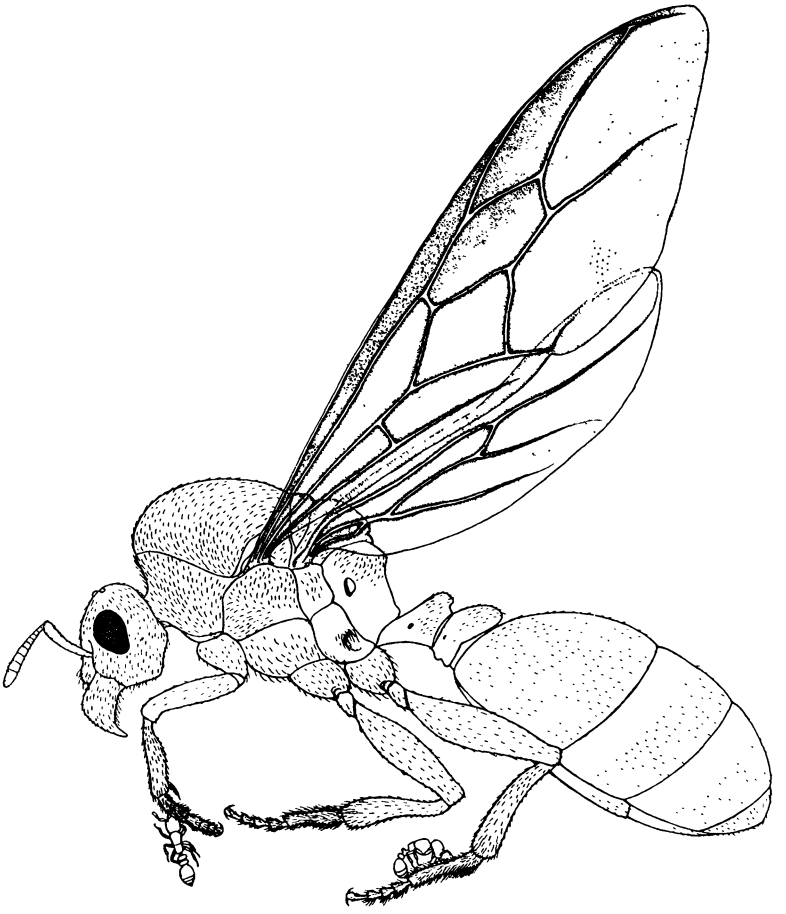

FIG. 80

Winged queen of *Carebara vidua* carrying the minute blind workers of her own species attached to her tarsal hairs.

form. When both species are large and aggressive they may perhaps find it advantageous to present a combined hostile front to the attacks of other ants.

(4) What Forel calls "parabiosis," a word I have translated as "tutelage," seems to be a more definite relation of mutual or unilateral protection. In a typical case which I recently observed in British Guiana, we have two species, a small black Crematogaster (*C. parabiotica*) and a large brown Camponotus (*C. femoratus*) together inhabiting a large ball of earth which they build up around the branch of a tree. In this ball, which Ule calls an "ant-garden," because it supports numerous epiphytes, the Crematogaster inhabits the superficial, the Camponotus the central portions. When it is slightly disturbed the little black ants rush out to attack the intruder, but a more serious disturbance

of the nest at once brings out the battalions of the much larger and extremely vicious brown species. The Crematogaster seem therefore to act as a skirmishing line for the Camponotus. Though the galleries of both species open freely into one another, and though the workers of both forage in long common files on the surrounding vegetation, they nevertheless keep their broods rigidly separated. The tutelary or parabiotic relation is evidently more mutualistic or cooperative than any of the foregoing cases of compound nests.

(5) An interesting series of small species includes the "guest ants" which live in still more intimate relations with other species. One of the best examples is *Leptothorax emersoni* which I first found many years ago associated with the considerably larger *Myrmica canadensis* in bog-like situations on our higher New England hills. The Leptothorax inhabit small chambers at the surface of the Myrmica nest and connect them by means of tenuous galleries with the chambers of their neighbors. The Leptothorax workers spend much of their time in the Myrmica nest where they mount the backs of the workers and assiduously lick their bodies and especially their heads and mouthparts. The Myrmicas seem greatly to enjoy this performance and from time to time reward their little guests with a droplet of regurgitated food. But while the Leptothorax arrogate to themselves the right to mingle freely with the Myrmicas and to flatter them into regurgitation, they resent the intrusion of the Myrmicas into their own habitations and insist on bringing up their own brood in perfect seclusion. Under natural conditions the Leptothorax are never seen to take any food, except from the surfaces and crops of their hosts, but if kept for some time by themselves in an artificial nest, they learn to eat honey and insects like other ants. And if both species are kept together in a glass nest without earth and therefore without materials for making separate chambers, the Leptothorax eventually though very reluctantly permit the Myrmicas to mingle the broods of both species and a true mixed colony is formed.

The ants that live in the various compound nests are not closely allied but belong to different genera or even subfamilies, a fact which may help to explain why they occupy separate nests and do not bring up their broods in common, for the rearing of the brood is a very delicate operation and would be apt to differ considerably in unrelated species. We may therefore be prepared to find that mixed colonies are formed only by closely allied species, *i. e.*, either by those belonging to the same genus or to closely allied genera, and this proves to be the case. But before considering the

various types of mixed colonies, two facts must be emphasized: First, many ants are fond of kidnapping the larvæ and pupæ belonging to other colonies of their own or allied species. Frequently these kidnapped young are devoured, but in well-nourished colonies they may be permitted to complete their development and the emerging workers may be adopted as *bona fide* members of the colony, even if they belong to a different species. It is therefore possible to produce a mixed colony artificially by giving a colony the mature brood of some other species. In this manner Miss Fielde succeeded in inducing species belonging even to very different subfamilies to live together in perfect amity. It is also interesting to observe that ants thus reared in the colony of an alien species may be very hostile to their own sisters that have been left to grow up in the parental nest. Second, the mixed colonies found in nature are not in the first instance produced by a mere kidnapping of the brood of an alien species, but by the young queen of a parasitic species, that is unable to start a colony independently, invading the nest of another species, which then becomes the host. The behavior of the invading parasite and the

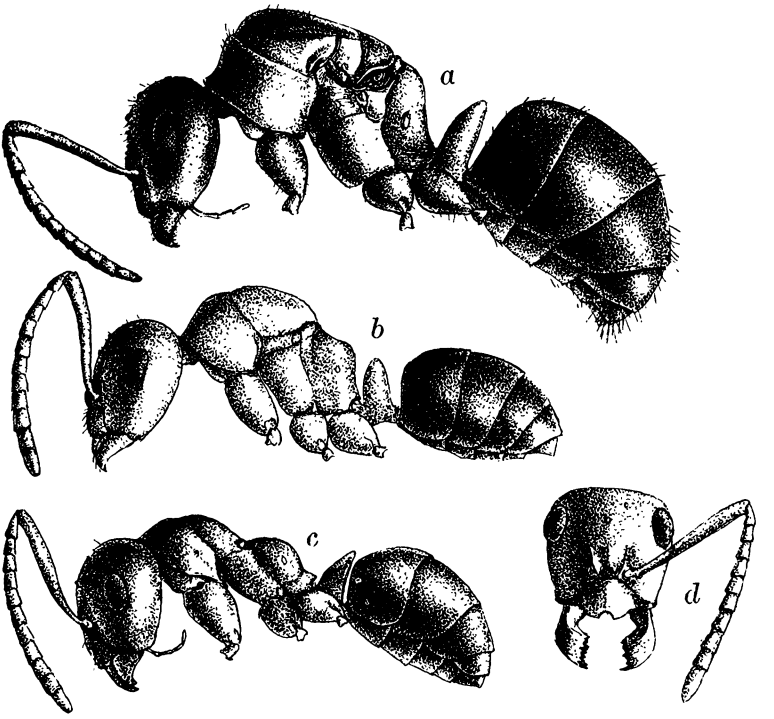

FIG. 81

Blood-red slave-maker (*Formica sanguinea*) in profile. *a*, Queen, with wings and legs removed; *b*, pseudogyne; *c*, worker; *d*, head of same from above, showing the characteristic notch in the clypeus.

host colony differ in different species, but in nearly all the observed cases the host queen, if present, is eventually killed and her place is taken by the alien intruder. Since the queen ant is really the reproductive organ of the colony considered as a superorganism, the host colony may be said to be castrated and its sterile worker personnel is constrained to devote all its energies to rearing the brood which is forthwith produced by the fecund parasite. With these general statements in mind we may turn to the three types of mixed colonies, those of the slave-makers, the temporary and permanent social parasites:

(1) The peculiar phenomena known as slavery, or dulosis, which occur in two genera of Formicinæ, Formica and Polyergus, and two genera of Myrmicinæ, Strongylognathus and Harpagoxenus, represent three phylogenetic stages, a primitive stage in *Formica sanguinea,* a culminating stage in Polygergus and a degenerate or evanescent stage in Strongylognathus and Harpagoxenus. The "blood-red slave maker," *F. sanguinea* (Fig. 81), is a common but rather local red ant, with black or brown gaster and is represented by numerous subspecies and varieties ranging over northern Europe, Asia and North America. It can be readily distinguished from the other species of the genus, at least in the Old World and the eastern United States, by the pronounced notch in the clypeus or small shield at the anterior end of the head. The worker and queen look as if they were hare-lipped. *Sanguinea* is one of the most intelligent of ants and therefore one of the most interesting to keep in artificial nests. Its habits were first studied more than a century ago by Pierre Huber, the son of the blind François Huber, and have ever since commanded the attention of myrmecologists, because its armies of workers make periodical forays on the colonies of the common black *Formica fusca,* carry the worker larvæ and pupæ into their nest and permit many of them to emerge and become members of their colony. Thus the colony is mixed, and the black individuals, on account of their color and provenience, have been called "slaves." It is evident, however, that this term is inappropriate, for a slave is "a man who is the property of another, politically and socially at a lower level than the mass of the people, and performing compulsory labor" (Nieboer), and none of these distinctions applies to the *fusca* workers in the *sanguinea* nest. They are more properly called "auxiliaries" (Hilfsameisen), but I shall use the old term on account of its brevity. At least one of the subspecies of *sanguinea* (*aserva*) does not make slaves, and the colonies of some of the other forms give up the habit after a time, for the *sanguinea* colony, when once established, is quite able to lead an independent

life. Darwin and others offered various explanations of the peculiar slave-making habit of *sanguinea*, but its meaning remained obscure till 1904 when I found that it had its origin in the behavior of the young queen. She is quite unable to found a colony independently and therefore, after her marriage flight, may adopt one of three courses: she may return to the nest in which she was reared or enter some other *sanguinea* nest, or she may invade a nest of *F. fusca*. As the first and second courses are sometimes adopted by other ants and do not lead to the formation of mixed colonies, they need no further consideration in this place and we may confine our attention to the last. As soon as the *sanguinea* queen invades a *fusca* colony, she becomes greatly excited and interested in the brood, seizes and collects in a small pile as many pupæ as she can snatch up and mounts guard over them. She slays any *fusca* workers that are bold enough to attempt to regain their property and is therefore soon left in undisputed possession of her plunder. Eventually *fusca* workers emerge from the cocoons and at once assume a friendly attitude towards the queen, feed her by regurgitation and behave towards her as if she were their own mother. She begins to lay eggs and the resulting larvæ are fed and reared by the black workers, so that when the *sanguinea* emerge a mixed colony is established. These workers show that they have inherited their mother's proclivities by kidnapping the brood of neighboring *fusca* colonies, but they do this as an army and carry the *fusca* brood to their nest. In some colonies, as I have stated, this kidnapping or slave-making proclivity may disappear after a time, and in *aserva* it seems to disappear very early or perhaps is not even inherited by the workers. In such cases, therefore, the personnel of old colonies may be made up entirely of *sanguinea* after the batch of *fusca* workers kidnapped and reared by the queen has died of old age. It is evident that slavery is at bottom a form of predatism and has its origin in the inability of the young queen to establish a colony without the aid of workers. Unlike the great majority of ant-queens, she has been unable to store enough food in her body to stand the strain of long fasting and nourishing her first brood. In another sense she is, of course, a parasite and the *fusca* workers represent the host. Owing to the fact that the colony may eventually cease to increase its worker personnel by the kidnapping of *fusca* brood, we may call this type of slavery temporary, acute or facultative.

The species of Polyergus, or "amazons," as they were called by Pierre Huber, have much the same distribution as *sanguinea* and have the same species of Formica as slaves, but their method of securing the latter is more highly perfected. The amazons

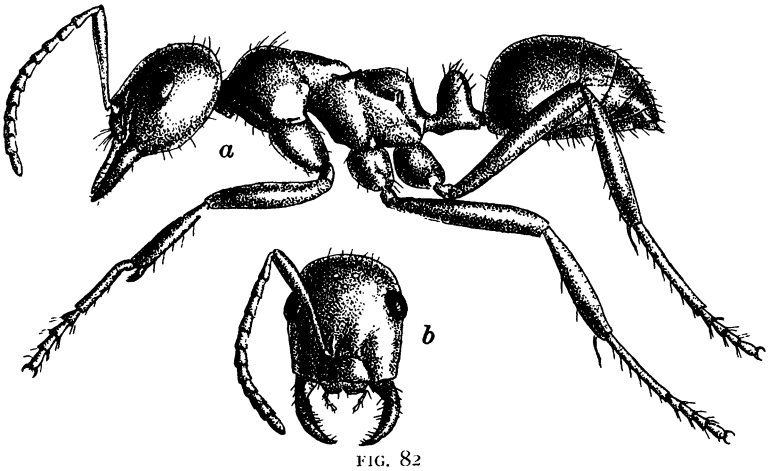

FIG. 82

a, Worker of *Polyergus lucidus*, the "shining amazon," a permanent slave-maker of the Eastern United States; *b*, head of same, showing the sickle-shaped mandibles.

are very beautiful red ants (except the Japanese *P. samurai*, which is black), and their mandibles are slender and sickle-shaped and perfectly adapted to fighting but of no use for digging in the earth or capturing food (Fig. 82). Hence these insects are unable to make nests or even to feed themselves or care for their own young, but are absolutely dependent on their slaves. Like *sanguinea*, the amazons make periodical forays, which for some unknown reason are always carried out in the afternoon, but their armies show a more perfected tactical organization and the subjugation and plundering of the *fusca* colonies are effected with much greater dispatch and precision—one might say with the most consummate *éclat*. At the approach of the amazons the *fusca*

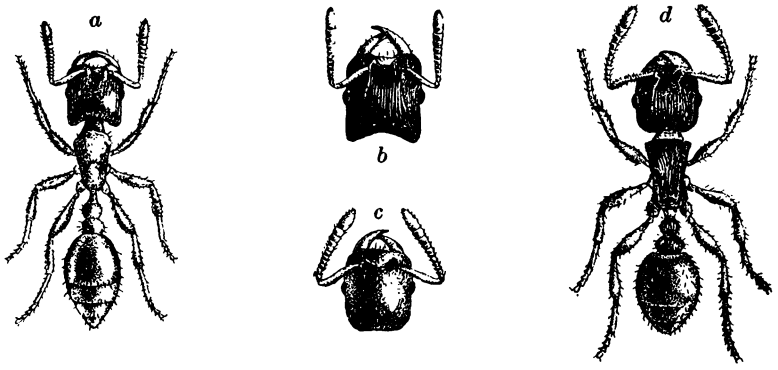

FIG. 83

c, Worker of *Strongylognathus testaceus*, a degenerate slave-maker of Europe; *b*, head of female of same; *c*, head of worker of *S. huberi*, an allied species; *d*, worker of the pavement ant (*Tetramorium caespitum*), the host of the species of Strongylognathus.

workers usually flee in dismay, but if they offer any resistance the amazons pierce their heads with the sickle-shaped mandibles. The young on emerging from the kidnapped pupæ excavate the nest, feed the Polyergus and bring up their brood but do not accompany the armies on their raids. The initial stages in founding the colony have been studied by Emery, who found that the young Polyergus queen secures adoption in some small, weak *fusca* colony after killing its queen by piercing her head. She then produces her brood which will later make the slave-raids on the *fusca* colonies. Since this raiding proclivity never lapses even in old colonies, Polyergus is to be regarded as a chronic, or obligatory slave-maker. An amazon crimson on a field sable with the device "*stultus sed pugnax*" might be an appropriate coat-of-arms for some of the military castes that have flourished during the course of human history.

In Europe there are several species of the interesting genus Strongylognathus (Fig. 83*a-c*), which have sickle-shaped mandibles like Polyergus and always live in the colonies of the common pavement ant, *Tetramorium caespitum* (Fig. 83*d*). Our fragmentary knowledge indicates that we have here some of the degenerate or evanescent stages of slavery. The workers of *S. rehbinderi* and *huberi* seem still to make forays on Tetramorium colonies and to carry home their brood, and Kutter has recently shown that *S. alpinus,* a form I discovered some years ago near the head-waters of the Visp, within sight of the Matterhorn, makes nocturnal slave raids and is accompanied by its slaves, which do most of the fighting and carry home the brood of their own species. In this case the slaves are really the masters and seem to use the Strongylognathus merely as a means of disconcerting or terrifying the colonies of *cæspitum* whose brood they are bent on kidnapping. Finally, *S. testaceus,* the best-known species of the genus, no longer makes forays and is tending to lose its worker caste. Wasmann, Mrázek, Forel and I have found that colonies of *cæspitum* infested by this species may retain the host queen. In order to establish her colony, therefore, the young *testaceus* queen probably associates herself with a young, nest-founding *cæspitum* queen. In the mixed colonies of other species of Strongylognathus the host queen appears to be eliminated as in the colonies of *sanguinea* and Polyergus.

(2) In 1904 I detected another method of forming mixed colonies, which I called temporary, although I might have called it acute social parasitism. It is practiced by a number of ants, especially by several North American species of Formica that have unusual queens. In some species they are peculiarly colored or

furnished with long yellow hairs, in others they are extremely small, smaller even than the largest workers (Fig. 84). The young queen of these ants enters the nest of another Formica belonging to the *fusca* or *pallide-fulva* group and is very apt to be adopted, probably on account of her smaller size or other physical attractions. The fate of the host queen in such invaded nests has not been ascertained but she is probably killed by her own workers. The parasite then proceeds to produce her brood, which is reared by the host workers, and a mixed colony results. As there is no inclination on the part of the queen's offspring to plunder other nests of the host species, and as all the host workers die off in the course of a few years, a pure colony of the parasitic species is left behind and may grow to be very populous and aggressive, without showing any signs of its parasitic origin—a beautiful analogue of some human institutions, which after starting in humble and cring-

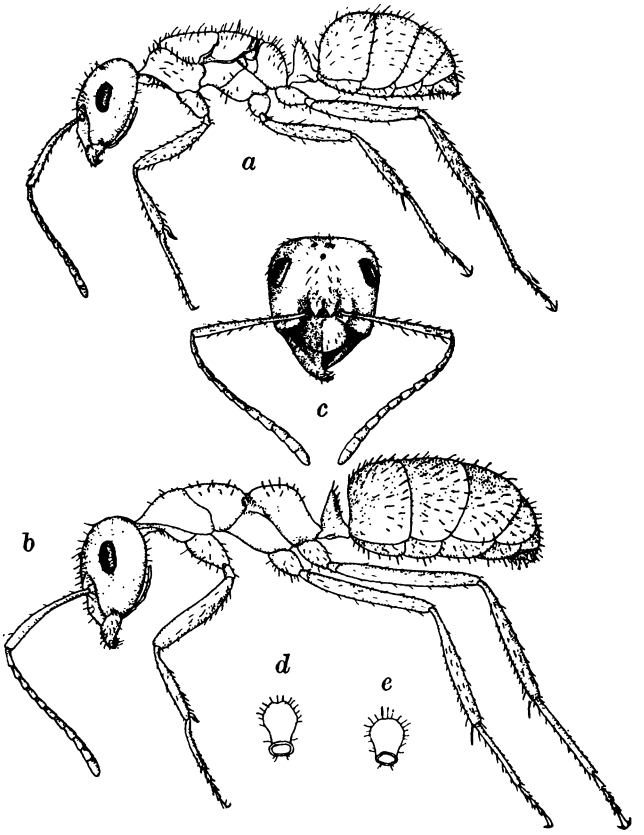

FIG. 84

A temporary parasite (*Formica microgyna*). *a*, queen, with wings removed; *b*, large worker drawn to same scale; *c*, head of same; *d* and *e*, petiole of worker and queen seen from behind.

ing parasitism have come to acquire during the centuries a most exuberant and insolent domination. Our common mound-building ant (*Formica exsectoides*) is one of these successful temporary parasites which starts its opulent colonies with the aid of the ubiquitous *F. fusca* var. *subsericea*. Since my observations were published many European Formicas, including the well-known mound-building *rufa*, and ants of several other genera (Lasius, Bothriomyrmex, Crematojaster, etc.) in various parts of the world have been found to be temporary social parasites. One of the most interesting of these is the Dolichoderine *Bothriomyrmex decapitans* which Santschi observed in Tunis. The young queen, on descending from her marriage flight, wanders about on the ground till she finds the nest of a *Tapinoma nigerrimum* colony, when she permits herself to be seized and "arrested" by its workers. These then proceed to drag her into their burrow by her legs and antennæ. After entering the nest the parasite may be attacked from time to time by the workers, but she takes refuge on the brood or on the back of the larger Tapinoma queen. In either of these positions she seems to be quite immune from attack, probably because her own odor is overlaid by that of the brood or the host queen. Santschi observed that the parasite often spends long hours on the back of the Tapinoma queen and that while in this position she busies herself with sawing off the head of her host! By the time she has accomplished this cruel feat, she has acquired the nest-odor and is adopted by the Tapinoma workers in the place of their unfortunate mother. The parasite thereupon proceeds to keep them busy bringing up her brood. They eventually die of old age and the nest then becomes the property of a thriving, pure colony of *Bothriomyrmex decapitans*.

(3) There are more than a dozen genera of ants from various parts of the world, which may be classed as permanent, or chronic social parasites. They have all completely lost the worker caste so that in this respect they closely resemble the parasites among the social wasps and bees. The young queens enter the nests of other ants and secure adoption, like the queens of the temporary social parasites. The host queen seems to be regularly assassinated by her own workers. At least this has been observed by Santschi in the case of *Wheeleriella santschii*, which lives in the nests of the common North African *Monomorium salomonis*. After fecundation the *Wheeleriella* queen roams about over the surface of the soil in search of a Monomorium nest. When near the entrance of one of them she is "arrested," to use Santschi's expression, by a band of Monomorium workers, which tug at her legs and antennæ and draw her into the galleries. Sometimes she may be

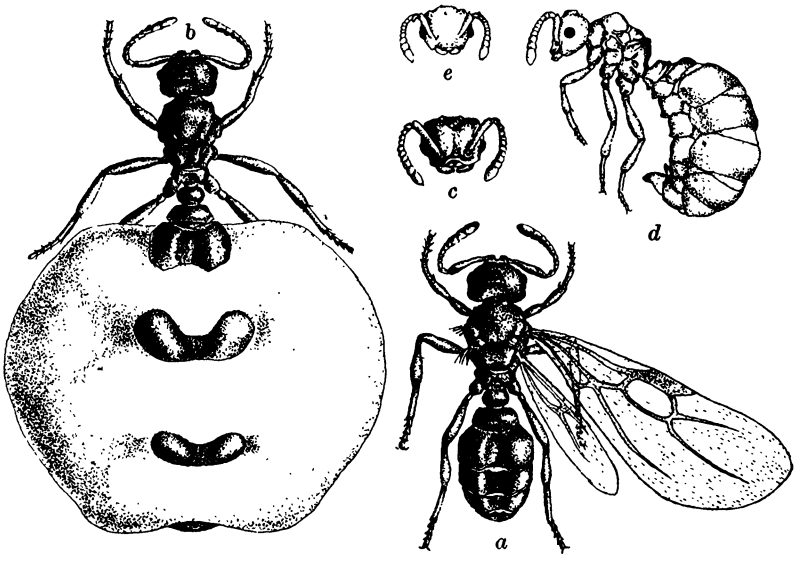

FIG. 85

A workerless, degenerate, permanent social parasite (*Anergates atratulus*) of Europe. *a,* virgin queen; *b,* old, egg-laying queen with enlarged gaster; *c,* head of same from front; *d,* male, which is wingless and pupoidal; *e,* head of same.

seen to dart suddenly into the entrance of her own accord and is arrested within the nest. There are no signs of anger on the part of the Monomorium, and she is soon permitted to move about the galleries unmolested. The workers then begin to feed and adopt her and in the course of a few days she lays her first eggs, which are accepted and cared for by the host. The parasite pays no attention to the much larger Monomorium queen, but the latter is eventually assassinated by her own workers. Other species, like the famous *Anergates atratulus* (Fig. 85) of Europe and the recently discovered *Anergatides kohli* of the Congo, are much more highly modified and represent the last stages of parasitic degeneration. In the former, which lives with *Tetramorium cæspitum,* the queen is small and winged (Fig. 85*a*), but after deälation and adoption her gaster swells enormously with eggs till she resembles an old termite queen (Fig. 85*b*). The male (Fig. 85*d*) is wingless and pupa-like and unable to leave the nest so that mating takes place between brothers and sisters ("adelphogamy" of Forel). The conditions in Anergatides, which is a parasite of *Pheidole melancholica,* are somewhat similar. In the workerless parasites the offspring of the intrusive queen are, of course, all males and females and are produced during the life-time of the host workers. The colonies are therefore mixed throughout their existence which is necessarily terminated by the death of the host.

While all myrmecologists now agree in recognizing the three types of social parasitism and their origin in the behavior of the young queens, there is still disagreement in regard to their phylogenetic derivation. I at first believed that they had all had their inception in the passive adoption of insufficiently endowed, young queens by colonies of their own species, and Wasmann has consistently adhered to this view. Emery and Viehmeyer, however, see in the aggressive, predatory behavior of the *sanguinea* queen a stage from which temporary and permanent social parasitism may be more naturally derived. I am now inclined to believe that these investigators are nearer the truth and that the adoption of queens by colonies of their own species is a distinct phenomenon, which may readily lead to the formation of new colonies by a kind of swarming, analogous to that of many social bees and wasps, but not to the series of parasitic developments which we have been considering.

All the parasitic ants are rare or local. The permanent, or chronic social parasites, especially, are so very scarce that they must be on the very verge of extinction—a fact which shows that parasitism, so far as the race is concerned, is anything but a promising or profitable business. But even the individual parasite buys its rare successes very dearly, for it must often run the gauntlet of great resistance and animosity on the part of a too healthy host and must at the same time carefully avoid seriously injuring that host and thus bringing about its own destruction. Parasitism in the queen ant may, indeed, be regarded as a kind of compensation or overcompensation for her inability to rear a brood of workers. One is reminded of the overcompensations (megalomania) resorted

PERMANENT SOCIAL PARASITES (ANTS WITHOUT WORKERS)

PARASITES	HOSTS	HABITAT	ANCESTRAL GENUS
Sympheidole elecebra	*Pheidole ceres*	Nearctic	Pheidole
Epipheidole inquilina	*Pheidole ceres*	Nearctic	Pheidole
Parapheidole belti	(?) *Pheidole sp.*	Malagasy	Pheidole
Sifolinia laurœ	(?) *Pheidole sp.*	Palearctic	Pheidole
Anergatides kohli	*Pheidole melancholica*	Ethiopian	Pheidole
Wheeleriella santschii	*Monomorium salomonis*	Palearctic	Monomorium
Wheeleriella adulatrix	*Monomorium subnitidum*	Palearctic	Monomorium
Wheeleriella wrougtoni	*Monomorium indicum*	Palearctic	Monomorium
Epœcus pergandei	*Monomorium minimum*	Nearctic	Monomorium
Epixenus andrei	*Monomorium venustum*	Palearctic	Monomorium
Epixenus biroi	*Monomorium creticum*	Palearctic	Monomorium
Myrmica myrmoxena	*Myrmica lobicornis*	Palearctic	Myrmica
Hagioxenus schmitzi	*Tapinoma erraticum*	Palearctic	Monomorium
Anergates atratulus	*Tetramorium cæspitum*	Palearctic	(?) Tetramorium
Pseudoatta argentina	(?) *Mœllerius balzani*	Neotropical	Mœllerius
Plagiolepis nuptialis	*Plagiolepis custodiens*	Ethiopian	Plagiolepis

to by some human being with pronounced inferiority complexes. Was it an inkling of this that led the ancients to make Hercules the tutelary deity of parasites? That the parasitic queen's inability has been acquired and fixed during the past history of the species is suggested by the singularly close genetic relations of the parasites to their hosts. In the great majority of cases, as indicated in the accompanying list, the parasite belongs either to the same genus as its host or to a genus descended from that of its host. This is equally clear from detailed lists of the other parasitic ants, wasps and bees and shows that the parasite originally led an independent life but took to exploiting some common, allied species of the same genus. Probably the exploitation was at first predatory as it still is in certain Psammocharid wasps and *Formica sanguinea*, because food was more expeditiously secured by such tactics. In the course of time the parasite's adaptations to its host became increasingly refined and were reflected in its structure as generic distinctions, as we see, *e. g.*, in the species of Polyergus, which are obviously modified Formicas. The descent to Avernus became steeper and more slippery, as the parasite, yielding to inertia, became chronically and abjectly dependent on its host and condemned itself to physiological and numerical inferiority ("misère physiologique"). The next stage is extinction, after a longer or shorter period of hopeless specialization ("degeneration"). This or a very similar story has been so often repeated in all the classes of the animal and plant kingdoms that the number of forms which during geological time have descended to the *limbus parasitorum* must be considerable.

Having considered the ants as parasites and hosts of one another, we may now turn to the cases in which they act as the hosts of insects belonging to very different orders, the myrmecophiles, or ant-guests. Here we enter on a vast and very intricate subject to which I shall be unable to do justice in the short time at my disposal. Fully 2,000 species of myrmecophiles have been described, and no doubt the number will be more than doubled when the nests of the many species of tropical ants have been carefully explored. The myrmecophiles include not only members of nearly all the different orders of insects but also many spiders, mites, millipeds and land-crustaceans—a weird, one might almost say demoniacal, horde of creatures, which have been induced to live in more or less intimate and maleficent relations with the ants by the obvious advantages of the association. Ant nests furnish admirable hiding or lurking places and are at night and during the winter months somewhat warmer than the surrounding soil. They often contain quantities of food or refuse, and the helpless brood,

callow and injured ants may be stealthily devoured. Furthermore, the ants may be wheedled into adopting and feeding alien insects, as if they were their own young or ants of the same species. All the forms of exploitation, therefore, from predatism, adoption and domestication to external and internal parasitism have been developed by the myrmecophiles. It may be said that these creatures have searched out and taken advantage of every vulnerable point in the ant's structure and behavior, just as every human idiosyncrasy, frailty and virtue has been exploited by some cunning human parasite.

There are two reasons why we must consider the myrmecophiles in these lectures. First, many of them live only with particular ants and really form a constituent though not an essential part of their colonies, for although they are not present in all colonies, they can not exist apart from the ants except while migrating from one nest to another. They are, in fact, a more integral component

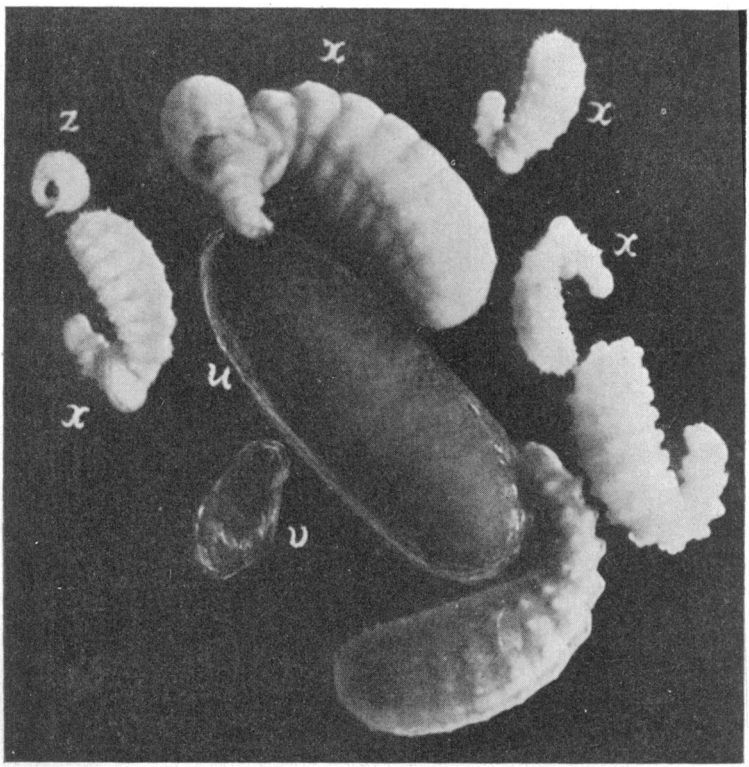

FIG. 86

Larvæ and pupæ of a ponerine ant (*Pachycondyla montezumia*) and its commensal (*Metopina pachycondylae*). The Pachycondyla larvæ marked *x* have each a Metopina larva around the neck; *z*, isolated Metopina larva; *v*, Metopina puparium; *u*, cocoon of Pachycondyla.

of the colony in which they occur than are the domestic animals in the human community. Many of our domestic animals are still able to return to an independent, feral life, but this is impossible for the more typical and highly specialized ant-guests. Second, the ant-guests afford a very striking, indirect or pathological demonstration of the extraordinary intensity of the brood-nursing propensities of ants. Any insect possessed of the glandular attractions, which I shall presently describe, can induce the ants to adopt, feed and care for it and thus become a member of the colony, just as an attractive and apparently well-behaved foreigner can secure naturalization and nourishment in any human community. But the procedure among the ants is more striking, because the foreigners are so very foreign, that is, belong to such alien and heterogeneous groups. Were we to behave in an analogous manner we should live in a truly Alice-in-Wonderland society. We should delight in keeping porcupines, alligators, lobsters, etc., in our homes, insist on their sitting down to table with us and feed them so solicitously with spoon-victuals that our children would either perish of neglect or grow up as hopeless rhachitics.

Although every species of myrmecophile has its own methods of securing food and lodgings in the ant nest I shall describe only a few examples to illustrate the exploitation of the trophallactic habit.

(1) There are probably several myrmecophiles that steal the food given to the larva, but the only case that has been adequately described is the larva of a small fly, *Metopina pachycondylæ*, which I found many years ago in Texas infesting the nests of a Ponerine ant, *Pachycondyla montezumia* (Fig. 86). This ant feeds its larvæ in a very primitive manner with pieces of insects and thus exposes itself to the inroads of the Metopina. Its small larva clings to the neck of the ant larva by means of a sucker-like posterior end and encircles its host like a collar. Whenever the ant larva is fed by the workers with pieces of insect placed on its trough-like ventral

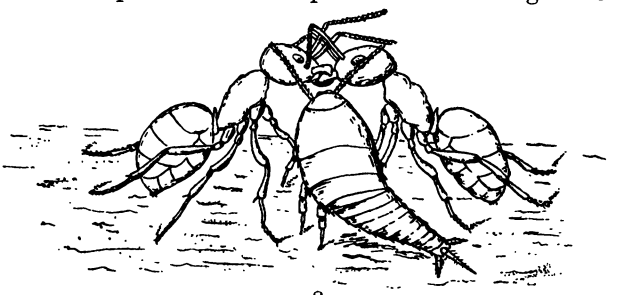

FIG. 87

Atelura formicaria about to snatch the droplet of food that is being regurgitated by one *Lasius mixtus* worker to another. (After C. Janet.)

surface, within reach of its mouthparts, the larval Metopina uncoils its body and partakes of the feast; and when the ant larva finally spins its cocoon it also encloses the Metopina larva within the silken web. The commensal, however, moves to the caudal end of its host and forms a small flattened puparium which is applied to the wall of the cocoon. This is obviously an adaptation for preventing injury from the jaws of the worker ants when the cocoon is being opened and the callow extracted from its anterior end. The ant hatches before the Metopina and the empty cocoon, with the puparium concealed in its posterior pole, is carried to the refuse heap. Here the fly emerges and escapes from the cocoon by the opening through which its host emerged. The Metopina consumes so little food and is so considerate of its host that it can hardly be said to produce any injurious effect on the colony; at any rate the larvæ which have borne commensals develop into perfectly normal workers. The ants clean the commensals when they are cleaning their own progeny and show no signs of being aware of their presence in the nest.

(2) *Lepismina* (*Atelura*) *formicaria* (Fig. 87) is a small, primi-

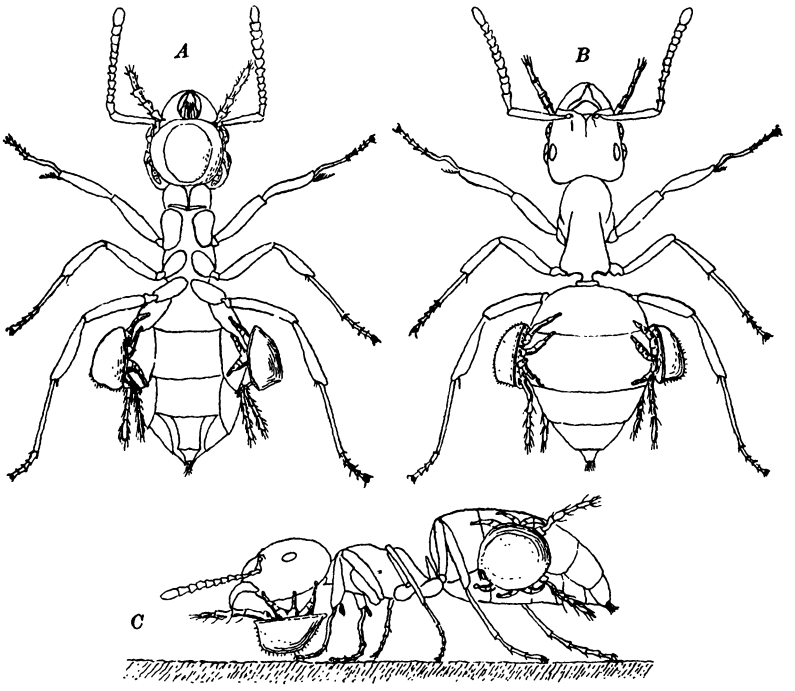

FIG. 88

Lasius mixtus worker carrying three symmetrically oriented mites (*Antennophorus pubescens*). *A*, ventral; *B*, dorsal; *C*, lateral view. (After C. Janet.)

tive insect which lives in the nests of *Lasius mixtus*. Its body tapers rapidly behind and is covered with slippery scales so that it is not easily caught by the ants. It is, moreover, extremely agile and circumspect, because it has not succeeded in ingratiating itself with its hosts. Janet, after providing a colony of *Lasius mixtus* with honey, was able to make the following observations on the behavior of the insect: "From the instant that the first foragers returned to the nest, the Lepismina showed by their excitement that they perceived the odor of honey. Soon a considerable number of ants were grouped in couples for the purpose of regurgitating. They elevated their bodies slightly and often raised their fore legs, thus leaving a vacant space under their heads. As soon as a Lepismina came near such a couple, it thrust itself into the space, raised its head, suddenly snapped up the droplet that was passing in front of it and made off at once as if to escape merited pursuit. But the ants standing face to face are not free enough in their movements even to threaten the audacious thief, who forthwith proceeds to take toll from another couple and continues these tactics till his appetite is appeased."

(3) A more subtle method of obtaining regurgitated food is adopted by the large mites of the genus Antennophorus (Fig. 88), which have been studied by Janet, Wasmann, Karawaiew and myself. These mites, which have conspicuously long fore legs and attach themselves to the bodies of the workers, whether present in odd or even number, always orient themselves in a symmetrical position with respect to their host. When only one Antennophorus is present it clings to the gula, or chin of the ant, with its fore legs directed towards the ant's mouthparts. When two are present, there is one on each side of the head or one on each side of the gaster; in the former case the antenniform appendages are directed towards the anterior, in the latter towards the posterior end of the ant's body. When there are three mites, one attaches itself to the chin and the two others to the sides of the gaster. Four place themselves in pairs on the sides of the head and gaster. If six are present, which rarely happens, four are arranged in pairs on the sides of the head and gaster while of the two remaining individuals, one attaches itself to the chin, the other to the mid-dorsal surface of the gaster. Janet believes that these symmetrical arrangements are for the purpose of balancing the burden and thus making it easier for the ant to carry. When attached to the head the mite obtains its food by drinking the regurgitated droplet as it is being passed to or from the mouthparts of the host, or it titillates the ant with its antenniform legs and induces her to regurgitate for its special benefit. The mites attached to the gaster obtain their

food by stroking other ants in the vicinity or by reaching out and partaking of the droplets as they pass from one ant to another. The ants try to rid themselves of the parasites when they first attach themselves, but after they have taken up their definitive, symmetrical positions, they seem to be tolerated with indifference.

Most of the species of Antennophorus have been described from Europe, but I have found two species (*donisthorpei* and *wasmanni*) rather common near the Arnold Arboretum in Boston. They live in essentially the same manner as the European Antennophori with our small yellow ants of the genus Lasius, and its subgenus Acanthomyops. All these Lasii are hypogæic and devote themselves to attending snow-white plant-lice and mealy-bugs on the roots of our forest trees, and since the mites occur only with these ants it would seem that they, the plant-lice, the mealy-bugs, the mites and the forest trees are all so many members of a peculiar, subterranean association, or biocoenose. The plant-lice and mealy-bugs pump the juices out of the plants and pass on to the soliciting ants the unassimilated portions in the form of honeydew, some of which the ants regurgitate to the mites that ask them for it by aping with their long, hairy forelegs the antennary movements of the hungry ants. In other words, the ants serve as cup-bearers, distributing to one another and to the indolent, sedentary Antennophori the nectar which the tapster plant-lice and mealy-bugs keep drawing from their vegetable hosts. Owing to this interesting biocoenotic arrangement the worker Lasii do not have to come to the surface of the ground to seek their food. The eyes of the

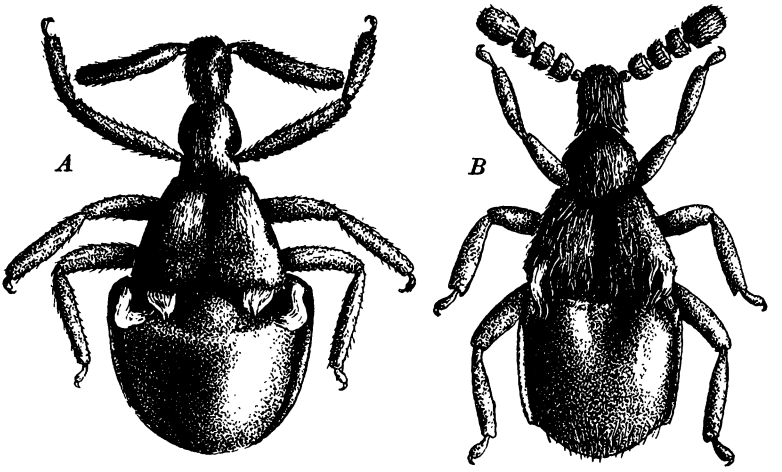

FIG. 89

A, Adranes lecontei of North America, and *B, Claviger testaceus* of Europe, two guest beetles, with golden yellow trichomes at the tips of their wing-cases and at the base of the abdomen.

workers have therefore become so minute that their visual powers must have nearly or quite disappeared. Perhaps we can best appreciate the relations of the ants to the mites if we fancy ourselves blind, condemned to live in dark cellars and continually occupied with pasturing and milking fat, sluggish cows, yielding quantities of strained honey instead of milk. Then let us suppose that occa-

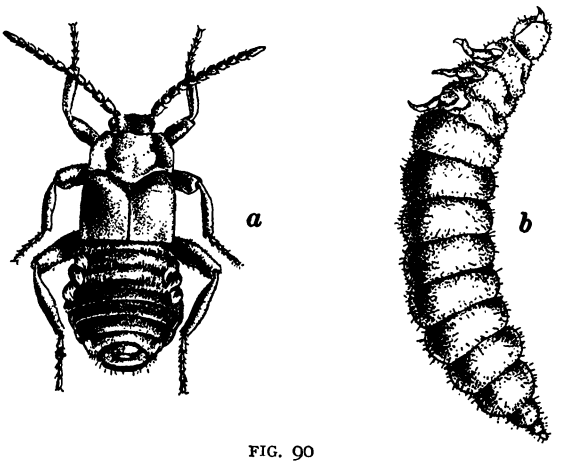

FIG. 90

a, A European guest-beetle (*Lomeschusa strumosa*) and *b*, its larva, which live with colonies of the blood-red slave-maker (*Formica sanguinea*).

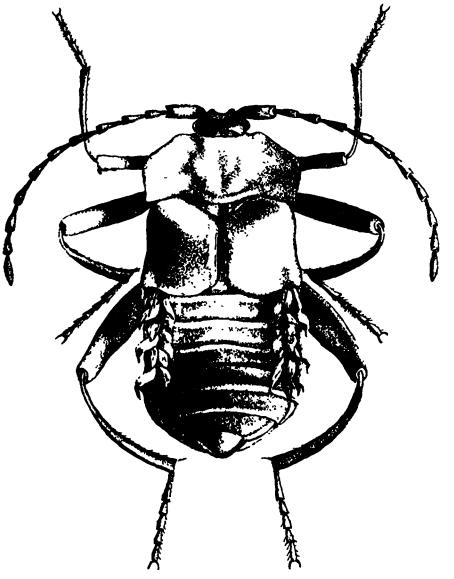

FIG. 91

Xenodusa cava, a North American beetle which breeds in the nests of Formica during the summer and passes the winter in the nests of Camponotus. Note the tufts of trichomes along the sides of the abdomen.

sionally there alighted on our cheeks or backs small creatures which, by placing themselves in positions symmetrical to the median longitudinal axis of our bodies, took great care not to annoy us, and stretched forth to us from time to time small, soft hands, like those of our friends, begging for a little of the honey, should we not under the circumstances treat these little Old Men of the Sea with much lenity and even with something akin to affection?

(4) The behavior of the myrmecophiles I have been considering is simple and transparent compared with that of the true ant-guests or symphiles, which are really the *élite* of all the insects that live in ant colonies. They comprise several hundred species of beetles belonging to a number of natural families but showing a very singular, convergent agreement in certain characters, such as a deep, oily red color and peculiar tufts of golden yellow hairs, or trichomes on various parts of their bodies (Fig. 89). Their antennæ and mouth-parts, too, are in many cases peculiarly modified, the former for soliciting, the latter for receiving regurgitated food. The trichomes surround the openings of singular glands, the aromatic, volatile secretions of which flow along the hairs and are licked off by the ants. So inordinately fond are the ants of these secretions that they cherish the beetles, feed them and carry them to safety when the nest is disturbed or to new nests when the old ones have to be abandoned. The beetles breed in the colonies and their larvæ are often treated with even greater solicitude than the ant larvæ.

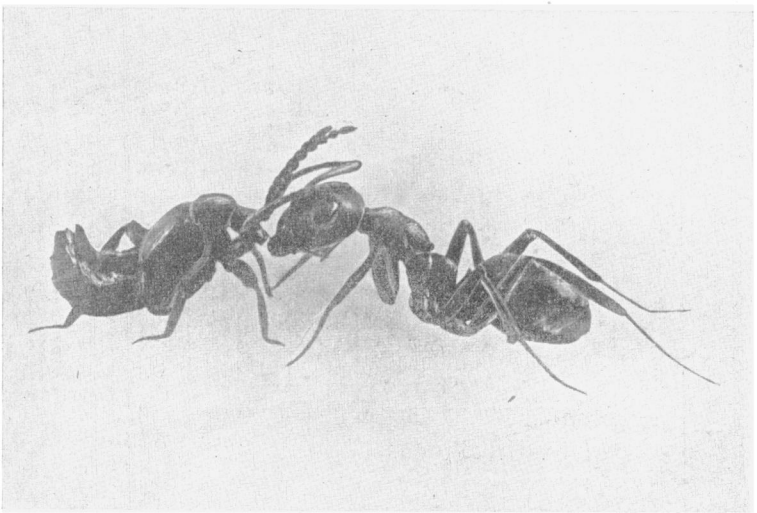

FIG. 92

Worker of the blood-red slave-maker, *Formica sanguinea,* feeding its guest beetle, *Lomechusa strumosa.* (After H. K. Donisthorpe.)

Probably the most remarkable of these true guests are the Lomeschusini, which have been studied by Wasmann for more than 30 years. They belong to the rove-beetles, or Staphylinidæ and comprise only three genera: Lomeschusa (Fig. 90) and Atemeles, peculiar to Europe and Northern Asia, and Xenodusa (Fig. 91), known only from the United States and Mexico. The species of Atemeles and Xenodusa have two hosts, those of the former living during the summer and breeding in Formica colonies but hibernating in colonies of Myrmica, the latter also breeding with Formica but hibernating with our large carpenter ants of the genus Camponotus. Lomeschusa, on the other hand, has only one host, *Formica sanguinea,* with which it lives throughout the year. The adult beetles of all three genera look much alike. They have long, mobile antennæ, short wing-cases and a voluminous abdomen, which can be curled up over the thorax and is provided on each side above with a segmental series of beautiful golden trichomes. Atemeles and Xenodusa beg their food from the ants by stroking their cheeks with the fore feet. Their larvæ are active, have long legs and employ the same method as the beetles in persuading the ants to regurgitate. They also devour the defenseless Formica larvæ. The adult Lomeschusa is more passive in its behavior and uses its antennæ in soliciting food (Fig. 92). Its larvæ (Fig. 90*b*) have very short legs and are unable to run about but lie among the ant brood. They eat the brood but are also fed by regurgitation. In all probability they secrete fatty exudates which are greatly appreciated by the ants. At any rate, the ants seem to prefer the Lomechusa larvæ to their own, or perhaps regard them as unusually promising ant larvæ. In consequence of this infatuation the Lomechusa larvæ often destroy the greater part of the brood, so that in *sanguinea* colonies heavily infested with the parasites the queen larvæ develop abnormally. Either these larvæ are neglected, or the ants actually endeavor to convert them into workers, because they feel that this caste is inadequately represented in the colony. But whatever be the treatment of the queen larvæ, they develop into pathological adults, known as "pseudogynes" (Fig. 81*c*)—abortive creatures, resembling workers in size and in the shape of the head and gaster, but with a more voluminous and convex thorax, approaching that of the queen. They are paler than the normal workers and very lazy, cowardly and incompetent. Usually they constitute 5 to 7 per cent., less frequently 20 per cent. or more, of the personnel of an infested *sanguinea* colony. Their appearance in a nest indicates that the colony is in a diseased condition and on the road to extinction, as the result of Lomechusa infection. Similar pseudogynes are also

produced in the Formica colonies infested with Atemeles and Xenodusa, but not in the Myrmica and Camponotus colonies in which the beetles hibernate, because they do not breed among their winter hosts and can not therefore interfere with the normal development of their brood.

Such being the effect on the colonies that harbor the Lomechusini, one naturally inquires why the habit of rearing the parasites has not long since led to the extinction of the Formicas. This question has been partially answered by Wasmann. He finds that the ants treat the Lomechusa larvæ like their own, even when they are ready to pupate. *F. sanguinea,* like many other ants, buries its full-grown larvæ in the soil in order that they may spin their cocoons and pupate within them. After pupation the cocoons are unearthed, cleaned and stacked up in the chambers of the nest. Now the full-grown Lomechusa larvæ also need to be buried in order to pupate, though they do not spin cocoons, but they must not be unearthed after pupation, like the ant brood, or they perish. The ants, however, are utterly ignorant of these different developmental requirements and therefore unearth as many of the Lomechusa pupæ as they can find. Thus death in the guise of what might be called a regulatory Nemesis overtakes all except the few pupæ that have been overlooked by the ants, but these few suffice to insure the survival of the species. More recently Wasmann has claimed that *sanguinea* takes a particular liking to certain pairs of beetles and eliminates the less attractive individuals from the colony. Of course, this would still further tend to reduce the incidence of parasitism and its baneful effects on the host.

The behavior of *sanguinea* and Lomechusa has seemed to Wasmann so unique and extraordinary that he has used it on every occasion as furnishing brilliant proofs of the absence of intelligence in ants, of the impotence of natural selection, of the possession by *sanguinea* of a singular, innate Lomechusa-fostering instinct, and therefore of a new type of selection, which he calls "amical selection," and, finally, even of the Divine Wisdom in maintaining the equilibrium in nature. Being a very accomplished Jesuit he has devoted many hundred pages and much scholastic casuistry to these "proofs." To the biologist who is under no compulsion to make his conclusions square with the philosophy of St. Thomas Aquinas, the behavior of *sanguinea* appears in a very different light, as a brilliant example of the perversion of appetites. Escherich has compared the infatuation of the Lomechusa-cherishing *sanguinea* with alcoholism in the human species. It might also be compared with a cat's infatuation with cat-nip, and the rearing of the Lomechusa larvæ by the ants would

seem to be due to the same kind of instinct perversion that we observe in the birds that rear cuckoos, the occasional cat that rears a puppy or the hen that adopts kittens. It would seem to be no more necessary to postulate a special Lomechusa-rearing instinct in *sanguinea* than a special ice-cream instinct in our children or a special Havana-cigar instinct in old bachelors.

That the behavior of *sanguinea* towards Lomechusa proves nothing in regard to intelligence, even when the word is used, as it is always used by Wasmann, in the scholastic sense, that is, as equivalent to reason, or ratiocination, has been shown by Hobhouse. After referring to Wasmann's conclusions, he says: "Difficult as it is to conceive the psychological conditions under which such contrasts are possible, we may still get some help from the analogy of human action. When comparative psychologists take occasional inconsistency as proving the utter absence of intelligence (in animals) they are using an argument which would equally disprove the existence of intelligence in man. After all, is an ant nourishing parasites that destroy its young guilty of a greater absurdity than, say, a mother promoting her daughter's happiness by selling her to a rich husband, or an inquisitor burning a heretic in the name of Christian charity, or an Emperor forbidding his troops to give quarter in the name of civilization? The mother really desires her daughter's happiness, but her conception of the means thereto is confused, and rendered self-contradictory by worldly ambitions. The inquisitor's conception of Christian charity is similarly corrupted by the subtle corporate egoism of a Church and the cruel pedantry of bad theology. Even the Emperor has some conception of civilization, but it is the civilization of militarism. In all cases there impinge on the avowed plan of action conflicting impulses of a kind not to stop the course of action, but to merge in it and distort it."

Hobhouse also comments trenchantly on Wasmann's conception of the maneuvers of the Divine Wisdom in maintaining the equilibrium of parasite and host, but I will pass over this matter, because it involves a consideration of the problem of evil and belongs to the philosopher and the theologian. The cases of social parasitism considered in the first part of this lecture and the behavior of *sanguinea* and Lomechusa suggest a few concluding remarks on a matter that is often overlooked. It is evident that a parasitic species is more seriously affected and at a much greater disadvantage than a host species, notwithstanding the suffering or death that may be inflicted on individual host colonies. Without exception, the hosts of all the known social parasites and Lomechusini are very common, prolific, widely distributed and therefore

very plastic or adaptable ant, and the instances of infection of these hosts are local or sporadic. This is even the case with *Formica fusca,* which occurs practically over the whole northern hemisphere and is infested by an extraordinary series of social parasites. It is enslaved by *F. sanguinea* and *Polyergus rufescens* and serves as the temporary host of many parasitic Formicas, including *rufa, truncicola, dakotensis, exsecta, exsectoides,* etc. We may conclude, therefore, that *fusca* and the other hosts of parasitic ants and Lomechusini have developed more or less resistance or even a certain local immunity to the inroads of the parasites, and that the parasites even when successful exploit merely that margin of super-abundant vitality and fecundity which every healthy organic species possesses. Hence the occasional destruction of colonies by the parasites does not seriously endanger the life of the host species. If this were the case the hosts would be scarce or would have disappeared long ago. The same considerations probably apply to the human species, for it would seem that only man's world-wide distribution, great fecundity and wonderful adaptability have enabled him to survive all the terrible exploitations to which he has been subjected.