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THE PARASITIC ACULEATA, A STUDY IN EVOLUTION.¹

By WILLIAM MORTON WHEELER.

(Read April 25, 1919.)

There is undoubtedly much to be said in favor of the opinion commonly held by entomologists that the fruitfulness of their investigations is apt to be directly proportional to the intensity of their specialization, but it is also true that this very specialization may often preclude an adequate appreciation or even a recognition of phenomena that would profoundly impress the worker who possesses more general biological interests. This statement is not inapplicable to the subject of the following study, which is an attempt to collate the data accumulated in their respective fields by a number of observers of ants, bees and wasps and relating to certain types of parasitism which keep recurring in various natural families of the Aculeata in response to frequently recurring stimuli or situations in the organic environment. The few who have published comprehensive accounts of the phenomena have failed to present them as clearly and cogently as the facts would seem to warrant. I am aware that my own treatment of the subject may leave much to be desired and especially that my account of the bees, a difficult and extensive group to which I have been able to devote comparatively little study, is rather summary, but every attempt to attain

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 155.

broader generalization has its attendant risks and inadequacies. If I succeed in directing renewed attention to an interesting series of facts and to some of the problems which they suggest, the purpose of this article will have been accomplished.

In considering the parasitic Aculeata I shall adhere to the following classification, which though in certain respects artificial and unsatisfactory from the standpoint of phylogenetic development, will nevertheless facilitate an understanding of the history of our knowledge of the subject:

I. Nonsocial Parasites.

1. Solitary Bees.
2. Solitary Wasps.

II. Social Parasites.

1. Ants.
 - a. Guest Ants.
 - b. Slave-makers.
 - c. Temporary Social Parasites.
 - d. Permanent Social Parasites.
2. Social Bees.
3. Social Wasps.

The solitary bees may justly claim our attention first, because they comprise such a large number of parasitic forms which have been objects of study for more than a century. The taxonomy of the bees, however, notwithstanding the number of able investigators they have attracted, is still in a very unsatisfactory state. The very numerous species are often distinguishable only by very minute or dubious characters, so that many of the genera are large, homogeneous and widely distributed. Even the generic characters are often very feeble as compared with those employed by taxonomists in other Aculeate families. Hence also the higher groups, such as the tribes and subfamilies are so poorly characterized that no two melittologists agree on their limits or number. The wing venation is extraordinarily uniform throughout the whole family and the taxonomic use of the mouthparts encounters the usual difficulties which beset the employment of delicately adaptive structures. All the members of the group are of comparatively recent phylogenetic development and very highly specialized in adaptation to the

pollenation of flowering plants, themselves a group of organisms of recent origin. As manifold morphological expressions of this adaptation attention has often been called to the peculiar modification of the mouthparts for extracting nectar from flowers, the singular branched hairs of the body and modification of the hind legs or hairs on the venter in the female for carrying pollen, and the highly developed visual and olfactory organs.

On the side of the instincts there are, further, the marvelous habits of nidification which have aroused the admiration of all students since the days of Réaumur. Still the general activities of the female bee—the male is, of course, an ethological nonentity as in other Aculeates—are strangely uniform in their general outlines:—the visiting of flowers, mating, nidification, provisioning the nest with pollen and honey, oviposition. But different species visit different flowers and build their nests in different places and of different materials. All this is true of perhaps 80 per cent. of the thousands of species, but a considerable number—between 15 and 20 per cent., representing fully 70 genera—have become parasitic and have therefore ceased to collect pollen and nectar or to construct and provision nests, but instead seek out the nests of other bees and oviposit in their cells, with the result that the larvæ reach maturity by devouring the provisions so carefully stored for their own offspring by more industrious mothers.

This peculiar habit has profoundly modified the structure of the parasites. Their mouthparts have not been affected to any extent because these bees still visit flowers assiduously for food, but the collecting apparatus has atrophied and the hairs on the body and appendages have been completely or almost completely lost, so that the species have sometimes been placed in a group by themselves called *Denudatæ*. Other peculiarities are also manifested. The loss of the collecting apparatus, which is one of the most striking secondary sexual characters of the female bee, excepting in the *Prosopidinae*, which swallow the pollen instead of collecting it on their hind legs or venter, has brought about a close resemblance of the sexes to one another. In a few cases the female has even taken on a male secondary sexual character, as in the genus *Androgynella*, recently described by Cockerell (1918). It comprises two species,

detersa of Australia and *subrixator* of the Philippines. In both species the female, though possessing a well-developed sting, has 13-jointed antennæ, a number peculiar to the male in all other bees and in fact in most other Aculeates. The specimens cannot be gynandromorphs, because R. E. Turner found the 13 joints in 14 females of *detersa*, so that Cockerell is justified in regarding it as "certain that this is a normal condition and must represent an early stage in the evolution of a parasitic species, like those of *Calioxys* and *Stelis*. From the standpoint of genetics, it is an extraordinary case, since the female seems to have dropped her secondary sexual characters and thereby assumed those of the male which were present in her genetic constitution." He adds that "presumably the male of *A. subrixator* cannot be distinguished from *Megachile subrixator*," which is a common species in the Philippines and in all probability the host.

Another peculiarity of the parasitic bees, to which Friese has called attention, is their often very vivid coloration. Many of the species are more or less red or yellow (*Sphecodes*, *Nomada*, *Epeolus*, etc.) or banded and spotted with patches of white or blue appressed hairs or scales (*Epeolus*, *Crocisa*, *Melecta*, etc.), or are brilliantly metallic (*Exærete*, *Aglaë*). The red color suggests that of certain myrmecophilous beetles (*Lomechusa*, *Heterius*, *Claviger*, etc.) and may have a similar meaning, but it is difficult to account for the spots and bands unless we assume that they are an expression of peculiarities of metabolism, associated with the active habits of the parasites, an interpretation which has also been suggested to account for the more vivid color patterns of the males as contrasted with the conspecific females of many animals. Perhaps the peculiar odors of certain parasitic bees, *e. g.*, of *Nomada*, odors which in some cases at least seem to play a rôle in the relations to the host, also point to such peculiarities in metabolism.

From an examination of the brains of two genera of parasitic bees, *Nomada* and *Psithyrus*, von Alten (1910) concluded that their fungiform bodies, supposed to be the seat of intelligence and therefore to correspond to our cerebral hemispheres, were more feebly developed than in the nonparasitic species. He even found that the fungiform bodies of the male parasites were relatively

larger than in the females. It can hardly be claimed, however, that the parasitic bee is psychically less endowed than its host, because the finding and entering of the latter's nest presupposes instinctive activities of a high order.

Our knowledge of the habits of parasitic bees is rather meager when compared with our knowledge of the species as taxonomic units. They occur in all parts of the world, but even the hosts of many of the genera, especially of the nonholarctic forms, have not yet been ascertained. Within recent years, however, Verhoeff (1892), Höppner (1904), and Graenicher (1905) have made some careful observations on the behavior of a few European and North American species. Verhoeff studied the activities of the *Stelis minuta* larva in the nests of *Osmia leucomelæna* which are in hollow blackberry stems. The *Osmia* makes a row of cells in the cavity, separating them with partitions of chewed up leaves, provisions each cell with a ball of honey-soaked pollen, the so-called "bee-bread," and lays an egg on it before closing the cell and starting another. Graenicher summarizes Verhoeff's observations in the following words:

"1. *Stelis minuta* deposits its egg earlier than the host-bee, and in the lower region of the bee-bread. 2. The larva of the parasite hatches a little earlier than that of the host-bee, whose egg is situated on top of the bee-bread. 3. Both larvæ, which at the beginning are of about the same size, partake of the bee-bread, the host-larva on top, the parasite below. 4. The latter gradually increases in size, and consequently advances towards the host-larva on top. 5. Finally the parasite, which in the meanwhile has become twice as large as the host-larva, comes in contact with the latter, kills it and eats it. Verhoeff informs us that there was a mutual exchange of hostilities between the two larvæ, each trying to grab the other with its mandibles, but that finally the parasite succeeded in burying its mandibles in the head of the host-larva. The latter was eaten up within 1 or 2 days."

Höppner's observations on the larva of *Stelis ornatula* in the cells of *Osmia parvula* and *leucomelæna* agree essentially with Verhoeff's, except that he saw no struggle between the parasitic and host larva. The former bored its way upwards through the bee-bread, sought out the *Osmia* larva as soon as possible and plunged its mandibles into the body of the latter without meeting with any resistance. Like Verhoeff he found the parasitic to be larger than the host larva.

Graenicher's observations are more extensive. He studied in Wisconsin the parasitism of *Stelis 6-maculata* on *Alcidamia producta*, of *Cælixys lucrosa* on *Megachile addenda* and of *Triepeolus helianthi* on *Melissodes trinodis*. In all these cases the general behavior of the parasite is very similar to that of *Stelis minuta* and *ornatula*, but he found that the just-hatched larva has sharp, falcate jaws, which are very large in *Cælixys* and *Triepeolus* and are replaced by smaller jaws with the next moult, after it has killed the host larva. The first stage *Triepeolus* larva, moreover, has peculiar leg-like appendages which enable it to crawl about in the cell. We are justified, therefore, in speaking of a hypermetamorphosis in these bees, comparable to that of so many other parasitic insects (Rhipiphoridae, Strepsiptera, Meloidae, Eucharine Chalcididae, Chrysididae, Mantispidae, etc.). I quote a portion of Graenicher's account relating to the *Stelis* larva.

"July 9, 1903. Nest collected at Milwaukee contains 4 cells. Third cell (from below) with a parasite. On top of the bee-bread an *Alcidamia* larva, about 3 days old. On the side of the bee-bread, about half way up a *Stelis* larva feeding on bee-bread. It is smaller than the host larva, and its head is directed upward, and toward the posterior end of the latter's body.

"July 13. The parasitic larva has grown considerably but is not as large as the host larva. At 1 P.M. the parasite moves upward a short distance, comes in contact with the host larva, and secures a hold on the latter's side behind the middle of the body. The victim at first makes an effort to free itself, but offers no serious resistance. The parasite remains in the same position the whole forenoon, sucking the liquid contents of the host's body. The latter gradually perishes and shrivels.

"July 14. The parasite has released its hold on the dead host larva, and is feeding on bee-bread. It has lately increased very much in size. From now on the parasite does not pay any more attention to the remains of the host.

"In the cell just considered a single parasite was present, but in a nest collected at Milwaukee, July 15, 1903, a cell was come across with 3 parasitic larvæ, all of them on the same side of the bee-bread as the head of the host larva. One of them was sitting above the middle, not far below the host larva, the second was lower down and directed laterally, and the third was below the second and quite close to it. In the evening the third parasite, which throughout the day (July 15) had been partaking of bee-bread and growing in length, reached the second and killed it. Four days later this same parasite killed the uppermost one and fed on its contents. Two days after this (July 21), the surviving parasite killed the host larva. Both were about equal in size."

These very similar observations of Verhoeff, Höppner and Graenicher on three very different genera of parasitic bees cast some doubt on the older and more meager observations which led Schmiedeknecht and Sharp to assume that the parasitic bee larva is merely a commensal that feeds so voraciously and grows so fast that it compels the host larva to perish from starvation. It was this assumption which led the earlier writers to call the parasites "cuckoo bees." It is possible, of course, that some parasites, *e. g.*, *Nomada*, which infests the nests of *Andrena* and *Halictus*, may conform to this older view, but renewed investigation is certainly demanded by the results of the authors I have been considering.

Graenicher (1906) has also made some valuable observations which show that vision as well as odor is an important factor in the parasitic bee's method of locating the nest of the host. Speaking of *Argyroselenis minima*, which is a parasite of *Colletes eulophi*, he says:

"It is quite evident that after having discovered the nest this parasitic bee pursued a course similar to that of a host-bee when constructing a nest. It started out to make a careful and repeated inspection of the environment of the nest, gradually covering more territory in different directions, but often returning to the nest as the main object of its attention. Being possessed of a good memory for visual impressions it became acquainted with the locality within 6 minutes, and experienced no difficulty in refinding the nest at its next visit after an absence of 14 minutes. It gradually acquired a thorough familiarity with the topography of the region, and on its return to the nest it was seen to fly towards the opening as directly as the owner itself.

"Such a parasitic bee when hunting for a nest of a host-bee is not always flying around in a haphazard way, trusting to its good luck in finding a nest here today, and one somewhere else tomorrow. When it has come across a suitable one it is very careful to keep this under observation, and in making its trips to and away from the nest it is directed by its visual memory in exactly the same manner as the host-bee itself. It would not be in the interest of such a bee to pursue a different course. The work of the host-bee in constructing a cell, and provisioning it with the food-supply must have progressed to a certain point before the parasitic bee may find it suitable for the reception of the latter's egg. For this reason such a bee has to make repeated visits to the nest, in order to be on hand when the right time comes. If it were in the habit of wandering around until it happened to come across a host-bee's cell in the proper stage of construction, then it might not get much chance to deposit an egg within its life-time of a few weeks duration, especially in rainy seasons. It is even possible that a parasitic bee has more than one nest under observation during the same period."

Graenicher found the behavior of the female *Triepeolus*, *Calioxys* and *Stelis* to be very similar to that of *Argyroserenis*.

There is one genus of bees, *Sphecodes*, which must be briefly considered, because it has been the center of a prolonged controversy. These insects are fairly common in Europe and North America and closely resemble the species of *Halictus* except in color, as they have the abdomen wholly or in part vivid red and in the hind tibiae which are very sparsely pilose and therefore suggest a degenerate condition of the pollen-collecting apparatus. More than a century ago de Walkenaer (1817) maintained that *Sphecodes* is a parasite of *Halictus*, and the same view was more or less emphatically maintained by Wesmael (1835), Lepeletier (1841) Spinola (1851), and Taschenberg (1866), but Fred. Smith (1851) and Sichel (1865) held that it nests independently. The controversy continued, however. Perkins (1887, 1889) believed that *Sphecodes* might be occasionally parasitic and Friese and von Buttel-Reepen (1903) regarded it as perhaps incipiently parasitic. Rudow (1902) repeated the old statement that it nests independently. Marchal (1890, 1894) and Ferton (1890, 1898) witnessed some serious combats between *Sphecodes* and the *Halicti*, whose nests it was trying to enter. Ferton (1905) saw a *Sphecodes subquadratus* breaking into the nest of *Halictus malachurus*.

"Not being able to seize by the head the sentinel bee which barred her passage, she tunneled towards the *Halictus* burrow and succeeded thus in seizing and killing the guardian, which she tossed backward out of the burrow. A second and a third *Halictus* that rose in the burrow in succession to replace the first, met the same fate."

Morice (1901) contended that such aggressive behavior showed that the *Halictus* was not a parasite, because some parasitic bees, *e. g.*, *Nomada*, seem to entertain friendly relations with their hosts. Three investigators, however, have succeeded in breeding *Sphecodes* from *Halictus* and *Andrena* nests. Breitenbach (1878) long ago took *S. rubicundus* from the brood-cells of *Halictus 4-cinctus* and Sladen (1895) found pupæ of the same species in the nests of *Andrena nigroænea* and *labialis*. Finally Nielsen (1903) gave cogent reasons for regarding *S. gibbus* as a parasite of *Halictus 4-cinctus*. He says:

"When quickly unearthing a nest which I had seen *Sphecodes* entering, I discovered it sitting in a cell nearly filled with honey. Later on I found several cells containing larvæ differing from those of *Halictus* and which can hardly be other than those of *Sphecodes*. Finally I found in the autumn a cell containing a dead specimen of a fully colored *Sphecodes* pupa. It is therefore proof that *Sphecodes* is a cuckoo with *Halictus*."

Nielsen calls attention to the fact that the parasitic habit of *Sphecodes* explains the great variations in size, puncturation, etc., which have led taxonomists to multiply species in the genus. He found that poorly nourished individuals are often only half the size of well-fed specimens. Perkins had previously noticed that small forms of *Sphecodes* live with small *Halicti* and *vice versâ*. Sichel, after studying 3,200 specimens of European *Sphecodes*, decided that they represented only three species. He sent 600 other specimens which he referred to two species to Foerster, who claimed that he could distinguish some 150 species among them, but wisely refrained from publishing descriptions. Similar variations are, of course, frequent in other parasitic insects, notably in Mutillidæ and in *Ceropales*.

The aggressive behavior of the female *Sphecodes*, which was also observed by Nielsen, suggests that she may enter *Halictus* cells which are already completed and destroy the egg of the host, so that her own progeny will not have to compete with the lawful owner of the bee-bread, as in the case of *Stelis* and the other parasites studied by Graenicher. At any rate our knowledge of the behavior of *Sphecodes* is in need of further careful investigation.

When commenting on the difficulties encountered by the taxonomic student of the bees, I omitted one of the greatest, viz., that presented by the numerous parasitic genera. In many cases these are known to be very closely related to the genera of their hosts, a fact which was noticed even by the early investigators, although its full significance became apparent only in the course of time, with the constant discovery of new species and genera in all parts of the world and with changes in the interpretation of general biological phenomena. The whole matter is so interesting that I may be pardoned for introducing some historical considerations.

The more than a century devoted by entomologists to the study of bees may be conveniently divided into a pre- and a post-

Darwinian period. Latreille, in a short paper, published in 1802 at the end of his remarkable volume on the habits of ants, and Kirby in the same year were the first to construct noteworthy classifications of bees. There was a remarkable agreement in their point of view, both dividing the family into short-tongued and long-tongued forms, subsequently called Andrenidæ and Apidæ, the Andrenatæ and Apiaries of Latreille and the supergenera *Melitta* and *Apis* of Kirby. The parasitic bees that were known in his day were intercalated by Latreille among the Apiaries in close proximity to their host genera. Lepeletier de St. Fargeau (1825) divided the bees into two groups, the “récoltantes,” or collecting, and the “parasites,” and subdivided the former according to the differences in their pollen-collecting apparatus. The views of Latreille and Lepeletier have dominated the classification of bees down to the present time. Certain German melittologists, notably Schmiedeknecht and Friese, have followed Lepeletier’s scheme, whereas Westwood (1840) and most subsequent workers have agreed with Latreille. As Westwood’s reasons are still interesting and include a good statement of the pre-Darwinian or special creation conception of the relations of the parasite to the host, I quote some of his remarks:

“Indeed it is to be observed that the variation in the structure of the species, thus varying in their habits, does not seem to warrant the establishment of them into separate families. This circumstance appears naturally dependent upon two considerations: 1st, it is essential that the parasite in its perfect state should possess a certain resemblance to the animal in the nest of which it deposits its eggs, so as to deceive the latter and its associates (Kirby in a footnote here calls attention to the resemblance of the Dipteron *Volucella* to *Bombus*); and 2d, the nature of the food of both being similar, the variation in structure is much less striking than if the parasite were carnivorous, as the Ichneumonidæ, and the animal attacked (as the caterpillars of Lepidoptera, etc.) herbivorous. The parasitic connection indeed goes no further than this, viz., that the larva of the parasite eats up the food of its fosterer, and so starves it to death; the larvæ of both are therefore pollenivorous, and the differences which will naturally be most striking, will consequently be found in those organs which are employed in the construction and provisioning of the nest of the working species, and which one may therefore expect to find in a less developed state than in those species which, from being parasitic, do not require their full development. Hence it is that we find the general structure of the parasitic bee closely resembling that of the bee, at the expense of whose young its own are destined to be

nourished; and hence, if we regard *Bombus* and *Psithyrus* of St. Fargeau, *Aglaë* and *Euglossa*, *Melecta* and *Anthophora*, or *Sphecodes* and *Halictus*, with reference to their general structure, they will be found most intimately allied; whilst if, on the other hand, we regard such portion of their economy as is connected with the formation and provisioning of their nests, it will be requisite to place them in different divisions. If we observe, however, the great variation existing among bees in this portion of their economy, it is evident that this cannot be regarded as a normal or typical character and that a distribution founded thereupon would necessarily be unnatural."

The publication of the "Origin of Species" could not fail to have its effect on the students of bees. In the light of evolution the parasitic species acquired a new meaning, for it was at once apparent that their resemblance to their hosts might have a genetic significance. One of the first to fall under the spell of the new conception was Hermann Müller (1871). He believed that the genus *Psithyrus* was of rather recent descent from its host genus *Bombus*, that *Melecta* and *Crocisa* were less recently descended from *Anthophora*, and that the phylogenetic origin of *Stelis*, *Cælixys*, *Epeolus* and *Nomada* was still more remote, although the derivation of *Stelis* and *Cælixys* from gastrilegid genera seemed clear. He was guided to these conclusions by a study of the antennæ. Referring to a table of the genera of bees he says: "An examination of this table shows that in all nonparasitic bees, without exception, the males have a shorter scape but a longer flagellum than the females, but that in some pronounced cuckoo-bees the very reverse is the case." Smell not only guides the males to the females, but also the parasites to their hosts and hence the olfactory organs of the female parasites must be highly developed. "A glance at the development of the male and female olfactory organs of the cuckoo-bees clearly supports the conclusion that in the antennæ of the females the adaptations for working in the brood-chambers have been lost *pari passu* with an increase in the olfactory organs and that these developments correspond in degree to the period of time at which the transition to a parasitic life took place." I am not aware that any study of the antennæ and their sense-organs has since been undertaken with a view to testing the correctness of Müller's conclusions. Allusion has already been made to Graenicher's discovery that the vision of the parasitic bees is an important factor in locating the nests of the host.

In 1883 Pérez published an important study of the parasitic bees and republished his general conclusions in a separate article in 1884. After careful morphological investigation he concluded that the parasitic genera must have evolved from the host genera and was able in a few instances to point out the very species from which the parasitic genus had originated. He recognized four distinct lines of development from as many host genera: *Psithyrus* from *Bombus*, *Stelis* from *Anthidium*, *Cælioxys* and *Dioxys* from *Megachile* and *Sphecodes* from *Halictus*. The series of genera known as the Nomadiniæ and comprising *Epeolus*, *Melecta*, *Crocisa*, *Ammobates*, *Pasites*, *Phileremus*, *Biastes* and *Nomada*, he derived from *Cælioxys* on the supposition that this genus had given rise to a whole series of parasitic forms which had acquired new hosts among the various genera of recoltant bees. He contended that Latreille's example in placing the parasitic genera next to their host genera should be followed in any attempt at a natural classification of the Apidæ. The truth of his contention has since been conceded and is clearly expressed in the classifications of Ashmead (1899), Robertson (1899) and Cockerell (1910). Dalla Torre (1896) and Friese in his work on the African bees (1909), however, adopt a compromise between the views of Latreille and Lepeletier, dividing the bees into podilegid, gastrilegid and social sections and appending to each a series of parasitic genera. Of the classifications I have seen Robertson's seems to be the most natural, but he is dealing with a limited fauna, in which the relations of the parasitic genera are few and fairly well known, whereas Dalla Torre and Friese, in an attempt to deal with the bees of remote regions or of the whole world and with dozens of imperfectly known parasitic genera, have some justification for the course they adopt. It is evident, nevertheless, that no satisfactory classification can be constructed till the precise affinities of all the parasitic genera to one another and to the host genera have been thoroughly elucidated.

The phylogenetic relationships even among the European and North American parasitic bees are still in part very problematical. Probably all agree that *Psithyrus* must be derived from *Bombus*, *Stelis* from *Anthidium* (*sensu lato*), and *Cælioxys* from *Megachile*, or some closely related, now extinct, genus. But the origin of the

Nomadine series is by no means clear. Friese in his earlier work (1889) could not decide whether it was to be derived from *Cælioxys*, as Pérez suggested, or from a form like *Eucera*. To-day even such an alternative seems too simple, for in all probability the long series of "Nomadine" genera now known consists of several heterophyletic groups. *Melecta* and *Epeolus* are derived from *Anthophora* by Robertson and others, and Saunders and Robertson would derive *Nomada* from *Andrena*, whereas such genera as *Ammobates*, *Blastes*, *Pasites* and *Phiarus* are now supposed by Friese (1916) to be connected with *Megachile* through genera like *Casarea* and *Paracælioxys*, the last being also the source of *Cælioxys* and of *Dioxys* and *Paradioxys* through the genus *Prodioxys*. Among the exotic parasitic genera it seems clear that some have arisen from host genera very different from those above mentioned. Thus there is every reason to suppose that *Thalestria* has arisen from *Oxæa*, *Aglaë* and *Exærete* from *Euglossa*, *Eucondylops* from *Allodape*, *Perezia* from *Osmia*.

It will be seen, therefore, that even if we make all due allowance for dubious cases there still remain a number in which the closest morphological affinity of the parasitic is with its host genus. This is evident from the accompanying table (Table I.) in which the most clearly established cases (fully 50 per cent.) are marked with an asterisk. In constructing this table I have profited by a number of valuable suggestions kindly communicated by Professor Cockerell. We must assume, I believe, that in some cases the primitive host genera are now extinct, that in some cases, therefore, the parasites have come to infest species of genera to which they have no morphological affinity, that many parasites are directly derived from other parasitic genera and that in some cases the phenomena of parasitic convergence are so pronounced and obliterate or obscure the generic affinities to such a degree that they can be elucidated only by the most painstaking study. For my immediate purposes, however, the present results will suffice, since they agree with the conditions in other groups of Aculeata, as will be shown in the sequel.

In marked contrast with the bees, the solitary wasps comprise few parasitic species, if we exclude the Mutillidæ, which I am not

TABLE I.

GENERA OF PARASITIC BEES.

Parasites.	Hosts.	Ancestral Genus.
* <i>Nomada</i>	<i>Andrena</i> , <i>Halictus</i> , <i>Eucera</i> , <i>Colletes</i> , <i>Panurgus</i>	<i>Andrena</i> .
* <i>Sphecodes</i>	<i>Halictus</i>	<i>Halictus</i> .
* <i>Parhalictus</i>	(?) <i>Halictus</i>	<i>Halictus</i> .
* <i>Chlerogas</i>	(?) <i>Thrinchostoma</i>	<i>Thrinchostoma</i> .
* <i>Melecta</i>	<i>Anthophora</i>	<i>Anthophora</i> .
* <i>Bombomelecta</i>	(?) <i>Anthophora</i>	<i>Anthophora</i> .
* <i>Ericrocis</i>	(?) <i>Anthophora</i>	<i>Anthophora</i> .
* <i>Crocisa</i>	<i>Anthophora</i>	<i>Anthophora</i> .
* <i>Protomelissa</i>	(?) <i>Anthophora</i>	<i>Anthophora</i> .
* <i>Melissa</i>	(?) <i>Anthophora</i>	<i>Anthophora</i> .
<i>Epeolus</i>	<i>Colletes</i>	<i>Anthophora</i> .
<i>Triepeolus</i>	<i>Melissodes</i> , <i>Tetralonia</i>	<i>Epeolus</i> .
<i>Argyroselenis</i>	<i>Colletes</i>	<i>Epeolus</i> .
* <i>Epeoloides</i>	<i>Macropis</i>	<i>Macropis</i> .
* <i>Leiopodus</i>	<i>Melitoma</i>	<i>Melitoma</i> .
<i>Osiris</i>	(?) <i>Tetrapedia</i>	<i>Tetrapedia</i> .
<i>Rhathymus</i>	(?) <i>Epicharis</i>	<i>Epicharis</i> .
<i>Mesocheira</i>	(?) <i>Centris</i>	<i>Crocisa</i> .
<i>Acanthopus</i>	<i>Centris</i>	(?) <i>Centris</i> .
<i>Eurytus</i>	<i>Centris</i>	(?) <i>Centris</i> .
<i>Mesonychium</i>	<i>Melitoma</i>	<i>Acanthopus</i> .
* <i>Aglæ</i>	<i>Euglossa</i>	<i>Euglossa</i> .
* <i>Exaerete</i>	<i>Euglossa</i>	<i>Euglossa</i> .
* <i>Perezia</i>	<i>Osmia</i>	<i>Osmia</i> .
* <i>Eucondylops</i>	<i>Allodape</i>	<i>Allodape</i> .
* <i>Stelis</i>	<i>Anthidium</i> , <i>Chalicodoma</i> , <i>Heriades</i> , <i>Osmia</i> , <i>Ceratina</i> , <i>Aldidamia</i> , <i>Chilos-</i> <i>toma</i>	<i>Anthidium</i> .
<i>Parevapis</i>	<i>Megachile</i>	<i>Stelis</i> .
<i>Euasps</i>	<i>Megachile</i>	<i>Stelis</i> .
* <i>Thalestria</i>	<i>Oxæa</i>	<i>Oxæa</i> .
* <i>Androgynella</i>	<i>Megachile</i>	<i>Megachile</i> .
* <i>Cælioxys</i>	<i>Megachile</i> , (?) <i>Anthophora</i>	<i>Megachile</i> .
<i>Dioxys</i>	<i>Osmia</i> , <i>Chalicodoma</i>	<i>Megachile</i> .
<i>Pasites</i>	<i>Nomia</i> , <i>Camptopæum</i>	<i>Ammobates</i> .
<i>Ammobates</i>	<i>Anthophora</i> , <i>Macrocera</i> , <i>Saropoda</i>	<i>Cæsarea</i> .
<i>Biaestes</i>	<i>Systropha</i>	<i>Ammobates</i> .
<i>Phiarus</i>	<i>Meliturga</i>	<i>Ammobates</i> .
<i>Holcopasites</i>	(?) <i>Calliopsis</i>	<i>Ammobates</i> .
<i>Oreopasites</i>	<i>Spinoliella</i>	<i>Ammobates</i> .
<i>Phileremus</i>	<i>Rhophites</i> , <i>Halictoides</i>	<i>Pasites</i> .
<i>Herbstiella</i>	(?) <i>Psænythia</i>	<i>Pasites</i> .
* <i>Psithyrus</i>	<i>Bombus</i>	<i>Bombus</i> .

including in my survey. The following are the only cases I have found in the literature. According to Ferton (1901) the Gorytid *Nysson dimidiatus* is a parasite of *Gorytes elegans*. The latter digs its burrow in the sand and provisions it with larval and adult Hemiptera; the *Nysson* finds it and often enters it during the absence of the *Gorytes*. If the latter happens to be at home the *Nysson* waits motionless about a dozen centimeters away, with its head turned towards the nest, till the *Gorytes* departs. Adlerz (1910) observed very similar behavior on the part of *Nysson maculatus* towards *Gorytes lunatus*. Apparently both species of *Nysson* destroy the *Gorytes* egg attached to the prey and lay their own in its place. In 1887, at a time when nothing was known of the parasitic habits of *Nysson*, Handlirsch called attention to the superficial resemblance of some of the species to parasitic bees.

Williams (1913) and the Raus (1918) have described an interesting sporadic case of parasitism in *Stizus uncinatus*, a wasp belonging to a very different family, the Bembicidæ. The *Stizus* digs its way into the nest of a Sphecid, *Chlorion thomæ*, after the latter has provisioned it with a cricket, oviposited and closed the entrance. After the Bembicid has entered the chamber it devours the *Chlorion* egg and deposits its own so that the larva can have the cricket all to itself. This case is extraordinary because the other species of *Stizus* (*S. tridens* and *errans*), whose habits have been studied by Fabre (1886) and Ferton (1899, 1908, 1910, 1911), dig their own burrows in the sand, glue their egg to the bottom of the cell and feed the hatching larva continuously with Hemiptera after the manner of other Bembicids (*Bicyrtes*). Ferton has also observed similar behavior in *S. gazagnairei* and *fertoni*. According to the same observer (1899, 1901, 1908) *S. fasciatus* feeds its young with immature crickets. Our American *Stizus* with the exception of *uncinatus*, seem to have similar habits. During the summer of 1917 I saw a flourishing colony of a small undetermined species near Tempe, Arizona. It comprised thousands of individuals, all nesting close together in the sand, like *Bembix*.

The remaining parasitic wasps belong to the family Psammocharidæ (Pompilidæ), all of which prey on spiders. In two of his papers (1890, 1891) Ferton has shown that some individuals of

Pompilus rufipes (now called *Psammochares*) have acquired the habit of robbing other individuals of their prey which they then bury and furnish with an egg. They even wage fierce battles for one another's spiders. These observations acquire added interest in connection with another very closely related species, *P. pectinipes*, which, according to Ferton (1901, 1902, 1905), enters the sealed nests of *P. rufipes*, eats its egg and deposits its own on the spider. Ferton was thus led to advance the opinion that we have in *pectinipes* a parasite that has just become detached phylogenetically from its host species.

"The parasitic habit," he says, "would therefore appear to have been built up in the following manner: *P. rufipes*, living in colonies, has acquired the habit of stealing the prey of its neighbor and even of fighting for the possession of prey not its own. Some individuals finally learned to steal the spiders that had been buried, either by driving away the rightful owner while she was sealing her burrow, or by ferreting through the soil occupied by the colony in search of sealed burrows. Their descendants, inheriting this habit, gave up constructing a nest and transporting the stolen prey to it and left it in the cell where it was discovered, simply substituting their egg for the one it bore. Thus *P. pectinipes* was evolved, scarcely distinct from the maternal stock in many of its anatomical characters but become a parasite on the species from which it arose."

In Sweden Adlerz (1910, 1912) found that *P. campestris* exhibits a similar parasitism on *P. unguicularis* and *P. aculeatus* on *P. rufipes* and *fumipennis*, and Ferton (1891) has shown that *P. viaticus* and *pulcher* resemble *rufipes* in their habit of appropriating the prey of other individuals of their own species.

Finally we have among the Psammocharids a distinct and peculiar genus, *Ceropales*, all the species of which are parasites on other genera of the family. Lepeletier (1827) was the first to regard *Ceropales* as a parasite, but Walsh was the first to breed it from the nest of another Psammocharid. Riley and Walsh (1869), in their paper on wasps and their habits, state that a male *Ceropales*, which they described under the name *C. rufiventris*, but which is now known as *C. robinsoni* Cresson, emerged from a mud cell that had been constructed and provisioned by *Agenia bombycina*. That they were fully aware of the importance of this observation is clear from the following remark:

"The inference is unavoidable—more especially as we had previously bred very numerous specimens of the same little mud-dauber from the same kind of mud-cells obtained in northern Illinois—that this gaily dressed Spider wasp (*Ceropales*) had sometime in the summer of 1867, laid an egg in one of the five mud cells found in south Illinois, and thus appropriated to the use of its future larva the supply of food laid up by the provident care of the unfortunate, dingy looking little mud-dauber for its own offspring. Otherwise it is impossible to account for two distinct kinds of wasp hatching out from the same lot of mud cells."

Pérez (1894) and Ferton (1897) made some very interesting observations in France on the behavior of *Ceropales maculata* and *cribrata*, showing that these wasps are parasitic on various species of *Psammochares* and *Aporus*, and Adlerz (1902) has succeeded in giving us a complete account of the behavior of *C. maculata* as he observed it in Sweden. This behavior is so interesting, especially in connection with Graenicher's observations on the parasitic bees, that I subjoin a translation of the German résumé of the paper:

"*Ceropales* has the habit of visiting the breeding grounds of *Pompilus* species and there alights on small eminences of the soil in order to spy on the Pompilids while they are dragging in their paralyzed spiders. The tense attitude of the wasp, her deflected antennæ and her movements as she turns towards a Pompilid that has just come within the range of her vision, are indicative of her keen interest. As Pérez and Ferton have observed, the *Ceropales* either alights on the spider while it is being borne along by the *Pompilus*, unobserved by the latter, or on a spider that is lying unguarded in the open or concealed above the ground, while its captor is busy digging her nest. In either case the *Ceropales* can be seen bending the tip of her abdomen under the spider for the evident purpose of ovipositing. Ferton saw a *Ceropales cribrata* follow a *Pompilus chalybeatus* into her burrow while she was dragging in a spider, but although a *Ceropales* larva was afterwards found on the prey, it is not certain that the egg was laid on this occasion. As will be seen from what follows, it might have been laid previously. The only time I saw a *Ceropales* enter a *Pompilus* burrow was when a *P. niger* was still busy excavating. No spider was therefore on hand and, of course, oviposition could not have occurred. It was merely a sign of impatience on the part of the parasite, which, after persistently watching the digger, stole down into the burrow as if to inspect the progress of the work. I was present also on a second exceptional occasion when a *Ceropales* pounced down with such violence on a *P. cinctellus* with its spider that the two wasps and the spider tumbled about together. The little *P. cinctellus* was so dismayed that she flew away in great haste and never returned. On this occasion the egg which the *Ceropales* probably laid during her subsequent tedious manipulation of the spider must have perished, because the spider was left in the open where it was exposed to ants and other predatory

insects. That the *Pompilus* suspects the hostile intentions of the *Ceropales* is clear from the behavior of a *P. viaticus* that hid with her spider among the dense grass-blades of a road-side and would not venture into the open because she was being watched by two female *Ceropales* each perched on a grass-blade, stretching its antennæ downward and edging nearer from time to time. The angry *Pompilus* finally gave chase to the parasites and only after they had flown away did she leave her concealment with her prey.

"When a spider on which a *Ceropales* has just alighted is examined, the egg cannot be seen at first because it is placed in such an unsuspected spot. At the base of the ventral surface of the abdomen the spider has two slit-shaped stigmata which open into the lung-books. The wasp inserts her egg into one of these. The stigmata look like pockets, with very closely fitting flaps. After the egg is in place the orifice of the pocket sometimes gapes slightly so that one end of the egg can be seen. This is apt to be the case in *Drassodes*, but in the large Lycosids the pockets are so capacious that they completely conceal the egg. The place is obviously selected because in it the egg is perfectly protected when the spider is later dragged into the burrow by its rightful owner, for it is evident that if the egg were merely attached to the surface, it would be exposed to serious injury while the spider is being drawn through the narrow burrow. The last abdominal segment of the female *Ceropales*, which is constructed like a short, flat, truncated ovipositor—a structure unique among the solitary wasps—evidently represents an adaptation to the narrow, slit-shaped stigmata, since the latter can be opened by means of such an instrument and the egg inserted. Not infrequently I have seen an egg in each of the lung-books of the same spider. Since the *Pompilus* later attaches its own egg to the side of the spider's abdomen, the situation becomes very complicated, as there are then three rival claimants for the same spider which is sufficient food for only one. A few successful breeding experiments have revealed the drama that is subsequently enacted in the dark burrow.

"After an embryonic period of two to three days, the *Ceropales* larva hatches. Its anterior portion, as far back as the tenth segment, extends straight out from the stigma, while its posterior portion remains concealed in the lung-book. Soon the exposed portion is seen to bend downward till the head touches the spider's belly and the larva begins to feed. As soon as the *Ceropales* in the other lung-book hatches the older larva evidently smells a rival, for it stops feeding, stretches itself out and moves its anterior end freely about in the air in the direction of its competitor. The latter is at first out of reach, but as soon as the older larva has fed and grown sufficiently in length it attacks its younger companion, which is quite unable to escape its fate. After its cannibal feast the *Ceropales* larva again bends down and continues to devour the spider. Not till several days have elapsed does the *Pompilus* larva hatch, although the egg was laid not more than a few hours after the *Ceropales* egg. When the *Pompilus* larva begins to grow the *Ceropales* larva becomes aware of a new rival and turns in its direction. When a little later it has grown sufficiently to reach the *Pompilus* larva, the latter's fate, too, is sealed. With the elimination of its last com-

petitor the *Ceropales* larva turns again to the spider and devours it completely except for a few unassimilable remnants. Then the larva weaves a network of pale brown threads among which on the following day it spins a pale brown cocoon. In one case which I observed the feeding period of the larva extended over a period of 12 days."

It will be seen that the general outlines of the behavior of the solitary parasitic bees and wasps are strikingly similar. Among the wasps we can recognize two types, that of *Nysson*, *Stizus uncinatus* and *Psammochares pectinipes* and that of *Ceropales*, whereas in bees only a single type, bearing a great resemblance to that of *Ceropales*, is known. It is probable, nevertheless, as I have indicated above, that the *Nysson* type may be represented among the bees by *Sphecodes*. The two types are shown in the accompanying diagrams in which the main activities of the parasite and its host are represented in parallel series.

Nysson.

Nysson Mating Finding Host Nest
Gorytes Mating Nidification, Provisioning, Oviposition.
 Destroying Host Egg Ovipositing Larva Appropriating Prey.

Ceropales.

Ceropales Mating Finding Host and Prey, Ovipositing.
Psammochares Mating Provisioning, Nidification
 Larva feeding Killing Host Larva Appropriating Prey.
 Oviposition Larva feeding

Stelis.

Stelis Flower visiting Mating Finding Host Nest, Ovipositing.
Alcidamia Flower visiting Mating Nidification, Provisioning
 Larva feeding Killing Host Larva Appropriating Food.
 Ovipositing Larva feeding

In all the cases the parasite takes possession of the food-supply (prey or bee-bread) by eliminating the egg or young larva to which it belongs as a result of the activities of the host, but this elimination may be effected in two ways, either by the adult or by the larval parasite. In the *Nysson* type the mother appropriates the prey and bequeaths it to her offspring, in the *Ceropales-Stelis* type the larval

parasite seizes the prey or food for itself, or, regarding the situation merely from the standpoint of the individual life-history of the parasite, we may say that it is predacious either in its first larval stage or as an adult on the egg or young larva of the host. The host egg or larva constitutes an obstacle to the parasite's enjoyment of the prey or bee-bread, and as the parasite is a true insect bolshevik and member of the I. W. W. its life purpose is completely expressed in the impudent imperative: "Get out, I want your place." Nor is it surprising that long before the Russian soviets the parasitic wasps and bees had learned that the quickest way to remove a living obstacle is to kill it.

There is some difficulty in deciding which of the two types of parasitism represented in the diagrams is the more primitive. Probably the more aggressive *Nysson* type was the earlier as indicated by the behavior of *Psammochares rufipes* and *pectinipes*. On this supposition the rôle of assassin, directed not only against the host larva, but also against any competing larva of its own species, was acquired later by the larval parasite as a result of neglect on the part of the mother to destroy the egg of the host. The same type of behavior, however, is also seen in many other insects when more than one egg is laid by the mother in a very limited supply of food, *e. g.*, among the larval egg-parasites (Proctotrupids) and the caterpillars that live in the heads of composite flowers (Rabaud, 1912, 1914). In the larval egg-parasites the large, sickle-shaped jaws are beautifully adapted for the purpose of killing competing individuals of the same species, and the similar mandibles described by Graenicher in larval bees of the genera *Stelis*, *Calioxys* and *Tripeolus* are equally useful in destroying both the competitors of the same species and the host larva.

The social parasites are most abundantly represented and have been most extensively studied among the ants. The literature on the subject is so voluminous that I am unable to deal with it here. Much of it is cited in my ant book (1910), where the subject is considered in greater detail, and in the first volume of Wasmann's "Gesellschaftsleben der Ameisen" (1915). As would be expected, the conditions become very complex when a social organism such as a colony of ants becomes parasitic on another colony. Among

the parasitic relationships four types can be recognized. One of these, corresponding to Wasmann's category of "compound colonies" is represented by a number of small species which live in little nests that communicate with the nests of the host by tenuous galleries. The two species bring up their brood separately, but the workers consort with one another freely and amicably in the galleries and chambers of the host. The relations of parasite and host, where they have been determined, are much like those exhibited between certain ants and their myrmecophiles (symphiles). The most typical of these guest ants is our North American *Leptothorax emersoni*, the behavior of which I have elsewhere described in detail. From the accompanying table (Table III.), in which all the known guest ants and their hosts are listed, it will be seen that none of the former is congeneric with its host. Emery's statement (1909), however, that: "The myrmecophilous ants are not derived from forms allied to their host species, but from other genera or even from other subfamilies," is not strictly true, though in all probability the guest-ants have developed, as he contends, from predatory thief-ants, of which quite a number of species are known to nest in the walls of the nests of termites and larger ants and to prey on their brood.

The three other types of parasitism, representing Wasmann's category of "mixed colonies," are the slave-makers, temporary and permanent social parasites, which agree in living so intimately with their host in the same nest that the two species bring up their broods in common. The differences between the three types is, however, very striking when we follow the development of the parasitic colony, although it is founded in every case by a single recently fecundated female, or queen, that succeeds in entering and establishing herself in the nest of the host species. The queen slave-maker, at least in species like *Formica sanguinea*, breaks into the host nest and appropriates and fiercely defends a portion of the host brood till it matures and surrounds her with a number of loyal workers, which are then able to rear the brood hatching from her eggs. The workers produced by such a queen have the extraordinary habit of making periodical, organized raids during the summer months on other colonies of the host species (usually *Formica*

TABLE II.
PARASITIC WASPS.

Parasites.	Hosts.	Habitat.	Ancestral Genus.
<i>Stizus unincinctus</i>	<i>Chlorion thomæ</i>	Nearctic	(?) <i>Sphæcius</i> .
<i>Nysson dimidiatus</i>	<i>Gorytes elegans</i>	Paleartic	<i>Gorytes</i> .
<i>Nysson maculatus</i>	<i>Gorytes lunatus</i>	Paleartic	<i>Gorytes</i> .
<i>Psammochares pectinipes</i>	<i>Psammochares rufipes</i>	Paleartic	<i>Psammochares</i> .
<i>Psammochares campestris</i>	<i>Psammochares unguicularis</i>	Paleartic	<i>Psammochares</i> .
<i>Psammochares aculeatus</i>	<i>P. rufipes</i> and <i>fumipennis</i>	Paleartic	<i>Psammochares</i> .
<i>Ceropales</i> (many species)	<i>Psammochares</i> , <i>Agenia</i> , <i>Aporus</i>	Holarctic	<i>Agenia</i> .
<i>Vespa austriaca</i>	<i>V. rufa</i> and (?) <i>consobrina</i>	Holarctic	<i>Vespa</i> .
<i>Vespa arctica</i>	<i>Vespa diabolica</i>	Nearctic	<i>Vespa</i> .

TABLE III.

XENOBIOTIC (MYRMECOPHILOUS) PARASITES.

Parasites.	Hosts.	Habitat.	Ancestral Genus.
<i>Leptothorax emersoni</i>	<i>Myrmica brevinodis</i>	Nearctic	<i>Leptothorax</i> .
<i>Symmyrmica chamberlini</i>	<i>Myrmica</i> (<i>Neomyrmica</i>) <i>mutica</i>	Nearctic	<i>Leptothorax</i> .
<i>Formicorexenus nitidulus</i>	<i>Formica rufa</i> and <i>pratensis</i>	Paleartic	<i>Leptothorax</i> .
<i>Formicorexenus ravouxi</i>	<i>Leptothorax unificatus</i>	Paleartic	<i>Leptothorax</i> .
<i>Formicorexenus corsicus</i>	(?) <i>Leptothorax</i> sp.	Paleartic	<i>Leptothorax</i> .
<i>Phacota noualhierii</i>	<i>Monomorium subnitidum</i>	Paleartic	<i>Monomorium</i> .
<i>Phacota sicheli</i>	(?) <i>Monomorium</i> sp.	Paleartic	<i>Monomorium</i> .

fusca or one of its varieties), and of carrying their larvæ and pupæ home and permitting a certain number of them to hatch as "slaves," so that the colony is maintained as an intimate mixture of two species, at least for a considerable period. The queen *Polyergus*, however, kills the queen of the host colony whose nest she enters and is adopted by the workers, and the slave-making, or dulotic raids of her offspring are even more perfectly organized than in *sanguinea*, since *Polyergus* in all its phases depends absolutely on the slaves, or host workers for its food, the rearing of its young and the construction of the common nest. It will be noticed from the table (Table IV.) that all the slave-making, or dulotic parasites belong either to the same genera as their hosts or to closely allied genera, though the latter represent two different subfamilies.

The recently fecundated queen of the temporary social parasites belonging to *Formica* species of the *rufa*, *microgyna* and *exsecta* groups, *Bothriomyrmex*, *Lasius umbratus* and *fuliginosus* or some species of *Aphenogaster*, enters the nest of the host in a conciliatory or at any rate non-aggressive manner, and after being adopted by the workers, supplants the host queen, when she is killed either by her own workers or by the parasite, which then proceeds to produce her own brood to be reared by the host workers. The offspring of the parasite, however, are not slave-makers, so that the host workers gradually die off, leaving a pure and eventually flourishing colony of the intrusive species. As shown in the table (Table V.), all the temporary social parasites belong to the same genera as their hosts, although these genera represent at least three different subfamilies.

The queen of the permanent social parasites enters the host colony in the same insinuating and conciliatory manner as the temporary social parasite and is definitively adopted in the same manner after the host queen has been eliminated, but the rate of development of the parasitic brood is very rapid, so that adult males and females are produced within the lifetimes of the host workers. This development of the sexual forms is the more accelerated because the worker caste has disappeared among the permanent social parasites, which represent the culmination, or, more properly speaking, the level of the greatest "degeneration" (specialization)

TABLE IV.
SLAVE-MAKING, OR DULOTIC PARASITES.

Parasites.	Hosts.	Habitat.	Ancestral Genus.
<i>Strongylognathus</i> sp.	<i>Tetramorium caespitum</i>	Paleartic	<i>Tetramorium</i> .
<i>Harpagoxenus sublaevis</i>	<i>Leptothorax acervorum</i>	Paleartic	<i>Leptothorax</i> .
<i>Harpagoxenus americanus</i>	<i>Leptothorax curvispinosus</i>	Nearctic	<i>Leptothorax</i> .
<i>Myrmoxenus gordigiani</i>	<i>Leptothorax servulus</i>	Paleartic	<i>Leptothorax</i> .
<i>Formica sanguinea</i>	<i>Formica fusca</i>	Paleartic	<i>Formica</i> .
<i>Formica sanguinea</i> subsp.	<i>F. fusca</i> vars. and <i>pallide-fulva</i> vars.	Nearctic	<i>Formica</i> .
<i>Polyergus rufescens</i>	<i>Formica fusca</i>	Paleartic	<i>Formica</i> .
<i>Polyergus rufescens</i> vars.	<i>Formica fusca</i> and vars.	Nearctic	<i>Formica</i> .
<i>Polyergus lucidus</i>	<i>Formica pallidefulva</i> subsp.	Nearctic	<i>Formica</i> .

TABLE V.
TEMPORARY SOCIAL PARASITES.

Parasites.	Hosts.	Habitat.	Ancestral Genus.
<i>Pseudomyrma flavidula</i>	<i>Pseudomyrma elongata</i>	Neotropical	<i>Pseudomyrma</i> .
<i>Aphenogaster tennesseensis</i>	<i>Aphenogaster fulva</i>	Nearctic	<i>Aphenogaster</i> .
<i>Aphenogaster maria</i>	(?) <i>Aphenogaster fulva</i>	Nearctic	<i>Aphenogaster</i> .
<i>Crematogaster (Atopogyne)</i> sp.	<i>Crematogaster</i> sp.	Ethiopian	<i>Crematogaster</i> .
<i>Crematogaster (Oxygyne)</i> sp.	<i>Crematogaster</i> sp.	Paleotropical	<i>Crematogaster</i> .
<i>Bothriomyrmex meridionalis</i>	<i>Tapinoma erraticum</i>	Paleartic	<i>Tapinoma</i> .
<i>Lasius (Formicina) umbratus</i>	<i>Lasius niger</i>	Paleartic	<i>Lasius</i> .
<i>Lasius (Formicina) subumbratus</i>	<i>L. niger</i> and <i>silkensis</i>	Nearctic	<i>Lasius</i> .
<i>Lasius (Dendrolasius) fuliginosus</i>	<i>L. (Formicina) umbratus</i>	Paleartic	<i>Lasius</i> .
<i>Formica (rufa and exsecta groups)</i>	<i>Formica fusca</i>	Paleartic	<i>Formica</i> .
<i>F. (rufa, microgyne and exsecta groups)</i>	<i>F. fusca</i> vars. and <i>F. pallidefulva</i> vars.	Nearctic	<i>Formica</i> .

TABLE VI.

PERMANENT SOCIAL PARASITES (ANTS WITHOUT WORKERS).

Parasites.	Hosts.	Habitat.	Ancestral Genus.
<i>Sympheidole elecebra</i>	<i>Pheidole ceres</i>	Nearctic	<i>Pheidole</i> .
<i>Epipheidole inquilina</i>	<i>Pheidole ceres</i>	Nearctic	<i>Pheidole</i> .
<i>Parapheidole belti</i>	(?) <i>Pheidole</i> sp.	Malagasy	<i>Pheidole</i> .
<i>Sifolinia lauræ</i>	(?) <i>Pheidole</i> sp.	Paleartic	<i>Pheidole</i> .
<i>Anergatides kohli</i>	<i>Pheidole melancholica</i>	Ethiopian	<i>Pheidole</i> .
<i>Wheeleriella santischii</i>	<i>Monomorium salomonis</i>	Paleartic	<i>Monomorium</i> .
<i>Wheeleriella adulatrix</i>	<i>Monomorium subnitidum</i>	Paleartic	<i>Monomorium</i> .
<i>Wheeleriella wrongtomi</i>	<i>Monomorium indicum</i>	Paleartic	<i>Monomorium</i> .
<i>Epæcus pergandei</i>	<i>Monomorium minimum</i>	Nearctic	<i>Monomorium</i> .
<i>Epixenus andrei</i>	<i>Monomorium venustum</i>	Paleartic	<i>Monomorium</i> .
<i>Epixenus biroi</i>	<i>Monomorium creticum</i>	Paleartic	<i>Monomorium</i> .
<i>Myrmica mymoxena</i>	<i>Myrmica lobicornis</i>	Paleartic	<i>Myrmica</i> .
<i>Hagioxenus schmitzi</i>	<i>Tapinoma erraticum</i>	Paleartic	<i>Monomorium</i> .
<i>Anergates atratulus</i>	<i>Tetramorium caspium</i>	Paleartic	(?) <i>Tetramorium</i> .

among the parasitic ants. The list of the species in the table (Table VI.) shows that they all belong to a single subfamily, the Myrmicinae, and, with the exception of *Hagioxenus*, to genera differing from though allied to their hosts.

The tables IV. to VI. are much more striking as illustrations of the natural affinities of the parasites to their respective hosts than the table of the bees (Table I.). This is undoubtedly due partly to the fact that the ant-parasites are structurally much less sharply distinguishable from their hosts and partly to the different views of myrmecologists and melittologists concerning the scope and dignity of the genus as a taxonomic category. The myrmecologist is being so constantly impressed with the great structural variations that may exist in the same colony of ants and often therefore among the offspring of the same mother, that he is apt to be a "lumper" with a vengeance, whereas the melittologist, especially on our radical and progressive American continent, seems to develop a veritable passion for erecting new genera or even subfamilies on very minute morphological characters. Thus Ashmead created a family Psithyridae and Cockerell a subfamily Psithyrinae for the bees of the single genus *Psithyrus*, although no one doubts that these insects are very closely related to *Bombus*, whereas no myrmecologist has dreamed of placing the aberrant, workerless parasite *Anergates atratulus* even in a distinct subfamily, although it differs much more profoundly from *Tetramorium* and other Myrmicine genera than *Psithyrus* from *Bombus*. No melittologist, moreover, ever thinks of placing a new parasitic bee in one of the known genera of recoltant bees, because the absence of the collecting apparatus is tacitly assumed to have decided generic or even subfamily value, but among the ants there are several genera (*Formica*, *Lasius*, *Aphaenogaster*, *Crematogaster*, *Leptothorax*) which are made to include both parasitic and nonparasitic species, because there are no morphological characters by which they can be satisfactorily distinguished.²

Leaving out of consideration the guest ants, the origin of which, as we have seen, can be accounted for in the same way as the myr-

² Forel has, indeed, placed *Formica sanguinea* in a separate subgenus, *Raptiformica*, and its slave in another subgenus, *Serviformica*, but in my opinion without sufficient justification.

mecophiles, there remains the interesting problem as to the phylogenetic relations of the slave-makers, temporary and permanent social parasites. Obviously the permanent parasites can be readily conceived as developing either from temporary parasites or from dulotic species. The fact that there are among the social bees and wasps, as will be shown in the sequel, certain forms which agree in all essential particulars with the permanent social parasites among ants, although for obvious reasons they cannot have arisen from dulotic forms, would seem to point to the origin of the permanent from the temporary type of social parasitism. On the other hand, *Polyergus* seems clearly to be in a stage transitional from dulotic to permanent social parasitism, and a more advanced stage appears to be represented by *Strongylognathus testaceus* which lives with *Tetramorium caespitum* and produces workers which are few in number and endowed with very feeble slave-making proclivities.

It is more difficult to determine the phylogenetic relations of the dulotic to the temporary parasites. Wasmann (1905), Emery (1909), Viehmeyer (1909, 1911), Brun (1912) and I have discussed this matter in several papers. Wasmann holds that temporary social parasitism, which I first discovered in various North American species of *Formica*, arose from the pleometrosis of such forms as *Formica rufa*. In a single colony of this and other acervicolous species the females may be very numerous and new nests may be formed by daughter queens departing from the maternal nest with contingents of workers, or recently fecundated queens may secure adoption in other nests of their own species. At first I was inclined to derive both dulosis and temporary social parasitism from such conditions, but Wasmann insisted on deriving dulosis from temporary social parasitism, a view which Emery, Viehmeyer, Brun and I have rejected as unsound on the principle that parasitism may readily arise from predatism, but that the reverse development is biologically highly improbable. I am now inclined to agree with Emery that pleometrosis and the adoption of queen ants by workers of their own species are probably phenomena *sui generis* which did not lead to social parasitism, that we must assume a predatory stage not unlike that of *F. sanguinea* as the starting point for dulosis and that temporary social parasitism

was a subsequent development. Probably the predatory *sanguinea* queen originally entered *fusca* nests for the purpose of devouring the brood, but later came to care for the larvæ and pupæ till they hatched. We may conceive that the number of appropriated *fusca* young was more than was needed as food and that the queen acquired a fostering relation towards the remainder by coming in contact with the buccal secretions or fat-exudates of the larvæ. In other words, trophallactic relations were established between the queen and the alien brood and led to a rearing of the latter (Wheeler, 1918). This might offer a simple explanation of dulosis, a phenomenon which has always seemed unique and difficult of explanation. At any rate it furnishes an hypothesis to be tested by a closer study of the relation of *F. sanguinea* to the larval *fusca*.

Among the social bees there is only one parasitic genus, *Psithyrus*, to which I have repeatedly alluded. Kirby was the first to distinguish these bees from their hosts, the species of *Bombus*, as long ago as 1802, but a genus was first established for them by Lepeletier in 1841. The habits of *Psithyrus*, as described by Hoffer (1881, 1888), Wagner (1907) and Sladen (1912), show that it is to be regarded as a permanent social parasite. Like the ants of this type, it lacks the worker caste. The female hibernates alone like the queen *Bombus* and enters and secures adoption in a young colony of the latter, usually after the first batch of workers has emerged. The *Psithyrus* female has a tougher integument and a stouter, more curved sting than *Bombus*, and though she visits flowers, she does not collect pollen or nectar. After entering the *Bombus* nest Sladen says:

"Her first care is to ingratiate herself with the inhabitants, and in this she succeeds so well that the workers soon cease to show any hostility towards her. Even the queen grows accustomed to the presence of the stranger and her alarm disappears, but it is succeeded by a kind of despondency. Her interest and pleasure in her brood seem less, and so depressed is she that one can fancy that she has a presentiment of the fate that awaits her. It is by no means a cheerful family, and the gloom of impending disaster seems to hang over it. But while the queen grows more dejected, the *Psithyrus* grows more lively, and takes an increasing interest in the comb, crawling about over it with unwonted alacrity and examining it minutely."

The queen is eventually killed by the parasite, which then begins to

lay her eggs. She is at first very prolific, "but she ages and fails more quickly than the *Bombus* queen. . . . The *Psithyrus* kills the *Bombus* queen before she has laid the full number of worker eggs, consequently nests containing *Psithyri* are not very populous, the number of workers seldom exceeding eighty." Neither queens nor males of *Bombus* are reared in such infested nests, but the workers take to ovipositing. Their eggs would, of course, produce males, but the *Psithyrus* devours them. She "pays close attention to her new-laid eggs for several hours, giving the workers no chance to molest them, but the workers soon get reconciled to them and henceforth they feed and tend the *Psithyrus* brood with as much devotion as if it were their own species; indeed, they seem sometimes to show a greater fondness for it." Sladen's concluding remarks are very interesting in connection with the case of *Psammochares rufipes* and *pectinipes*. He says:

"The origin of *Psithyrus*, more especially of its peculiar parasitical instincts, is an interesting question. If a specimen of *Psithyrus* be compared with a specimen of *Bombus* it is seen that the resemblance is not merely superficial but extends to nearly all the important details of structure, so that it is impossible to avoid the conclusion that *Psithyrus* has sprung from *Bombus*, and this at quite a recent period in the history of life. Moreover, the *Bombi*—and this is particularly interesting—show parasitical tendencies leading to the parasitism of *Psithyrus*. We have seen (pages 55-58) how the *Bombus* queens may enter the nests of their own species and kill one another, and how, in the case of the twin species, *B. terrestris* and *lucorum*, *terrestris* has extended this habit so as to prey on *lucorum*, killing the *lucorum* queen and getting the *lucorum* workers to rear her young in practically the same manner as the *Psithyri* prey on the *Bombi*. It is a remarkable fact that the sting of the *terrestris* queen differs from that of the *lucorum* queen and approaches that of *Psithyrus* in being somewhat stouter and more curved, and having its thickened basal portion more parallel-sided when viewed sideways than in *lucorum*. There is, however, no evidence to show that any species of *Psithyrus* has sprung from the particular species of *Bombus* on which it preys, such resemblances as it may show to it in coat-colour, etc., being pretty clearly attributable to mimicry or exposure to the same conditions of life, and not to ancestry."

Among the social wasps only two parasitic species are known, *Vespa arctica* and *V. austriaca*. The former belongs to our Canadian faunal zone and infests the nests of *V. diabolica*, as Fletcher (1908) has shown; the latter has long been known in Europe where it occurs in the nests of *V. rufa*. Recently Bequaert (1916) has

succeeded in finding *austriaca* in the United States and surmises that it may here be a parasite of *V. consobrina*, "which, although very different in coloration, is very probably the American race or subspecies of *Vespa rufa* L." A good account of what is known of the habits and distribution of *austriaca* may be found in the papers of Robson (1898), Carpenter and Pack-Beresford (1903) and Bequaert. This wasp is so closely related to *V. rufa* that Carpenter and Pack-Beresford regard them as a single species, and the *austriaca* queen as producing both *rufa* and *austriaca* offspring. Their reasons for this assumption are, however, too weak to invalidate the view of the great majority of authors who hold that *austriaca* bears the same relation to *rufa* that *Psithyrus* does to *Bombus*. Both *arctica* and *austriaca* lack the worker caste and eliminate the queens of the colonies which they enter. Males of the host species sometimes develop in colonies infested by *austriaca*, so that, unlike *Psithyrus* and the workerless ants, this parasite seems not to destroy the eggs laid by the host workers.

In conclusion I would record a few reflections that have been suggested by the foregoing survey of the various Aculeate parasites. The tables show in a rather imposing manner that many of these parasites have arisen from their respective host genera, but apart from such forms as *Psammochares pectinipes*, *Vespa austriaca* and some of the parasitic bees like *Perezia* and *Eucondylops* there is little evidence among existing parasites of a direct derivation from their host species. This is what we might expect, for in the first place the origin of most of the parasites is so remote that even if they had remained permanently associated with the species from which they arose, both host and parasite would by this time have diverged in structure to such a degree that their genetic affinities would no longer be clearly discernible, and in the second place, many parasites are probably no longer associated with their original hosts, which have become nearly or quite extinct, so that their parasites have been compelled to adapt themselves to new hosts or cease to exist. Under such circumstances a parasite would naturally attach itself to a species more or less closely allied to its primitive host.

That this has been the course of parasitic evolution seems to be

indicated by the fact, which has not, I believe, been emphasized by other students of the subject, that most of the Aculeate hosts belong to dominant genera. By dominant genera I mean those that are represented by a considerable number of species, some of which are very abundant in individuals and widely distributed as distinguished from genera that are monotypic or represented by few species of rare or sporadic occurrence. Such genera are *Andrena*, *Halictus*, *Anthophora*, *Megachile*, *Osmia* and *Bombus* among the bees, *Vespa*, and *Psammochares* among the wasps, and among the ants *Formica*, *Lasius*, *Tapinoma*, *Pheidole*, *Crematogaster*, *Aphenogaster*, *Tetramorium*, *Monomorium* and *Leptothorax*. It is, nevertheless, surprising that no hosts of parasitic ants are known to occur in genera like *Camponotus* and *Polyrhachis*, which comprise hundreds of species and are widely distributed, the former in all parts of the world, the latter in the old world tropics. Probably the dominant genera, owing to their abundance in individuals and the wide distribution of their species, would act like great nets set to capture any parasites that have overstepped the bounds of good parasitic manners by bringing their original host species to the verge of extinction. This would account for the close generic affinities which we have seen to be so evident between parasite and host, for a parasite that had endangered or destroyed its original host species would itself more readily escape extinction if the host were already a member of a dominant genus containing many closely allied species, because this would permit a comparatively easy re-adaptation of the parasite to a new host species. Although the parasites would probably differ in their powers of adaptation, the very similar habits of species in the same genus, especially among the bees, would greatly facilitate such a transfer of the parasitic relation.

Still even if we grant that the Aculeate parasite has arisen from its original host species, we are confronted with two troublesome questions, for it will be asked: What induced certain individuals to become parasites on other individuals of their own species? And if a parasite originated in this way, what is to prevent it inbreeding with its host and thus losing its peculiar tendencies by swamping, or "panmixia"? One of the difficulties involved in the first question lies in deciding on the stimuli that would so affect some of the

individuals of a species as to compel them to give up the industrious and nonparasitic habits that have become elaborated and fixed as an integral part of their genetic constitution.. I believe, however, that such stimuli exist and that they are frequent and comparatively simple. If we take such a constantly recurring external stimulus as temporary scarcity of prey or food, we can understand how some individuals of a common species that has outrun its food supply or has emerged in seasons or places of scarcity, might find it as easy as advantageous to steal the provisions of other individuals. This is, in fact, a common practice among normally non-parasitic Aculeata, *e. g.*, in *Bembix* and *Psammochares*, in bumblebees, and honey-bees. And if this external is reinforced by an internal stimulus, such as the urgent need for oviposition, we can see how a parasitic group of individuals might readily arise within the confines of a single species. This urgency of oviposition is very apparent in many parasitic Aculeata, especially among the parasitic bees, which often lay several eggs in a single cell of the host, though only one larva is able to develop. *Psithyrus* and some of the parasitic ants seem to reveal the same urgency. It is even probable that this internal stimulus is more fundamental than the external stimulus above mentioned and that it may incite the insect directly to appropriate the provisions collected by other individuals whose ovarian eggs mature more slowly or in smaller numbers. When the parasitic habit is once started it tends necessarily, owing to the saving of energy which would otherwise be expended in work, to accelerate the maturation of the ova and thus to become more and more confirmed by one of the circular processes so familiar to the physiologist.

Urgency of oviposition will, I believe, account also for the many cases in which Aculeates have been observed in the act of appropriating valuable nesting materials or partly constructed nests of other individuals. Fabre (1890) saw wall-bees (*Chalicodoma muraria*) take possession of the partly constructed masonry nests belonging to other females of the colony and destroy their eggs, and Adlerz (1904) observed other bees (*Trachusa serratulæ*) enter each others' burrows and steal the pine-pitch with which they glue together the pieces of leaves for their nests. Drory (1872) saw

South American stingless bees (*Melipona*) overpower other individuals of their species and bite away the propolis with which their hind legs were charged.

The difference of sexual maturity between parasite and host suggests an answer to our second question, for the time of mating would of course depend on the time of sexual maturity and one group of individuals may be effectually isolated so far as its further phylogenetic development is concerned from another group of the same species, if the mating periods fail to coincide in the two groups. Thus interbreeding of the parasite with the host might be avoided in a very simple manner, and parasite and host, though reared on the same food and in the same environment would nevertheless tend to pursue divergent paths in their subsequent history. It would be interesting, therefore, to collect accurate data on the rate of larval development, and the time of emergence and mating of parasitic Aculeates and their hosts with a view to testing the strength of the hypothesis here suggested.

That certain Aculeates respond so readily and in such a uniform manner to simple stimuli like the urgency of oviposition and dearth of food by becoming parasitic on other Aculeates may be attributed to a peculiar modification of their constitution during their long phylogenetic history, some of the main outlines of which have been clearly revealed by morphological studies. Hymenopterists agree that the higher Aculeates are descended from primitive wasps whose modern representatives constitute the families Scoliidae, Thynnidae and Mutillidae and that their ancestors in turn are to be sought among groups like the Ichneumonidae. The latter have been called parasitic, but it is clear that their larvæ, which feed on the tissues of other insects and eventually kill their hosts are really practicing a refined, protracted and very economical predatism. They may be more properly designated as *parasitoids*, as Reuter (1913) has suggested. The Scoliidae, Thynnidae and Mutillidae, which seek out the larvæ of other insects in concealed places, *i. e.*, in the soil or in nest-cavities, immobilize or kill them by stinging and then deposit their eggs on them, therefore occupy a position, ethologically as well as structurally, midway between the higher solitary wasps and the Ichneumonidae. The higher wasps in constructing nests

and provisioning them with paralyzed insects merely elaborate the same fundamental behavioristic theme or pattern, the main features of which were also retained by the solitary bees even after they had ceased to capture insect prey and had become pollenivorous and nectarivorous. The social wasps and bees have merely modified certain details in the behavior of the solitary species. Among the ants the modifications are more profound, but the most primitive subfamily, the Ponerinæ, still exhibits many Sphecid traits. We may assume, therefore, that the ancient parasitoid habits of the Ichneumonid ancestry still abides as a latent, phylogenetic memory, or mneme, in the constitution of the whole Aculeate group. Hence it is not surprising that this mneme can be revived in response to such recurrent external and internal stimuli as dearth of food and urgency of oviposition. Under these conditions the solitary Aculeate readily becomes parasitic and reverts to a type of behavior essentially like that of the Mutillidæ, Thynnidæ and Chrysididæ. In the parasitic social Aculeates new behavioristic modifications have developed as the result of the complex and peculiar living environment presented by the social habit of the host, the trophallactic relations of the mother insect and her offspring and the existence of a worker caste.

The general conclusions that may be drawn from the foregoing survey of the parasitic Aculeata in particular and of insect parasites in general may be stated as follows:

1. We may distinguish two intergrading types of parasitism among insects. One of these is true parasitism and is represented by the lice, fleas, Mallophaga, many Diptera (Cestridæ, Pupipara) and some Hemiptera, which live on mammals and birds and do not destroy their hosts. The other is parasitoidism, which is really a refinement of predatism and is eminently characteristic of large sections of the Hymenoptera and Diptera (Tachinidæ). It leads sooner or later to the death of the host. The difference between the two types is largely due to differences in the size and vigor of the hosts.

2. Parasitoids are of two classes, one of which is best represented by the so-called Parasitica among the Hymenoptera and the Tachinidæ among the Diptera, which have no genetic relationship

with their hosts. The other class of parasitoids is represented by the Aculeates which have sprung directly from their host species (intraspecific parasitoids), though they may subsequently acquire hosts among other species of the same genus or of other genera and may in turn be the ancestors of parasitic species.

3. The derivation of all the existing Aculeata from primitive insectivorous wasp-like ancestors may account for the retention of a rather uniform pattern of behavior among the parasitic species. The parasites, both among the solitary wasps and the solitary bees, behave in a very similar manner, though the former are reared on insect prey, the latter on pollen and honey. In both groups the object of the parasite is to secure the provisions accumulated by the host for its own progeny. This involves a destruction of the egg or young larva of the host. The social parasites, however, have passed beyond this destruction of the host brood to a stage involving the fostering of the host brood as a means of insuring the rearing and alimentation of their own young. This change may have been due in the first instance to the formation of trophallactic relations between the parasite and the host brood.

4. The origin of parasitism among the Aculeata may be attributed to urgency of oviposition and temporary or local dearth of the supply of provisions for the offspring.

5. In all the different forms of parasitism among the Aculeata, there are traces of the primitive predatism or parasitoidism from which it arose, although in some of the social parasites this is represented only by the aggressive or conciliatory intrusion of the recently fecundated female into the host colony. Even the more extreme forms of behavior, such as those of the temporary and permanent social parasites, were derived from predatory behavior like that manifested by *Formica sanguinea* and its various subspecies and varieties.

6. Although many cases of parasitism are known to occur among the Aculeata, and although many others will doubtless be discovered in the future, nevertheless the total number must be small in comparison with the thousands of nonparasitic species. Contemplation of such a series as we find among the ants, beginning with *Formica sanguinea*, which is an abundant, vigorous and aggressive species

and ending with *Anergates atratulus*, a small, sporadic, and apparently evanescent species, without workers and with wingless, nymphoid males, suggests that parasitism among the Aculeates tends to such extreme specialization ("degeneration") as to lead to extinction. If we possessed a knowledge of the whole evolution of the Aculeate group, we should probably find that the total number of parasitic species which it produced during the ages was very great, but that the vast majority of them, after reaching the *Anergates* or a similarly specialized, or degenerate stage, lingered on precariously for a time and then disappeared.

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