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RECOGNITION AMONG INSECTS

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INTRODUCTION

It has always been a matter of conjecture as to how the various lower animals recognize each other, and by what means the sexes of any species distinguish one another. At first thought it might be claimed that sight is the chief means by which any animal having eyes can recognize other animals, but after a second thought we recall that the eyes in the lower animals are not as highly developed as they are in the higher animals; and we know that many of the lower animals live in dark places and that some of them are partially or totally blind. For example, the eyes of some beetles and spiders inhabiting caves function little or not at all, and despite this fact, these animals seem to distinguish one another as easily as do those with normal eyes living in light places. Relative to blind or partially blind species, touch may be the chief means by which they recognize one another, but during the courtship of cave spiders the writer (1910) observed that the males recognize the females of the same species at short distances and even before the males touch the webs of the females. Touch, therefore, can not be the chief means of recognition for cave spiders and perhaps not for any other animal. Since we know so little about the senses of hearing and taste in the lower animals, we may safely eliminate them as the chief factors in recognition.

That the lower animals do recognize one another without using the tactile organs, and as their sense of sight is not sufficiently developed to be the chief factor in recognition, we may assume that the most important factor is some chemical sense, perhaps similar to our olfactory sense. If the olfactory organs are the chief means of recognition, they must constantly receive stimuli in the form of odors, and these odors must be emitted by the animals themselves. If this is true, it would seem that the odor emitted by one animal should be at least slightly different from that of any other animal, and reasoning in this way Jaeger (1876) believes that most animals emit odors peculiar not only to the individual, variety, race, and species, but also to the genus, family, order, and class, and that these odors are the chief means by which one animal recognizes other animals. Without the aid of the eyes he claims that the degenerate human olfactories are able to distinguish a horse from a cow, a goat from a roe, a dog from a cat, a martin from a fox, a crow from a pigeon, a parrot from a hen, a lizard from a snake, and even a carrion crow from a hooded crow. Blackman (1911) remarks that the anal mucous membrane of our domestic animals, particularly the dog and cat, contains glands whose secretion emits a comparatively mild odor which probably serves as a secondary sexual purpose, but in other carnivores, such as the otter, badger, wolverine, mink, martin, ferret, ermine, weasel, and skunk, the scent may be far from mild and in many cases is used either as a means of defense or offense.

The chief object of the present paper is to show that the chemical sense (usually called the olfactory sense) in the lower animals, but particularly in the honey-bee, is so highly developed that we do not have any more conception of it than does the honey-bee (if it could think as we do) of our wonderfully developed sense of sight which is able to distinguish accurately the size, form, and color of objects.

If recognition among the lower animals is accomplished by means of odors stimulating the olfactory organs, then these animals must have means of producing the odors, and therefore such organs may be called scent-producing organs. The experimental results embodied in the present paper are mostly from observations made upon the honey-bee by the writer, while the part dealing with the scent-producing organs is a brief historical review of the literature on this subject.

ODORS EMITTED BY INSECTS

Our experiences with the higher animals prove that practically all of them emit odors, which in most cases probably play a secondary rôle to that of sight, but it is shown in the following pages that the odors emitted by the honey-bee are the chief means of recognition.

A. Odors Emitted by the Honey-Bee

It has always been more or less a matter of conjecture as to just how the different individuals of a colony of bees recognize one another. Considering the five special senses of sight, hearing, touch, smell, and taste which we experience, we may safely eliminate taste, because the writer has recently (1916a) shown that bees do not have a true gustatory sense, for it is only one phase of the olfactory sense. Since it is more or less dark inside the hive, sight certainly can not play a very important part in recognition, and since it has never been proved experimentally that bees can hear we can not consider hearing as the chief factor, and despite the fact that the writer (1916a) has demonstrated that the tactile sense is quite acute, the sense of touch in all probability is not as important as is the sense of smell. The following pages give the experimental results concerning the power of recognition among bees, which were brought about by means of the olfactory sense, and the rôle played by the other senses is not considered.

Relative to the odors emitted by the honey-bee, von Buttel-Reepen (1900) says:

> I believe that the following odors are present in a colony of bees:
>
> 1. The individual odor. It can be easily demonstrated that the queen odor varies with different individuals, and on the same ground (germinal variation), an individual odor should be assigned to the workers.
>
> 2. All offspring of one mother (queen) have a common inherited family odor in addition to the individual odors, belonging only to the progeny of one queen.
>
> 3. The brood and chyle odor.
>
> 4. The drone odor.
>
> 5. The wax odor. Since the wax is a glandular secretion, an exuded product, it may be safely taken for granted that, considered apart from the specific odor of wax, the individual odors of the wax-generators adhere to the honey-comb. Accordingly the wax structures of different colonies have different odors.
>
> 6. The honey odor. That the honey of each colony (mixed with a secretion of the salivary glands) has its specific odor is readily seen from the old practice of bee-keepers to which Bethe also alludes. If a queen be daubed with honey from a queenless colony, she will be accepted readily by that colony when inserted.

7. The hive odor (exhalation odor, colony odor). The hive odor is composed normally by a mixture of the preceding odors, or of some of them. Single bees, therefore, besides their individual odors, possess the family odor and especially the common adhering hive odor, which forms the dominant factor in the various actions toward hive mates and hive strangers —that is, in mutual recognition between bees.

Von Buttel-Reepen furthermore describes an abnormal hive odor which is caused by abnormal conditions among the occupants of the hive, and abnormal odors which are generated by disease (dysentery, foul brood, etc.).

To support the preceding views, von Buttel-Reepen gives no proofs other than his experiences as a bee-keeper, which are far from being conclusive, and the present writer, who has experienced much difficulty trying to prove his views experimentally, has had only partial success.

To know the part that odors play in the behavior of bees will be of considerable importance to bee-keepers, because the introduction of queens, uniting, and various other manipulations may be performed more successfully.

I. ODORS EMITTED THAT MAY BE PERCEIVED BY A PERSON

From April to October, 1913, the writer devoted practically all his time to a study of the odors produced by the honey-bee, and not being satisfied with some of the results obtained, several of the experiments were repeated the following summer. When this study was first begun, only the more pronounced odors—the hive or bee odor, brood odor, honey odor, and wax odor—could be distinguished by the writer, but before the close of the first summer he was able to distinguish the three castes of bees merely by smelling them. The details are as follows:

Old workers constantly give off the characteristic bee odor; and when seized, they emit another distinct odor which comes from the poison ejected through the sting. No difference between the odor of a guard and that of a fanner could be distinguished; the odor from each closely resembles the hive odor, that is, the odor which comes out of a hive when the hive cover is removed. A worker carrying pollen gives off besides the bee odor another odor which comes from the pollen.

The younger the workers the less pronounced is the bee odor emitted. To the human nose the odor emitted by nurse bees and wax generators is much less pronounced than is the odor from old workers.

Workers just emerged from the cells have a faint sweetish odor, but lack the characteristic bee odor, and workers removed from the cells just before they begin cutting their way out emit a fainter sweetish odor.

Old queens have a strong, sweetish odor, while the odor from queens just emerged from their cells is much less pronounced. The queen odor is very pleasant and is as characteristic for queens as is the bee odor for workers.

The majority of old drones have a faint odor, while almost every young drone has a stronger odor. This odor is slightly different from that of young workers and is less sweetish.

While considerable experience was required of the writer before he was able to distinguish differences between the odors emitted by the three castes and only slight differences or none at all between the odors emitted by different individuals of the same caste, the following experiments show that this power of distinguishing odors is quite different with the bees themselves.

2. HIVE ODOR

To determine if workers carry the hive odor and to ascertain the significance of this odor if carried by them, one-half the frames and about two-thirds of the bees were removed from hive No. 5, and were placed in a new hive some distance from the old one. The brood, honey, and pollen were divided as equally as possible and the queen was left in the old hive. The queen was a year old and this colony had never been united, so that probably nearly every worker in this hive was a daughter of this queen. The old and new hives may now be called hives No. 5a and 5b respectively.

To ascertain if the workers in these two hives had become enemies[1] eight days after hive No. 5 had been divided, ten triangular glass observation cases were constructed. These were made of three narrow wooden strips, two of which were 10 and the third 6 inches long, each being half an inch wide. Cheese-cloth served as bottoms and glass as tops for the cases. The apices and bases of these cases rested on two supports above a rigid table and the table legs rested on a concrete floor, near a window.

Twenty middle-aged workers from a frame in hive No. 5b were put into each of these cases. Ten middle-aged workers were removed

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[1] The words enemy and friend here as elsewhere in this paper are used anthropomorphically owing to lack of more appropriate terms.

from a frame in hive No. 5a. One of these 10 bees was put into each case; all 10 were attacked quite forcibly. This proves that the bees from these two hives had become enemies.

To determine if these sister bees, which had become enemies by having their original colony divided, could be made friends again, ten cases similar to those already described were used. These cases, however, were an inch deep and wire screen served as tops and bottoms. These cases were numbered 1 to 10 and may hereafter be known as the wire-screen cases.

Fifty middle-aged workers were removed from a frame in hive No. 5a and were placed in each of three of these cases (Nos. 1 to 3). Fifty workers from a frame in hive No. 5b were likewise placed in each of three more of these cases (Nos. 4 to 6). As controls 50 middle-aged workers from a frame in hive No. 29 were placed in each of two more of these cases (Nos. 7 and 8), and in a like manner 50 workers from hive No. 49 were placed in two more of these cases (Nos. 9 and 10). A large lump of queen-cage candy (made by kneading confectioner's sugar in a small amount of honey) was kept continually in each case. A piece of cotton wet with water was also constantly kept in each case. The cases containing the bees from hive No. 5a, one of those containing bees from hive No. 29 and one of those with bees from hive No. 49 were kept in the south room of the laboratory, while the other five cases were kept in the north room of the laboratory. The apices and bases of these cases rested on supports above rigid tables by open windows so that the air could pass freely through the cases.

Three days later a worker from each of cases Nos. 4 to 6 was put into each of cases Nos. 1 to 3; likewise, a worker from each of cases Nos. 1 to 3 was put into each of cases Nos. 4 to 6. All six introduced bees were received peacefully without even the least signs of hostility. This proves that these sister bees had become friends again, provided they responded normally. To test this possibility, 15 minutes later a worker from hive No. 23 was put into each of the six cases; all six introduced bees were attacked quite forcibly. After another interval of 15 minutes a worker from a frame in hive No. 5a was put into each of the six cases; all six introduced bees were attacked quite forcibly. Fifteen minutes later a worker from a frame in hive No. 5b was put into each case; as usual, all six introduced bees were attacked quite forcibly. An hour later still workers from cases Nos. 7 to 10 were put into these six cases; all six introduced alien bees were attacked only lightly.

Concluding from the foregoing experiments, the following conditions are indicated: Hive No. 5 had a hive odor and after this colony had been divided eight days each new colony thus produced had formed a new hive odor different from the hive odor of the other new colony. The workers of any colony carry the hive odor formed by their own colony. After a confinement of three days in the wire-screen cases, workers do not produce a new hive odor, but lose the hive odor that they bore when removed from their hive. That they are not able to form a new hive odor in these cases and that they lose the hive odor carried by them is probably due to air constantly passing through the cases. The workers, therefore, from hives Nos. 5a and 5b confined in cases Nos. 1 to 6 became friends again because their respective hive odors had disappeared, and they failed to attack each other even lightly because they were offspring from the same mother. These workers fought those from cases Nos. 7 to 10 only slightly because the latter had lost their respective hive odors and the slight hostility exhibited was due to the fact that the bees in cases Nos. 7 to 10 were offspring from different queens.

The foregoing experiments were repeated three times with bees from hives Nos. 5a and 5b. Each of the three lots of bees was put into cases Nos. 1 to 6 as already described for lot No. 1 in the preceding experiments and workers used as controls from different hives were put into cases Nos. 7 to 10 as before described. After a confinement of three days in the cases all of these workers were tested. Of the 18 workers tested one at a time from hives Nos. 5a and 5b, 16 were received peacefully without the least signs of hostility; the bees showed slight signs of hostility toward the other two but did not attack them. On the fourth day after confinement 18 more workers were tested one at a time; all 18 were received peacefully without signs of hostility. After a confinement of only one day in these wire-screen cases and when tested one at a time, each introduced bee was attacked only lightly. The workers used as controls in all of these experiments were tested and the results were always the same as described for the first lot.

Hive No. 73 was equally divided on October 15, making two new colonies, Nos. 73a and 73b. The brood, honey, and pollen were also divided as equally as possible and the queen was left in the hive on the old stand. Five months previously this colony had been united whereby strange bees from another queen were mixed with those already in this hive. By October 15, all the bees added by uniting were certainly dead. Three days after the colony had been divided, workers from hives Nos. 73a and 73b were placed in the glass observation cases as already described for bees from hives Nos. 5a and 5b. Upon testing them it was evident that they had become enemies and the hostility was certainly due to the hive odor carried by the bees from their respective hives.

Workers from hives Nos. 73a and 73b were put into wire-screen cases Nos. 1 to 6, and workers used as controls from hives Nos. 40 and 80 were put into wire-screen cases Nos. 7 to 10. After a confinement of four days in these cases they were tested as usual. The results were the same as those described for the bees from hives Nos. 5a and 5b.

Hive No. 7 was formed by uniting two colonies on May 25. On September 2, this colony was equally divided and at this date it very probably contained workers which were the daughters of two queens. Six days after the colony had been divided, workers from the two new colonies, Nos. 7a and 7b, were quite hostile to each other. Workers from hives Nos. 7a and 7b were put into wire-screen cases Nos. 1 to 6, and workers used as controls from hives Nos. 44 and 72 were put into wire-screen cases Nos. 7 to 10. After a confinement of seven days in these cases they were tested. Of the six introduced workers from hives Nos. 7a and 7b, five were received peacefully while one was attacked slightly. The results obtained by using the controls were the same as those for the other controls as already described.

On July 17, colony No. 56 was made by uniting eight frames containing bees, brood, and stores from four different hives. The bees, therefore, were offspring from at least four different queens. This hive did not thrive well because much difficulty was experienced in getting a good laying queen accepted. On August 19, this colony was equally divided. Four days later the bees in the two colonies, Nos. 56a and 56b, had become enemies. Three lots of workers from hives Nos. 56a and 56b and workers from various other colonies were put into the wire-screen cases as usual, and were tested on or after the third day of confinement. Of the 18 workers tested from hives 56a and 56b, five were received peacefully and the bees did not even attempt to attack them; they attempted to attack seven others, but did not seize them; five others were attacked lightly, and one other was attacked considerably. The results obtained by using the controls were the same as in all the foregoing experiments.

It should be stated that all the controls, described for the first lo of bees from hives Nos. 5a and 5b, were also employed in all o the other experiments, and the results obtained are practically the same. The time of introducing a bee to be tested in the various sets of experiments was so alternated that no error in regard to the sequence of time of introducing could have affected these results.

The following experiments were performed to determine the gradual change in the hive odor: On May 20 at 11 o'clock, colony No. 2, swarmed, and the swarm was placed in a new hive (No. 26). Twenty-four hours later 20 workers from a frame in hive No. 2a (the old hive) were put into each of the 10 observation cases, then 10 workers from a frame in hive No. 2b were tested as usual. Of the 10 workers tested, six were received peacefully; the bees showed signs of attacking one; and three were attacked slightly. Forty-eight hours after the bees had swarmed, the preceding experiment was repeated. Of the 10 workers tested, three were received peacefully; four were attacked slightly; and three were attacked considerably. Seventy-two hours or on the third day after the bees had swarmed, nine of the ten bees tested were received hostilely.

The foregoing experiments were repeated by using workers on the first, second, and third days after colony No. 82 had been equally divided. On the first day after the colony had been divided, four workers were received hostilely; on the second day seven were received hostilely; and on the third day all 10 of the workers tested were attacked. Similar results were also obtained by using bees from seven other colonies which had been divided.

All the foregoing experiments seem to prove that each colony of bees has its own particular hive odor and when a colony is divided each portion forms a hive odor different from that of the other portion, and also different from the hive odor of any other hive and probably different from that of the original hive, and the new hive odor is formed gradually and is sufficiently different at the end of the third day from that of any other hive to cause total hostility. The hive odor is carried by the workers and disappears in three days when the workers are confined in wire-screen cases.

The bees in the wire-screen cases described under hive odor, will also be discussed under individual and family odors.

(a) FUNCTION OF HIVE ODOR

Concluding from the experiments dealing with the hive odor, the success attained in uniting bees from two or more colonies in order to increase the number of colonies depends upon the formation of a new hive odor. When first united the new colony will contain just as many hive odors as there are colonies from which the bees were taken. To have peace among the different members of the new colony, a new hive odor, common to every individual in the hive, must be produced. The new hive odor is brought about by a thorough mixing of all the old hive odors with all the individual odors (see pp. 13 to 19) emitted by the members of the new hive, and success is more readily attained when smoke is added.

In practical bee keeping it is impossible to have an emerged queen devoid of a hive odor. So soon as a queen emerges from her cell she mingles with the workers and soon takes on the hive odor. To introduce an emerged queen into a foreign hive by the indirect method, she is put into a queen cage, which is then placed inside the foreign hive. By the time the workers have eaten through the candy to her, she has lost the hive odor that she previously carried and has taken on the hive odor of the foreign hive.

No difficulty is encountered on account of the hive odor when a queen cell, containing a queen ready to emerge, is transferred from one hive to another, because such a queen carries little or no hive odor.

The introduction of queens by means of the direct method is simple. The hive is filled with smoke, the queen is then run into the hive, and the entrance is closed. The smoke confuses the workers and throws them into a state of excitement, causing them to fill themselves with honey. More smoke is blown into the hive, and by the time the workers have become quiet, the introduced queen has taken on a sufficient amount of their hive odor to protect her.

(b) IMMERSION TO DESTROY HIVE ODOR

In view of the fact that the hive odor is probably the most important factor employed in the maintenance of the social life of a colony of bees, it is at the same time the most perplexing factor that man has to contend with in dealing with bees. This is due to the fact that uniting, introducing queens, etc., are artificial manipulations, and the processes involved are not in accord with the natural laws.

If the hive odor can be eliminated before such manipulations are undertaken, the difficulties encountered in uniting and in the introduction of queens might be overcome. To ascertain whether the hive odor may be destroyed by immersing bees in various liquids, the following experiments were performed. Twenty workers from the alighting board of hive No. 14 were placed in each of the 10 glass observation cases. Ten workers from the alighting board of hive

No. 28 were put into a queen cage and the cage with bees was immersed in water for 15 minutes. The apparently lifeless bees were then removed from the cage and were allowed to become dry. When dry and when they could walk and fly normally, one of them was introduced into each of the 10 cases. This set of experiments was repeated seven times. Of the 80 immersed workers tested, 40 were attacked more or less and 40 were received peacefully, although the bees seemed to regard some of the latter also as strangers. As a control the bees placed in the cases were taken from a frame of hive No. 25, and 10 guards from the entrance of the same hive were immersed in water for 15 minutes. When dry one of the immersed guards was introduced into each case; six of them were attacked lightly and four were received peacefully, although they were cleaned roughly.

Workers immersed in 5 per cent alcohol for one minute and then in water for 14 minutes were invariably attacked when introduced among strange bees; in all 30 such workers were tested.

Workers from a frame of hive No. 36 were put into the cases and 10 workers from the entrance of the same hive were immersed in 10 per cent alcohol for five minutes and then in water for 10 minutes. When these immersed bees were tested all were attacked.

Twenty workers from each of hives Nos. 15 and 17 were placed in the queen cages. They were immersed in 10 per cent alcohol for five minutes and then in water for 10 minutes. When dry each lot was put into a case, and later when mixed they were still hostile to each other. This set of experiments was repeated by taking two lots of bees from the entrance of the same hive. This time the bees were immersed in 10 per cent alcohol for 10 minutes and then in water for 10 minutes; all 40 revived as usual. When mixed they were not hostile to each other, but when strange workers were introduced, the strangers were attacked. The immersed bees also attacked hive mates taken from the entrance of their own hive. This experiment was repeated by immersing 200 bees from the entrance of hive No. 56. These workers were later quite hostile to strange bees as well as to hive mates.

Fifty workers from a frame each of hives 38a and 38b were immersed in each of 10 per cent alcohol and water for 10 minutes. When dry each lot of bees was placed in a wire-screen case. A hive mate that had been confined with others in a wire-screen case for four days and that by test had lost its hive odor, was placed in each case of immersed bees. Each introduced bee was attacked quite forcibly. This experiment was repeated once; one bee tested was received peacefully and one was attacked slightly.

Twenty workers from hive No. 60 were placed in each of the 10 observation cases. Twenty-five workers from the entrance of hive No. 19 were immersed in carbolic acid (one quart of water containing four drops of acid) for 10 minutes and then in water for 20 minutes. When dry one immersed bee was put into each of the above cases; nine were attacked and one was cleaned roughly. Upon repeating this experiment once all 10 were attacked.

Strange drones were tested in the same manner as described above. Thirty were immersed in water for 15 minutes and when dry one was put into each case as usual; 14 were attacked and 16 were received peacefully. Thirty strange drones were immersed in 5 per cent alcohol for one minute and then in water for 10 minutes. When tested, 26 of the immersed drones were attacked and four were received peacefully.

Concluding from the preceding results, it is not known whether the immersion of the bees in the liquids employed eliminated the hive odor which they carried, or whether it was merely changed, but the latter view seems the more reasonable. At most this method of procedure does not seem to have any practical significance relative to eliminating the hive odor carried by queens so that they may be more successfully introduced. It would be of interest to know the effect on the introduction of queens should they first be subjected to harmless gases before they are introduced.

3. INDIVIDUAL ODOR

On the preceding pages it is stated that each colony of bees has its own characteristic hive odor; also, a new or different hive odor may be formed in three days, and after confining workers three days in wire-screen cases the hive odor carried by them from their hives disappears and the bees are unable to form a new hive odor in these cases.

To determine how a new or different hive odor is formed, the following experiments were carried on at the same time with the experiments described on the preceding pages. Two cases similar to the wire-screen cases were employed, but these had tight-fitting bottoms and tops made of cheese-cloth and glass; they were placed flat on top of a table. To start with workers bearing as little hive odor as possible, 60 cells, all in the same comb of hive No. 60 and containing workers just ready to emerge, were uncapped with a pair of forceps. The bees were then gently removed from their cells and 30 were placed in each of the two cases (Nos. 1 and 2), and a piece of candy and a piece of cotton wet with water were also put into each case. Six days later a worker was taken from case No. 1 and was put into case No. 2; then a worker from case No. 2 and was put into case No. 1; both introduced workers were attacked lightly. After an interval of five minutes the following controls were used: Two sister workers just removed from sealed cells of hive No. 60 were put into these cases; both were attacked slightly. Five minutes later a fanner from the entrance of hive No. 60 was put into each case; each introduced fanner was attacked lightly. Five minutes later still a fanner from the entrance of hive No. 19 was put into each case; again each fanner was attacked slightly. After a confinement of nine days in these cases the young workers were quite hostile to each other.

That a lot of isolated sister bees can not form a new hive odor unless confined in a container with close-fitting walls is evident, because the sister bees in wire-screen cases Nos. 1 to 3 were often tested in the same manner as described above after a confinement of several days. They never showed signs of hostility, and the same may be said about the sister bees in wire-screen cases Nos. 4 to 6, and about those in cases Nos. 7 and 8, and also about those in cases Nos. 9 and 10.

The foregoing experiments were repeated by using workers 21 days old, when just ready to emerge from sealed cells. They were confined in a wire-screen case for 21 days. On the first day after being put into the close-fitting cases Nos. 1 and 2, they were slightly hostile to one another; on the fourth day they were considerably hostile and on the sixth day they attacked one another still more.

These experiments were repeated by using workers bearing a hive odor. One hundred middle-aged workers, all from the same frame in hive No. 49, were put equally into the two close-fitting cases Nos. 1 and 2. After a confinement of three days in these cases they were tested in the usual manner; the bees attempted to attack both introduced sister workers. One hundred more sister bees from the same hive were used in the same manner; on the third day when tested, one introduced bee was attacked quite forcibly and one was attacked lightly. One hundred sister workers from hive No. 56 were likewise used; on the third day of confinement when tested, they showed no signs of hostility toward one introduced bee, but attempted to attack the other one; on the fourth day they were slightly hostile to two more of their sisters. One hundred workers from hive No. 19 were likewise tested on the fifth day; they attempted to seize one introduced bee and to sting the other one when introduced. One hundred workers from hive No. 23 were also tested on the fifth day; they attempted to attack one introduced bee and did attack the other one lightly; on the thirteenth day two more were attacked lightly. One hundred workers from hive No. 73 were tested on the seventh day; both introduced bees were attacked lightly.

According to the foregoing experiments it is evident that 30 or more workers confined in a close-fitting case are able to form a new hive odor. This hive odor on the third day differs enough from that formed in another similar case by sister bees to cause the bees to attack each other more or less. The longer the bees are confined in such captivity the more hostile they are to each other, however, on about the tenth day of confinement middle-aged workers become black and shiny, and their abdomens are much distended, due perhaps to an accumulation of waste matter in the intestines. After the tenth day their hostility does not usually increase because the bees from then on gradually become less active. These results indicate that each worker emits an odor which is at least slightly different from that emitted by any other worker, and if this is true the hive odor is chiefly composed of a combination of all the individual odors.

Experiments dealing with the individual odor of bees were performed on a larger scale by employing two Benton queen-mating boxes and two wire-screen cages. The inside dimensions of a queen-mating box are 15 by 9 by 9 inches. Small frames made purposely for these boxes were used in the same manner in which full-sized frames are used in standard hives. Each box has a cover which fits rather snugly. The entrance was closed with wire screen and the feed box was filled with water. Each cage consists of a frame work made of narrow wooden strips nailed firmly together, and all six sides of the frame work are covered with wire screen. The inside dimensions of each cage are 12 by 10 by 10 inches. The cubical contents of a box and of a cage, therefore are practically the same. Small frames belonging to the queen-mating boxes were suspended in the cages and a small tin pan containing water was put on the floor of each cage. The four containers may be called boxes Nos. 1 and 2, and cages Nos. 1 and 2.

Two frames with nice comb containing much honey and pollen were removed from hive No. 81. Each comb was equally divided into halves and each half was inserted into one of the small frames and then the frame with comb was put into one of the containers. Next, a half frame of bees from hive No. 81 was shaken into each container, the lid of the container was then securely fastened and all four containers were placed on hive bodies inside the laboratory by an open window so that the wind could blow through the cages.

Four days later 20 workers from cage No. 1 were put into each of five glass observation cases already described, and then one worker from cage No. 2 was put into each of these five cases. Twenty workers from cage No. 2 were put into each of five other glass observation cases, and then one worker from cage No. 1 was introduced into each of these five cases. No signs of hostility were shown toward any one of the 10 introduced workers. A few minutes later a sister worker from a frame in hive No. 81 was put into each of the 10 cases. The bees showed no signs of hostility toward one introduced worker; they lightly attacked seven; and two were attacked quite forcibly. After confining the bees in the cages seven days, the experiments were repeated and the same results were obtained. A few minutes later sister bees from boxes Nos. 1 and 2 were put into the cases. Eight of the introduced workers were attacked lightly and two were attacked considerably.

After confining the bees seven days in the queen-mating boxes, they were tested in the same manner as described for the bees from the cages. Of the 10 workers introduced, four were attacked lightly and six were attacked considerably.

After confining bees in these boxes and cages seven days they become more or less black and shiny and the abdomens are much distended with waste matter in the intestines. They are less active than usual and are perhaps more or less abnormal in some ways but after being confined seven to ten days, they seem to respond to odors normally.

All of the foregoing experiments were repeated by using bees and comb from hive No. 67. In these experiments, however, 20 workers from one cage were placed in each of the 10 cases and a worker from the other cage was introduced a few minutes later into each case. Thus for the cages, 20 workers, one at a time were put into the cases and all of them were received without any signs of hostility. The same procedure for the boxes was followed, and of the 20 workers introduced, the bees attempted to attack two; 10 were attacked lightly; and eight were attacked quite forcibly. When several of the workers from the boxes were placed on the alighting board of their own hive (No. 67), some of them were attacked by their sister guards and when a guard from the alighting board of their own hive was introduced into each case containing workers from the cages, 11 guards were attacked lightly and nine were attacked quite forcibly.

The experiments with bees in the boxes and cages further substantiate the view that a new hive odor may be formed in three days when middle-aged bees are confined in a container having tight-fitting walls, and that the hive odor must be composed of a combination of all the odors emitted from the individual bees. Also, when bees are confined in a container having wire-screen sides, no hive odor can be formed, because the air passing freely through such a container carries away the individual odors just as fast as they are given off by the bees. Furthermore, sister workers are hostile to sisters of any age if the latter are mostly devoid of a hive odor, or if they carry a hive odor which is slightly different from the hive odor of the former. Several workers just emerged from their cells, if confined in a close-fitting case, may accumulate a hive odor by the fifth or sixth day. This hive odor differs enough from that formed by other sister bees of the same age in another similar case to produce hostility when the sisters from the two cases are mixed.

To ascertain if workers confined singly for a few days in close-fitting cases are able to form hive odors, and to furnish another proof, if possible, whether a hive odor is nothing more than a combination of the various individual odors, the following experiments were performed: Nineteen small triangular observation cases were constructed. Two of the sides were 5 inches and the third side was 4 inches in length. The depth was ½ inch, the top was glass, and the bottom was wire screen.

To be sure that young workers bearing as little hive odor as possible might be used, half of a comb containing just emerging bees was removed from hive No. 19 and was placed in one of the cages described on page 15. Five days later most of the bees had emerged and two days after this date one of these young workers was introduced into each of the 19 cases. When put into these cases they had been emerged probably four or five days on an average and were sufficiently old to possess the characteristic bee odor. A small piece of candy and a small piece of cotton wet with water were also put into each case. A thick cloth was spread out on top of a table and these cases were put side by side on top of this cloth, then another cloth was spread over the tops of the cases. After a confinement of four days in these cases, five of the bees had died, and the remaining

14 live ones were tested. They were grouped in pairs by one being removed from its own case and then being introduced into another case containing a sister. When first put together, three pairs attempted to fight, but soon became friends; two pairs fought lightly; one pair fought quite forcibly; and one pair fought fatally. These experiments were repeated once by using 19 more of the same lot of bees from the same cage. The bees by this time were probably eight or nine days old on an average. After being confined singly four days, all were dead but eight; these were tested as usual. Two pairs showed no signs of hostility; one pair attempted to fight; and one pair fought lightly.

The foregoing experiments were repeated by employing middle-aged workers which had been confined three or more days in one of the wire-screen cases. As already shown these bees had lost the hive odor. After a confinement of four days in the small observation cases, three of them had died; the remaining 16 were tested as usual. Two pairs fought fatally; one pair attempted to fight, and five pairs showed no signs of hostility. This set of experiments was repeated twice with middle-aged sister workers that had lost the hive odor by being confined in a wire-screen case. After a confinement of four days, only 26 live ones for both sets remained and they did not appear entirely normal. When tested 10 pairs of them showed no signs of hostility; one pair attempted to fight; one pair fought quite forcibly, and one pair fought fatally.

The small cases described above were discarded and 50 smaller ones were constructed. Two sides of the latter cases were 4.5 inches and the third side was 3.5 inches in length, the bottoms being wood and the tops glass. The tops and bottoms fit so snugly that practically all of the odor emitted by a bee remained inside the case. After confining a single middle-aged worker from frame D of hive No. 67 in each of these cases for nine days, the remaining live bees were tested as usual. Three pairs showed no signs of hostility; three pairs attempted to fight; two pairs fought lightly; four pairs fought quite forcibly; seven pairs fought fatally, whereby in one case both bees were killed. When these results had been recorded, the remaining live bees were again placed singly into the cases, and an hour later a sister bee from frame D of hive No. 67 was introduced into each case. Twenty-seven pairs showed no signs of hostility; three pairs fought slightly; and one pair fought quite forcibly.

The preceding experiments were repeated by using middle-aged workers from a frame of hive No. 19. After a confinement of six days, the remaining live bees were tested. Ten pairs showed no signs of hostility; three pairs fought slightly; one pair fought quite forcibly; and five pairs fought fatally.

The tops and bottoms of the 50 small cases were removed and wire-screen tops and bottoms were used in order to have open cases. A middle-aged worker from a frame of hive No. 67 was put into each case. The cases were then placed side by side on supports near an open window so that the air could pass freely through the cases. Since it was too cool for this kind of experiment most of the bees died, but after carrying on two sets of these experiments the following data were obtained: Three days after being thus confined, seven pairs showed no signs of hostility; seven pairs fought lightly; three pairs fought quite forcibly and three pairs fought fatally. The hostility that resulted may have been due to the hive odor that had accumulated during the nights, because the cases of bees were left wrapped in cloths from 4.30 p. m. till 9.00 a. m.

4. FAMILY ODOR

To determine whether the honey-bee emits a family odor, the following experiments were performed. The observation hive (No. 81) became queenless about June 19, and since it contained no eggs and no brood except worker pupæ and few drone pupæ about ready to emerge on this date, two frames containing eggs and young larvæ removed from hive No. 23 were added to it. By June 26 almost all of the brood in this hive was sealed and no eggs nor young larvæ were seen, and on this date a virgin queen from hive No. 68 was introduced. On July 3, the new queen was laying nicely and many eggs were present.

On July 26, 20 old workers from a frame of hive No. 81 were put into each of the 10 glass observation cases described on page 6, when 10 young workers just ready to emerge from a comb in the same hive were removed from their cells by means of uncapping the cells with a pair of forceps. Since a period of 21 days is required for the development of workers, counting from the time the eggs are laid to the time when the adult bees emerge, it is plain that these young workers were the daughters of the new queen, while all the other bees in the same hive were daughters of other queens. These young bees as usual had a faint sweetish odor and failed to give off any odor resembling the hive odor. Young bees removed from their cells by the method just described may be regarded practically devoid of the hive odor for the following reasons: (1) They emit a faint odor which to the human nose fails to resemble the hive odor in the slightest degree; (2) they have not mixed with the other bees in the hive whereby they might have taken on the hive odor; and (3) it is not reasonable to think that a large amount of the hive odor penetrates the caps of the cells and adheres to the bodies of the bees. One of these 10 young workers was introduced into each of the 10 cases containing the old workers from the same hive. The old bees were more or less hostile to seven of the young ones, and received the other three without any signs of hostility.

The preceding experiments were repeated four times. In all five sets of experiments, the old bees were hostile to 38 young ones, while they showed no signs of hostility toward the other 12. These experiments were again repeated five times, but the old workers were taken from the alighting board of hive No. 81. Forty-nine young bees were received hostilely and no signs of hostility were shown toward the remaining one. Of the 100 young workers tested in the 10 sets of experiments, 87 were received hostilely, while 13 were received peacefully.

As a control for the foregoing experiments, 20 old workers from a frame of hive No. 38a were put into each of the 10 observation cases. A young worker removed from a sealed cell of a comb in hive No. 38b was introduced into each of the cases as usual. After repeating this set of experiments four times, the following data were obtained: Of the 50 young workers tested, two were received hostilely and 48 were received peacefully. As stated on page 21, all the bees whether young or old in hives Nos. 38a and 38b are supposedly offspring from the same queen and these experiments were not performed until the old workers in the two hives had become enemies to each other.

The experiments just preceding were repeated three times by using old workers from hive No. 23 and young workers removed from sealed cells of hives Nos. 2, 6 and 56. Of the 30 young workers tested, 22 were received hostilely and eight were received peacefully.

As described on page 15, half of a comb containing emerging workers was removed from hive No. 81 and was put into one of the wire-screen cages. Twenty of these young bees when four or five hours old were tested in the usual manner by introducing them into cases containing old workers from hive No. 49. Nineteen were received hostilely and one was received peacefully. When three or four days old, 30 of the same lot of young workers were introduced into cases containing old workers from their own hive (No. 81); all 30 young were received hostilely. It should be recalled that the old bees and young ones used in this set of experiments were not sisters, and the lack of a hive odor being carried by the young ones is probably the chief reason why they were received hostilely, rather than to attribute the hostility to a strange family odor.

As already described on page 7, 50 workers from hive No. 38a were placed in each of wire-screen cases Nos. 1 to 3; 50 from hive No. 38b into each of wire-screen cases Nos. 4 to 6; 50 from hive No. 49 into each of wire-screen cases Nos. 7 and 8; and 50 from hive No. 29 into each of wire-screen cases Nos. 9 and 10. It will be remembered that all the workers in hives Nos. 38a and 38b were daughters of the same queen and that each new colony had formed a new hive odor before the workers were put into these cases. After a confinement of three days in the wire-screen cases the hive odor carried by the bees from their hives had disappeared, and as already stated each individual worker is constantly throwing off an odor which is slightly different from the odor emitted by any other worker, whether that worker be a sister or alien bee. When sister workers in cases Nos. 1 to 3 were mixed, no hostility was exhibited, because the individual odor of each sister possesses a family characteristic which is common to all the workers of the same queen and which is inherited from that queen. The family characteristic may be called the family odor, although it is only a part of the individual odor. The same interpretation may be used to explain why sisters in cases Nos. 4 to 6 did not attack each other when mixed; likewise why sisters after being confined three days in cases Nos. 1 to 6 did not attack each other when mixed. In these tests the two different hive odors had disappeared and it seems only reasonable to think that the bees recognized each other as friends by means of the family odor. The reason why sisters in cases Nos. 7 and 8, or those in cases Nos. 9 and 10, did not fight when mixed may possibly be attributed to the family odor. When alien workers from cases Nos. 9 and 10 were mixed with those in cases Nos. 1 to 6, or with those in cases Nos. 7 and 8, instead of much hostility being exhibited, the bees fought each other only lightly. This fact may be explained by the view that they recognized each other as strangers by means of the family odor, which in the daughters of one queen is only slightly different from that in the daughters of another queen.

5. QUEEN ODOR

On June 27 at 1 o'clock, 20 workers from a frame of hive No. 69 were put into each of the glass observation cases Nos. 1 and 2;

on this date this colony had emerging queens. A light colored queen that had just emerged was introduced into case No. 1 and a dark colored one was put into case No. 2; both queens were received peacefully and the workers fed them.

On July 1 at 1 o'clock, the above queens were transferred from cases Nos. 1 and 2 to cases Nos. 3 and 4 which contained workers from hive No. 70. When the light colored queen was introduced, a worker grabbed one of her feet, but soon let it loose; then she was fed and accepted peacefully. When the dark colored queen was introduced, the workers seized her legs and wings and held her for half an hour, after which they accepted her more or less peacefully.

On July 2 at 1 o'clock, 20 workers from a frame of hive No. 69 (the hive from which the queens were taken) were put into each of cases Nos. 1 and 2. A few moments later the light colored queen was introduced into case No. 1. At once the workers seized her legs and held her for three minutes, then they let her loose, cleaned and "caressed" her. The dark colored queen was put into case No. 2. The workers ran after her and one of them seized her leg, but did not hold it long, then they "caressed" her.

On July 3 at 1 o'clock, 20 workers from a frame of hive No. 28 were put into cases Nos. 3 and 4 as usual. The light colored queen was transferred from case No. 1 to case No. 3, and immediately upon being seized by a worker she killed the attacking bee, after which all the workers balled her, that is, clustered closely around her for five minutes; later they "caressed" her. The dark colored queen was transferred from case No. 2 to case No. 4, and the workers balled her for 25 minutes.

On July 5 at 9 o'clock, 20 workers from a frame of hive No. 50 were put into each of cases Nos. 1 and 2, and then the queens were transferred from cases Nos. 3 and 4 to these cases. Immediately after being introduced into the cases, the workers balled and tried to sting each queen, and consequently the dark colored queen was stung in the thorax, but she was not apparently injured. By 11 o'clock the queens had not yet been accepted; at this hour, 20 workers from a frame of hive No. 68 were put into each of cases Nos. 5 and 6, and the queens were then transferred from cases Nos. 1 and 2 to these cases; at once the queens were balled, and the light colored queen was crippled in one hind leg. On July 7 at 8 o'clock, the light colored queen was found dead in case No. 5.

On July 7 at 1 o'clock, another set of 20 workers from hive No. 68 was put into case No. 4, and on this date the bees in case No. 6

(sisters to those now in case No. 4) had accepted the dark colored queen. Immediately upon transferring the queen to case No. 4, a worker grabbed her and stung the under side of her thorax; she died immediately. To the writer this queen emitted a slightly stronger odor than did the light colored one.

Much more experimentation along this line would be required to prove conclusively that queens have individual and family odors and that they carry the hive odor on their bodies wherever they go, but since there are many evidences in practical bee keeping which support this view, we shall not dwell on it longer.

6. DRONE ODOR

Since the human nose is able to detect the very faint sweetish odor emitted by drones, the following experiments were performed to ascertain if this odor has any practical value to the drones themselves. Twenty middle-aged workers from a frame of hive No. 60 were put into each of the 10 glass observation cases. After the workers in these cases had become perfectly quiet, a drone from the same hive was introduced into each case; all 10 drones were received without any signs of hostility. This set of experiments was repeated nine times. In all 10 sets of experiments 100 drones were used, and each one of them was received without any signs of hostility.

These experiments were again repeated 10 times, but instead of using workers and drones from the same colony, the workers in each set of experiments were taken from a frame of a colony having drones, and the drones for the same set of experiments were taken from a different colony. Of 100 drones tested, 22 were attacked lightly and the workers attempted to attack the other 68.

The preceding experiments were again repeated 10 times, but the workers were taken from various droneless colonies. Of the 100 drones tested, each one was attacked quite forcibly.

There are three possibilities which may be suggested to explain why no hostility was exhibited toward a single drone of the 100 tested in the first 10 sets of experiments: (1) The drones probably carried the hive odor of their own hive, which might have rendered them immune to attacks; (2) the drone odor emitted by them might have also protected them; and (3) since they and the workers were offspring from the same queen, the drones might have had a family odor like that of their sisters. The workers might have regarded the family odor as a friendly token. The slight hostility noted in the second 10 sets of experiments might have been due to a combination of a foreign hive odor and an alien family odor held in check by the drone odor. Since the workers used in these experiments were from colonies having drones, it is probably true that they were already accustomed to the drone odor, therefore this odor probably served as a check to prevent all the drones from being attacked considerably. Why all of the 100 drones tested in the third 10 sets of experiments were attacked considerably, might have been due to the combination of all three of the above enumerated possibilities. In these last experiments there was (1) a foreign hive odor, (2) a drone odor, to which the workers employed were not accustomed because their colonies were droneless, and (3) an alien family odor.

All the preceding experiments were performed in July, 1913, after the drone-killing time and when drones were comparatively few, but very similar results were obtained during the following May before the drone-killing time, and when drones were abundant. These experiments were repeated several times on July 15, 1914, and the results obtained were similar to those described. Other duties prevented the writer from continuing this experimentation in view of determining the relation between the odors produced and the factor causing the killing of drones. Those who maintain that bees are reflex machines, believe that a constant external stimulus is required during the drone-killing time, and reasoning from this point of view it might be possible that various factors cause the drone odor to change so that it might serve as the external stimulus to indicate to the workers that the drones must be killed.

According to the data obtained in all of the foregoing experiments, there is little evidence for the existence of a family odor in drones, but since it has already been shown that workers have a family odor, it is reasonable to think of drones also inheriting a family odor. These experiments do not prove conclusively that drones carry the hive odor, but since workers and queens carry the hive odor, it is logical to regard the drones in the same light. This possibility is further strengthened by the fact that all the combs, frames and even walls of the hive body are scented with the hive odor. After leaving small blocks of wood or queen cages in the hives for a few days and then removing them they give off the hive odor. According to the results obtained in the foregoing experiments, it may be inferred that drones when entering a strange hive are rarely molested if this hive contains several drones, but when drones enter a droneless colony they may be subjected to more or less hostility, although it is generally believed that drones go unmolested at all times and under all conditions from hive to hive, except during the drone-killing time. It, therefore, seems that the drone odor serves as a check to reduce the hostility caused by a foreign hive odor which is carried on the bodies of the drones.

7. ODOR EMITTED BY GUARDS

In order to have a standard by which to judge the hostility exhibited when testing guards, fanners, middle-aged workers inside the hive, nurse bees, and pollen carriers all belonging to the same colony, 20 workers from the alighting board of a hive were put into each of the 10 glass observation cases. These workers included both guards and fanners taken promiscuously from the alighting board. Ten more guards and fanners taken promiscuously from another alighting board were introduced into the cases as usual. This set of experiments was repeated nine times. Of the 100 strange workers tested, each one was attacked fatally and most of them soon died, perhaps on account of being stung.

Twenty middle-aged workers from a frame of hive No. 79 were put into each of the 10 cases. A guard from the alighting board of the same hive was introduced into each case. This set of experiments was repeated nine times by using workers each time from a different hive. Of the 100 guards tested, 54 were received without any signs of hostility; the bees offered to attack two; nine were attacked very lightly; and 35 were attacked lightly.

8. ODOR EMITTED BY FANNERS

Twenty middle-aged workers from a frame of hive No. 81 were put into each of the 10 glass observation cases. A fanner from the alighting board of the same hive was introduced into each case. This set of experiments was repeated by using bees from two other hives. Of the 30 fanners tested, 14 were received without any signs of hostility; the bees offered to attack one; three were attacked very slightly; and 12 were attacked slightly.

9. ODOR EMITTED BY MIDDLE-AGED WORKERS INSIDE HIVE

Twenty guards from the alighting board of hive No. 48 were put into each of the 10 glass observation cases. A middle-aged worker from a frame of the same hive was introduced into each case. This set of experiments was repeated three times by using bees from three different hives. Of the 40 middle-aged bees tested from inside the hive, 29 were received without signs of hostility; the guards offered to attack one; four were attacked very lightly; and six were attacked lightly.

These results explain why the workers in the top super of a tier of supers on a hive body are attacked by the guards of their hive should they escape from the super and try to pass into the hive through the entrance.

10. ODOR EMITTED BY NURSE BEES

Twenty middle-aged workers from a frame of hive No. 67 were put into each of the 10 glass observation cases, then a nurse bee from hive No. 23 was introduced into each case. Of the 10 nurse bees tested, the workers offered to attack two; four were attacked lightly; and four were attacked quite forcibly.

No experiments to test the odor emitted by wax generators could be devised, other than ones similar to those described just above, but the above experiments really deal with the hive odor rather than with the odor peculiar to nurse bees.

11. ODOR EMITTED BY POLLEN CARRIERS

To determine whether strange pollen carriers are accepted with less hostility than are strange workers without pollen, the following experiments were prosecuted. Twenty middle-aged workers from a frame of hive No. 73 were put into each of the 10 glass observation cases. A pollen carrier entering hive No. 81 was introduced into each of the 10 cases. Five of the 10 introduced pollen carriers were received peacefully and were fed, while the other five were attacked lightly. In three instances the bees in the cases ate the pollen on the legs of the pollen carriers. This set of experiments was repeated twice by using strange workers from various hives. Of the 20 pollen carriers tested, the bees showed no signs of hostility toward three; they attempted to attack seven; and 10 were attacked lightly. In five instances the pollen on the legs of the bees was eaten. These experiments were again repeated twice, but in these two sets strange workers from the entrances of various hives were put into the cases and the pollen carriers were taken from the entrances of other hives. Of the 20 pollen carriers tested, no signs of hostility were shown toward four; the workers attempted to attack five; 10 were attacked lightly; and one was attacked quite forcibly. The workers cleaned and ate the pollen from the legs of most of these pollen carriers.

To ascertain if workers from inside a hive would peacefully accept pollen carriers entering their hive, 20 workers from a frame of hive No. 7 were put into each of the observation cases. A pollen carrier about to enter the same hive was put into each case. This set of experiments was repeated with bees from hive No. 73. Of the 20 pollen carriers tested, 16 were accepted peacefully and four were attacked very lightly.

Twenty guards from hive No. 44 were put into each of three observation cases, then a pollen carrier about to enter the same hive was introduced into each case. One pollen carrier was attacked very lightly and two were attacked lightly.

Twenty pollen carriers about to enter hive No. 7 were put into each of five observation cases, then a guard from the same hive was introduced into each case. The pollen carriers showed no signs of hostility toward one guard; two were attacked very lightly; one was attacked quite forcibly; and one was killed. A few minutes later a guard from hive No. 29 was put into each case; four of the guards were attacked quite forcibly, and one was killed. While catching these pollen carriers the writer saw the guards on the alighting board attack and carry away a pollen carrier, and when the pollen carriers were put into the cases, three instances of fighting were seen among them. This hostility indicates that the attacked pollen carriers probably belonged to other hives, while the slight hostility of the workers used in the other experiments toward the pollen carriers seems to indicate one of two conditions as follows: (1) The workers and pollen carriers were probably hive mates, but the hive odor carried by the latter might have sufficiently disappeared in the field to cause the pollen carriers to be received with slight hostility, and (2) the workers and pollen carriers probably were not hive mates, but the hive odor carried by the latter might have so nearly disappeared that the workers could not distinguish them as strange bees.

It was planned to carry on similar experiments by using nectar carriers, but this was dropped for lack of time. In practical bee keeping we know that nectar carriers often enter strange hives without being molested, showing that the nectar they carry makes them immune to attacks, or that the hive odor carried by them has sufficiently disappeared to allow a peaceful reception.

12. EFFECT OF ODOR FROM BEE STINGS

To determine whether the odor from the stings of workers increases the hostility exhibited when strange workers are put together, 20 middle-aged workers from a frame of hive No. 67 were put into each of the 10 glass observation cases. The stings of 10 workers taken from the alighting board of another hive were extracted by letting the bees sting a meat rind. After having lost the stings these workers were active, though they did not have the energy and vitality of normal bees and when one of them was introduced into each case, it never offered to return the attack as does a normal bee. Each one was attacked less than is a normal bee under the same conditions. This difference in hostility is probably due to the abnormality caused by the extraction of the stings.

The effect of the odor from bee stings was tested in another way. Twenty middle-aged workers from a frame of hive No. 67 were put into each of eight cases. The extracted stings of 15 guards from hive No. 15 were placed in a small vial, and eight fanners from the alighting board of hive No. 67 were put into the vial containing the stings. After an interval of five minutes they were removed from the vial and one was introduced into each case; three fanners were attacked slightly, and the workers offered to attack the other five. As a control four guards from the alighting board of hive No. 67 were placed into an empty and odorless vial for five minutes. They were then removed and one was put into each of four cases; all four were attacked slightly. Another control was employed by using bees from hive No. 81. In this set of experiments middle-aged workers from a frame and fanners from the alighting board were used in the same manner as above described, but instead of using extracted stings of strange bees, stings of sister guards were used. The eight fanners were placed in the vial containing stings of sister guards. After an interval of five minutes they were removed and one was introduced into each case; six fanners were attacked slightly and the workers offered to attack the other two.

The foregoing results indicate that the odor from the poison which exudes from the sting does not increase the hostility exhibited when strange workers are put together, although we know from practical experience that when two or three bees sting a person's hand, other bees often attack the same hand immediately, indicating that the last bees were guided to the hand by means of the odor emitted from the poison of the first bees, but these two examples of hostility are not exactly parallel.

(a) EFFECTS OF ODORS FROM GLUE AND FINGERS

Twenty middle-aged workers from a frame of hive No. 7 were put into each of the 10 observation cases. The tip ends of the abdomens of 10 bees from the alighting board of the same hive were covered with liquid glue. When the glue was dry one of these workers was introduced into each case; all 10 were attacked considerably. Sometimes the attacking bee grabbed the glued end of the abdomen.

After a short interval the writer rubbed his fingers along the dorsal sides of the thoraces and abdomens of 10 workers from hive No. 7 and then these bees were put into the cases with their hive mates; all 10 were attacked slightly.

(b) EFFECTS OF ODORS FROM CANDY AND HONEY

Many times when the observation cases contained hungry workers, like guards and fanners, strange workers that had been allowed to eat much candy or honey were introduced into the cases containing the hungry bees. In all such instances the hungry bees do not attack the others, but beg food of them and when food is not forthcoming they offer to attack the bees having food.

B. Odors Emitted by Other Insects

Entomologists have observed that practically all insects have some means or other to produce odors, but comparatively few results dealing with the odors emitted have been published, and most of these appear as widely scattered notes. Under the above heading a brief discussion of the results of a few authors will be given, although under the following headings, which deal mostly with the morphology of the scent-producing organs, a more complete discussion of the literature will be presented.

The earlier entomologists observed the various means by which insects defend themselves, but they were usually ignorant concerning the origin of the various liquids secreted. For example, Burmeister (1836, p. 506) says:

> Other insects secrete peculiar fluids, in which they partly envelope themselves and partly thereby secure themselves from the attacks of their enemies. The *Aphrophora spumaria* is one of these, which envelopes itself in a thick white frothy fluid, that comes out of the anus . . . . We find other coverings in the *Aphidæ* and tortoise-beetles, which envelope themselves with a white woolly or fibrous substance, the origin of which we are not yet acquainted with, but it appears likewise to be produced by a peculiar secretion of the skin. Other insects, as the *cantharides,* burying-beetles, carrion-beetles, carrion-flies, wasps, etc., emit upon being touched such a nauseous stench, that this must prevent every insectivorous bird from using them as food.

On page 509 Burmeister further says:

> The generally known means of defense of the bomb-beetle (*Brachynus crepitans*) is of a peculiar description; it consists in its ejecting from its anus against its enemy a vapoury moisture accompanied by a slight sound, and which vapour has great resemblance to the gas of aquafortis.
>
> We have before noticed some peculiar organs of secretion in several larvæ, as for instance, in that of *Picris machaon*, which are projected at the approach of danger; they appear, in fact, to be glandular organs which partly secrete odours and partly liquids, for the purpose of chasing the enemy. . . . . Among the beetles similar organs are found in the genera of *Cantharia* and *Malachius*, which in these are seated at the sides of the thoracic and ventral segments, and are likewise projected in time of danger.

Kirby and Spence (1823) remark that a fly, *Hemerobius perla*, and an ant, *Formica fœtida*, emit an odor similar to that of human ordure. *Formica fuliginosa* imparts a strong odor to everything it touches. Many wild bees (*Melitta* and *Andrena*) are distinguished by their pungent and alliaceous odor. *Crabro flavum*, a wasp, emits a penetrating odor like that from ether.

Müller (1878 c-d) claims that odors may have been acquired by butterflies either for protection or to attract the opposite sex. In most cases protective odors appear to be equally strong in both sexes. Sexual odors may be divided into the following classes: (1) Those which attract or allure the opposite sex from a distance, and (2) those which excite the opposite sex during courtship. The male of *Didonis biblis* is able to emit as many as three distinct odors. When seized either sex of this butterfly protrudes a pair of protuberances from between the fourth and fifth abdominal terga; these protuberances emit a strong disagreeable odor. The male has a second pair of similar protuberances between the fifth and sixth terga; these emit an agreeable odor. The wings of the male emit a musky odor. In butterflies as a rule, Müller says that the scent-producing organs of males are located on the wings, but in a few genera (*Danais, Lycorea, Ituna, Morpho,* and *Didonis*) they are found on the abdomen, and in some Hesperidæ on the hind legs. Relative to moths these organs lie on the abdomen or legs, although not wanting on the wings.

Rye (1878) reports that a particular water beetle found in India emits a liquid, resembling walnut juice, which gives off a strong but not an unpleasant odor.

Lelièvre (1880) found that both sexes of *Thais polyxena* emit an odorous exhalation.

Dimmock (1882) says that most Staphylinidæ have a pair of "evaginable" organs, one on each side of the anus, which give off a disagreeable odor when protruded.

Pérez (1882) claims that each species of the bee, *Prosopis,* examined gives off a constant and characteristic odor which is unlike that emitted by any other species of the same genus.

Von Dalla Torre (1885) says that in many Zygænidæ each sex has a sac between the fourth and fifth abdominal segments, which exhales a very unpleasant odor. The males have, in addition, a pair of sacs between the fifth and sixth abdominal segments which emit an agreeable smell.

Howard (1889) says that the coccid, *Gossyparis ulmi,* gives off a pungent odor which is quite noticeable.

Haase, according to Plateau (1890), states that there are three types of scent-producing organs in Lepidoptera as follows: (1) The defensive ones produce an irritating and nauseating liquid; (2) the attractive ones are for bringing the males from a distance to the females; and (3) the seducing organs are possessed only by the males, and are found only in those species of which both sexes fly well. The odor emitted is aromatic and resembles that from vanilla.

Swale (1894) noticed that the staphylinid beetle, *Olophrum piceum,* is able to emit a quite disagreeable odor.

Hamm (1895), while collecting Lepidoptera, carried a bag, which a week previous had confined a female moth of *Bombyx quercus.* Several males of this species were atracted to the bag, and he attributes the cause of the attraction to the scent of the female still retained in the bag.

Keays (1895) placed a female of *Corycia taminata* in a box, and when it was removed, the box contained a filthy odor which was retained for hours thereafter.

Webster (1899) states that the odor emitted from the San José scale, *Aspidiotus perniciosus,* may be detected from a considerable distance.

Cockerell (1899) says that he has seen a male of *Margarodes hiemalis* "run over the ground until it detected a spot where a female was buried, and then dig down to the female. It must certainly have detected its mate by the sense of smell."

Johnson (1899) asserts that in the coccids, *Aspidiotus perniciosus* and *Chionaspis euonymi,* the odor emitted is perhaps for sexual purposes or for attracting other insects. In another scale insect, *Leca-*

nium nigrofasciatum, he regards the foul odor as a protection against the attacks of birds.

The odors emitted by certain social Hymenoptera have perhaps been studied more than those of all the other insects combined. For many years ants and bees have been regarded as having a colony odor (nest or hive odor). Jaeger (1876) was among the first to suggest that the colony odor is inherited, and speaking about bees Bethe (1898) called the hive odor "hive substance" and thought of it including both the family odor and colony odor. Bethe believes "that these family odors, common to all the members of one family, and differing slightly from those of other families of the same species play an important part in the life-history of the social hymenoptera. This family difference is due to the varying proportions of the constituent odors" (Geisler, 1907). Von Buttel-Reepen and the present writer have shown that the hive odor and family odor are two distinct odors and that only the family odor is inherited.

Fielde (1901) claims that a certain species of ants bears three distinct odors as follows: (1) A scent deposited by her feet, forming an individual trail, whereby she traces her own steps; (2) an "inherent" and inherited odor, manifested over her whole body, identical in quality for queens and workers of the same lineage, and a means for the recognition of blood relations; and (3) a nest odor, consisting of the commingled odors of all the members of the colony and used to distinguish their nest from those of aliens. Miss Fielde (1903) says that the odor of ants changes with their age, and that "A cause of feud between ants of the same species living in different communities is a difference of odor arising out of difference of age in the queens whose progeny constitutes the communities, and difference of age in the ants composing the community." She calls this odor the "progressive" odor and further (1904) claims that "Fear and hostility are excited in the ant by an ant-odor which she [the ant] has not individually encountered and found to be compatible with her comfort." The same author (1905) calls the family or "inherent" odor the "specific" odor which is transmitted by the mother ant to all her offspring of both sexes within the species. Miss Fielde claims that ants not only differentiate the innate odors peculiar to the species, sex, caste, and individual, but also the "incurred" odor of the nest and environment, and furthermore they can detect "progressive" odors, due to change of physiological condition with the age of the individual. She says that "as worker ants advance in age their progressive odor intensifies or changes to such a degree that they may be said to attain a new odor every two or three months."

Wheeler (1913, p. 182) writing about the odors of ants says:

> The specific odor may be readily detected even by the blunted human olfactories. Thus the odor of *Formica rufa* is pungent and ethereal, of *Hypoclinca gagates* and *mariæ* smoky, of *Acanthomyops* like the lemon geranium or oil of citronella, of the species of *Eciton* and some *Pheidole,* like mammalian excrement, of *Cremastogaster lineolata* fainter but equally unpleasant, of *Tapinoma* like rotten cocoa-nuts, etc. Undoubtedly ants are very quick to react to these various odors as well as to the "nest-aura," or odor which every colony derives from its immediate environment, brood, etc.

Concluding from the experiments on ants made by various observers, the family odor in these insects seems to play an important rôle by enabling the offspring of one queen to distinguish members of their family from those of alien families. Relative to ants the family odor is probably as important as is the nest odor, but in the honey-bee where certain social habits have been advanced to a higher degree, the family odor is of little or no use, because the hive odor has assumed such an important rôle in the recognition of the members of the same or of a different colony. Each colony of bees has its own hive odor and a small portion of which adheres to the body of each member of that colony, so that a bee is never entirely devoid of the hive odor. Should workers be forced to remain in the open air for at least three days, which is scarcely possible, they would lose their hive odor, and should they try to enter their own hive they would be attacked by their sister guards because the family odor emitted by them would not be a sufficient proof to the guards that they were friends; of course if the guards had also lost their hive odor, they would let these sisters enter unmolested.

Howlett (1915), endeavoring to lure the fruit fly, *Bactrocera* (*Dacus*), by using various chemicals, gives the following three probable explanations why the male flies are attracted so remarkably to methyl-eugenol and iso-eugenol: (1) The odors emitted from these substances may closely resemble the odors emitted by the females, and therefore they would serve as a sexual guide; (2) these odors may also resemble those emitted by certain plants, and in this case they would attract the females to the proper plants for breeding purposes; and (3) in a second case the odors would attract both sexes to these plants in order that the insects obtain suitable food.

C. SUMMARY OF ODORS EMITTED BY INSECTS[1]

It is certain that a queen gives off an odor, and it seems reasonable that the odors from any two queens would be slightly different. All the offspring of the same queen seem to inherit a particular odor from her. This odor, called the family odor, perhaps plays little or no part in the lives of bees, for it is certainly masked by the other odors. Drones seem to emit an odor peculiar to their sex, but little can be said about it. It seems certain that each worker emits an individual odor which is different from that of any other worker. It is also probable that the wax generators and nurse bees emit odors slightly different from those of the field bees.

Of all the odors produced by bees, the hive odor is probably the most important. It seems to be the fundamental factor or principle upon which the social life of a colony of bees depends, and perhaps upon which the social habit was acquired; without it a colony of bees could not exist. The hive odor is composed chiefly of the individual odors from all the workers in a hive, and is supplemented by the odors from the queen, drones, combs, frames and walls of the hive, etc. From this definition it is easily understood why no two colonies have the same hive odor. The hive odor of a queenless colony is perhaps considerably different from that of a colony which has a queen. The absence of a queen odor in the hive odor probably explains why the workers in a queenless colony are irritable and never work normally. All the bees—workers, queen, and drones—in a colony carry the hive odor of that colony on their bodies among the hairs. This odor serves as a sign or mark by which all the occupants of a hive know one another. Since the queen and drones are "aristocrats," they seem to disregard the sign that has been thrust upon them, but whenever a queen enters the wrong hive, she soon "realizes" that she wears the wrong badge.

Worker bees returning to the hives from the field pass the guards unmolested, because they carry the proper sign, although the hive odor that they carry is fainter than when they left the hive, and it is also partially masked by the odors from the nectar and pollen carried by these bees.

Bees kept in the open air for three days lose all the hive odor carried on their bodies, but each bee still emits its individual odor. When a colony is divided the hive odor in each half soon changes

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[1] A part of this summary has already been published in the Amer. Bee Jour., July, 1916, pp. 232 and 233, and in the Roots' revised ABC and XYZ of Bee Culture, 1917, pp. 639 and 640.

so that by the end of the third day the original colony possesses a hive odor so different from that of the other half of the colony, that when the workers are removed from the two new colonies and are placed together in observation cases, they fight one another as though they had been separated all their lives.

While a foreign hive odor calls forth the fighting spirit in workers, the queen odor always seems pleasant to workers regardless of whether the queen belongs to their hive or to another hive. Even though the queen odor forms a part of the hive odor, it is probable that this odor to the workers stands out quite prominently from the hive odor. That workers do not miss their queen for some time after she has left the hive, indicates that her odor thoroughly permeates the hive odor and that whenever this odor grows faint the workers "know" that she is not among them.

There has been much speculation concerning the ruling spirit or power in a colony of bees. The present writer is inclined to believe that a normal hive odor serves such a purpose. The hive odor is a means of preserving the social life of the bees from without, and the queen odor which is a part of it insures continuation of the social life within. As already stated the workers "know" their hive-mates by the hive odor they carry. This odor insures harmony and a united defense when an enemy attacks the colony. The queen odor constantly informs the workers that their queen is present. Even though she does not rule, her presence means everything to the bees in perpetuating the colony. Thus by obeying the stimuli of the hive odor and queen odor, and being guided by instinct, a colony of bees perhaps could not want a better ruler.

All insects apparently emit odors, but only those of honey-bees and ants have been carefully studied; while the family odor among ants seems to play an important rôle, it is probably of little or no use among bees, because the hive odor has assumed such an important part in recognizing the members of the same or of a different colony. The progressive odor among ants is perhaps more highly developed than it is among bees, because the duties of ants are more varied than are those of bees and since slavery among ants is common.

SCENT-PRODUCING ORGANS OF INSECTS

In the preceding pages it is shown that insects, particularly ants and bees, recognize one another chiefly by means of odors, and since this is true they must have some means of producing these odors, because a hard substance like chitin is practically odorless to us and certainly is not a good source of odors for insects. At first thought it might be argued that the blood of insects serves as a source for all odors, for the blood of different insects probably gives off slightly different odors, but it has never been shown that the blood of insects actually comes to the surface of the body; that the blood comes to the surface is more impossible for insects, owing to their chitinous covering, than it is for the higher animals. Of course devices for the blood to come to the surface might have been evolved, but after understanding the structure of the various types of scent-producing organs it will be seen that a much better specialization has been brought about, and instead of an insect pouring its vital fluid upon its external surface, gland cells have been evolved to extract the best constituents from the blood to serve as a source for odors; according to this specialization a smaller amount of liquid is required, because its volatility and ability to produce effective odors has been many times increased.

A. Scent-Producing Organ of Honey-Bee

It is reported that Nassonoff first described the morphology of the scent-producing organ of the honey-bee. His original work in Russian can not be had here, but acording to Zoubareff (1883), Nassonoff did not describe the structure of this organ as seen by the present writer (1914), and he suggested that the gland cells of the organ produce perspiration. Sladen (1902) called this organ a "scent-producing" organ, but did nothing more than to describe the articular membrane between the fifth and sixth abdominal terga (propodeum not counted) of worker bees.

Externally this organ appears as a white transverse stripe near the distal end of the abdomen, but is visible externally only in worker bees that are fanning, however, it is present in all workers and queens, but has never been found in drones. The white stripe is the articular membrane and it is so folded that it forms a pouch which encircles about one-half of the abdomen and terminates on either side of the abdomen just above the articulation of the tergum and sternum. Just beneath the pouch lie many unicellular glands, each of which is connected with the bottom of the pouch by means of a chitinous tube through which the secretion passes into the pouch. The gland cells are modified hypodermal cells; they are granular and have conspicuous nuclei which contain many globular, refractive bodies. Each chitinous tube arises in the cell at the center of a clear area, the ampulla, which contains many radial streaks.

Judging from the morphology, we may reasonably conclude that the gland cells secrete a substance throughout their cytoplasm. This substance collects in the ampulla which serves as a reservoir, and from the ampulla the secretion passes through the chitinous tube to the exterior where it runs into the pouch. That the gland cells secrete an odorous substance is shown by the fact that when the articular membranes forming the pouches are excised, they appear wet and give off the characteristic bee odor, while the other articular membranes neither appear wet nor emit an odor. This view is further supported by the following: A virgin queen, emitting a very sweet and pleasant odor, was severed between the thorax and abdomen; when tested the thorax did not emit the sweet odor, while the abdomen did. The abdomen was then split into dorsal and ventral halves, and when tested only the dorsal half gave off the sweet odor. The dorsal half was next severed between the fourth and fifth terga, and in this case the portion containing the last two terga emitted a sweeter odor than did the other portion.

The groovelike indentations in the chitin forming the pouch may serve two purposes: (1) To give more flexibility to the chitin, and (2) to retain the volatile secretion and to help prevent a too rapid evaporation of it. So long as the abdomen is straight, the pouch is well protected and the liquid can not evaporate rapidly, but when the abdomen is considerably bent, the entire pouch is more or less exposed to the outside air.

The gland cells in old workers and queens are highly developed and are proportionately the same size, but the size of them increases little after the bees have emerged, and not until a few days later do they function in full capacity, judging from the fact that the odor emitted by workers just emerged gradually becomes more pronounced up to the fifth or sixth day.

The present writer failed to find gland cells connected with the articular membranes in the abdomens of drones, but they were not looked for elsewhere, and it is possible that some kind of a scent-producing organ may yet be found in drones. This assumption seems reasonable for sometimes when the abdomens of young drones are slightly squeezed, a very thin and whitish liquid may be seen on the abdominal articular membranes. At other times a clear liquid may be observed on the articular membranes between the fourth and fifth, and fifth and sixth abdominal terga; and it has already been stated that drones emit a faint sweetish odor.

B. Scent-Producing Organs of Other Insects

A complete review of the literature pertaining to the scent-producing organs of insects has never been presented. Packard (1895, 1903) gives a fair review of this literature up to 1898, and Deegener (1912) briefly discusses the most important papers on this subject appearing between 1898 and 1912, but still the review is far from being complete. It is hoped that a good review of the work already done on this subject will aid and encourage future investigators who care to continue work along this line.

Deegener (1912), briefly reviewing the literature concerning the scent-producing organs of insects, divides them into the three following divisions: (1) Stink glands are found in Forficulidæ, Orthoptera, Hemiptera, Neuroptera, Lepidoptera, and Coleoptera, and reflex bleeding occurs in Coleoptera, Orthoptera, and Hymenoptera; (2) scent glands are found in Lepidoptera in general, and in other insects as Trichoptera, Coleoptera, and Apis; and (3) defense glands are separated from the stink glands only with difficulty.

Packard has divided these organs into repugnatorial and alluring organs, and a third class including those for recognition only might also be added. Since it is usually impossible to determine whether such organs are used primarily for defense, to allure, or for recognition, the present writer has called all of them scent-producing, for in perhaps most cases it is the odors produced that renders them of primary value; and he has not attempted any classification other than to divide them on the basis of their distribution, which is a convenient method for description. This review deals only with the literature pertaining to the scent-producing organs of imago insects, and does not include those papers dealing with these organs in larvæ.

1. UNICELLULAR GLANDS WIDELY DISTRIBUTED OVER THE BODY SURFACE OF BEETLES, ETC., AS SCENT-PRODUCING ORGANS

Aubé (1837) observed that a fetid and colorless fluid oozes from the surface of the elytra and thorax of beetles. This secretion is produced only when the insect is irritated and a moment after the irritation the insect is covered with many small drops of the liquid.

Burnett (1854) asserts that in some beetles the secretion is emitted from all parts of the body surface. In bugs the liquid is secreted by a single, yellow or red pyriform gland situated in the center of the metathorax, and opens between the posterior legs. In Formicidæ there is an anal gland which ejects a caustic and acrid fluid; this gland is simple and is composed of one reservoir whose neck opens into a simple tube.

Hoffbauer (1892) who has made a special study of these glands in the elytra and pronotum of beetles, thinks that their secretion is probably for protection and he divides them into simple and compound glands. A compound gland is nothing more than a collection of the unicellular simple glands. The efferent canal may be either narrow, flaskshaped, or champagne-corklike, and it may or may not come to the surface at the base of a hair. Each gland cell may or may not possess a small reservoir.

Cuénot (1896b) asserts that when the beetles, *Melasoma populi* and *M. tremulæ,* are irritated an odorous and opaline liquid may be seen on the elytra. This liquid is secreted by unicellular glands grouped in rosettes around a common efferent canal. These glands are found in the thickened portion of the elytron at the basal end. He regards the liquid secreted as an important means of defense.

Tower (1903) found simple and compound glands in beetles varying a great deal in complexity.

> The simplest glands are single hypodermal cells modified for a glandular function, and are uniformly distributed over the entire body surface. In the elytron they arise in the pupal stage by the direct modification of one of the hypodermal cells of the wing lamella.

Instead of a gland opening at the bottom of a pit, it often opens at the top of a cone or stalk situated in a pit. In regard to the compound glands he says:

> I suspect that these large glands of *Leptinotarsa decemlineata* are the cause of the peculiar odor that insect possesses which renders it obnoxious to most insectivorous animals. These glands persist in full functional activity as long as the beetle lives, although the hypodermis and unicellular glands will long since have degenerated.

Casper (1913) found hypodermal glands widely distributed over the entire body surface and legs of *Dytiscus marginalis,* and Lehr (1914), who resumed the search for hypodermal glands in other parts of the same insect, found them widely distributed in the wings and elytra.

The present writer (1916b) found unicellular glands widely distributed over the thorax, abdomen, legs, and elytra of the coccinellid beetle, *Epilachna borealis.* The wings contain none of these glands and the head with its appendages were not examined. Each gland cell lies beneath a pore in the chitin, and each pore possesses a spherical reservoir, from which runs an efferent canal to the exterior.

A chitinous tube passing through the inner portion of the pore connects the ampulla in the cell with the reservoir. The secretion is easily seen on the surface of the chitin; it has a bitter taste and emits a repugnant odor. For more details concerning the secretion and the structure of the gland cells see page 51.

Under the foregoing heading may be mentioned the wax glands, and the adhesive glands in the tarsi of various insects. While the primary function of these glands is certainly to produce wax and to enable insects to walk on smooth perpendicular surfaces, a secondary use is probably that of recognition; in regard to insects that follow their trails, for example ants, the secondary use seems quite plausible. For details concerning all these glands the reader is referred to Dreyling's paper (1906) on the wax glands of bees; to Packard (1903, p. 362) and others for information concerning the wax glands of Aphididæ and Coccidæ; to Packard (p. 111), Schröder (1912, pp. 10-13) and others for description of the unicellular glands in the feet of various insects.

2. CARUNCLES AS SCENT-PRODUCING ORGANS

(a) CARUNCLES OF A BEETLE

Laboulbène (1858) describes some caruncular structures in *Malachius bipustulatus* as being two pairs of beautifully red organs. They are remarkably large, soft, eversible, Y-shaped and are thrust out from the sides of the first and third thoracic segments. He was unable to detect an odor emitted from a single insect, but when several live insects had remained in a glass tube for a short time he detected a slight odor. When irritated these beetles evert the caruncles and direct them toward the enemy. He imagines that these organs emit an insensible odor to us, but a perceptible one to their enemies and that they are organs of defense.

Liegel (1878) was the first to describe the anatomy of the caruncles of *Malachius*. He asserts that they are everted by blood pressure and are retracted by muscles. Since he failed to find glands in them, he refutes the view that Laboulbène advances, and he thinks that they aid in respiration.

(b) CARUNCLES OF A COCKROACH

Gerstaecker (1861) describes a peculiar organ in the Indian cockroach, *Corydia*. This organ in both sexes consists of two pairs of caruncular, evaginated saclike appendages which are located on the pleura of the first and second abdominal segments. He thinks that they are perhaps similar in function to the caruncles described by Laboulbène.

Haase (1889a) says that the delicate chitin of these evaginated sacs is covered with finely netted ridges and that secreting tubules carry the secretion of the unicellular glands to the exterior through fine pores.

Klemensiewicz (1882) found oblong unicellular glands lying just beneath the hypodermis of the caruncles in the same species that the above two writers examined. The external end of each cell is attenuated and passes through the hypodermis and chitin. An efferent canal leads from the exterior opening and ends in the cell near the nucleus.

At this place might be mentioned the function of the cornicles of aphids. According to the latest researches, the aphids smear the secretion from these tubules on their enemies; the secretion thus has a protective function and perhaps its odors are also repellent (Wheeler, 1913, pp. 343-346).

3. PALPI OF A TRICHOPTERON AS SCENT-PRODUCING ORGANS

Müller (1887) says that each male of *Sericostoma personatum* that he held under his nose emitted a distinct odor resembling the odor from vanilla, and he thinks that this odor came from the wide maxillary palpi. Instead of the male palpus having four long joints as found in that of the female, it has but one joint and this is ladlelike with a flange on all sides. Inside the flange the surface of the ladlelike joint is covered with a tuft of fine hair. When males and females were kept together in a large vessel he noticed that a male placed himself against a female whereby the tuft of hair unfolded. He regards the hair and flange as a means for preventing a too rapid evaporation of the odoriferous secretion which he imagines comes from the interior of the joint, although he did not work out the anatomy of this organ.

4. GLANDS IN THORAX AS SCENT-PRODUCING ORGANS

(a) GLANDS IN PROTHORAX OF WALKING-STICKS

Scudder (1876) says that both sexes of *Anisomorpha buprestoides* are able to spurt a strong fluid or vapor from a pair of pores on the thorax; he considers this as a means of defense. Each pore lies at the bottom of a large deep pit on either side of the upper anterior surface of the prothorax. In *Diapheromera* the pores are smaller and do not occupy a position along the dorsum in which they are found in *Anisomorpha* and *Autolyca*. In *Autolyca pallidicornis* each of the two glands is a straight, ribbonlike blind sac with stout walls. It extends from the posterior extremity of the mesothorax where it is broadly rounded to the anterior part of the prothorax where it is cylindrical. Here the secretion comes to the exterior through the slitlike aperture.

Haase (1889b) considers the preceding means of defense as an argument against the doctrine of Wallace and Poulton. According to this doctrine the non-edible species are not eaten, presumably because they have a glaring defensive color. Walking-sticks do not have such an appearance and yet are not eaten, for they defend themselves by use of stink glands.

Maynard (1889) also asserts that both sexes of *Anisomorpha buprestoides,* when irritated, are able to squirt two streams of a vaporous fluid 6 inches from the prothorax. When expelled the liquid is milky but almost instantly it changes to a vapor and has a pungent or peppery odor.

(b) GLANDS IN METATHORAX OF CERTAIN HEMIPTERA

Leidy (1847) describes the odoriferous glands of the electric light bug, *Belostoma,* as follows:

> These consist of two moderately long cœcal tubes situated within the metathorax, beneath the other viscera, and extending into the anterior part of the abdomen. They are convoluted together in such a manner, that after one or two turns the closed extremity is brought close to the termination, both of which extremities are concealed by the passage over them of the ventral cord. They open externally between the coxæ of the posterior legs.

Leidy (1849) describes the odoriferous glands of Hemiptera as follows:

> In Hemipterous insects these bodies are situated within the posterior part of the metathorax or anterior part of the abdomen, and consist of one or two, more or less long and convoluted cœca, which open exteriorly, usually between the coxæ of the middle and posterior legs.

Künckel (1866) asserts that the scent-producing organ of *Pentatomidæ* consists of a sac in the ventro-anterior portion of the abdomen. The sac opens to the exterior through two ostioles in the metathorax near the base of the hind pair of legs. The same author (1895) says that the Cimicidæ, Pentatomidæ, Coreidæ, and Lygæidæ are provided with two systems of scent-producing organs. The larvæ and nymphs have a tergo-abdominal system and the adults have a sternal metathoracic system like the one described above. Künckel (1886) claims that the repugnant odor of young bed bugs, *Cimex* *dectularius,* comes from three invaginated sacs. These sacs lie just beneath the first three abdominal terga. Each opens to the exterior in the articular membrane by a pair of round apertures, one of which lies near and on either side of the median line. Gissler (1890) figures the scent-producing organ of the nymph of the common pine aphid, *Lachnus strobi.* Here an external opening of the gland lies on either side of the fifth abdominal tergum.

Mayer (1874) found a quite complicated scent organ in *Pyrrhocoris apterus.* Close to the median line of the metathoracic sternum, a slit opens into a saclike cavity. Midway between the two ends of this cavity a flask-shaped vessel, the reservoir, leads off at right angles. The kidney-shaped gland lies between the reservoir and the integument; the collecting tube, whose free end is dichotomously forked, passes lengthwise through the center of the gland and unites with the neck of the flask-shaped reservoir. The walls of the gland are composed of oblong secreting cells. In the inner end of each cell a secreting tubule arises flasklike and runs into the collecting tube. The secretion is stored in the reservoir, and except when the insect is irritated is prevented from escaping into the saclike cavity by a valvelike apparatus. A sweet odor similar to that from chloroform is emitted from this organ.

(c) GLANDS IN THORAX OF BEETLES

Lacordaire (1838) reports that *Dytiscus* and *Gyrinus,* when picked up, emit through the articulations between the head and prothorax, between the latter and the mesothorax and between the metathorax and abdomen a milky and fetid liquid.

Plateau (1876) noticed that *Dytiscus* and *Acilius* emit, sometimes at the same moment, two different kinds of liquids. The one having a milky appearance issues from between the head and the tergite of the prothorax, the other is yellowish and exudes from between the meso- and metathorax. At each place where the liquid is emitted the secretory organ is composed of many unicellular glands which lie just beneath the hypodermis. The milky liquid is not venomous and thus can not be used in the capture of prey, and also it probably does not aid the sexes to find each other, because it does not have a pronounced odor. It can not be a means of defense because it is neither acid, nor strongly odorous and the quantity secreted is entirely too small for this purpose. The yellowish liquid perhaps forms an attractive coat on the surface of the body.

(d) GLANDS IN THORAX OF CERTAIN MOTHS

Fenn (1890) reports "that *Liparis salicis* has the power, when annoyed, of ejecting a pale greenish or yellowish fluid from (apparently) glands, situated on the thorax above the eyes." In *Arctia caia* there are two glands located just in front of the red "collar" of the thorax and they secrete drops of greenish fluid, which is acrid and is distasteful to birds.

Reid (1891) reports that acrid glands are possessed by a number of Lepidoptera besides the above named species, but he thinks that the secretion is to soften the cocoons so that the imagoes may more easily emerge, rather than primarily to serve as a protective fluid during the adult life.

5. ANDROCONIA OR SCENT SCALES OF MALE BUTTERFLIES AS SCENT-PRODUCING ORGANS

Deschamps (1835) was the first to study the scent scales of butterflies, although he credits the discovery of them to Baillif about 1825. Deschamps found them in 37 species, representing three genera. He called them plumules on account of their feathery tips and observed that they are much smaller than ordinary scales and are found only on the wings of insects.

In order that an intelligible description of the scent scales may be presented at the outset we shall quote Kellogg (1894) who says:

> The androconia are found almost without exception on the upper side of the wings, and are more commonly met with on the forewings than on the hindwings. They are often found in certain limited spots, or in folds of the wings. This is usually the case among the Nymphalidæ, a familar example being the pouch of the hindwings of *Danais archippus*. Among the Papilionidæ they are limited to folds on the wings, as those found along the inner margin of the hindwings of *Papilio*. In the Hesperidæ the androconia are found in costal folds or in the familiar discal spots or streaks. Among the Lycænidæ and Pieridæ they are most often scattered over the wing-surface being concealed in the general wing covering.

Mayer (1860) observed the scent scales while examining the "powder" on the wings of various butterflies.

Watson (1865a-b, 1868a-b) found the scent scales usually on the upper side of the wings of males. He found them in 507 species, representing 30 genera, belonging to six families. He asserts that these scales are so constant in different individuals of the same species as to be of valuable use in taxonomy. He thinks that they are to aid in respiration and also may be inflated with air and thus serve as a buoyancy.

Wonfor (1868, 1869) found these scales on the wings of males, belonging to several genera and he regards them as a sexual character.

McIntire (1871) reports having distinguished these scales from the ordinary ones.

Anthony (1872) also distinguished these scales from the other kind.

Müller (1877b) says that the male butterflies of the many species which he examined are distinguished from their respective females by the presence of these peculiar scales on the wings. The same author (1877c-d, 1878e) asserts that many male butterflies smell their respective females from an unbelievable distance. He thinks that an odor is emitted from these scales, and for this reason calls them "Duftschuppen." From the manner in which they are grouped he regards them as a good device for collecting the secreted liquid and for preventing a too rapid evaporation of it. Their generic differences are considerable and they vary somewhat in shape on the front and hind wings of the same species, but their specific differences as a whole are insignificant. He regards them as a secondary sexual character. Müller (1878f, 1879a) describes the scent scales found in the feltlike spots on the upper side of the male wings of three more genera.

Scudder (1877, 1881) asserts that these scales should be called androconia because only the males have them. He says:

> These androconia are very capricious in their occurrence; a number of allied genera may possess them, while a single genus, as closely allied, may be quite destitute. . . . . In the highest butterflies, they are long, slender and invariably feathered at the tip. . . . . With the exception of the Heliconii, they may generally be distinguished from ordinary scales by the absence of any dentation at the tip. In the *Voracia,* they are fringed, and, with a single known exception, their extreme base is expanded into a sort of bulb; elsewhere, even in the other Pierids, they are not fringed, but have a smooth rounded edge. . . . . In the Equites where also they have been supposed to be wanting they differ but little from the ordinary scales but are much smaller and more coarsely striate. In the *Urbiculæ,* where no one has hitherto recognized them, they present the greatest variety in the same individuals; in one group (Hesperides) there are hairlike androconia, and others which are exceedingly large and spindle-shaped. In the Astyei, besides hairlike and gigantic androconia, there are usually some which are spoon-shaped, with long handles.

Weismann (1878) predicts that an etherlike oil is secreted in the cells surrounding the bases of the scent scales. He imagines that this secretion passes through the scales to the exterior because the structure of the scales indicates a conducting device. The simplest type of these scales is hairlike and it is penetrated by a single axial canal, which opens freely at the tip. Another type possesses many longitudinal canals whose external openings lie at the tip of the fringe that crowns the scale, or the surface of the scale is perforated by fine holes like a sieve. The odor that comes from a wing may be likened to that from a lemon, or a balm-tree blossom.

Aurivillius (1880a-b) calls these scales a secondary sexual character and based on their shape he has divided them into seven different types. This author found them in 110 species, representing seven families.

Von Dalla Torre (1885) says that the females of many lepidopterous insects give out odors perceptible to the males, and thereby induce copulation. It seems proven that by extending the ovipositor the female can cause the dissemination of the odor which attracts the male. In all male specimens of *Callidryas argante* examined, a musky odor was emitted from the scales when exposed on the wings. In *Prepona lærtes* the odor is like that from a bat, and in *Dircenna xantho* it resembles that from vanilla. That we are unable to perceive a distinct odor from these scales in every species does not argue against the idea that the scales emit an odor, because the sense of smell is much more highly developed in the Lepidoptera than in man.

Haase (1886b, 1887, 1888a-b) made a special study of the scent scales of many families belonging to the Indo-Australian butterflies. He found them usually grouped in brightly colored felt patches and considers them as a secondary sexual character. The odor emitted by several species is similar to that from vanilla. The scales lie so protected while at rest that an unnecessarily rapid evaporation is prevented.

Thomas (1893) says: "When scattered irregularly over the wing they are always underneath the large scales and therefore well protected." He was the first to prove by making sections through the wing that a secreting cell lies at the base of each scale. There is often a canal extending from the base to the tip of the scale where the secretion may find a direct outlet, or it may disappear in the spongy mass found at the end of these androconia.

Kellogg (1894) caught a male of *Pieris rapæ,* and after rubbing the upper surface of the front wing with the finger, he then smelled his finger and at once perceived a distinctly pleasing aromatic odor. This test therefore proves that the scales emit an odor.

Spuler (1895) shows that the dorsal surface of a scale is usually covered with many longitudinally parallel ridges while the ventral surface is smooth. There are also sometimes smaller transversely parallel ridges. The chitinous layers of the two surfaces are held in place by many chitinous supports. The peduncle of the scale is hollow and its cavity is connected with those between the chitinous supports. According to his drawings the above characteristics hold good for both the ordinary scales and scent scales.

Leoni (1898) observed that *Pieris napi* and *Colias hyale* emit a delicious odor from the dorsal surface of the wings.

Köhler (1900) does not attribute a great significance to the scent scales, because while present on the wings of 78 species of *Lycæna,* they are wanting in 32 species of the same genus. He also says that the name androconia is not appropriate, because he has observed a few scent scales in a female belonging to this genus.

Guenther (1901) found that some of the scales on the wings are innervated while others are furnished with gland cells, however, he believes that all of the scales are probably innervated.

Illig (1902), who has prepared a comprehensive monograph on the morphology of the scent-producing organs of insects asserts that the peduncle of each scent scale arises from a flask-shaped socket in which the neck of the flask is quite wide. The inserted end of the peduncle is open and it extends through and slightly beyond the bottom of the flask. A large gland cell lies just beneath and against the base of the flask. Many chitinous ridges running parallel the full length of the scale lie on the dorsal surface, whereas the ventral surface is smooth. The two sides of the scale are firmly held in place by many chitinous supports. The interior of the peduncle and the cavities between the supports are filled with a netlike contents or matrix. In the feathered type the scales are tipped with hollow hairs while in the other types myriads of small pores are found between the parallel ridges. These pores run through the chitinous layer and communicate with the internal matrix. The secretion from the gland cell passes through the matrix in the peduncle and into the matrix which fills the cavities between the supports, then it slowly but gradually finds its way to the exterior, either through the hollow hairs at the tip or through the pores which are widely distributed over the dorsal surface of the scale.

Freiling (1909) has also carefully worked out the finer anatomy of various scent-producing organs of insects. The large gland cell at the base of each scent scale has a conspicuous nucleus, many vacuoles and some of them have a reservoir. From the reservoir runs a canal to the base of the peduncle where the secretion passes through definite canals through the matrix of the peduncle into the matrix of the scale, then it infiltrates through the pores and forms a film over the entire dorsal surface of the scale. The bases of some of the scent scales are innervated.

6. GLANDS AT FEMORA-TIBIAL ARTICULATIONS OF BEETLES AND ANTS AS SCENT-PRODUCING ORGANS

Lacordaire (1838) was one of the first investigators to describe the phenomenon of ejecting liquid from various parts of the body of certain insects. He says that when *Dytiscus* and *Gyrinus* are picked up, they emit through the articulations between the head, thorax, and abdomen a milky and fetid fluid. *Meloe* emits from the articulations of the legs a yellowish-orange liquid whose odor is not disagreeable. Coccinellidæ and Chrysomelidæ emit an analogous liquid at the same places, but it has a different odor and is quite strong.

Leydig (1859) was the first to make sections through the femoro-tibial articulations of *Timarcha, Coccinella,* and *Meloe.* He thinks that the discharged liquid is blood for the following seasons: (1) No gland cells nor glandular apparatus of any kind were recognized; (2) the discharged liquid and blood have the same color; and (3) the discharged liquid contains presumably blood cells. He admits that this view is not well founded because he could not find any openings in the articular membrane through which the blood could pass.

Magretti (1881) imagines that the discharged liquid from *Meloe* is secreted by gland cells in the legs.

Beauregard (1885) saw a layer of large hypodermal cells beneath the chitin in sections through the articulations of the legs of *Meloe.* He imagines that these large cells are gland cells.

De Bono (1889) believes that the discharged liquid from *Timarcha* is a glandular secretion.

Cuénot (1890) says that the discharged liquid from the legs of the meloid beetles, *Cantharis, Meloe, Mylabris,* and *Cerocoma,* is completely odorless, but it is slightly poisonous. He thinks that this liquid is blood, although he did not study sections passing through the articulations. The same author (1894) states that when one touches *Timarcha, Adimonia, Coccinella,* or *Meloe,* the beetles at once feign death. They fold the legs and antennæ under their bodies, fall to the ground and for a longer or shorter time assume a perfectly inactive attitude destined to deceive their enemies. At the moment when the insects roll on the ground, drops of a slightly viscid liquid are ejected from the mouths of *Timarcha* and *Adimonia,* but from the femoro-tibial articulations of the coccinellids and meloids. This liquid is yellowish or reddish in color. The discharged liquid of *Coccinella* has a strong and very disagreeable odor, and that of *Timarcha* is odorless, but has a persistent and astringent taste. He proved by experiments that this liquid is for defense.

The ejection of a liquid from the articulations of the rudimentary wings of certain Orthoptera has been studied by Cuénot (1896a) and others. Cuénot (1896b) summarizes his investigations by saying that *Timarcha, Galeruca, Megalopus,* coccinellids, and meloids among the Coleoptera, and *Eugaster* and *Ephippiger* among the Orthoptera possess the phenomenon of reflex bleeding. When disturbed they feign death and eject drops of blood from the mouth, femoro-tibial articulations and from the articulations of the first pair of wings. In all these species the blood comprises toxic, caustic, or repulsive products. It is an important means of defense against lizards and batrachians.

Lutz (1895) asserts that in the Coccinellidæ, blood coming from the distal end of the femur issues through a slit on either side of the articular membrane which surrounds the chitinous rods (Selane) to which the extensors of the tibia are attached. The blood exudes by a forced contraction of the abdomen and by the flexors of the tibia, and it is a voluntary act. It is a means of defense because the blood is actually quite repulsive to insectivorous animals. In *Timarcha, Meloe,* etc., as in the coccinellids, the device of ejecting blood from the femoro-tibial articulations is to permit the blood to escape from the legs rather than through the mouth.

Packard (1895) states that many beetles, such as the oil beetles *Meloe, Cantharis,* and *Lytta,* emit drops of blood from the femoro-tibial articulations as a means of defense. The cantharadine produced by these insects is formed in the blood and in the genital organs. It is so extremely caustic that scavenger insects feeding upon the dead bodies of these beetles leave untouched the parts containing cantharadine. Coccinellids are also protected by a yellow mucilaginous and disagreeable fluid which is emitted from the sides of the thorax.

Izquierdo (1896) says that liquids discharged by insects as a means of defense may be divided into three groups: (1) Those from organs which are furnished with glands. Such organs are found in all families of insects and their exits may be found in the thorax, abdomen, at the anus, or in the last portion of the intestine; (2) liquids which are discharged from the femoro-tibial articulations; and (3) liquids that are discharged from the mouth.

Porta (1903) says that the discharge of the secretion from *Coccinella, Timarcha,* and *Meloe* is caused by a reflex phenomenon brought about by any excitement. The liquid is secreted by a glandular follicle in the reticulum of connective tissue, which is situated in the wall of the middle intestine. The liquid has an acid reaction, and it is perhaps only a bile secretion. He gives three reasons why this liquid is not blood: (1) It is inadmissible that insects should constantly pass such an important fluid; (2) after a prolonged excitation the liquid ceases to exude; and (3) it has an acid reaction while we know that blood in all animals has an alkaline reaction. He fails to explain how this secretion reaches the exterior from where it is produced.

Berlese (1909) seems to think that the discharged liquid from *Meloe* is a mixture of blood and a secretion from hypodermal glands. In a diagram showing the anatomy of the leg at the femoro-tibial articulation, he figures a receptacle for containing the blood and shows how the blood is ejected through an aperture at this place in the leg. He also shows unicellular glands lying just beneath the hypodermis on both sides of the articulation. Each gland cell is almost spherical, has a conspicuous nucleus and a central vesicle, the ampulla, from which runs the efferent tube through the hypodermis and chitin to the exterior.

Schön (1911) found unicellular glands beneath the femoro-tibial articulations of *Camponotus* and the tibio-tarsal articulations of *Formica.*

The present writer (1916b) has examined the femoro-tibial articulations of the meloid beetles, *Cysteodemus armatus* and *Epicauta pennsylvanica,* and of the coccinellid beetle, *Epilachna borealis.* No slits nor openings, except gland pores, were seen in the femoro-tibial articulations of these beetles. As already mentioned on page 39, hypodermal gland pores are widely distributed over the integument of *Epilachna borealis.* Usually one, but sometimes two pores, lie near the base of almost every hair. Besides lying near the bases of the hairs, the pores on the tarsi and around the femoro-tibial articulations lie in groups. Two groups are located at the extreme proximal end of the tibia and two at the distal end of the femur around the articular membrane. All four groups contain 100 pores as an average. The articular membrane contains about 400 pores of another type.

These beetles always appear wet, and the more they are irritated the wetter they become. The wet appearance is caused by a hypodermal glandular secretion passing to the exterior through the pores. When irritated the beetles eject small drops of the amber-colored secretion from the femoro-tibial articulations through the four groups of pores near the articular membrane and those in the membrane. The discharge of the secretion is accomplished by putting the gland cells under a high blood pressure. This is made possible by a muscular contraction in the femur whereby the blood is forced into a specially devised chamber containing the gland cells which belong to the pores in and near the femoro-tibial articulation.

The gland cells are of two types: those with reservoirs are several times larger than those without reservoirs. The former are widely distributed throughout the entire insect, while the latter is found only under the articular membrane of the femoro-tibial articulation; in other respects the two types are alike. Each gland cell has an ampulla and a conducting tube which either runs from the ampulla to the reservoir in the chitin or from the ampulla to the surface of the articular membrane. An efferent tube leads from the reservoir to the surface of the chitin.

The glandular secretion is bitter and has an offensive odor. Its chief purpose is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species.

7. TUFTS OF HAIR ON TIBIÆ OF MALE MOTHS AS SCENT-PRODUCING ORGANS

Swinton (1877) observed tufts of hair on the tibiæ of the second pair of legs in various genera of Noctuidæ; on the tibiæ of the third pair of legs in various genera of Geometridæ, and on the tibiæ and first tarsal joint of the Deltoids. An odor is emitted from each of these tufts of hair.

Bertkau (1879a-b) found that the tarsi of the third pair of legs in the males of *Hepialus hecta* are completely aborted. The tibiæ are completely filled with elongated glands which open into pores in the chitin. From each pore arises a long scalelike hair. These hairs form a tuft on the inner side of the tibia and project slightly beyond the distal end of this segment. The same author (1882a) made sections through the tibiæ of *Hepialus hecta* and found large gland cells which are slightly club-shaped and reach entirely across the leg. Their nuclei lie in the broader ends of the cells while the narrower ends extend into the pores and communicate with the club-shaped hairs, which are firmly fastened in the pores by semicircular plates. The secretion of these unicellular glands is a volatile oil which runs into the hairs. The oil infiltrates through the upper surface of the hairs and may often be noticed as minute yellowish-green drops. The odor emitted is aromatic and quite noticeable.

Müller (1879b) found a scent-producing organ on the inner side of the tibia of the third pair of legs in the males of *Pantherodes pardalaria*. The tuft of long hair lies in a groove and may be spread out fanlike. The same author (1879c) describes a similar organ on the tibia of a small species of *Erebidea*.

Bailey (1882) noticed fan-shaped brushes of hair on the legs of all the males of *Catocala* examined. He thinks that they may be aphrodisiac in function.

Barret (1882, 1892) detected an odor in the males of *Hepialus hectus,* which he thinks is emitted by the aborted hind legs. It is similar to the odor from ripe pineapples and it seems to attract the females. In every fresh male examined of *H. humuli* an odor was perceived, but in old ones no odor was detected. The same author (1886), while watching some males and females of *Hepialus hectus,* saw the females fly toward and against the males and he thinks that they were attracted by the odor from the males.

Edwards (1882) reports that he has seen these tufts of hair in the males of *Parthenos nubilis, Catocala desperata,* and *C. amatrix*.

Kirby (1882) reports that he noticed fanlike tufts of hair on the front legs of *Catocala fraxini*.

Johnson (1891), while watching a male and female of *Hepialus lupulinus* pairing in the air, thought without the slightest doubt that the female throws off a faint odor and that the vibration of the wings assists in diffusing it.

Deegener (1902) says that the tibiæ of the third pair of legs in the males of *Hepialus hectus* are greatly swollen. They are club-shaped with the distal end the broader. The interior of the tibia is filled with large gland cells which stand at right angles to the pore field; between the gland cells are spaces filled with blood. A spatula-shaped hair, arising from the bottom of each pore, has longitudinally parallel ridges on the surface similar to those on the upper surface of the scales of butterfly wings. Between the upper and lower chitinous walls of a hair are canals to convey the liquid secreted by the gland cells. The same author (1905) describes a similar organ in the males of *Phassus schamyl*. Instead of the hairs in this species being spatula-shaped, they are usually scalelike with the distal end divided into two or three lobes. They have both the longitudinally and transversely parallel ridges. It may be assumed that the liquid secreted by each large gland cell passes through the pore into the cavity of the scale which is filled with a granular matrix and then it infiltrates to the exterior through pores that are closed with very thin chitin. It may also be assumed that some of the secretion passes out of the pore around the base of the scale and then runs down the surface of the scale between the ridges. He thinks, therefore, that the scales are a means of spreading the liquid over a large area for quick evaporation.

Illig (1902) describes the scent-producing organs in the males of *Syrichthus malvæ* as fan-shaped tufts of long and slender hairs which lie on the proximal ends of the tibiæ of the hind legs. Muscle fibers are attached to the bases of these hairs to move them and a large gland cell lies at the base of each hair. Since the hairs do not open at their tips, the secretion evidently comes to the exterior through the pores around the bases of the hairs; but on the surface of the spatula-shaped hairs of *Hepialus hecta* he thinks that he saw fine pores through which the secretion probably issues. In *Pechipogon barbalis* the scent-producing organ consists of three tufts of hair on the front legs. The largest tuft lies at the distal end of the femur; one of the smaller ones midway between the ends of the tibia, and the other small tuft at the distal end of the tibia. The morphology of these three tufts and of their unicellular glands is very similar to that of *Syrichthus malvæ*.

8. PAIR OF LATERAL TUFTS OF HAIR AT ANTERIOR END OF ABDOMEN OF MALE MOTHS AS SCENT-PRODUCING ORGANS

Stefanelli (1870) says that only the males of *Sphinx convolvuli* emit an odor. The odor is strong but agreeable, resembling amber or musk. It comes from two lateral grooves on the first abdominal segment. The openings of the grooves are guarded by bunches of yellowish hair.

Tozzetti (1870) describes the scent-producing organ of the same species as follows: It consists of a pair of deep grooves, each one of which lies in the pleura of the first and second abdominal segments on either side. The groove is filled with long, slender, scalelike hairs. Each hair has a peculiar ringlike base whose lowermost portion extends into a long process which is inserted into a chitinous socket. Beneath the socket lies a unicellular gland containing a large nucleus.

Swinton (1877) saw this organ in *Acidalia remutata* and during copulation he observed that it expands. He also noticed it in *Acherontia satanas;* here it may be expanded into a stellate shape and a pungent odor of jessamine is emitted.

Müller (1878a-b) ascertained that the strong musky odor of a certain Brazilian sphinx moth comes from the organ described above.

Arnhart (1879) found a similar organ in *Acherontia atropos.*

Fügner (1880) saw the same organ in *Sphinx ligustri.* The odor emitted is musklike.

Von Reichenau (1880a-b) first described this organ in *Sphinx ligustri.* He says that a muscle is attached to the base of the hairs so that they may be expanded. Each hair is hollow and is filled with a secretion emitting a musky odor.

Hall (1883) noticed that *Acherontia atropos* emits a musky odor when the thorax is compressed.

Bertkau (1884, 1887) describes this type of organ as a shallow pocket, lined with hairs, in the pleura of the first and second abdominal segments. The slit-shaped opening of this longitudinal pocket is securely closed by hairs and it lies near the posterior edge of the pleuron of the second segment. Muscle fibers are present at the bases of the hairs and at the bottom of the pocket. The chitin is perforated by many fine pores, and from each pore runs a secreting tubule to a unicellular gland which is a modified hypodermal cell.

Haase (1884, 1886a) calls this type of organ in *Acherontia* a secondary sexual character because it is found only in the males. The hairs serve chiefly to spread the volatile oil which issues from the pores at the bottom of the pocket. During a forced expiration the hairs spread out raylike and thus greatly increase the available surface to assure a quicker evaporation of the oil.

Pollack (1887) observed similar scent-producing organs in *Hadena atriplicis* and *H. litargyria.*

Illig (1902) considers this organ in *Acherontia atropos* and *Sphinx ligustri* as a bunch of hair lying in a longitudinal groove, located as already stated. A large unicellular gland is connected with the base of each hair. Since the surface of the hair has longitudinal ridges and because the chitin between these ridges at times appears porous, it may be assumed that the secretion infiltrates through the apparent pores.

9. VARIOUS STRUCTURES AT VENTRO-POSTERIOR END OF ABDOMEN OF CERTAIN LEPIDOPTERA AS SCENT-PRODUCING ORGANS

(a) INVAGINATED SACS, TUFTS OF HAIR AND SCENT GROOVE OF CERTAIN MOTHS

Morrison (1874) saw two long, pale-yellow and hairy appendages projecting from under the extreme end of the abdomen of a male *Leucarctia acreæ.*

Stretch, Grote and Weed (1883) report having seen these appendages in the same species. Weed also saw them in *Pyrrharctia isabella* and pronounces them scent-producing organs.

Smith (1886) also describes these appendages of *Leucarctia acreæ*. They project from a narrow opening between the seventh and eighth sterna, and when not protruded they form two invaginated sacs. They are lined with hairs and are united at the base where they are attached to the integument. When protruded the hairs are on the outside of the evaginated sacs. In *Pyrrharctia isabella* these organs are four snow-white tufts of hair and in both species an intense odor, somewhat like that of laudanum, is emitted when the sacs are evaginated.

Freiling (1909) asserts that the abdominal scent-producing organ in the female of *Taumatopoca pinivora* is a large paired tuft of hair on both sides and above the anus. In the female of *Stilpnotia salicis* this organ is also a paired scent tuft. In the female of *Orgyia antiqua* it is a scent groove between the eighth and ninth segments just above the anus; here the articular chitin is very thin and it is probably an elastic membrane. Under a high magnification he saw a small quantity of secretion on this membrane. The gland cells are modified hypodermal cells and they lie in groups like several bunches of grapes with their stems attached to a common base. The interior of each bunch is greatly vacuolated and a string of vacuoles extends into each cell. He thinks that the secretion passes from the individual cells through the center of the bunch to the thin membrane where it passes to the outside by infiltration, although he saw no pores in this chitinous membrane. This organ in the female of *Bombyx mori* consists of the "Sacculi laterales," so called by Techomirow, although he did not understand their function. Freiling considers these the most complete and most highly developed scent-producing organ found in any female lepidopteron. This organ is a pair of invaginated and greatly folded sacs; each sac lies on either side of the abdomen, and both of them unite and open to the exterior by a long groove between the eighth and ninth segments. The layer facing the lumen of the invaginated sac is a thin and soft chitinous membrane, and it is thickly studded with small prickles. The layer of the sac facing the body cavity of the abdomen is composed of a one-celled layer of unicellular glands which are greatly vacuolated. He thinks that the secretion from the glands infiltrates through the thin chitin to the exterior. These sacs are evaginated by blood pressure and are retracted by muscles. He proved experimentally that the females have a powerfully attractive force of some kind which causes the males to congregate around them, although he was never able to detect any odor coming from these sacs. With a piece of filter paper he drew some of the secretion from the outer surface of the evaginated sacs and then placed the paper in front of a freshly emerged male. The same reactions were obtained as when a male had been given access to a female in a box; at once the male threw himself upon the paper as if it were a female. While experimenting with silkworm moths, Kellogg (1907) obtained similar results and he says: "If the cut-out scent-glands are put by the side of and but a little apart from the female from which they are taken, the males always neglect the nearby live female and go directly to the scent-glands," and try to copulate with them.

(b) STYLED KNOBS AND INVAGINATED SACS OF CERTAIN BUTTERFLIES

Müller (1877a) regards a pair of small styled knobs, found only in the females of maracujá butterflies, as a scent-producing organ. In shape they are similar to the halteres of flies and lie on the posterior edge of the abdominal penultimate segment. The knobbed portion of the organ, which he thinks secretes a fluid, is covered with scales.

Illig (1902) says that the scent-producing organ in the male of *Danais pexippus* and *Euplœa* consists of two large chitinous, invaginated sacs, one of which lies on either side of the abdomen and opens to the exterior by a wide aperture between the seventh and eighth sterna. Scalelike hairs are attached to only the anterior portion of these sacs and a gland cell is found at the base of each hair. The secretion probably finds its way to the exterior through the socket around the base of the hair. This organ is evaginated by blood pressure and retracted by muscles.

Freiling (1909) says that in the female of *Gonopteryx rhamni* this organ is an invaginated sac lined with scalelike hairs, opening between the seventh and eighth sterna. In the female of *Euplœa asela* the organ consists of a circle of scalelike hairs on the eighth segment around the anus and of a pair of invaginated sacs lined with hairs. These sacs open to the exterior between the seventh and eighth sterna. In the males of *Euplœa asela* and *Danais septentrionales* this organ is a pair of invaginated sacs, one of which lies on either side of the abdomen with its external opening at one side of the anus between the seventh and eighth segments. Most of the scent hairs are attached to the anterior portion of the sac and when the sac is evaginated and the tuft of hair is expanded, this organ greatly resembles a cylindrical fan whose contents are turned inside out to form the circular part of the fan. Freiling asserts that scent hairs are more common than scent scales in abdominal scent-producing organs. A few of these hairs are innervated and vacuoles seem to be always absent in the large gland cells at the bases of the hairs, but a secreting tubule is invariably present. The scent hairs may have parallel ridges with myriads of fine pores in the chitin between the ridges, or they may have many stubby, thornlike projections, each of which is pierced by a small canal through which the secretion passes to the exterior. The scent hairs are filled with a matrix substance.

10. ANAL GLANDS AS SCENT-PRODUCING ORGANS

(a) ANAL GLANDS OF COCKROACHES

Bordas (1901) describes a voluminous organ in the posterior end of the abdomens of males belonging to *Periplaneta orientalis* and *P. americana*. This organ is a slender sac with a series of dichotomously branched tubes running into its anterior end. The posterior, or narrower end of the sac opens to the exterior by an oval aperture in a chitinous projection under the penis. The gland itself lies in the ventral portion of the abdominal cavity at the right, and all of its tubes are surrounded their full length by a layer of unicellular glands. A cross section of one of these tubes shows three layers in its wall as follows: (1) The outer layer is a thin membrane; (2) the middle one is a layer of trapezoidal gland cells; and (3) the inner one is the chitinous lining of the tube. Each gland cell has a large nucleus and a vesicle from which runs a filamentous, secreting tubule to the chitinous canal, the collecting tube. This gland secretes a volatile, strong and nauseating liquid, sometimes acrid and alliaceous, recalling the odor of a mouse or that from old cheese in decomposition; it secretes continuously but in time of danger its action is accelerated.

Harrison (1906) describes a supposedly new organ in *Periplaneta orientalis*. This glandular organ lies on the ventral side in the sixth abdominal segment and opens to the exterior between the sixth and seventh sterna. From the external opening the organ extends upward and forward as two distinct lobes.

(b) ANAL GLANDS OF BEETLES

Dufour (1811) first described the anal gland of the bombardier beetle, *Brachinus displosor*. This gland is paired and one half of it lies on either side of the abdominal cavity. Each half is divided into the three following parts: (1) The spherical reservoir lies under the last dorsal segment of the abdomen just under the rectum and opens at the side of the anus; (2) the preparator is a large saclike organ lying just behind the reservoir; and (3) the long threadlike duct is the anterior continuation of the preparator.

He found an organ similar to the preparator in several other carabids and also in *Blaps*. These beetles, when excited, discharge an acrid and caustic liquid through the two apertures near the anus. Dufour (1826) remarks that the Dytiscidæ are able to discharge a colorless and disagreeable fluid from the anus. Silphidæ emit from both the mouth and vent a fetid liquid having an ammoniacal odor; the members of this family have a single anal gland.

Meckel (1846) says that the reservoir of the anal gland in *Dytiscus* contains a yellowish-white emulsion. The secretion has a rancid odor, an acid reaction, and a defensive function. The gland cells are comparatively large, and in the collecting tubes leading from these cells may be seen drops of the secretion. In *Carabus auratus, C. coucellatus,* and *Chlænius vestitus* the gland consists of grapelike bunches; in *Chlænius velutionus* of three short, broad sacs which empty into a canal (the efferent canal) leading to the exterior; in *Aptinus* the gland is five lobed; in *Brachinus* it consists of convolutions of blind sacs which unite at a common point with the efferent canal; in *Bombylius* and the water beetles the gland is a long, convoluted, and closed vessel.

Karsten (1848) remarks that this organ in *Brachinus complanatus* is paired. Either external opening lies above and to one side of the anus, and the posterior end of either kidney-shaped reservoir communicates with its respective external opening. From the anterior end of the reservoir runs a collecting tube which soon divided into twelve glandular tubes, each one of which has a central canal, and its peripheral end is free. The gland cells are spindle-shaped and stand perpendicularly to the central canal, which is filled with a greenish fluid.

Candèze (1874) reports that certain carabid beetles throw a burning and extremely fetid liquid on their enemies.

Gissler (1879) remarks that the repugnatorial gland of *Eleodes gigantea* and *E. dentipes* is paired. The secretion has an intensely penetrating odor and causes the eyes to shed tears. When irritated, these beetles stand on their first two pairs of legs with the abdomen high in the air and the liquid is thrown right and left.

De Rougemont (1879) describes the organ causing the explosions in *Brachinus crepitans* as a paired structure in which the collecting tube is a double canal. Its inner tube which is filled with air is arranged spirally inside the cylindrical outer tube. The anterior end of this double tube is divided into two branches which are also filled with air and the walls of these branches are composed of gland cells. A brown liquid, butyric acid, is found in the reservoir. The author thinks that this acid is passive as long as it remains in the reservoir, but when it is discharged to the outside by the force of the condensed gas inside the collecting tube, it becomes active and produces a strong odor.

Bertkau (1882b) describes the anal gland of both sexes of the click beetle, *Tacon murinus,* as a saclike cavity which is protruded when its secretion is discharged; the sac is retracted by a muscle. The spherical gland cells lie in the walls of this large sac. The long, fine, and entwined secreting tubules arise beside the nuclei of the gland cells and several of them run into the sac at the same point. Each tubule begins as a faint swelling in the cytoplasm of the unicellular gland, but he noticed no vesicle. The lower portion of the sac serves as a reservoir where the secretion is collected.

Williston (1884) reports that when either sex of *Eleodes longicollis* is disturbed, it discharges a pungent and vile smelling fluid from the anal glands.

Townsend (1886) placed some carabids, *Calathus gregarius,* in a bottle, and subsequently the bottle was filled with white smoke, which he concludes was brought about by the anal glands.

Loman (1887) discovered that a beetle, *Cerapterus maculatus,* from Java causes loud explosions when the secretion of its anal glands is discharged. He found that this secretion, which is to guard off enemies, contains free iodine.

Gilson (1889a-b) describes the anal glands of *Blaps mortisaga* as two cylinders which unite to form a short tube. This tube opens at the lower part of the last intersegmental space of the abdomen. Each cylinder is a sac whose walls are covered with a large number of whitish lobes. While the sac is a reservoir, each lobe is a collection of unicellular glands. He says that these cells constitute the most complete type of unicellular glands and one of the most complicated forms of all cells. Besides having a conspicuous nucleus, each gland cell has a radiating vesicle, a central ampulla, a secreting tubule and a sheath around the tubule. The cytoplasm of the cell contains radial streaks which radiate toward the vesicle. The club-shaped ampulla arises at the center of the vesicle and runs to the outside of the vesicle where it continues as the secreting tubule, which winds about considerably, passing through the lumen of the lobe in order to open into the reservoir. The sheath of the tubule arises inside the cell but encloses the tubule for only a short distance. The secretion is an odorous oil in which swims a considerable number of crystalline and yellow needles.

Leydig (1890) says that the glands of *Anchomenus* deviate from those of *Brachinus* in that they do not consist of long pouches, but of round sacs similar to those in carabids. He is not certain how the secreting tubules arise in the cells; Leydig in 1859 was the first to describe the finer structure of these unicellular glands.

Pórter (1895) experimented with eight individuals of *Eriopis convexa* (Coccinellidæ), one of *Chelymorpha varians* (Chrysomelidæ) and five of *Læmosthenes complanatus* (Carabidæ). In all of these he concludes that the liquid emitted by or near (por) the anus is not the product of a secretion, but it is blood because this liquid and some blood taken directly from the dorsal blood vessel both contain corpuscles (leucocytes) of the same form, same dimensions, same coloration, similar micro-chemical reactions and the same amœboid movements.

Bordas (1898) describes the anal glands of Dytiscidæ as a very voluminous structure. They are paired and consist of two white, intestinelike tubes, wound into an ovoid mass and located in the last abdominal segments. The gland consists of the three following layers: (1) The outer one is a thin peritoneal membrane; (2) the middle one consists of muscular fibers; and (3) the inner one lining the lumen of the collecting tube is an epithelial layer composed of rectangular secreting cells. The collecting tube runs into a reservoir whose muscular layer is more powerful than that in the gland just mentioned. When excited, the insect discharges a yellowish liquid into the surrounding water, making a slight brownish cloud by the aid of which the insect may easily escape its enemy. The same author (1899a-b) says that when *Brachinus* is disturbed an acrid liquid is discharged which produces a crepitation; the liquid at once changes into a little cloud of pungent and corrosive vapors and the detonations may be repeated 10, 15, or 20 times in succession. He has studied these glands in several genera of Carabidæ and in each species he found grapelike unicellular glands, secreting tubules, a collecting tube, a reservoir, and an efferent canal leading into the cloaca. Bordas (1899c) asserts that 24 genera and 56 species of Coleoptera, representing the families and subfamilies—Cicindelidæ, Carabinæ, Harpalinæ, Feroniinæ, Brachininæ, Dytiscidæ, Gyrinidæ, Staphylinidæ, and Silphidæ possesses anal glands. Bordas (1899d) says that the collections of gland cells may be oblong, grapelike, or may form a solid layer around the collecting tubes their full length. Each unicellular gland has a central nucleus and a vesicle which lies near the inner end of the cell from which runs a secreting tubule to the lumen of the collection of cells. The collecting tubes are usually filamentous and tortuous; the reservoir is ovoid, oblong, or kidney-shaped, and the efferent canal may be long or short.

Dierckx (1899a-e), whose descriptions and drawings of the anal glands are the most comprehensive of all the researches pertaining to these particular structures, calls them the pygidial glands, because their external openings are a pair of apertures on the pygidium or the last abdominal segment. He used many species of Carabidæ and Dytiscidæ. Each unicellular gland possesses besides a nucleus, a spherical, cylindrical, pyriform-shaped, or multilobed, radial vesicle which communicates with the lumen of the collection of cells by a filamentous, intravesicular tubule. Near the external opening of the efferent canal he discovered a new gland which he calls the "glande annexe." This structure is also composed of unicellular glands with magnificent radial vesicles. These cells are arranged around the efferent canal into which the secreting tubules empty just at the exit. The secretion of the anal gland is colorless, has a faint odor, and is very volatile. In Dytiscidæ the pygidial gland is double. Each half consists of a long intestinelike collecting tube which is surrounded by the unicellular glands, of an ovoid reservoir with feeble muscles, and of a short and tortuous efferent canal leading to the exterior. Each secreting cell has besides a large nucleus, from one to four vesicles which lie in a group. The secretion has an agreeable odor and judging from the anatomy of the reservoir a quick discharge is impossible, nevertheless an explosion brought about by this gland never occurs. In *Dytiscus* the defensive apparatus is the rectal pouch greatly enlarged by water charged with gas. When disturbed, the insect empties its rectal pouch whereby the excremential substances are blown against the enemy. He thinks that the anal glands of Dytiscidæ are to facilitate respiration.

Dierckx (1899f) asserts that the pygidial gland in *Stophylinus cæsareus* is paired. It seems to be a pair of invaginated sacs which are evaginated by blood pressure and retracted by muscles. The gland cells lie in the walls of the sacs and a secreting tubule runs from a vesicle in each cell and empties its contents into the invaginated sac. The same author (1900) claims that among the carabid bombardiers, *Pheropsophus* holds the record for the complexity of its defensive organ. There are twelve collecting tubes which empty into the hilum of the kidney-shaped reservoir. The free end of each collecting tube is divided into about a dozen short glandular tubes, and the reservoir empties into a chitinous capsule whose walls are surrounded by the cells of the "glande annexe." The capsule empties into an efferent canal which runs to the exterior. Dierckx (1901) presented his second large paper concerning the pygidial glands of beetles. He has worked out the finer anatomy of various representatives belonging to the Carabidæ, Paussidæ, Cicindelidæ, and Staphylinidæ. In the various species examined the collecting tubes may vary in number from one to several for each reservoir. The gland proper may be a widening of the free end of the collecting tube, or a kidney-shaped mass containing the many ramifications of the free end of the collecting tube, or this free end may possess several short branches which are not massed together, or the gland cells may be arranged in bunches like grapes at the free end of the collecting tube. He found the "glandes annexes" in most of the species examined, and claims that they produce the yellow and clammy constituents in the substance secreted.

Francois (1899) claims that the pygidial gland of *Aptinus displosor,* a carabid belonging to Brachynini, is more complicated than that of *Brachinus.* In this species there are three collecting tubes for each reservoir, and the free end of each tube is terminated by four or five pairs of small groups of secreting cells, arranged grapelike. The reservoir runs into a chitinous capsule which opens to the exterior by an aperture under the exit of the cloaca. This gland has a special innervation.

Escherick (1899) concluding from the works of Dierckx, Bordas, and Francois about the pygidial glands, remarks that all beetles possessing these glands may be divided into two main groups: (1) Those in which the collecting tube is simple, *i. e.,* without an inner tube; the glands may be acinous or tubular; and (2) those in which the collecting tube is double, *i. e.,* with an inner chitinous tube.

Seidlitz (1899) reports a scent-producing organ in *Blaps, Glasunovia,* and *Dermestes.*

Brandes (1899) states that in certain beetles bunches of bristles are found on the head and thorax, and he thinks that these bristles form a bridge between the scent organs of other orders of insects and the anal glands of other beetles.

(c) ANAL GLANDS OF ANTS

Forel (1878) was able to find anal glands in only the workers and queens belonging to the subfamily Dolichoderidæ (a division of Formicidæ). He has found them in *Bothriomyrmex meridionalis, Tapinoma erraticum, T. nigerrimum, Liometopum* (?) *sericeum, Dolichoderus* (*Hypoclinea*) *attelaboides,* and *D. bispinosus.* The gland in each of these species is very similar to that of *Bothriomyrmex* which he describes in detail. Just above the anus lies a slit-shaped external opening which leads into the efferent canal of the paired gland. Both reservoirs, which occupy about half of the space at the posterior end of the abdominal cavity, run into the same efferent canal. At the outer side of each reservoir lie the unicellular glands, arranged grapelike. A large collecting tube runs from the bunch of cells and empties funnel-like into the base of the reservoir. Each spherical cell has a large nucleus containing many nucleoli. Wound around inside the cell he saw a chitinous secreting tubule surrounded by a transparent sheath; the tubule runs into the collecting tube. A protoplasmic sheath containing nuclei encloses the secreting tubule outside of the cell, and even the collecting tube is likewise enclosed. Tracheal branches run between the gland cells and seem to be closely connected with the secreting tubules. The reservoirs are well supplied with muscles and also with tracheal branches. Forel claims that most ants have a more or less strong and characteristic odor; the two species, *Lasius emarginatus* and *L. fuliginosus,* have different odors; in these the scent-producing organ lies in the mandibles (Oberkiefer) and metathorax.

II. INVAGINATED SACS AND POUCHES AT THE DORSO-POSTERIOR END OF ABDOMEN AS SCENT-PRODUCING ORGANS

(a) INVAGINATED SACS AND POUCHES OF CERTAIN ORTHOPTERA

Vossler (1890) describes this organ in the ear-wig, *Forficula auricularis,* as two pairs of lateral structures in the third and fourth abdominal terga. Each one of these consists of a reservoir having a narrow neck which opens to the exterior through a slit. Muscles are attached to the neck of the reservoir to open and close the slit. The walls of the reservoir are composed of unicellular glands, each of which besides having a nucleus has also a vacuolated area from which runs a secreting tubule into the reservoir. In the reservoir he found a yellowish or brownish liquid, which may be thrown from 5 to 10 centimeters from the insect.

Garman (1891) reports that the males of the cricket, *Hadenœcus subterraneus,* protrude a pair of white, fleshy appendages from slits between the ninth and tenth abdominal terga. He thinks that these appendages are protruded only during the period of sexual excitement.

Minchin (1888) describes a new organ in *Periplaneta orientalis.* This organ consists of a pair of shallow, lateral pouches near the median line in the articular membrane between the fifth and sixth abdominal terga. The pouches are covered with the fifth tergum, but connect with the exterior by a pair of slit-shaped openings. These pouches contain numerous, stiff and branched hairs, and just beneath the chitinous lining of the pouches lie unicellular glands which extend into the enlarged bases of the hairs. He thinks that probably the secretion from these cells runs into the hairs which serve as a means of diffusing the odor. The same author (1890) describes a second glandular organ in the same species. This organ consists of a pair of tubular ducts which lie just above the pouches of the first organ, and they open to the exterior through apertures near the slitlike openings of the pouches.

Krauss (1890) observed in the roach, *Aphlebia bivittata,* invaginations whose common exit may be seen on the seventh abdominal tergum. These invaginations are filled with hairs.

Oettinger (1906) describes the scent-producing organ in the roach *Phyllodromia germanica,* as two double pouches, one of which is located in the articular membrane between the fifth and sixth, and the other betwen the sixth and seventh abdominal terga. They are found only in the sexually matured males. Each pouch is a double invagination, being divided in the median line by a tonguelike partition, and muscles are attached to the walls of the pouches. When the muscles contract the lumen of the pouch is constricted whereby the secretion is forced to the exterior. Beneath the chitinous lining of the pouch lies an irregular layer of supporting cells. The layer next to the abdominal cavity is composed of long, cylindrical and extremely large gland cells, each of which has a reticular netlike contents and a conspicuous nucleus having several nucleoli. A secreting tubule arises near or even against the nucleus, pierces the contents of the cell and runs to the lumen of the pouch. The gland cells as usual are modified hypodermal cells. In *Periplaneta orientalis* the pouch is lined with hollow hairs into which the secreting tubules of the unicellular glands run. He thinks that these organs bear a close relation to the sexual behavior of these insects.

(b) INVAGINATED POUCH OF HONEY-BEE

Under this heading belongs the description of the scent-producing organ of the honey-bee, but since a brief review of it has already been given on pages 36 to 37, further remarks are unnecessary.

C. SUMMARY OF SCENT-PRODUCING ORGANS OF INSECTS

In the first part of this summary the scent-producing organs are grouped on the basis of their devices for disseminating the odors and for storing the secretion, while in the second part they are grouped according to the order of the insects being discussed.

A review of the literature shows that the substance produced by any scent-producing organ is secreted by unicellular glands which so far as known are modified hypodermal cells. On this point Gazagnaire (1886) remarks that glandular cells of hypodermal origin are widely distributed in insects. They secrete the various fluids exuding through the chitin, and since their histology is so similar it might be admitted that they have the same general structure. For description, scent-producing organs may be divided into five types based on their devices for disseminating the odor and for storing the secretion as follows: (1) No special device for disseminating the odor or storing the secretion; (2) gland cells associated with hairs and scales as a means of scattering the odor more effectively; (3) "evaginable" sacs lined with hairs connected with gland cells as a device for storing the secretion and distributing the odor; (4) articular membranes serving as pouches for storing and preventing a too rapid evaporation of the secretion; (5) specialized tubes and sacs acting as reservoirs for storing and discharging the secretion.

The first type is the simplest of all five types. It is best represented as unicellular glands uniformly distributed over the entire body surface as found in several beetles. In this type of scent-producing organ the secretion passes through the chitinous tubes to the exterior where it spreads over the surface of the chitin surrounding the exits of the tubes.

In regard to spreading the secretion over a wider area, the second type is much more highly developed than is the first type. This is accomplished in most cases by the secretion spreading over the surfaces of many large hairs arranged in tufts which may be expanded into a fan-shaped figure. In the second type the secretion from the gland cells passes into the hairs and scales and then spreads over their surfaces, whereby the odor from the secretion is more effectively disseminated.

In regard to storing the secretion in an " evaginable " sac, the third type is a little further advanced than the second type. The sacs are evaginated by blood pressure and retracted by muscles, and the odorous substance may be more or less retained in the invaginated sacs, but when the sacs are evaginated, like the fingers of a glove, all the odor escapes.

In regard to storing the secretion, the fourth type is more highly organized than any one of the preceding types. The scent-producing organ of the honey-bee belongs to this type, and it is one of the most highly developed organs of its kind. At this place might be mentioned some unicellular glands found in ants. In the petiole of the worker ant of *Myrmica rubra,* Janet (1898) found an invaginated chamber; at the bottom of the chamber may be seen the exits of the tubes which lead to a bunch of unicellular glands. He also found in the same ant two small groups of unicellular glands beneath the articular membrane between the ninth and tenth abdominal terga. These glands are also connected with tubes which run to the exterior. Both of these organs may possibly be scent-producing organs, and may be similar in function to that of the honey-bee.

Relative to storing and discharging the secretion as a means of defense, the fifth type is the most highly organized of all the five types of scent-producing organs. It is thus seen that there is a wide variation in organization between the lowest type and the highest type. All of those organs belonging to the first four types are used in all probability for alluring purposes and as a means of recognition, while those of the fifth type are perhaps used mostly as a means of defense. Of the scent-producing organs used only for recognition, that of the honey-bee is probably the most highly organized.

ORTHOPTERA

In the ear-wig, *Forficula auricularis,* the scent-producing organ consists of two pairs of lateral, saclike invaginations located in the third and fourth abdominal terga. The walls of these sacs, the reservoirs, are composed of unicellular glands.

In both sexes of the roach *Corydia* two pairs of caruncles or evaginated saclike appendages serve as the scent-producing organ. These appendages are located on the pleura of the first and second abdominal segments. Unicellular glands lie in their walls. In the roach *Periplaneta* there appear to be at least three scent-producing organs. The males have anal glands and probably the females (the writers did not determine the sex) have a pair of lateral pouches in the articular membrane between the fifth and sixth abdominal terga. These pouches are lined with hollow hairs into which the secretion from the unicellular glands empties. The same individuals also have a pair of tubular glands lying near the pouches. The same species has a fourth glandular structure lying in the sixth abdominal segment and opening between the sixth and seventh sterna. In the male roach *Phyllodromia germanica* the scent-producing organ consists of two double pouches, one of which lies in the articular membrane between the fifth and sixth, and the other between the sixth and seventh abdominal terga. The unicellular glands lie beneath the chitinous lining of these pouches.

In both sexes of the walking-sticks the secretion from the scent-producing organs is discharged through a pair of pores on the prothorax. The glands are paired, are ribbonlike blind sacs with stout walls, and lie in the mesothorax and prothorax. The gland cells certainly lie in the walls of these sacs, although information in regard to this point is wanting.

In two genera, *Eugaster* and *Ephippiger,* belonging to the Locustidæ, reflex bleeding occurs. The liquid issues from a pair of vesicles on the thorax near the bases of the front pair of wings. More information concerning the source of this liquid is lacking.

In the male cricket *Hadenœcus subterraneus* the scent-producing organ is a pair of appendages protruded from slits between the ninth and tenth abdominal terga.

HEMIPTERA

Scale insects emit an odor, but the anatomy of the scent-producing organs has never been studied and the external openings of the glands have never been located.

In the adult heteropterous Hemiptera, the scent-producing organ is a pair of tubular glands located in the posterior part of the metathorax or in the anterior part of the abdomen. The secretion from the glands is emitted through a pair of pores between the bases of the second and third pairs of legs. In *Pyrrhocoris apterus* a quite complicated organ is found; here there is a saclike cavity in the metathoracic sternum. A reservoir connects with the sac and a dichotomously branched, collecting tube runs from the kidney-shaped mass of unicellular glands to the reservoir.

TRICHOPTERA

The scent-producing organs of the male caddice fly, *Sericostoma personatum,* are the wide maxillary palpi. These appendages give off an odor, but the anatomy of them has not been studied.

COLEOPTERA

The simplest type of a scent-producing organ in beetles is composed of unicellular glands distributed over the entire body surface. In some beetles these unicellular glands are grouped and thus form glands varying considerably in complexity. In *Malachius* two pairs of caruncles serve as the scent-producing organs; unicellular glands lie in the walls of these structures. In *Dytiscus, Gyrinus,* and *Acilius* two different kinds of liquids issue from unicellular glands located in the articular membranes between the thoracic segments. The liquid emitted at the femoro-tibial articulation during the reflex bleeding of certain beetles seems to be secreted by two types of unicellular glands at this location.

The highest type of a scent-producing organ in all insects is the anal glands of beetles. These glands have been found in the following families and subfamilies: *Cicindelidæ, Carabinæ, Harpalinæ, Feroniinæ, Brachininæ, Dytiscidæ,Gyrinidæ, Staphylinidæ, Silphidæ,* and *Paussidæ.* They are usually paired, vary considerably in complexity and are probably present in both sexes. The most complex form consists of an efferent canal, a spherical capsule, a reservoir, collecting tubes and unicellular glands, each of which contains a radial vesicle from which runs a secreting tubule to the collecting tube.

LEPIDOPTERA

Butterflies.—The scent scales on the wings constitute the almost universal type of scent-producing organs in male butterflies. A unicellular gland lies at the base of each scent scale. A pair of invaginated sacs located at the ventro-posterior end of the abdomen, has been found, however, in the males of *Danais septentrionales* and *Euplœa asela.* These sacs are partially lined with scent hairs and at the base of each hair lies a unicellular gland. In the female of *Euplœa asela,* the same organ is present, but in addition there is a circle of scalelike, scent hairs around the anus. In the female of *Gonopteryx rhamni,* the scent-producing organ is a single invaginated sac similarly located. In the females of the maracujá butterflies, a pair of styled knobs located at the posterior end of the abdomen serves as a scent-producing organ.

Moths.—The most common type of scent-producing organ in male moths is a tuft of scent hairs on the tibiæ of the third pair of legs. Occasionally, however, tufts of hairs are found on the tibiæ of the first and second pairs of legs. A unicellular gland lies at the base of each scent hair. Another quite common type in male moths is composed of a pair of scalelike, scent hairs located at the base of the abdomen. Each tuft lies in a groove on either side of the body in the pleura belonging to the first and second abdominal segments. A large unicellular gland lies at the base of each scent hair. In the males of *Leucarctia* and *Pyrrharctia,* a pair of invaginated sacs located at the ventro-posterior end of the abdomen serves as a scent-producing organ; these sacs are lined with hairs.

In the female moths *Taumatopœa* and *Stilpnotia* the scent-producing organ consists of a paired tuft of scent hairs near the anus. This organ in the female of *Orgyia* is a scent groove in the articular membrane between the eight and ninth segments just above the anus. Unicellular glands lie just beneath this thin membrane. The scent-producing organ in the female of *Bombyx mori* is the most highly developed of any found in the female Lepidoptera. This organ is a pair of invaginated and greatly folded sacs located at the posterior end of the abdomen; beneath the chitinous lining of these sacs lie the unicellular glands.

HYMENOPTERA

Ants emit characteristic odors, but as yet little is known about their scent-producing organs, nevertheless, a well-developed organ has been found in the petiole, besides unicellular glands beneath the articular membrane between the ninth and tenth abdominal terga, and also some around the femoro-tibial and tibio-tarsal articulations. A quite complicated, paired anal gland has been found in a few species belonging to one subfamily of ants. Many wild bees and wasps emit strong odors, but their scent-producing organs seemingly have never been described. This organ in the honey-bee consists of a pouch which is formed by the articular membrane between the fifth and sixth abdominal terga. Unicellular glands lying just beneath the membrane secrete a volatile substance which admirably serves as a source for odors.

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