

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 63, NUMBER 9

THE OLFACTORY SENSE OF INSECTS

BY

N. E. McINDOO, Ph. D.,
Bureau of Entomology, Washington, D. C.



(PUBLICATION 2315)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
NOVEMBER 21, 1914

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

THE OLFACTORY SENSE OF INSECTS

By N. E. McINDOO, PH. D.,
BUREAU OF ENTOMOLOGY, WASHINGTON, D. C.

CONTENTS

	PAGE
Introduction	I
Sense of smell in general	2
Spiracles as seat of olfactory organs	3
Structure near spiracles as seat of olfactory organs	5
Glands of head and thorax as seat of olfactory organs	6
Œsophagus as seat of olfactory organs	6
"Internal superior surface" as seat of olfactory organs	7
Different parts as seat of olfactory organs	7
Folded skin beneath antennæ as seat of olfactory organs	7
Rhinarium as seat of olfactory organs	7
Plate between eyes and beneath antennæ as seat of olfactory organs	8
Mouth cavity as seat of olfactory organs	8
Epipharynx as seat of olfactory organs	9
Palpi as seat of olfactory organs	9
Antennæ as seat of olfactory organs	
(1) Without experiments	11
(2) With experiments	14
Various structures on antennæ as olfactory organs	24
Caudal styles ("abdominal antennæ") as seat of olfactory organs.....	35
Organs on bases of wings and on legs as olfactory organs	36
Olfactory organs on the appendages and sternum of spiders.....	49
Summary of author's experiments	51
Literature cited	56

INTRODUCTION

Since no one has ever collected the views of the various writers on the sense of smell in insects, the literature that bears directly on this subject is here briefly discussed for the use of students on this subject. Abstracts and translations of this literature have been made by the writer and his wife, Emma Pabst McIndoo, and the discussion is from these abstracts and translations. Minor details may have been incorrectly stated in some cases, but it is believed that each view as a whole is given correctly. The views of a few authors have been cited from others, because the original works were not accessible. After a short discussion of the sense of smell in general, the

names of the various writers and their views are grouped under heads according to the seat of the olfactory organs which these writers favor. A few writers fail to advocate any particular view but they criticize certain ones. Such writers are placed under the head which they criticize.

This discussion was originally written as the second part of the author's (1914a) paper on "The Olfactory Sense of the Honey Bee." On account of the great length of this paper it was necessary to omit the discussion. Since the first part of the paper was published a few more references have been collected and the author (1914b) has written a second paper on the same subject concerning the Hymenoptera. Several letters have also been received requesting that a complete discussion be published. Another reason for publishing this discussion is to reveal the chaos which now exists on this subject, so that students may hereafter replace such chaos by facts.

The author is grateful in various ways to Dr. E. F. Phillips, in charge of bee culture investigations, and to Miss Mabel Colcord, librarian of the Bureau of Entomology, for invaluable aid in securing references.

SENSE OF SMELL IN GENERAL

Aristotle is the earliest author whose writings on the sense of smell in insects are available. He says:

As for insects, both winged and wingless, they can detect the presence of scented objects afar off, as for instance bees and cripes detect the presence of honey at a distance; and they do so recognizing it by smell. Many insects are killed by the odor of brimstone; ants, if the apertures to their dwellings be smeared with powdered origanum and brimstone, quit their nests; and most insects may be banished with burnt hart's horn, or by burning of gum styrax.

Virgil was a beekeeper as well as a poet. The ancients used roasted or burnt crabs in the treatment of certain bee diseases, but Virgil warned beekeepers that the odors arising from such materials are injurious to bees. He also reports that certain strongly scented plants were rubbed on the tree where a swarm of bees was collecting, so that these odors might prevent them from going farther.

Pliny states that the odors of origanum, of common lime, and of sulphur kill ants. Gnats hunt for acids and do not approach things which are sweet.

Varro (1735) infers that bees can distinguish odors, and that they are sensitive to perfumes which come from odoriferous objects; in this respect their preferences differ greatly.

Aliani (1744) asserts that bees smell anything with a foul odor or anything smeared with odors, and that they cannot tolerate an offensive smell, nor do they like sweet, delicious odors.

Rösel and Klemann (1747) remark that it is clearly understood that certain butterflies have a very acute sense of smell and that one sex certainly perceives the odor of the other from a distance.

Romanes (1877) is certain that moths smell, although they may detect the odor from ammonia through their whole system.

The Peckhams (1887) in their experiments on wasps used two essential oils—peppermint and wintergreen—maple syrup, and warm and cold chicken bones. They say:

We conclude from these experiments that wasps have a strong sense of smell, but that they pay little attention to odors, however powerful, which do not denote the presence of something which they can utilize as food.

From the foregoing it is evident that the belief in a sense of smell in insects is general and that some insects are able to distinguish between various odors. From the time of Aristotle to the present no one has ever denied that insects can smell, yet no one has ascertained the relative sensitiveness for any particular species.

SPIRACLES AS SEAT OF OLFACTORY ORGANS

Sulzer in 1761, according to Lubbock (1899), was the first to suggest that the spiracles are the seat of the olfactory organs. Later, however, he abandoned this view and adopted the antennal theory in 1776.

Dumeril (1797) asserts that all insects possess a more or less acute sense of smell. He was the first to advocate strongly the view that insects, like all other animals that live in the air, have their olfactory organ located at the entrance of the respiratory system. The air charged with odoriferous particles passes into the tracheæ through the spiracles and here these particles stimulate multitudes of nerves and thus the sensation of smell is produced. He thought that the tracheal walls consist of a membrane which is clothed with olfactory nerves, against which the odoriferous particles from foreign bodies strike. Later the same author (1823) remarks that the perception of odors is then, like all the other sensations, physical—a kind of touch in which the bodies, should that be their nature, impinge upon the olfactory nerves. Dubois (1890) held the same opinion, saying that the first excitation is a mechanical one, like that which occurs in the sensation of touch. Hermbstädt (1811) asserts the opinion

now generally prevalent, that taste and smell are chemical senses, while sight, hearing and touch are purely mechanical.

Baster (1798), cited from Perris (1850), believes that olfactory stimuli are received by the tracheæ, either at their apertures or throughout their whole extent.

Lehmann (1799), according to Lacordaire (1838), was the first who actually performed experiments to determine the location of the olfactory apparatus. He made a round aperture, surrounded by wax, in a glass bottle, in the center of which was a paper diaphragm. The antennæ or entire head of an insect was then inserted into this aperture. He next introduced into the bottle strongly odoriferous substances, such as burnt feathers, burning sulphur, etc. None of the insects subjected to this test reacted, but when the same substances were placed near the remaining part of the insect, the specimen made violent movements which showed the effect these substances had upon it. He concluded, therefore, that the head is not the seat of olfaction and that it must lie in the tracheæ near their external openings. As the antennæ are covered with hard chitin, while the tracheal walls are clothed with very thin, chitinous membranes, critics contend that such strong irritating odors mechanically irritate the tracheæ and that these odors cannot so affect the antennæ on account of the hard chitin.

Cuvier (1805) thinks that since all other air-breathing animals have the organs of smell located at the entrance of the respiratory organs, we should find it at the entrance of the tracheæ in insects, as Baster suggested. He added that the internal membrane of the tracheæ, being moist, appears properly to fulfill this office, and that in the insects in which the tracheæ form numerous vesicles these tracheæ appear to be excellently suited for the seat of smell. The antennæ do not seem to fulfill any of these required conditions.

Straus-Durckheim (1828) believed that the seat of olfaction is located at the entrance of the tracheæ because he discovered, in the environs of the spiracles, nerves which are large enough to belong to a special sense organ.

Lacordaire (1838), after discussing the experiments of Huber and Lehmann, says that from all the preceding we can conclude that we know nothing positive about the seat of smell and that the hypothesis which locates it in the respiratory organs is yet the most rational of all.

Brullé (1840), after briefly discussing the sense of smell in articulate animals, remarks that the organ of smell is not known in these

animals, unless it is to be assigned to the apertures of the respiratory organs.

Of the foregoing six authors who advocate the theory that the spiracles are the seat of olfaction, Lehmann is the only one who experimented on the subject. The others seem to think that an analogy with higher animals is sufficient proof. Lehmann's experiments indicate that the seat of smell is not located in the head and assumes that the tracheæ are the only other place in which these organs could be located. No one has found any nerves or any kind of sense organ, which suggest an olfactory function, in the walls of the tracheæ or in the spiracles of the bee. This theory has been long since abandoned.

STRUCTURE NEAR SPIRACLES AS SEAT OF OLFACTORY ORGANS

Joseph (1877) postulated three conditions necessary for an olfactory apparatus: (1) It must come in contact with moving air; (2) it must be continually moistened, and (3) the olfactory substance must be in the form of a gas. If one of these three conditions is lacking, olfaction is impossible. According to these conditions no one has sought the seat of smell in any place other than at the entrance of the tracheæ, and the assumption that insects smell with their antennæ or buccal organs is completely inadmissible. In spite of the fact that their antennæ had been removed and in spite of their clumsy flying, a number of *Necrophorus vespillo* (carriage beetles) found a carcass wrapped in paper at a distance of 20 feet. The same result was obtained with the flesh-fly (*Musca*) *Sarcophaga carnaria* and with other insects. A short distance from the spiracles, toward the median line of the thorax and abdomen, he reports finding a peculiar structure which he called the "regio olfactoria." This olfactory region is completely covered by a delicate membrane perforated by pores, the largest of which are for gland exits and the smallest for hairs. Beneath this membrane lies a peculiar layer of cells.

Thus, not favoring the view that the spiracles are the seat of smell, and in order to comply with the above three conditions, Joseph assumed the existence of an organ near the spiracles which communicates with the air cavities of the tracheæ. Of course, being connected with the tracheæ and being continually moistened by the glands, it is easy to see that the necessary conditions would be fulfilled. No drawing of this organ is given and no such structure is found in the honey bee.

GLANDS OF HEAD AND THORAX AS SEAT OF OLFACTORY ORGANS

Ramdohr (1811) states that many species of insects, and among them the bee, have a well-marked sense of smell. He failed to find olfactory organs in the spiracles, but conceived the idea that odors come into the mouth through the lumen of the proboscis. He found behind the mouth a tube which is divided into three branches, the smallest of which runs along the œsophagus above the first thoracic ganglion and soon divides into two smaller tubes which pass into the thorax and seem to connect with the large tracheæ coming from the first spiracle. The other two branches pass at right angles into the sides of the head, where they expand into four small sacs which differ from air tubes in having walls that are soft, thick and transparent. A thick tissue of the finest tracheæ covers these various tubes. Ramdohr also mentioned nerves running to his supposedly olfactory organ. He was led to believe that air carrying odors passes through the lumen of the proboscis into these small sacs and, as their walls are soft and perforated with minute air tubules, that they act as an organ of smell. Referring to Snodgrass (1910) and judging from the foregoing description, Ramdohr probably mistook the thoracic salivary gland for the branch accompanying the œsophagus, and the salivary glands in the posterior part of the head for the other two branches.

ŒSOPHAGUS AS SEAT OF OLFACTORY ORGANS

Treviranus (1816) infers that the smelling organs in various families of insects are located in the throat. In all the insects discussed the œsophagus is dilated, as in the bee, in front of the stomach into a large sac-like reservoir, which he thought is perhaps for the purpose of drawing air into the throat. He believed that in the presence of strong-smelling substances the antennæ do not produce noticeable movements. He further stated that the olfactory apparatus of higher animals and the antennæ and palpi of insects are as different in structure as organs can ever be. In order to smell, higher animals must inhale the odoriferous particles. On the contrary, the antennæ and palpi do not conform with this general rule; in most insects these appendages are not coated with a mucous skin and the interior is carefully guarded against the entrance of odoriferous air. Treviranus therefore infers that the sac-like reservoir "honey stomach" in the bee, is for the purpose of drawing odorous air into the œsophagus.

“INTERNAL SUPERIOR SURFACE” AS SEAT OF OLFACTORY ORGANS

After discussing the various views concerning the location of the organs of smell, Burmeister (1836) concludes as follows:

Thus insects, according to my opinion, would smell with the internal superior surface, if I may so call it, which is provided all over with ramifications and nets of nerves, since this is always kept moist by the blood distributed through the body and by transpired chyle, the same as is surmised of the superior *Mollusca*.

Further, the same authority wrote.

Various authors consider the antennæ as olfactory organs, but with what right? A hard, horny organ, displaying no nerve upon its surface, can not possibly be the instrument of smell, for we always find in the olfactory organ a soft, moist, mucous membrane, furnished with numerous nerves.

What Burmeister means by “internal superior surface” is not clear.

DIFFERENT PARTS AS SEAT OF OLFACTORY ORGANS

Schelver (1798), cited from Lacordaire (1838), and Comparetti (1800), according to Perris (1850), place the seat of smell in different parts for different families, as follows: The club of the antennæ in lamellicorns, the proboscis in the *Lepidoptera*, and certain frontal cells, which have never been seen since by any one else, in the *Orthoptera*.

FOLDED SKIN BENEATH ANTENNÆ AS SEAT OF OLFACTORY ORGANS

Rosenthal (1811), cited by Burmeister (1836), “described a folded skin at the forehead, beneath the antennæ, to which two fine nerves passed, and which he considers the organ of smell in the flies *Musca domestica* and (*Musca*) *Calliphora vomitoria*; and he observed, after the destruction of the part, a deficiency of the function which had previously strongly exhibited itself.”

The honey bee has no such structure as that described by Rosenthal.

RHINARIUM AS SEAT OF OLFACTORY ORGANS

Kirby and Spence (1826) regard the rhinarium as the location of the organs of smell. The rhinarium or nostril-piece is the foremost portion of the clypeus just above the labrum; it consists of circular pulpy cushions, covered by a membrane transversely marked with fine striæ. These fleshy cushions, like the upper surface of the tongue, are beset with minute black tubercles carrying bristles.

No such structure as the rhinarium exists in the bee.

PLATE BETWEEN EYES AND BENEATH ANTENNÆ AS SEAT OF
OLFACTORY ORGANS

Paasch (1873) claims that no nerves coming from the brain lead to the tracheæ and that the olfactory organ need not necessarily be connected with the breathing apparatus. He reasons that its location should correspond with that found in higher animals. He found a peculiar plate situated between the eyes and beneath the antennæ and extending to the base of the proboscis. This plate possesses a groove whose edges are beset with stiff bristles, and many tracheal branches; it also has nerve connections. This he regards as the olfactory organ. This plate does not exist in the honey bee.

MOUTH CAVITY AS SEAT OF OLFACTORY ORGANS

After having cut off the antennæ of some queen bees, Huber (1807) was rather inclined to regard these appendages as the olfactory organ, but later (1814) after many experiments he concluded that the organ of smell resides in the mouth itself or in the parts depending upon it.

The following is a brief summary of his later work concerning the olfactory sense: Not only do bees have an acute sense of smell, but they possess the memory of sensations. For example, in the fall we placed some honey in a window and the bees came to it in great number. The honey was removed and the shutter of the window was closed all winter. The following spring, when we opened the shutter, bees returned to the same window, although there was then no honey at this place. They remembered that it had been there previously and an interval of several weeks had not effaced the acquired impression. Bees not eating appear more responsive to odors, while those eating honey are reluctant to move when odors are brought near them. To ascertain how different odors affect bees he used mineral acids and volatile alkalies presented on a pencil brush to the opening of the mouth; these did not affect them. Musk placed in front of the hives did not irritate the bees much. Assafoetida mixed with honey was put at the entrance of hives; the bees ate the honey and were not annoyed by this odor which is obnoxious to us. Bees are greatly affected by the odors from camphor and the poison from bee stings.

To locate the region of the body in which the olfactory organ is found, Huber brought a pencil brush, which had been dipped into turpentine oil, near the abdomen, thorax and head. He saw a response only when it was in the region of the head and decided that the organ of smell is located only in the head. He next placed an ex-

tremely fine pencil brush wet with the same oil near the eyes, antennæ, proboscis and mouth cavity. The only response observed was when the brush came near the mouth cavity. He obtained the same result, only more pronounced, when oil of origanum was used. The mouths of several bees were filled with flour paste and when this was dry they were released. Honey, turpentine and oil of cloves, either in fixed or volatile alkalies, did not produce any response.

EPIPHARYNX AS SEAT OF OLFACTORY ORGANS

Wolff (1875) found many peculiar hairlike organs on the epipharynx of the honey bee; each organ consists of a small cone with a pit in the summit bearing a small hair. He regarded these cones as having an olfactory function and believed that the mandibular glands pour a liquid upon the surface of the epipharynx which keeps these cones moist and capable of absorbing odoriferous particles. He explained the inhalation of these particles into the preoral cavity as brought about through the contraction of the air sacs situated near the mouth.

Harting (1879), in discussing Wolff's olfactory organs, inferred that Wolff tried to homologize the epipharynx with the nose of higher animals whereas there is not the slightest reason for such an homology.

To determine whether the mouth cavity and the epipharynx are the seat of the olfactory organs, the author repeated Huber's experiment of filling the mouth cavity with flour paste. With the aid of a small pencil brush the mouth cavities of 20 worker bees were thus filled. When the paste had become perfectly dry, the bees were put into observation cases. They seemed otherwise entirely normal, but lived only $7\frac{1}{2}$ days as an average, whereas unmutilated workers in the same cases lived 9 days and 3 hours. When tested with the oils of peppermint, thyme and wintergreen, their average reaction time was 2.68 seconds. The average for the same odors with normal workers was 2.64 seconds. It would seem that neither the buccal cavity nor the epipharynx has anything to do with olfaction.

PALPI AS SEAT OF OLFACTORY ORGANS

Lyonnet (1745) thinks that the palpi should be considered as the organs of smell rather than those of taste.

Bonnsdorf (1792) and Knoch (1798), according to Perris (1850), regarded the palpi as olfactory organs, but Knoch believes that the maxillary palpi only are for smell, while the labial palpi are for taste.

According to Marcel de Serres (1811), even if insects have their olfactory organs located at the entrance of the respiratory organs, the view that the palpi serve as organs of smell does not contradict the former view, because the palpi communicate both internally and externally with the air. This view resembles Duponchel's theory (1840), except that the latter author considers the antennæ of certain water insects as having a respiratory function. Duponchel thought that the antennæ were provided with minute perforations through which the air passed.

Newport (1838) performed many experiments with certain insects (Sylphæ) and he concludes that they find their food by smell but he did not think that the olfactory organs are found either in the antennæ or spiracles. He says:

Hence, I think it must appear * * * from the motion of the palpi and the avidity with which the insect darted upon the food when held in front of it, it seems but fair to conclude that the sense of smelling must certainly reside in the head.

We may include Newport with those who believe that the palpi are the seat of olfaction.

Driesch (1839) favors the opinion that the seat of the olfactory organ is located in the palpi.

Perris (1850) found that after the amputation of the palpi insects showed none or only a very little sensibility to odors. In the articulates the sense of smell resides in the antennæ and in the palpi; but the antennæ are destined to perceive odors from both afar and near, while the palpi perceive odors from afar only. As far as the palpi are concerned he thinks that the seat of smell lies in their last joint. Cornalia (1856) also shared this view.

Plateau (1885) performed many experiments by cutting off the palpi. He ascertained that the amputation of both maxillary and labial palpi did not destroy the olfactory sense.

Wasmann (1889) favors the view that the group of delicate peg-like papillæ on the tips of the palpi probably function as olfactory organs.

To ascertain whether the palpi of the honey bee bear the organs of smell, the author cut off the labial palpi and maxillæ of 19 workers at their bases. When put into observation cases these bees appeared normal in all other respects, but certainly were not completely normal, for they lived only 24 hours on an average. When tested with the oils of peppermint, thyme and wintergreen, honey and comb, pollen and leaves and stems of pennyroyal their average reaction time was 4

seconds, whereas for the same odors with unmutilated bees the average was 3.4 seconds. Since these appendages carry several porelike organs, we may either attribute the 0.6 second difference in reaction time to the view that these appendages really aid in receiving odor stimuli, or to the injury caused by the operation, or to both of these views combined.

Breithaupt (1886) describes some porelike sense organs on the base of the proboscis of the bee. To determine whether these have an olfactory use, the author cut off the proboscides of 22 workers. These bees seemed normal in most respects, but lived only 7 hours on an average. When tested with the oils of peppermint, thyme and wintergreen the average reaction time was 2.9 seconds, while for the same odors with unmutilated bees the average was 2.6 seconds. We can probably attribute this difference of 0.3 second to the abnormality of the mutilated bees.

Janet (1911) describes a sense organ in the mandible of the honey bee which he thinks may have an olfactory function. To ascertain this experimentally, the mandibles of 20 workers were amputated close to the base by the author. These bees appeared completely normal, although they lived only 7 days on an average. When tested with the oils of peppermint, thyme and wintergreen, honey and comb, pollen, and leaves and stems of pennyroyal, they gave an average reaction time of 4.8 seconds, while the average for the same odors with unmutilated bees was 3.4 seconds. We may attribute this slight difference in reaction time either to the injury caused by the amputation, or to the view that the mandibles help to perceive odors, or to both.

ANTENNÆ AS SEAT OF OLFACTORY ORGANS

(1) WITHOUT EXPERIMENTS

Reaumur (1734) was the first to suggest that the olfactory organs of insects lie in their antennæ.

Lesser (1745) says that the sense of smell of some insects is more acute than that of man. He gives as two proofs of this, (1) that they find their food with this sense, (2) that they scent food farther than man does. He says that the antennæ are "noses" and that they enable their owners to smell odors near or far away.

Baster (1770) remarks that no one doubts that insects can smell, for flies, purely through olfaction, find their way to tainted meat. He also states that water insects can smell. Baster states that no insects, whether living in the air, under water, or in the earth, have the seat of smell in the antennæ.

Sulzer (1776) contends that insects have an acute sense of smell and spoke of bees coming for honey when it is placed in a spoon under a window. He believes that the olfactory apparatus is located in the antennæ.

Fabricius (1778) infers that the seat of smell belongs to the antennæ.

Bonnet (1781) asserts that diverse insects have the sense of smell exquisitely developed, but that we do not know where the seat of this sense lies. He suggests the antennæ as a possible location.

In discussing the probable uses of the antennæ, Olivier (1789) regarded them as olfactory in function.

Latreille (1804) regards the fact that many male insects have the antennæ better developed than the females of the same species as evidence that these appendages are the seat of olfaction. The greater number of insects that live in animal matter, in decayed vegetables, or in stagnant water generally have the antennæ better developed than those that live elsewhere. A more perfect olfaction would be necessary to these insects, and the organization of the antennæ seems to be adapted for this purpose.

After discussing Marsham's account of ichneumon flies, Samouelle (1819) states, "From these remarks may we not infer that the antennæ may be the organ of smelling?"

De Blainville (1822) and Robineau-Desvoidy (1828), cited from Perris (1850), state that the antennæ are olfactory organs.

After briefly discussing the various views concerning the seat of olfaction, Carus (1838) confesses that the opinion of Rosenthal, combined with that of Réaumur, appears to him to be the best. Hence he believes that the seat of olfaction lies in the folded skin beneath the antennæ as well as on the surface of the antennæ.

Since the antennæ of the male are often better developed than those of the female, Percheron (1841) states that the antennæ of the male aid the eyes in searching for the female. He infers that the antennæ are used for smelling.

Goureau (1841) thinks that the antennæ may be organs of olfaction besides being organs of touch and hearing.

Pierret (1841) also favors the view that the seat of olfaction lies in the antennæ.

Robineau-Desvoidy (1842) speaks of an olfactory apparatus as nothing less than an ordinary organ of touch which is capable of receiving invisible stimuli. By analogy he thinks that the antennæ must be the organs of smell.

Slater (1848) firmly believes that the antennæ are olfactory organs. He says that the antennæ seem to be the real organs for this sense or for a sense closely allied to it.

According to Dufour (1850) both the organs of audition and olfaction are found on the antennæ. The distal joints, which have a spongy texture, are the ones that bear the sense of smell, for here the odoriferous atoms can fall upon this special texture and the impulse can be transmitted to the cerebral ganglion.

Claparède (1858) asserts that absolutely nothing warrants us in locating in the antennæ the sense of hearing rather than that of olfaction or any other function, but he favors the view that the organs of smell are there.

Dönhoff (1861) from various experiments contends that bees learn the location of honey and of the queen through the antennæ. He placed a stick near the antennæ of a bee and these appendages remained quiet. When a stick wet with honey was similarly placed, the bee at once extended these appendages in the direction of the stick. When one places a foul-smelling substance like tobacco juice near the antennæ, the bee moves away. When one places a stick wet with honey or tobacco juice near a bee with amputated antennæ the insect shows no response of any kind. He thinks that the olfactory organ was removed by cutting off the tip of the antennæ.

Noll (1869) asserts that butterflies have a fine sense of smell as shown by the way in which they find prepared food when placed in a box covered with screen wire and having only a slit through which these insects may enter. This is shown by the way in which the males are able to find the females. He regards the antennæ as the olfactory organs, at least for the male.

Wonfor (1874) says:

That it is the sense of smell which directs the blow-fly to the deposition of the larvæ is shown by the fact that she has laid them on *stapelias*, a carrion-odoured hothouse plant, and on silk with which tainted meat had been covered. Notwithstanding the view of Hicks he considers one of the functions of the antennæ as that of smell.

Fabre (1882) remarks that it is incontestable that insects have a very highly developed sense of smell. Carrion beetles run from all sides to the place where a dead mole lies. If we admit that the seat of smell lies in the antennæ he contends that it is difficult to comprehend how such an appendage of hard chitinous rings, articulated end to end, is able to fulfill the office of a nose. The organization of a true nose and that of the antennæ have nothing in common.

Henneguy (1904) state that the organ of olfaction is probably located in the antennæ and the buccal palpi.

(2) WITH EXPERIMENTS

Dugés (1838) was the first to experiment with the antennæ of insects. He cut off the antennæ of two male (*Bombyx*) *Eudia pavonia minor* and then these insects were unable to find a female that they had previously been able to locate while their antennæ were intact. Also, after having extirpated the antennæ of many blow-flies, (*Musca*) (*Calliphora vomitoria*), and a large viviparous fly, *Sarcophaga carnaria*, he ascertained that they were unable to find putrid meat as before. He felt satisfied that olfaction resides in the antennæ.

Lefebvre (1838) was the first observer to experiment with a bee. He placed a long needle, whose end had been plunged into ether, near a piece of sugar which a bee was eating. The bee moved its antennæ towards the needle and then passed them several times between the legs. He brought this needle near the legs and spiracles, and since he noticed no response from these parts, he concluded that the antennæ are olfactory organs. As a control he used a needle without ether in the same manner. Next he mutilated the antennæ of several wasps (*Iscpa*). All their organs for perceiving odor stimuli seemed to be at the extremity of these appendages.

Küster (1844) declares that bees have a very acute sense of smell. He reports some that found a store of honey; even a week after they had carried away all the honey they still continued to come to the same place in search of more food. Since vertebrates carry their olfactory organs on the front of their head, under and between the eyes, he tried by analogy to locate the corresponding organs of the bee on the antennæ.

Perris (1850) repeated Dugés' experiment by holding many specimens of different families and genera over the mouths of vials containing alcohol, turpentine, or ether. At times he obtained the same results as did Dugés, at other times none at all, using the same individuals after intervals of one-half hour; but more often the antennæ or palpi exhibited more or less violent movement. He also repeated the experiments of Huber on various insects by stopping up their buccal cavities with wax, paste and gum. When they were set free he did not notice any signs of inconvenience. By such experiments he failed to locate the seat of the organs of smell in or near the mouth as Huber did. After having placed a brush dipped in turpentine, ether or wild thyme near the spiracles he concluded that odor-stimuli are not received by the respiratory apparatus.

In his summary Perris says: (1) By amputating the extremity of the antennæ the olfactory sense is not destroyed but it is weakened,

and by cutting them off at the base the sense of smell is totally or partially destroyed; (2) covering the antennæ with a layer of india rubber renders these organs insensitive; (3) sometimes a little sensibility is shown when the palpi are amputated. Thus in the articulates the organs of smell reside in the antennæ and in the palpi, but the antennæ recognize odors from afar and from near by, while the palpi recognize only distant odors. In the plumose, flabellate or pectinate antennæ olfactory organs are present in all the branched parts. In the simple and setaceous or filiform antennæ the organs of smell are principally in the last joints and diminish toward the base. In antennæ terminated with a club the organs of smell are exclusively in the club. He believes that the organs of smell are present in the last joint of the palpi.

Cornalia (1856) says that the manner in which insects move the antennæ shows that these appendages serve for searching when the odor is scattered. He observed a male *Bombyx mori* that was trying to enter a small box in which a female was enclosed. After he had cut off the antennæ of this male it approached the box with uncertainty and sometimes did not go to the box at all. The same result was obtained by covering the antennæ. His view is similar to that of Perris in that the seat of olfaction lies in both the antennæ and palpi.

Garnier (1860) is certain that articulated animals perceive odors. Bees that go foraging for a long distance quickly recognize their hives without the aid of their acute vision. An organ of olfaction, wherever one may observe it, is an expansion of very fine skin, abundantly supplied with vessels and nerves, and moistened with a viscid fluid which permits the intimate contact of the odor. He does not state where the olfactory apparatus lies in insects, but he denies that the antennæ performs such a function, because when the knobs of the antennæ or the entire antennæ of individuals of the Genus *Necrophagus* were detached, the insects returned immediately to the body of a mole from which they had been temporarily removed.

Balbani (1866) put unmutilated female butterflies in one box and in a second box he placed males of the same species. Some of the latter had their antennæ cut off. As soon as the box containing the females was placed under that of the males, the unmutilated males moved their antennæ, vibrated their wings and quickly moved their legs, while the mutilated ones remained perfectly quiet. In this experiment he says that sight and hearing were excluded and thinks that olfaction brought about by the antennæ is entirely responsible for these responses of the males.

Forel (1874, 1885) says that myricids (ants) appear to have the sense of touch highly developed in the antennæ, while in the antennæ of *Tapinoma* (ants) the sense of smell is better developed. If individuals of either genus are deprived of their antennæ they cannot guide themselves and are not able to distinguish companions from enemies or even to discover food placed at their sides. While deprived of the anterior part of the head and of the entire abdomen they preserve all their faculties. The same author (1878a) claims that the moving-back and forth of the wings enables insects to scent certain substances by means of their antennæ. Olfaction may cause certain flying insects to proceed in a given direction.

Forel (1878b) used three wasps that had previously fasted. The first was left intact, both antennæ of the second were cut off, and the anterior part of the head up to the compound eyes of the third was cut off. After a short rest a needle dipped in honey was brought near the first insect. It at once directed both antennæ toward the needle with rapid movements and followed the needle when it was slowly moved away. Exactly the same thing took place in the wasp with the anterior part of the head cut off, and thus with the nerve endings of the mouth, the pharynx, and Wolff's olfactory organs lacking. It was quite different with the one with the removed antennæ. It remained near the needle motionless, did not react to honey at all, and did not follow the needle.

Forel (1908, p. 92) cites some of his experiments performed in 1878. He found the putrid bodies of a hedgehog and a rat infested by a swarm of carrion-feeding beetles belonging to several genera. He collected more than 40 specimens from the carcasses and removed their antennæ. Then he placed them all at one place in the grass and moved the dead bodies a distance of 28 paces from the beetles and concealed them in a tangle of weeds. Examination the next day revealed the fact that not one of the mutilated beetles had found the carcasses, and repeated experiments gave the same results. No beetle without its antennæ was ever found on the dead animals, although at each examination new individuals of the several species were present. On the supposition that the mutilation itself might make the beetles abnormal to such an extent that they did not care to eat, Forel next cut off all the feet on one side of the body from a dozen beetles with their antennæ intact and changed the location of the dead bodies again. The next day five of this lot were found on the carcasses.

Trouvelot (1877) performed various experiments on the antennæ of many butterflies, several *Promethes* silkworm moths, and some

ants. From these experiments he concludes that the antennæ are the organs of smell, but he thinks that the sense of smell in insects is very different from that sense in the human species. He regards it as a kind of feeling or smelling at a great distance by some process now entirely unknown.

Layard (1878) relates the experiments of a certain French naturalist who immersed a long-snouted weevil in wax so that it was covered all over except the tip of the antennæ. When tested with oil of turpentine it became violently excited and endeavored to escape. Another had only the tips of its antennæ coated with wax, and neither turpentine nor any other strong-smelling substance affected it. From this he infers that the organ of smell is present in the tips of the antennæ of weevils.

Slater (1878) says:

That wasps have an acute scent and seek their prey or their food by its means, will be generally admitted * * *. When a wasp is flying it keeps its antennæ advanced and extended, so as to be in the most favourable position for receiving an impression from odoriferous substances.

Chatin (1880) states that when one brings a needle wet with ether, creosote, essence of wild thyme, or clove oil near the head of a bee it moves its antennæ, vibrates them vigorously, and directs them away from the odorous substance; if one repeats the same experiments near the spiracles no such movements are manifested. Also, when the antennæ are cut off no responses occur.

Lubbock (1882) experimented with a large female ant. He placed a feather of a pen almost against the antennæ of this ant without it moving in the least. Next he dipped the pen in essence of musk and repeated the experiment. The antennæ were at once retracted. With a second ant he used essence of lavender and observed the same results. Many more of his experiments indicate that ants have a highly developed sense of smell.

Porter (1883) experimented on a butterfly with a piece of gum camphor on the end of a broom straw. He says:

Whenever I put the camphor end near to its head and mouth parts, it would begin to struggle with all its might to get away from the fumes of the camphor; thus showing not only that it disliked the smell of camphor, but also that it did not smell with its antennæ. After experiments have shown the same thing of other insects.

This butterfly was affected little, if at all, by the extirpation of its antennæ while some humble bees become very sick after the loss of their antennæ; they, however, recovered after awhile. Some other humble bees are not affected at all by such an operation.

Graber (1885) severely criticizes the view that the antennæ are the seat of the olfactory sense. He experimented on many species with various odors, and makes the following claims: (1) Ants (*Formica rufa*) and flies (*Lucilia caesar* L.) without antennæ still possess the sense of smell; this fact shows that the perception of odors is not accomplished by the antennæ alone. (2) In *Silpha thoracica* deprived of antennæ, the odor of the essence of rosemary is manifestly perceived, while assafoetida does not affect the insects at all. Thus the antennæ are those parts of the body which are most sensible to odors. (3) From the comparative experiments on the excitability of the antennæ, the palpi, and the cerci (caudal styles) in *Gryllotalpa gryllotalpa* L. (*vulgaris*), the palpi are more sensible to odors than the antennæ. (4) The palpi of *Lucanus* are sometimes the most easily excited, at other times the antennæ, according to the odors employed. From similar experiments on *Periplaneta*, some intact, others several days after they were operated on, it seems that the reception of odor stimuli is accomplished by the cerci. Graber is inclined to the view that insects do not have any special olfactory organ, and that when the odoriferous emanations are intense they may be perceived by the surfaces of the body that are covered with thin chitin and provided with terminal excitable nerves.

Plateau (1886) used four *Blatta* (cockroaches), two with their maxillary and labial palpi cut off and their antennæ left intact and the other two with the antennæ cut off and the palpi left intact. These four insects were put into a large circular dish 8 inches in diameter. This vessel contained a bed of fine sand and in the center there was a round pasteboard box 2 inches in diameter and 2 inches high. Food was put into this box, and these insects were observed each day for a month. Each day he saw one or two *Blatta* eating the food, and in every instance these were the insects with un mutilated antennæ, and he concluded that the antennæ are the olfactory organs in *Blatta*.

Graber (1887) repeated Plateau's experiments by using many cockroaches and declares that it is sufficiently proved that cockroaches deprived of their antennæ smell little or none at all, and that the antennæ in these insects actually function as olfactory organs. He also says that for cockroaches (and some other insects) it is shown that the olfactory sense lies in the antennæ but this is not the case in all insects.

Dubois (1895) touched the scent glands situated at the tip end of the abdomen of a female moth with a glass rod and then brought this rod, which had no odor perceptible to him, near a male of the same

species that had its antennæ cut off. The male at once vibrated its wings and started toward the rod.

Fielde (1901a), who has made a special study of ants, claims in her various papers that ants have a keen sense of smell. The same author (1901b) asserts that,

The power of perceiving the individual track lies in the tenth segment of the antennæ. When deprived of this segment the ant is no longer able to find her way in with the pupæ, but wanders about helpless and bewildered. Ants deprived of nearly all of the eleventh and twelfth segments continued to carry the pupæ through the runs of the maze, though with diminished physical vigor. The ant could pick up her scent so long as a tenth segment was intact, and no longer.

Miss Fielde clipped the antennæ with sharp scissors and 15 days after the operation about 40 per cent of the ants recovered from the effect of the shock.

Before their recovery the ants were listless and abnormally irritable; and they attacked with self-destructive violence any moving thing that touched them. One antennæ performs all the functions of a pair. * * * Every *Stenamma fulvum piceum* has an odor manifest in all parts of her animate body, and discerned by herself and by other ants through the eleventh segment of the antennæ.

The commingled odors of all the ants in the nest constitute what she calls the "aura" of the nest.

It is diffused in air or ether from the animate occupants of the nest, and it is discerned by the ant through the twelfth, the distal, segment of the antennæ.

When deprived of the distal segment the ants were not alarmed when introduced into the nest of aliens; they did not flee, nor did they endeavor to hide; thus their behavior is strikingly different from that of unmutilated ants. Also she found (1907) that queens deprived of their antennæ did not behave normally.

So long as the eighth and ninth segments of the antennæ are uninjured, the ant may continue to lift and care for the eggs, larvæ, or pupæ, but after the removal of these segments she loses all interest in the young and performs no further work in the nursery. * * * Marked ants of two hostile colonies, when clipped across the tenth segments, associated freely and amicably with one another during several days in the care of the pupæ belonging to one of the two colonies.

A paper by the same author (1903a) summarizes the foregoing and adds observations on some of the segments not heretofore mentioned. The following perceive these particular odors: The eleventh or distal segment, the nest odor; the tenth, the colony odor; the ninth, the individual track; the eighth and seventh, the inert young; the sixth

and fifth, the odor of enemies. Miss Fielde (1903b) claims that feuds between the same species living in different communities are caused by a difference of odor. Also, (1904) fear and hostility are excited by a strange ant odor. She (1905) decides that ants have a specific and progressive odor; the former is received by organs near the proximal end of the funiculus, while the latter is received among ants by organs in the penultimate joint of the funiculus.

Piéron (1906), basing his conclusion on the interpretations of Fielde and others, remarks that recognition in ants by odor is well established, and that sections of the antennæ have shown that the organs of smell are those of recognition.

Wheeler (1910) believes that the olfactory organs of ants are located in the antennæ, but he refutes Miss Fielde's theory that each segment of the antenna perceives a particular odor. He asserts:

She says: "The organ discerning the nest-aura, and probably other local odors, lies in the final joint of the antenna, and such odors are discerned through the air; the progressive odor or the incurred odor is discerned by contact, through the penultimate joint; the scent of the track by the antepenultimate joint, through the air; the odor of the inert young, and probably that of the queen also, by contact, through the two joints above, or proximal to those last mentioned, while the next above these also discerns the specific odor by contact."

This statement not only lacks confirmation by other observers, but seems to be the only one which implies that the olfactory organs of an animal may exhibit regional differentiations. This has not even been claimed for dogs, which nevertheless possess extremely delicate powers of odor discrimination and association. This would be no serious objection, however, if we were able to discover the slightest support for Miss Fielde's hypothesis in the structure of the antennæ. We do, indeed, find in the funiculi a variety of sensillæ, as has been shown in Chapter IV, but none of these is confined to a single joint or to two joints. Miss Fielde, moreover, completely ignores the tactile organs of the antennæ and makes this surprising statement:

"During five years of fairly constant study of ants I have seen no evidence that their antennæ are the organs of any other sense than the chemical sense."

Many of her interpretations of the behavior of ants with mutilated antennæ are open to the obvious objection that she tacitly denies the existence of perception where there is no visible response or where the animal inhibits certain of its activities. If we add to this objection the very limitations of the method, *i. e.*, the necessity of removing all the joints distal to the one whose function is being tested, and the consideration that the hypothesis is not needed to explain the facts, it will be seen that we are not sufficiently justified in regarding the ants' antenna as an organ made up of a series of specialized "noses."

Barrows (1907) says:

I have found that *Drosophila ampelophila* (the vinegar fly) has a large saclike pit, which contains sense cones, situated in the end of the terminal (third) segment of the antennæ.

Gum on the antennæ did not prove satisfactory for abolishing sense of odors, nor could they be burnt off without considerable injury to the fly. He etherized some flies and cut the joint off with fine scissors and declares that the ether did not affect the results of the experiments with odors.

It, therefore, seems certain that the sense of smell is absent, or at least greatly reduced in flies that have lost the terminal joints of the antennæ.

He thinks that these flies when normal find their food wholly by smell.

When one antenna is lost and the other antenna is stimulated by food odor, circus movements are carried out in such a way as to prove that the fly orients normally by an unequal stimulation on the antennæ.

Kellogg (1907) informs us that the female silkworm moth protrudes a paired scent organ from the hindmost abdominal segment. A male moth with antennæ intact and with eyes blackened finds a female immediately and with just as much precision as when his eyes are not blackened. A male with the antennæ extirpated and eyes not blackened does not find the female unless by accident. Males with antennæ intact become greatly excited when a female is brought within several inches of them. If the excised scent glands are laid near the female from which they were taken, the males always neglect the near-by live female and go directly to the scent glands and try to copulate with them. A male with its left antenna removed, when within 3 or 4 inches of a female with protruded scent glands, becomes greatly excited and moves in circles around her to the right. A male with right antennæ off circles to the left.

Sherman (1909) discusses the sense of smell in insects without even giving any references or without performing any experiments.

He says: "The organs of smell are the antennæ." Insects that feed upon decaying matter find their food almost entirely by smell. When their antennæ are removed they are unable to find their food even though it is quite near and in full view. "This indicates that the sense of sight is defective and that of smell very acute."

To ascertain if the antennæ of honey bees, ants and hornets carry the olfactory organs, the author performed the following experiments. Worker bees with one antenna pulled off are much less pugnacious than are those with the antennæ intact, and they "pay less attention" to each other. They appear otherwise normal, except that their ability to communicate is considerably decreased. In observation cases they live only $6\frac{3}{4}$ days while workers with unmutilated antennæ live $9\frac{1}{8}$ days under the same conditions. When tested with the three essential oils—peppermint, thyme and wintergreen—

their reaction time was 4.6 seconds, which is exactly double the reaction time when workers with unmutated antennæ are used.

Bees with one antenna pulled off and with 2 to 8 joints of the other one cut off never "pay any attention" to each other and very seldom are seen fighting, but are just as apt to fight a hive-mate as a stranger. The greater the number of joints severed, the less number of days they live and the more abnormal are they. On an average they live only 5 days and 11 hours. When tested with the three essential oils the following reaction times were obtained:

	Seconds		Seconds
2 joints missing....	15	6 joints missing....	27
4 " "	44	7 " "	98
5 " "	56	8 " "	88

Bees with both antennæ pulled off live only 19 hours in observation cases and are completely abnormal in behavior. They always fail to respond to odors. When both antennæ are cut off at the bases, the bees live only 2 hours. They are also entirely abnormal and fail to respond to odors.

Bees with their antennæ covered with either shellac or celloidin do not live long and are quite abnormal. Bees with the antennæ covered with vaseline soon remove this substance and then behave normally again. Bees having the antennæ covered with liquid glue are abnormal until they remove the glue with their antenna cleaners. To prevent this removal the tarsi of the front legs including the antenna cleaners were burnt off with a red-hot needle. One-fourth of the bees so mutilated died within 12 hours, but the remainder appeared quite normal in every other way. On the second day the entire flagellum of each antenna was covered with liquid glue. These workers were quite abnormal and most of them did not live long. However, after gluing the flagella of many bees, 21 were finally obtained that were fairly normal and their reaction time to the three essential oils was 2.9 seconds, while the reaction time of the same odors for unmutated bees was 2.6 seconds. These 21 workers lived only 24 hours on an average. The odor from the glue did not affect these results.

Both antennæ of 95 workers were burnt off with a red-hot needle. These workers were quite abnormal and lived only 17 hours. Seven of them recovered sufficiently from the operation to respond to odors; while the others failed to respond. The reaction time of the 7 workers used to the three essential oils was 4 seconds.

Since the effect of the shock caused by mutilating the antennæ may have produced the abnormality in all the bees experimented with, 30 workers were immersed in water for 15 minutes. When removed

they appeared entirely lifeless and the antennæ were pulled off at once. They revived and lived thereafter only 19 hours. When tested with odors they failed to respond and like all the other bees made completely abnormal, they scarcely moved when touched with a pencil.

Since bees whose antennæ are mutilated after they become adults are abnormal, the antennæ of 400 worker pupæ were cut off. Several days later these workers emerged normally from their cells, but lived thereafter only 5 days.

The funiculi of 12 workers of *Formica* were cut off. These ants were then returned to a Fielde nest. They were slightly hostile to each other and to their unamputated sisters. They failed to eat food and to catch flies, but their unamputated sisters continually ate food and soon caught flies. The funiculi of 50 more workers of *Formica* were cut off. When returned to their cage, these ants were quite irritable and invariably attacked one another, and as a result several were killed.

The funiculi of 2 soldiers, 10 large workers and 7 small workers of *Camponotus* were cut off. When returned to their nest these ants attacked one another for three hours, then they became very inactive and responded to odors only slowly. The next day they were still quite inactive and "paid no attention" to anything, except when they came in contact with each other, they still fought one another. When tested with odors they failed to respond. At no time did they eat or drink.

The funiculi of 30 winged virgin females of *Formica* were cut off. When placed in experimental cases they were quite abnormal. Five of them failed to respond to odors and scarcely moved when touched with a pencil. These ants were discarded from the experiments. When tested with the three essential oils, the other 25 gave a reaction time of 4.38 seconds, while the reaction time for unamputated sister females was 2.12 seconds. Confined in a Fielde nest, these mutilated ants lived only 19 hours.

The funiculi of 30 winged virgin females of *Formica* were covered with liquid glue. These ants were completely abnormal and five of them failed to respond to odors. When tested with the three essential oils the other 25 gave a reaction time of 5.78 seconds. They lived 6 days on an average.

The flagella of 25 *Vespula maculata* were cut off. In behavior these mutilated hornets were abnormal and lived only 1 day and 13 hours in observation cases. When tested with the three essential oils some of them responded promptly; some responded slowly, and a few failed to respond at all. All of those which failed to respond to

odors scarcely moved when touched with a pencil. These were discarded and the flagella of the others were cut off. The 25 used in these experiments gave a reaction time of 3.09 seconds which is 0.66 second greater than the same reaction time for normal hornets.

In conclusion under this head it is seen that about four-fifths of the writers cited advocate the view that the antennæ are the seat of the organs of olfaction. Most of these observers have not said whether the mutilated insects that they used were normal. The inactivity or state of rest of many of these specimens indicates abnormality. In regard to Miss Fielde's ants, only 40 per cent recovered from the effect of the shock and in all probability all of these were more or less abnormal. When the antennæ of ants, hornets and bees are mutilated in the slightest degree, as ascertained by the author, the insects are more or less abnormal. The results obtained by using any insect with mutilated antennæ are, therefore, in all probability more or less erroneous. Judging from the author's experiments there is no reason to assume the presence of the olfactory organs in the antennæ, because the differences in reaction times between the reaction times of the mutilated insects and those of uncut antennæ may be attributed to the abnormality of the insects which is probably always caused by the operations. At most it can be claimed only that the antennæ may assist in the receiving of odor stimuli.

Since the organs in the antennæ of ants, hornets and bees, and probably all insects, fail to receive most, if not all, odor stimuli, the true olfactory organs must be looked for elsewhere.

VARIOUS STRUCTURES ON THE ANTENNÆ AS OLFACTORY ORGANS

Before entering into a discussion of the antennal organs of insects, a brief description illustrated with drawings of the antennæ of the honey bee and their organs will first be given.

The antenna of the bee consists of two portions: the proximal part, called the scape, and the distal portion, the flagellum. Each portion is more or less cylindrical in shape. The scape consists of a single long, slender joint, while the flagellum consists of 11 short joints in the worker and queen and of 12 in the drone.

When an antenna is examined under the microscope with a strong transmitted light its surface is seen to be covered with small bright spots and also various kinds of hairs. In order not to overlook any of these peculiar structures, several pairs of these appendages from young bees just emerged from their cells were removed and perma-

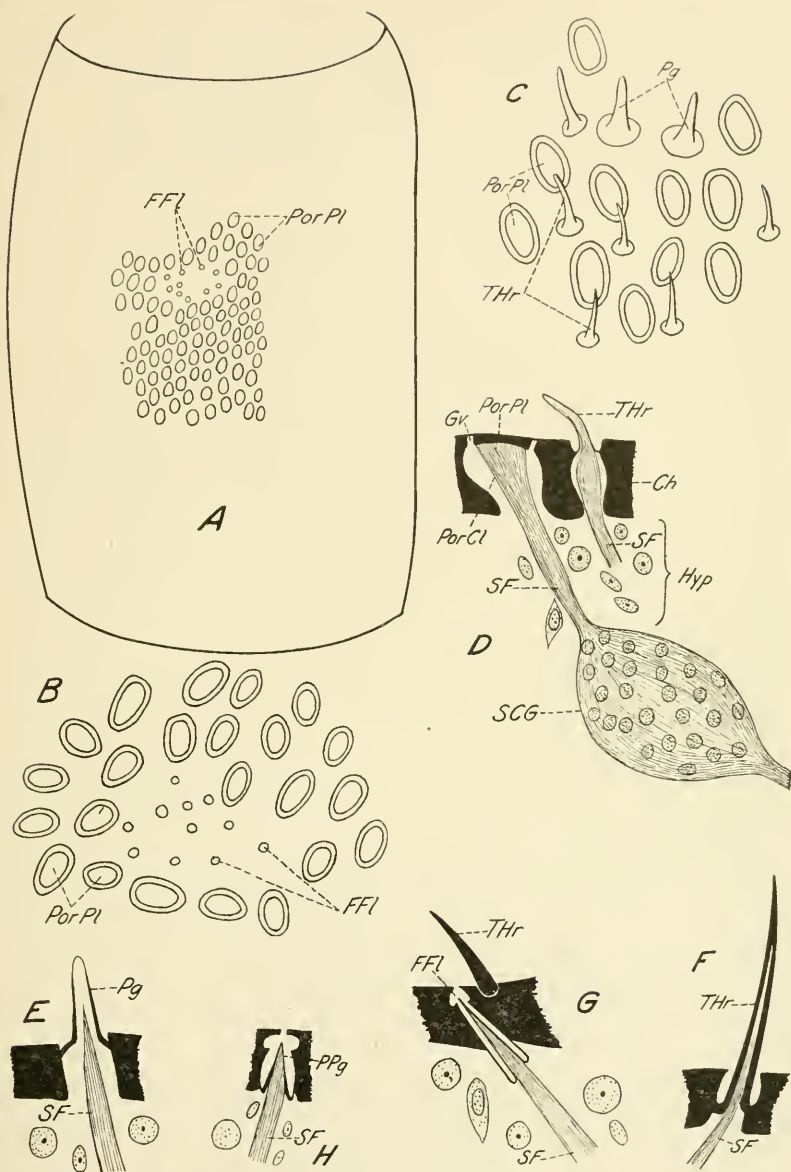


FIG. 1.—Antennal organs of the honey bee copied from Schenk. A, an antennal joint of a drone, showing a few of the many pore plates (*PorPl*) and a group of Forel's flasks (*FFI*), $\times 150$; B, pore plates and Forel's flasks from a drone's antenna, $\times 600$; C, pore plates (*PorPl*), pegs (*Pg*), and tactile hairs (*THr*) from a worker's antenna, $\times 600$; D, internal anatomy of a pore plate and of a tactile hair; E, the same of a peg; F, the same of a tactile hair; G, the same of a Forel's flask; H, the internal anatomy of a pit peg. D-H, $\times 600$.

nently mounted. In these antennæ there is no dark pigment to obscure any of the antennal organs. To illustrate these various structures modified copies of Schenk's drawings (1903) are given (fig. 1).

Figure 1, A, shows the small bright spots (*PorPl*) on the drone antenna magnified 150 times. This drawing also shows still smaller bright spots (*Ffl*) which are difficult to find. Formerly the larger bright spots were termed "pits" but later they were called "pore plates," "pore canals," and "sensilla placodea," while the smaller spots bear the names "Forel's flasks" and "sensilla ampullacea." In this discussion the former will be known as *pore plates* and the latter as *Forel's flasks*. Figure 1, B, represents these organs of the drone bee enlarged 600 diameters. Figure 1, C, shows the pore plates (*PorPl*) and two kinds of hairs from the antenna of a worker, enlarged 600 diameters. The stouter of these hairs (*Pg*) bear the names, "pegs," "clubs," and "sensilla basiconica," and the more slender ones (*THr*) "hairlike structures" and "sensilla trichodea." In this discussion the stout hairs are designated *pegs* and the slender ones *tactile hairs*. A fifth antennal organ whose external opening is not drawn by Schenk has the same superficial appearance as Forel's flasks and probably cannot be distinguished from them externally. These structures have been termed "pit pegs," "champagne-cork organs," and "sensilla cœloconica." They are here designated *pit pegs*.

Figure 1, D-H, show the internal anatomy of the five antennal sense organs. Figure 1, D, shows the structure of a pore plate and of a tactile hair. The chitin (*Ch*) is solid black, the sense fibers (*SF*) and sense cell ganglion (*SCG*) are represented by fine broken lines. Since the sense fibers in Schenk's drawing are defective and are not attached to the plate (*Pl*) as the writer has observed them many times in his sections, and as Schenk represents them in *Vespa*, they are here drawn as they really exist. The plate is a hard and comparatively thick chitinous disc completely covering the pore canal (*PorCl*). However, at its margin there is a deep groove (*Gv*) entirely surrounding the plate. To stimulate the sense fibers attached to the plate the odors must first pass through this hard chitinous plate.

Figure 1, E, shows a peg with its sense fibers running half-way to the tip of the hair. At its base the chitin is relatively thick while at the tip it is thin. If this structure is an olfactory organ, the odors must first pass through the thin chitin at the tip of the peg to stimulate the sense fibers. Figure 1, F, is a tactile hair. Figure 1, G and H, represent a Forel's flask and a pit peg respectively. Both of these

are nothing less than hairs inside of pits, and the only difference between them is the shape of the flask. If they are olfactory organs, odors must enter the small apertures and pass through the thin chitin at the tip of the hairs inside the pits, to stimulate the sense fibers.

In drones, the antennal organs are found on only the distal nine joints of the flagellum and in workers and in queens on the distal eight joints. According to Schenk, the pore plates are present on all of these joints, and while they are abundant on both the dorsal and ventral sides of the male antennæ, in the female antennæ nearly all of them occur on the dorsal side. On both antennæ of a male there are about 31,000 and on those of a female only about 4,000; however, those of the female are considerably larger. Pegs are entirely absent from the drone antennæ, while they are abundant on those of workers and of queens. As a rule they are at the distal end of the joint on the dorsal side. The male antennæ are always devoid of tactile hairs whereas those of the female have many. Forel's flasks and pit pegs are moderately numerous in both sexes, but slightly less abundant in the female antennæ.

Some of these antennal organs, or at least modifications of them are present in the antennæ of all species of insects with probably one or two exceptions. In butterflies and moths pore plates are entirely absent and pegs are almost wanting. However, the place of the pegs seems to be taken by end rods, which are very similar in structure but are more club-shaped. Butterflies and moths also have bristle-like tactile hairs.

Pore plates, pegs, Forel's flasks, pit pegs and end rods have all been considered as olfactory organs by various authors, who, in trying to prove their views, assert that odors can pass through the hard chitin of these organs so that the nerve fibers inside may be stimulated. While these authors declare that this is possible in insects, they acknowledge that it would be impossible in the higher animals.

Erichson (1847), according to Hicks (1859c), first observed the pore plates and hairs on the antennæ of insects. He considered the pore plates as olfactory organs for two reasons: (1) He thought that the numerous hairs on the antennæ protect and keep these plates moist, so that odors can pass through them, and (2) they are more numerous in those insects whose smell is acute.

Burmeister (1848) describes the pits found on the antennæ of lamellicorn beetles. These are a variety of the pit pegs, and he attributes an olfactory function to them.

Vogt (1851), according to Wonfor (1874), discovered that the antennæ are covered with minute pores which are apparently filled

with fine hairs. He thinks that these structures perform a function combining those of smell and touch.

Bergmann and Leuckart (1852) say that when one brings a drop of ether on the tip of a needle near the head of an insect it moves and strokes its antennæ. They speak of many pits on the antennæ; from the base of these pits arise small papillæ which they regard as olfactory organs.

Leydig (1860, 1886) made a thorough investigation of the pore plates discovered by Erichson. He found these pore plates not only in the antennæ of most insects but also discovered that they are modified into peculiar, peglike organs in the remaining insects, and in the crustaceans and myriapods. Leydig regarded these organs of questionable function as olfactory. In 1860 he thought that the palpi have a function similar to that of the antennæ.

Lespés (1858) compares the pore plates to the ears of higher animals and denies their olfactory office.

Hicks (1859b and c) thinks that the pore plates are cavities filled with fluid, closed in from the outer air by a delicate membrane to which a nerve is attached. He regards the pore plates as auditory organs and says:

If we assign an olfactory function to these organs, one difficulty presents itself, viz: that for the odorous particles to affect the nerve they must reach it through a membrane and a stratum of fluid.

Landois (1868) experimented with the stag beetle (*Lucanus cervus*). He does not doubt that this beetle can smell, for if exposed to the fumes of sulphuric acid, or ammonia or to tobacco smoke it draws in its antennæ quickly. If the ends of the antennæ are removed it still draws in the remainder of these appendages with the same rapidity as when the antennæ are intact. He found two kinds of sense hairs on the antennæ of this insect and pits filled with small hairs. He thinks, however, that olfaction is performed by none of these organs.

Grimm (1869) describes three kinds of hairs and a pitlike organ on the antennæ of beetles but does not regard any of these as an olfactory apparatus. He put a beetle with entire antennæ into a box which had a glass cover and an opening at the bottom covered with thin cloth. After this beetle had become quiet he put a piece of dung to the opening. The beetle at once came to the opening and tried to tear the cloth. Later he cut off its antennæ and repeated the experiment, and the beetle came to the opening as before. By repeating these experiments many times he concluded that the antennæ of

beetles do not function as smelling organs. Also he infers, like Leydig, that there may be some olfactory rods or pegs on the palpi of this beetle.

Gegenbaur (1870) briefly discusses the antennal organs described by Erichson, Burmeister and Leydig but fails to express his own opinion concerning their function.

Lowne (1870) believes that the olfactory apparatus of the blow-fly is located in the third antennal joint. This joint is remarkably dilated and is covered with minute openings which communicate with little sacs in the interior.

Müller (1871) found stiff hairs and pore plates on the flagella of the antennæ of a female bee, but only pore plates on those of the male bee. He thinks that the pore plates are olfactory organs and that male bees have a better olfactory sense than the females for the following reasons: (1) A male bee has one more joint in the flagellum; (2) all of these joints are longer, and (3) wider, and (4) the pore plates are so close together that they crowd out the stiff hairs.

Claus (1872) thinks that many insects have a well developed olfactory sense and that the surface of the antennæ is the seat of the sense of smell, basing this conclusion upon the work of Erichson and that of Leydig.

Chadima (1873), after examining the hairlike structures on the antennæ and palpi of crustaceans, insects and myriapods, which Leydig (1860) regarded as most probably olfactory organs, says that the smelling organs of arthropods have not yet been found. He states that none of these hairs is perforated at its tip. He thinks investigators will have more success in solving this problem if they look on the olfactory sense as being connected with the breathing apparatus.

Forel (1874) counted five different kinds of organs on the antennæ of ants—(1) olfactory knobs or pegs, (2) tactile hairs, (3) pore plates, (4) Forel's flasks and (5) pit pegs. Forel (1902) judging from the works of Hicks, Leydig, Hauser, Kräpelin and himself remarks that all the reputed olfactory structures of the antennæ are modified pore canals bearing hairs. They come under three chief forms—pore plates, olfactory knobs, and olfactory hairs. At times the last two can hardly be distinguished from one another. Chitin, even if very thin, always covers the end of the nerve. Forel's flasks and pit pegs have no relation to smell because they are lacking in the insects with acute smell (wasps) and are present in great abundance in insects (bees) with poor sense of smell. The same author (1908, pp. 95 and 96) still regards the pit pegs and Forel's flasks as a

physiological enigma. They are generally absent, but are present in ants and aphidids, are quite abundant in the domestic bee, are present but not abundant in bumble bees, and are absent in wasps; nevertheless, he thinks they have nothing to do with olfaction. In dragonflies and cicadas the antennæ are rudimentary and the sense of smell is poor. The organs of smell of insects are in general situated in the antennæ, especially in their swollen or perfoliate parts where the antennal nerve ramifies. "These 'horns,' these 'ears' form, therefore, a famous nose in spite of Wolff and Graber." Thus Forel believes that the antennæ are the olfactory organs, yet he does not state what particular antennal organs receive the olfactory stimuli.

Bertè (1877) states that none of the antennal organs in fleas is for olfaction.

Lubbock (1877) discusses the antennal organs but does not venture to suggest their functions.

According to Vom Rath (1888), Lubbock (1883) found the same structures on the antennæ as did Forel (1874), although the details are somewhat different. Neither Forel nor Lubbock ventures to ascribe an olfactory function to any one of the five antennal organs, but by their many experiments, particularly on ants, both are thoroughly convinced that the antennæ carry the olfactory apparatus.

Graber (1878) describes a pitlike sense organ in the antennæ of flies. This was long before described by Leydig as an olfactory apparatus, but Graber regards it as an auditory organ.

Mayer (1878, 1879) regards the pitlike organs or pore plates as being most probably olfactory in function.

Reichenbach (1879) thinks that the small pits filled with hairlike structures are the olfactory organs in insects.

Hauser (1880) studied the behavior of various insects before and after the removal of the antennæ. When the antennæ were cut off many individuals soon became sick and died, although some of them lived thereafter for many days. In insects with their antennæ dipped in melted paraffin, the behavior was similar to that of those with the antennæ amputated. He placed 12 individuals (beetles) *Philonthus æneus* R. one at a time in an inverted beaker whose bottom was removed. He slowly placed a clean glass rod in front of the head and the insect gave no response. He then repeated the operation with a glass rod dipped in carbolic acid. When this was 4 inches away the insect was much affected, it lifted and moved its head in different directions and made quick forward movements with its antennæ. When the glass rod was brought nearer it moved away quickly and

drew its antennæ through its mouth. The reaction to turpentine and acetic acid was more violent. Next he cut off the antennæ. On the second day after the operation he repeated the experiments, but the insects failed to respond to any one of these three strong odors. After the operation the beetles ate with a greater appetite and some of them lived more than two months thereafter. From these experiments he concludes that the beetles lost the olfactory sense by the removal of the antennæ.

Experiments with species of several other genera gave the same results but those with beetles of the genera *Carabus*, *Melolontha*, and *Silpha* were less satisfactory. These never completely failed to respond to strong-smelling substances. If they are exposed for a long time to the odors the insects deprived of their antennæ become restless and walk away from the glass rod, yet all the movements are less energetic. The entire reaction is indefinite and weakened. Experiments with Hemiptera gave a still less favorable result. After the loss of the antennæ these insects reacted almost as well as they did with their antennæ intact.

Hauser performed the following experiments to ascertain the value of the antennæ in the search for food. He placed beetles (*Silpha*) in a large box whose bottom was covered with moss. In one corner of the box he put a small glass with a small opening, the glass containing foul meat. As long as the insects possessed their antennæ they regularly found the meat in the glass after some time, while after the removal of the antennæ they never came in contact with it. Similar experiments were performed with flies of three genera. A vessel containing spoiled meat was placed on a table by an open window. Soon several flies came to the meat. Then he closed the window and cut off the antennæ at the third joint. Thereafter not one of these flies came in contact with this meat.

Hauser next ascertained the value of the antennæ to the male in finding the females. Male and female beetles and butterflies were placed in large boxes. As long as they were normal in every respect they mated freely, but when the antennæ were cut off they copulated only occasionally.

Hauser, who worked extensively and thoroughly on the antennæ of insects of all orders, found many differences in the various orders but among different Hymenoptera the differences in distribution and structure of the antennal organs are comparatively slight. According to him, *Vespa* (a wasp) possesses about three times as many pegs as does the honey bee, and for this reason *Vespa* has better olfactory

perception. *Formica* (an ant) has far more pegs than pore plates, contrary to the rule in hymenopterous insects. In conclusion Hauser asserts that in almost all insects the olfactory organ consists of (1) a large nerve arising from the cephalic ganglion which runs out into the antenna, (2) a recipient end apparatus which represents rod cells modified from hypodermal cells with which the fibers of those nerves are connected, (3) a supporting and accessory apparatus which is formed by the pore plates and pegs filled with a serous fluid. When both pore plates and pegs are present they both function in smelling according to their number; when one of these organs is absent then the other one functions entirely as an olfactory receptor.

Kräpelin (1883), according to Schenk (1903), considers the pore plates and pegs as smelling organs and translating from Vom Rath (1888) Kräpelin thinks that the olfactory organ is also located in the palpi.

Schiemenz (1883) regards the pegs as touch organs, while the pore plates and Forel's flasks probably serve as olfactory organs.

Sazepin (1884) worked chiefly on the antennæ of myriapods, but he also spent some time in working out the anatomy of the antennæ of *Vespa*. By comparing the anatomy of the myriapods' antennæ and with that of *Vespa* he found that as a whole there is a great similarity, but while the olfactory pegs in *Vespa* are closed at their tip, they are open in what he calls the olfactory pegs in myriapods.

Witlaczil (1885) worked on the antennæ of certain bugs. Since their antennal pits, called olfactory pits by Hauser, are covered by a membrane he thinks that they can scarcely be called olfactory organs.

Vom Rath (1887, 1888), like most authors on this subject, regards the olfactory sense as located in the sense pegs of the antennæ and probably also in the pore plates. By making a comparative study of all the antennal organs in arthropods, Vom Rath (1895) found a great similarity in the structure of each set of organs. The sense pegs are not by any means confined solely to the antennæ but are found on all the mouth parts, in the mouth cavity, and even over the entire body. It is possible that many pegs serve for the reception of the stimuli of weak odors from a distant object and others for the olfactory perception of those nearer. It may be that the pegs of each kind, and also the pore plates, are especially responsive to certain kinds of odors. He believes that the pegs on the palpi possess an olfactory function and possibly for odors close at hand. Moreover, these pegs elsewhere may have the same function.

Ruland (1888), who made a thorough comparative anatomical study of insect antennæ, contends that only such hair structures as those which are perforated at the tips can be sensitive to chemical stimuli. Pegs are found in all orders of insects and, since myriapods and crustaceans possess similar structures, these organs may be considered as the chief form of olfactory organs in the arthropods. Ruland regards the pit pegs and Forel's flasks found in most insects as simple pit pegs, while the compound pits, as seen in the antennæ of flies and butterflies, he calls compound pit pegs. He believes that all three sets of these organs are organs for the reception of stimuli from certain olfactory substances. To determine whether all of the hair structures are perforated at their tips, he put the antennæ into boiling caustic potash. After such treatment he observed that they were all open at the end. In the investigations made by the author it was learned that caustic potash within a short time not only destroys all of the internal tissue but it soon dissolves thin chitin. All who have studied these structures before and since 1888 assert that these hairlike organs are tipped with very thin chitin through which the odorous particles must pass. In the observations made by the author these structures in the antennæ of the honey bee have not shown a single hair which is open in the slightest degree at the tip and it is probable that in Ruland's treatment the caustic potash dissolved the thin chitin at the tip.

Nagel (1892, 1894, 1909, the views set forth in the first reference being cited by various authors,) states that, in his opinion, the antennæ are generally the olfactory organs of insects—not, however, without exception. That insects, after amputation of the antennæ, seem incapable of perceiving odors is not sufficient proof that the antennæ are olfactory organs. He declares (1894) that organs with thick chitinous walls cannot function in smelling, but he thinks that the olfactory pegs, being tipped with thin chitin, are capable of receiving olfactory stimuli. He asserts that these olfactory pegs are found on other parts of the body besides the antennæ. He (1909) does not doubt that in many insects the palpi may assist in smelling. In the antennæ of a May beetle there are four different kinds of pitlike organs (varieties of pit pegs), all of which may be olfactory in function. In the Hymenoptera the antennæ are the only seat for their highly developed olfactory sense. In some Hymenoptera both pore plates and pegs, while in others only the pore plates, function in smelling. In ants the pegs and knee-shaped bristles probably serve this purpose; in Lepidoptera the pit pegs function for smelling when the

insect flies, the end rods serving such a purpose while the insect is resting; in Diptera the pit pegs, similar to those of butterflies, are the olfactory organs. Nagel repeated most of Hauser's experiments and seems to be convinced that the antennæ are almost always, if not always, the seat of the organs of olfaction. When one or more of these organs are absent the next best, histologically considered, must perform the olfactory work; and when all the antennal organs are wanting, as in *Ephemera vulgata*, a pseudoneuropteran, he imagines that the insect cannot smell.

Dahlgren and Kepner (1908) regard the knob-shaped, pitlike antennal organs of *Necrophorus* as the olfactory organs. They found glandlike cells beneath the hypodermis which they believe to be associated with these pits and perhaps aid in receiving odor stimuli.

Nearly all of the foregoing observers have overlooked the sense organ found in the second antennal joint of insects. This is called Johnston's organ. In *Cespa* the upper end, or the nerve rod, of the organ penetrates the articulating chitin between the second and third joints and comes to the surface. From its structure an olfactory sense might be attributed to it. According to Child (1894a and b), who experimented extensively with mosquitoes, this organ serves as a combined touch and auditory apparatus and has nothing to do with olfaction.

Lubbock (1899) says:

Forel and I have shown that in the bee the sense of smell is by no means very highly developed. Yet their antenna is one of those most highly organized. It possesses—besides 200 cones [pegs], which may probably serve for smell—as many as 20,000 pits [pore plates]; and it would certainly seem unlikely that an organization so exceptionally rich should solely serve for a sense so slightly developed.

From this fact and his numerous experiments Lubbock regards the antennæ as the seat of the organs of olfaction, yet he does not commit himself as to the particular antennal organs which receive the odor stimuli.

Börner (1902) states that only a few of the hair structures on the antennæ of *Collembola* may be regarded as olfactory organs.

Schenk (1903) claims that the fact that the males of *Apidæ* (bees) do not possess any pegs does not argue against the view that these structures are olfactory organs for (1) the pit pegs, which certainly have an olfactory function, are common to the antennæ of males, queens and workers, and (2) in hunting for the females the olfactory sense appears to be of second place to sight. In the summary of his observations on *Lepidoptera* Schenk asserts that the pit pegs function

as smelling organs, because they are more highly developed and more advantageously distributed on the antennæ in the males so that they may be of the greatest use in scenting the females. The end pegs also aid in olfaction, particularly when the insect is resting. He does not think that the pore plates in Hymenoptera have an olfactory use, and he regards this view as based on insufficient data. Olfaction in the Vespidae (wasps) is accomplished by the pegs, because the pit pegs are almost absent, while in the bees the pegs and pit pegs both are olfactory in use; but since the male bees do not have these pegs, the sense of smell is entirely performed by the pit pegs.

Röhler (1905) made a special study of the antennal organs in a grasshopper, (*Trypalis*) *Acridella nasuta* L. On the antennæ he found only three kinds of organs, viz: bristles, pegs and pit pegs. Of these three he regards only the pit pegs as olfactory in function, and the females have only about two-thirds as many of them as have the males. This additional number of pit pegs greatly aids the males in finding the females.

Cottreau (1905) discusses the sense of smell of insects in a popular way, without performing any experiments or citing any references. He says that the olfactory organs are the pits and papillæ, distributed abundantly on the antennæ and without doubt in certain regions on the mouth parts.

In discussing olfaction and antennal sense organs of insects Berlese (1906) seems to infer that there can be no doubt that the antennæ are really the seat of the smelling organs.

In a comprehensive study of the morphology of the chitinous sense organs of *Dytiscus marginalis*, a water beetle, Hochreuther (1912) finds seven different kinds of organs. Of these seven only the hollow pit pegs (hohle Grubenkegel) are probably olfactory in function. They not only occur on the antennæ and mouth parts, but a few are found on the thorax and perhaps a few on the coxæ of the first two pairs of legs.

CAUDAL STYLES ("ABDOMINAL ANTENNÆ") AS SEAT OF OLFACTORY ORGANS

Packard (1870) discovered that the caudal styles of the female *Chrysopila* (a fly) possess a peculiar sense organ. On the posterior edge of the upper side of each style there is a single, large, round sac with quite regular edges. Its diameter is equal to one-third of the length of the style. Dense, fine hairs project inward from its edge, and the bottom of this shallow pit is a clear, transparent membrane devoid of hairs. Since this same insect possesses no antennal organs

Packard believes that this structure is an olfactory apparatus. He calls this a "simple nose," while in the caudal styles of the cockroach there is a "compound nose."

ORGANS ON BASES OF WINGS AND ON LEGS AS OLFACTORY ORGANS

While examining the organs on the halteres of flies, Hicks (1857) discovered on the bases of the wings peculiar structures which he called vesicles, arranged in a single row extending some little distance up the vein on both sides of the wing, but principally on the upper side. By examining insects of other orders he ascertained that these organs are not confined to the Diptera. He believes that they are found in all insects, and they were present in all specimens examined by him. They exist on both sides of the wing, but chiefly on the upper side of the base on the subcostal vein and in the Hemiptera on the costal vein. Those on the hind wing are generally larger in size and greater in number.

In Moths they are very apparent, being greatest in the Noctuæ [Noctuidæ] and Bombycidæ. There are about 100 vesicles on the upper surface of the posterior wing, and half that number beneath, besides some few on the nervures [veins]. In the butterfly they are smaller, but arranged in more definite groups, about three in number. In Coleoptera and Neuroptera they are arranged in long rows along the subcostal nerve; they are more apparent in Coleoptera than in Neuroptera. In the Hymenoptera, for instance the bee, they are found in a rounded group of about forty on each side.

Are they organs of smell, as suggested by Mr. Purkiss? As the olfactory organ has never yet been decided on, it seems to me not improbable that they be the organs of that sense; for, first, it is not likely that they should be the organ of hearing, as they are in constant motion, and situated near the source of the hum of the wings, so that other sounds would be drowned, 2ndly, it is not necessary that the power of smell should be in the head. It is situated in the commencement of the air passages in the upper animals probably because the current of air or water passing the olfactory nerves is there most powerful; but in the spiracle-breathing insects the greatest currents are in the neighborhood of the wing, and near the greatest thoracic spiracle. The motion of the halteres also permits a greater exposure to odors floating in the air.

He claims that the organs on the halteres and on the base of the wings are similar in structure and probably have the same function, that of smell. He was able to trace a nerve to each group of organs, the one going to the hind wing being the larger.

Hicks (1859a) presented a second paper concerning these organs in which he asserts:

I may here repeat that each of these structures consists of very thin and transparent, hemispherical or more nearly spherical projections from the

cuticular surface, beneath which the wall of the nervure is deficient, so as to allow a free communication with its interior; these organs are arranged in rows on the halteres and in variously shaped groups in the wings.

He examined one or more species of about two dozen genera representing all of the insect orders. He observed these organs in the honey bee, in *Vespa*, and in all other species examined by him except *Corysus* [*Corizus*], the bedbug (*Cimex lectularius*), an apterous beetle, and the flea (*Pulex irritans*). Usually these structures consist of two groups on the upper, and one scattered group on the under side of the subcostal vein, amounting in *Ophion* to from 200 to 300 above, and perhaps 100 beneath, with a smaller group at the end of the vein. In the Diptera these vesicles are found both on the wings and halteres. In the Coleoptera they are highly developed and occur in numerous groups on the subcostal vein, mostly at the widest part, but are also scattered along it to the joint of the wing. In *Carabus* (a beetle) they are found on veins other than the subcostal. In many beetles the vesicle is overarched by a hair, which probably protects the organ. He could distinguish no differences in the sexes except that the vesicles were slightly larger in the females, due to their greater size. These organs are most perfectly developed in the Diptera, slightly less perfectly developed in the Coleoptera, rather less so in the Lepidoptera, only slightly developed in the Neuroptera, scarcely at all in the Orthoptera, and only a trace of them exists in the Hemiptera. He gives several drawings, but they represent only the superficial appearances.

Hicks (1860) discovered these same vesicles on the trochanter and femur, chiefly on the former, in all the insects he examined. In *Formica rufa* (an ant) these structures are numerous and exist both on the trochanter and femur. A few small groups of these vesicles are also present on the proximal end of the tibia in this ant. In the honey bee these organs are not so abundant on the legs but are located at the same places as on the ant. The vesicles on the legs, like those on the wings, consist of a thin, delicate membrane

stretching over, and closing in from the air, a tubular aperture in the chitin-layer of the part. This aperture may be circular or oval, the tube varying in length according to the thickness of the integument, curved as in the Hornet, or forming a globular cavity as in *Silpha*. The delicate membrane which covers over this aperture is generally level, sometimes leaving a ridge or a minute papilla in its center.

Hicks gives drawings showing the disposition of these vesicles or pores on the wings and legs of many of the species examined. He saw nerves running to all of these organs and gives a very good idea

concerning their structure, although since our modern technique of making stained sections was entirely unknown in his time we should not expect his drawings to represent the finer anatomy of these pores. He used the following technique:

After cutting off the wing and washing it well in water or spirits of wine, and draining off the major part by blotting paper, I immerse it in spirits of turpentine for a week or two, after which it is placed in Canada balsam between glass in the normal way, taking care not to heat it, as that renders the nerve too transparent. In those parts which are too dark for observation, I have been enabled to render them colorless by Chlorine.

In regard to smell in insects and the function of the pores on the legs Hicks says:

The delicacy with which odours are perceived by many insects argues an olfactory apparatus of considerable perfection; and it seems to me not impossible that these latter named organs [those on the legs] may be in some way connected with the sense of smell, or perhaps with some sense not to be found in the Vertebrata.

To summarize Hicks' three papers, he discovered these pores on the halteres and on the bases of the wings of all Diptera examined; on the bases of all four wings of the four-winged tribes; on the trochanter and femur of all insects, and occasionally on the tibia. He examined many species representing various insect orders and found these pores even on the lower insects, such as the earwig. In such wingless insects as the worker and soldier ants, he infers that these pores are much more abundant on the legs than they are on these appendages in the winged insects. Hicks suggested an olfactory function for all of these pores, whether on the legs or wings, but he performed no experiments of any kind.

Weinland (1890) and several others have made a special study of the halteres or balancers of flies and the sense organs on the bases of these appendages. Weinland distinguishes four kinds of structures on the halteres, all of which are similar in most respects and differ only in minor details. Their internal anatomy is similar to that of Hicks' vesicles. Of these four structures Weinland calls only one of them Hicks' papillæ, and neither he nor anyone else except Hicks and Bolles Lee (1885) has ever attributed an olfactory sense to any of the structures on the balancers.

Guenther (1901) studied the nerve endings found in butterfly wings. He spent a short time on the anatomy of Hicks' vesicles but failed to recognize them as the ones which Hicks first described in 1857. Guenther calls them sense domes (*Sinneskuppeln*). He describes the external appearance of them as being light spots whose

thin chitin is arched in the shape of a dome. Each light spot is surrounded by a dark, chitinous ring. The internal anatomy consists of a sense cell, sense fiber, and a flasklike cavity with its chitinous cone. All of these parts are almost identical to those in Hymenoptera described by the author but Guenther failed to see the sense fiber join the aperture at the bottom of the flask. Thus his drawing shows a thin chitinous arch or dome which completely closes the external end of the flask, the sense fiber running up against this chitinous dome. If he had prepared more sections and used light colored stains such as safrain and not dark stains like hämatoxylin, he could certainly have seen the sense fiber join the aperture in the dome. Guenther tries to liken these pores to the membrane canals of Vom Rath. A similar dome-shaped membrane was found in the antennæ of lamellicorn beetles by Hauser, Kräpelin, Vom Rath, and others, but these bear a little hair at their center. Hauser attributes an olfactory function to such structures, but Guenther shares the opinion with Vom Rath and Graber that they have an auditory rôle.

Janet (1904) found porelike sense organs in large numbers in all the ants that he examined. These pores are either widely separated or, more frequently, united into groups. They occur on the labial palpi and on the tongue, and there are some on the pharynx, besides many on the legs. Janet recognizes those on the legs as the same vesicles or organs that Hicks describes in 1860. In a wasp (*Vespa*) and an ant (*Formica*) their disposition is almost identical with that in the honey bee. Janet's drawings of the superficial aspects of these pores are very similar to those of the author but on account of the small size of the specimens he seems to have had trouble in understanding their internal anatomy. According to him, all the pores, whether on the mouth parts or legs, have a similar structure, and they resemble the structure of the olfactory pores found in the honey bee; however, there are a few slight differences. He calls the chitinous cone an umbel, which is always separated from the surrounding chitin by a chamber. This chamber communicates with the exterior by means of the pore. The sense fiber, or his manubrium, runs into the umbel, and he thinks that it spreads out over the inner surface of the umbel and does not open into the chamber. Thus the umbel forms a thin layer of chitin which separates the end of the sense fiber from the external air. The rôle of these organs is evidently to permit the end of the nerve to become distributed on a surface relatively large and separated from the air only by a thin layer of permeable chitin. Janet fails to give drawings that show the sense fibers run-

ning all the way to the umbel and apparently has not seen the way in which the nerves actually end in the umbels.

Janet (1907) describes and gives a drawing of one of these same organs that he found near the articulation of the wing of a queen ant. Its morphology is the same as described above. Thus in ants, according to Janet, we see that Hicks' vesicles are not only found on the legs, but also near the wing articulations and probably also on the mouth parts. According to their anatomy, as Janet describes it, these organs function as some kind of a chemical sense and in fact are as suitable to perceive olfactory stimuli as are the antennal organs, if not more suitable.

Wesché (1904) remarks that a certain bot-fly has a highly developed sense of smell, equal to that of many mammals. This fly has large antennæ containing sense organs that are larger than those in some other flies; some of these organs are known to function as a keen olfactory sense.

I think that where the antennæ are not particularly sensitive, the palpi have this structure to compensate. We thus see that the palpi, like the antennæ, can bear organs of three senses—touch, taste, and smell; but I do not think that any one palpus has more than two of these senses developed at the same time.

Besides making such broad statements concerning the senses of insects, the same writer describes and gives drawings of some sense organs that he thinks entirely new. Some of these he found on the legs, which are without doubt Hicks' vesicles. He observed these organs in *I'esda* and in many Diptera and his description of their superficial appearance fits what has been seen by the author. Wesché remarks that these organs are possibly auditory or for some unknown sense; however, he says nothing about their internal anatomy or any literature relating to them.

Freiling (1909) spent a short time studying the anatomy of Hicks' vesicles as found in the wings of butterflies. While Guenther found these sense domes (*Sinneskuppeln*) in great numbers, irregularly scattered on the veins near the base of butterfly wings, Freiling regards them as regularly distributed in the same location. The superficial appearance, as he has drawn it, is similar to that of the bee. He shows a large bipolar sense cell with its sense fiber running to the apparent opening in these organs but he thinks that the sense fiber ends [clublike] just beneath the apparent aperture. He worked three weeks trying to get good sections of these organs and succeeded in getting only one specimen from which he obtained fairly good sections. Freiling gives only one drawing each of the external and the

internal structure of these organs, and the latter is drawn diagrammatically. In this he fails to show the chitinous cone, and the end of the sense fiber is represented as separated from the exterior by the thin layer, forming the dome. On this incorrect interpretation of the anatomy, he, like Guenther, speculates on their probable function and concludes that these sense domes may serve as some kind of a barometric device or as an apparatus for measuring the force of the air against the wing.

Berlese (1909, pp. 678-684) calls all the dome-shaped organs of insects "sensilli campaniformi o papilliformi." The campaniform type is found on the mandibles, antennæ, legs and wings. Their domes never project above the general surface of the surrounding chitin. The papilliform type occurs only on the halteres. Here the domes project above the surface of the chitin. In schematic drawings he shows how the domes may have been derived from a portion of the chitin originally not arched. Berlese regards the function of these organs as unknown.

While studying the morphology of the chordotonal organs in the honey bee and ants, Schön (1911) found two rows of small cones on the proximal end of each tibia. A sense cell lies just beneath each cone and the peripheral end of the sense fiber runs into the cone. These sense cells connect with the chordotonal organ located in the middle and distal end of the tibia. Schön has certainly mistaken Hicks' vesicles for cones, because the external appearance of these vesicles often resembles cones when observed without the cylindrical tibia being properly rotated. These organs always lie near the edge of the tibia, and when one looks down upon them their apertures look like cones, but when the tibia is rotated slightly, so that they lie on the median line of the tibia, the optical illusion becomes evident.

Hochreuther (1912) describes and gives drawings of the dome-shaped organs (kuppelförmigen Organe) in a manner somewhat similar to that of Janet. Each organ is located at the bottom of a chitinous flask, the mouth of which communicates with the exterior. Instead of the peripheral end of the sense fiber coming into direct contact with the air in the flask, it apparently stops just beneath the chitinous dome. No true chitinous cone is present, but his terminal strand (Terminalstrang) resembles it somewhat in general appearance. He finds a few of these dome-shaped organs on the epicranium near the margin of the eyes, 11 on the first and second joints of the antennæ, a few on the dorsal side of the labrum, very few on the dorsal side of the mandibles, several on the maxillæ, about 18 on the first four joints of the first legs, about 10 on the first three joints of

the second legs, and a few on the trochanter of the third legs. He evidently has not examined the wings. Thus according to Hochreuther these organs are rather widely distributed. Since the per-

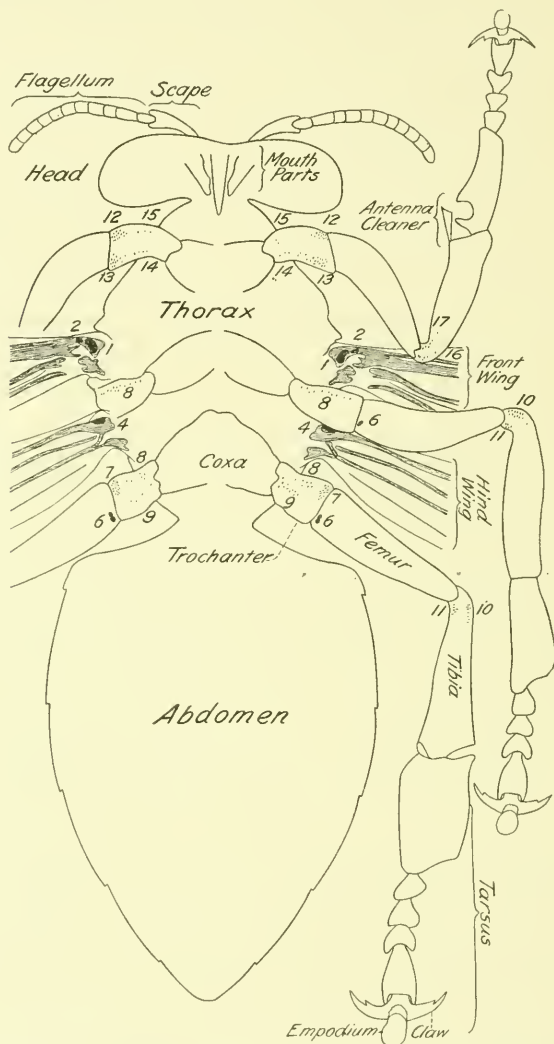


FIG. 2.—Diagram of ventral view of a worker bee, showing the location of the different groups of olfactory pores as indicated by the numbers.

ipheral ends of the sense fibers do not come into contact with the outside air, but connect with the tops of the domes, he suggests that they receive some kind of mechanical stimuli, although he performed no experiments to determine their function.

The following results were obtained by the author. The disposition of Hicks' vesicles (called olfactory pores by the author) is best understood by referring to the numbers in figures 2, 3 and 4 of the

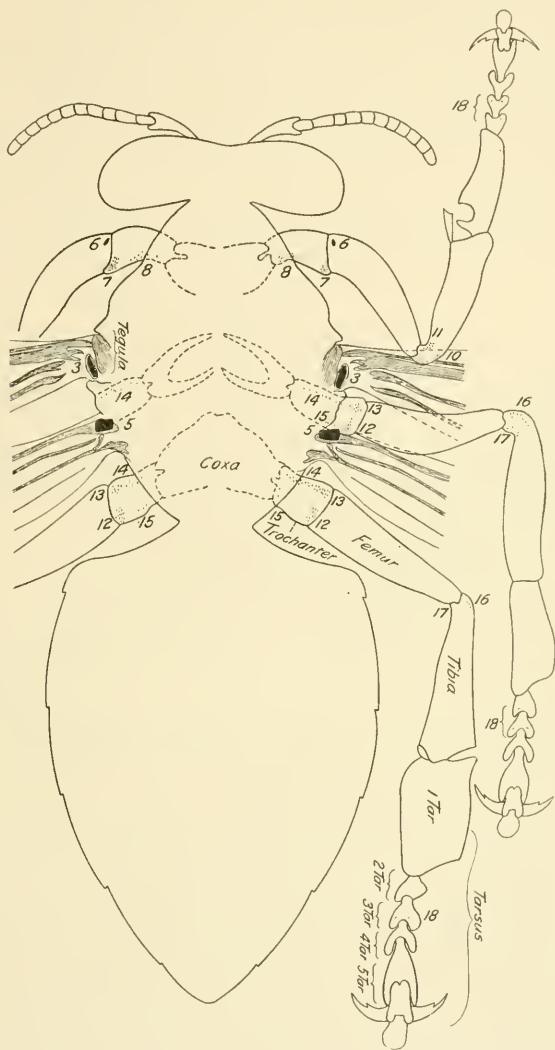


FIG. 3.—Diagram of dorsal view of a worker bee, showing the location of the different groups of olfactory pores as indicated by the numbers.

honey bee. Groups 1 to 5 lie on the bases of the wings as indicated by the numbers 1 to 5. Groups 6 to 18 lie on the legs. Group 19 to 21 lie on the sting of the worker and queen (fig. 4). The same organs are found on the mouth parts of all the hymenopterous insects

examined, but they have not yet been thoroughly studied. The antennæ of the honey bee and probably the antennæ of all Hymenoptera do not carry any of the organs first described by Hicks.

The olfactory pores in other hymenopterous insects are similar in position to those of the honey bee. Among the 29 species examined, these pores vary much in the number of groups and in the number of pores contained in the individual groups. As a rule, the lower the insect the fewer the groups and more isolated are the pores. *Cimber*, regarded as the lowest hymenopteron, has the least number of groups of all the species examined, but it stands fourth in regard to the number of isolated pores. Its total number of pores is larger

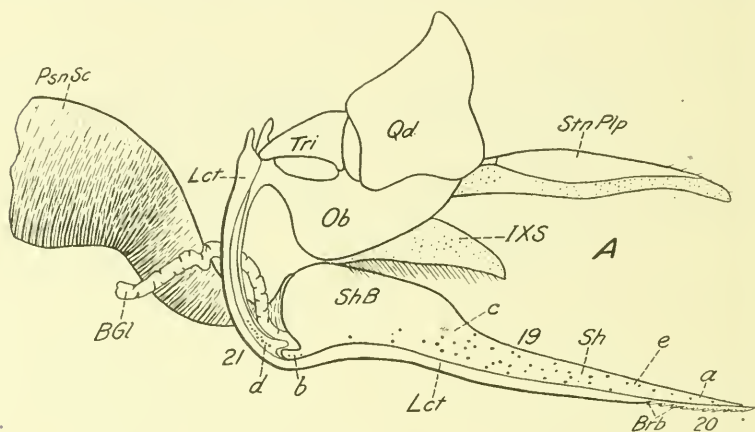


FIG. 4.—Diagram of lateral view of a worker bee's sting and its accessory parts, showing the location of the olfactory pores as indicated by the numbers.

than that of many of the higher forms. Among ants the variations are also great. For the legs of ants the number of pores varies from 211 to 356 and for the winged ants the total number varies from 463 to 1,090. The smallest specimen among the ants and the second smallest one of all the Hymenoptera examined is a female with 463 pores as the lowest number. The drone honey bee with 2,608 pores has the highest number. The smallest specimen examined is a wasp with 688 pores. The following table including 6 of the 29 species examined will illustrate the variations in the number of olfactory pores as found on the three pairs of legs and the two pairs of wings. The letters "F," "M," "H" and "G" stand for front, middle, hind and grand, in the order named. The "Total" means all the pores found on all 6 legs, and the "G. total" means all the pores found on all 6 legs and all 4 wings combined.

TABLE I
Average number of olfactory pores on the legs and wings of Hymenoptera

Average number of stigmatal pores										Average number of stigmatal pores																					
Apidae.					Bombidae.		Vespidæ.		Formicidæ.				Braconidæ.		Cimbicidæ.																
<i>Apis mellifica</i> Linn.					Bombus sp.		<i>Vespula maculata</i> Linn.		<i>Formica obscuriventris</i> Forel.				<i>Microgaster mametree?</i> Vier.		<i>Cimbex americana</i> Leach.																
♂		♀		♀	No. of isolated pores.		No. of isolated pores.		No. of isolated pores.		No. of isolated pores.		No. of isolated pores.		No. of isolated pores.																
No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.	No. of groups.	No. of isolated pores.															
119	77	6	96	57	6	128	96	8	132	95	8	90	67	6	41	79	8	32	80	8	40	71	8	21	42	6	112	17	2 F. legs.		
111	75	5	99	60	6	146	86	8	72	88	8	102	70	6	37	79	8	33	83	8	32	76	8	39	30	6	92	12	2 M. legs.		
140	88	7	89	51	6	137	101	8	53	83	8	80	64	6	38	82	8	31	83	8	36	77	8	36	43	6	118	24	3 H. legs.		
610	452	694	523	473	356	342	332	211	375	Total.		
.....	1232	6	840	6	970	6	704	6	1036	6	402	6	320	6	319	6	468	6 F. wings.		
.....	766	4	470	4	540	4	400	4	448	4	134	4	98	4	92	4	373	4 H. wings.		
608	28	1762	...	28	2204	...	34	1627	...	34	1957	28	892	...	34	760	...	34	760	...	34	760	...	622	...	28	1216	...	17 G. total.

In size the olfactory pores vary much. Those of an ant vary more in size than do those of the hornet or honey bee. The pores on the wings are always much smaller than are those on the legs and they vary less in size. In proportion to the sizes of an ant and of a worker honey bee, the pores of the ant are much larger.

Under the microscope with transmitted light the olfactory pores appear as bright spots. At the first glance they resemble hair sockets (fig. 5, *PorApHr*) from which the hairs have been pulled, but after

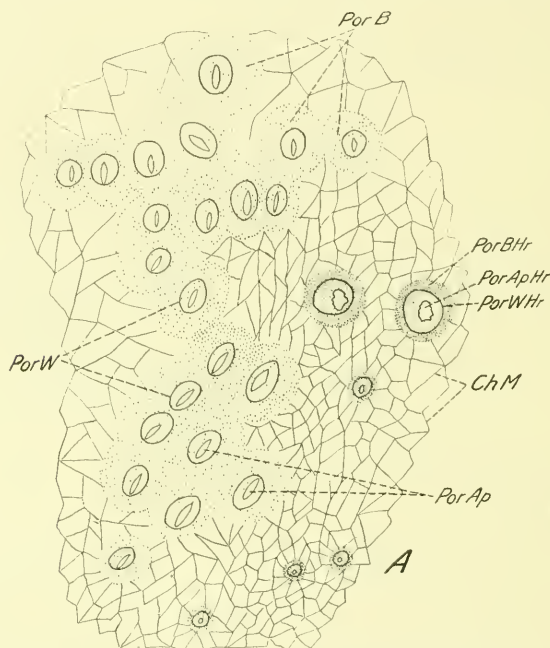


FIG. 5.—Group 6 of the olfactory pores from the hind leg of a worker bee, showing the external appearance, $\times 700$.

a closer examination a striking difference is usually seen. Each bright spot is surrounded by a dark line, the pore wall (figs. 5 and 6, *PorW*). Outside this line the chitin (fig. 5, *PorB*) may be light or dark in color, but inside the line the chitin (figs. 5 and 6, *ChL*) is almost transparent, and at the center there is an opening, the pore aperture (figs. 5 and 6, *PorAp*).

The olfactory pores consist of inverted flasks in the chitin and of spindlelike sense cells lying beneath the mouths of the flasks (fig. 6). About two-thirds of the space at the bottom of the flask is occupied by a hollow chitinous cone (fig. 6, *Con*) which is not separated from

the surrounding chitin, but only stains less deeply. In a typical olfactory pore the neck (Nkf1) of the flask is wide and the mouth (Mf) is flaring. The sense fiber (SF) of the sense cell (SC) pierces the bottom of the cone and enters the round, oblong, or slitlike pore aperture (PorAp). The nerve fiber (NF) soon runs to a nerve. It is thus seen that the cytoplasm (Cyt) in the peripheral end of the sense fiber comes in direct contact with the air containing odorous particles and that odors do not have to pass through a hard membrane in order to stimulate the sense cells as is claimed for the antennal organs.

To determine the function of these pores the wings, legs and stings of many worker honey bees were mutilated. The behavior of the mutilated bees was carefully studied, and they were tested with odors

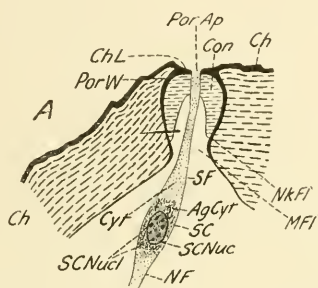


FIG. 6.—Cross section of a typical olfactory pore with its sense cell (SC) from the tibia of the hind leg of a worker bee, $\times 700$.

in the same manner as were unmutated ones. The stings of 100 workers were pulled out. These bees lived 30 hours on an average. Twenty of them were tested with odors. They responded only slightly more slowly than unmutated bees. The wings of 28 workers were pulled off. When tested with odors, these bees responded one-eighth as rapidly as normal bees. The bases of the wings of 20 workers were covered with liquid glue. When tested, these bees responded also one-eighth as rapidly as unmutated ones. The pores on the legs of 20 workers were covered with a mixture of beeswax and vaseline. When tested, these bees responded two-fifths as rapidly as unmutated workers. The wings were pulled off and the pores on the legs of 20 workers were covered with the beeswax-vaseline mixture. When tested with odors, these workers responded one-twelfth as rapidly as unmutated workers. All of the workers with mutilated wings and legs lived just as long in the observation cases as did unmutated workers, and they were absolutely normal

in all respects except that they reacted to odors more slowly. Controls proved that the odors themselves from the glue and beeswax-vaseline mixture did not affect the reaction times.

The preceding experiments were repeated by using ants and hornets with mutilated wings and legs. When tested with the odors from the oil of peppermint, oil of thyme, oil of wintergreen, honey and comb, leaves and stems of pennyroyal, and formic acid from other ants, four deälated females of *Formica* gave a reaction time of 2.89 seconds. The reaction time for winged females of the same species is 2.45 seconds. The niches from which wings of these four females arises were examined. In seven of the eight niches, pores were seen.

All four wings of each of 25 virgin females of *Formica* were pulled off. When tested with the above six odors, these ants gave a reaction time of 2.85 seconds. After an examination it was found that 62 per cent of the detached wings had broken off just beyond the groups of pores, thus the pores on only 38 per cent of the wings were lost. When the wings are shed naturally only 21 per cent of the pores are lost, while 79 per cent are not prevented from functioning, because the wings devoid of pores always break off at a weak place in the chitin just distal to the groups of pores. Furthermore, sections through the stubs of the wings of deälated females show that the sense cells are normal.

The wings of 7 males of *Formica* were pulled off. When tested with the six odors, these ants gave a reaction time of 3.50 seconds, while the reaction time for the same ants before the wings were pulled off is 2.63 seconds. They were normal in all respects other than their slowness in responding to odors. Only 8 per cent of the pores belonging to the wings were left intact while 92 per cent were pulled off with the wings.

The bases of the wings of 25 winged females of *Formica* were covered with liquid glue and the pores on the legs were covered with the beeswax-vaseline mixture. Confined singly these ants were not able to remove the glue, but they did remove much of the vaseline and smeared some of it over their spiracles, which certainly accounts for their short lives. When tested, they gave a reaction time of 5.21 seconds, which is slightly more than twice the reaction time for their un mutilated sister females.

• When tested, 25 deälated females of *Camponotus* gave a reaction time of 3.25 seconds. Their wing niches were filled with liquid glue thus covering the pores on the stubs of the wings, and the pores

on the legs were covered with the beeswax-vaseline mixture. These females now appeared normal in all respects other than their slowness in responding to odors. When tested, they gave a reaction time of 7.94 seconds, which is more than twice the reaction time obtained before using the glue and vaseline.

The wings of 25 males of *Camponotus* were pulled off. These ants appeared normal in all respects except their slowness in responding to odors. When tested, they gave a reaction time of 3.49 seconds, which is one and a fourth times the reaction time of unmutilated males. Only 12 per cent of the pores on the wings were left intact.

The wings of 21 workers of *Vespula maculata* were pulled off. These hornets appeared normal in all respects other than their slowness in responding to odors. When tested with the three essential oils, they gave a reaction time of 6.35 seconds, which is almost three times the reaction time for sister hornets with wings intact. Only 22 per cent of the pores on the wings were left intact.

OLFACTORY ORGANS ON THE APPENDAGES AND STERNUM OF SPIDERS

In 1878 Bertkau noticed some slitlike cuticular organs on the legs of spiders. Since that date five other observers, including the present writer, have studied these structures. They are called lyriform organs on account of their shape.

The author (1911) made a special study of the morphology and physiology of the lyriform organs of spiders. He used in his studies 39 species representing 27 of the 38 families. These organs in spiders exist both as isolated slits and as groups containing several slits, and their position is relatively constant. The groups are located at the distal end of each joint of the legs, pedipalpi, chelicera (mouth parts), pedicel, and spinnerets. They exist on both sides of the fore-going appendages and as a rule each joint of the legs and pedipalps possesses the following number of groups: Coxa 1, trochanter 3, femur 2, patella 3, tibia 3, metatarsus 1, and occasionally the tarsus 1; each cheliceron usually has 4, each pedicel 2, and only occasionally is a group present on one of the spinnerets. The isolated slits not only occur irregularly scattered on the joints of all the above-named appendages, but also on the remaining mouth parts, on the sternum, and a few on the ventral side of the abdomen. Thus it is seen that the disposition of the lyriform organs is similar to that of Hicks' vesicles; however, the vesicles are situated at the proximal instead of the distal ends of the joints and less seldom exist as isolated struct-

ures irregularly distributed, as are the isolated slits. A few of Hicks' vesicles exist on the mouth parts but none is found on the sternum and abdomen, except those in the sting, which might be compared in position to the lyriform organs on the spinnerets of spiders. Since spiders have no wings, possibly all the slits on the mouth parts, sternum, pedicle, and the ones on the abdomen exclusive of those on the spinnerets, replace all the pores that exist on the wings of insects.

A great difference in the number of groups and isolated slits was found in the different species. The spiders that hunt for their food and use no webs in capturing their prey, without exception have the most slits, while those that live in caves and catch their food entirely by means of webs have the least number. The common cobweb spider (*Theridium tepidariorum*) catches its prey wholly by webs; it does not live in caves and may be considered as intermediate between hunting spiders with highly developed lyriform organs and cave spiders with degenerated lyriform organs. By counting all the slits on the surface of this cobweb spider, we find that an average spider possesses 1,770 slits, whereas considering an average worker bee, we have already seen that it possesses 2,270 pores. As stated by the other observers, lyriform organs have now been found in 7 of the 9 orders belonging to the Arachnida.

A lyriform organ is composed usually of several single slits which lie side by side and more or less parallel with each other. This group of slits is generally surrounded by a border, produced by a difference in pigmentation, which gives the lyre shape to the organ. Inside the border the pigmentation is usually much lighter than outside; hence a group appears as a light spot, while the superficial appearance of a slit reminds one of a long, slightly bent spindle that has an aperture either at the center or nearer one end than the other. A cross section of a slit shows that the aperture passes entirely through the cuticula and unites with the sense fiber of a large spindlelike sense cell lying at the base of the thick hypodermis. Thus a cross section of a slit with its sense fiber may be likened to a greatly flattened funnel. The innervation of a lyriform organ is identical with that of a group of olfactory pores, except that in the former the sense fibers unite with the base of the apertures, whereas in the latter the sense fibers connect with the top of the apertures.

So far as the writer knows, structures similar to lyriform organs and Hicks' pores have never been looked for in crustaceans. It is very probable, however, that this class of arthropods possesses some kind of organs that take the place of lyriform organs and Hicks' pores.

While experimenting with odors, it was found that spiders possess a true olfactory sense. Many individuals of two species representing two widely separated genera were used. They responded not only to five different essential oils, which are sometimes regarded as irritants, but also to both fresh and decayed buttercup flowers, decayed snails, squash bugs, and Phalangids. The usual reaction is to move away from the odor, but they also quickly moved their pedipalpi, chelicera and legs, and very often rubbed their legs and other appendages. The average reaction time of a ground spider (*Lycosa lepida*) to oils of peppermint, thyme and wintergreen was 9 seconds and for a jumping spider (*Phidippus purpuratus*) 4.6 seconds, while for the worker bee the same average is only 2.6 seconds. The differences in reaction time may be explained by the fact that *Lycosa* is rather sluggish, *Phidippus* is very active, while the bee is extremely lively. However, as a worker bee possesses 500 pores more than a spider and since it responds about twice as quickly it would appear that its sense of smell is more highly developed.

All the lyriform organs (single slits not included) on the legs, pedipalpi, chelicera, mouth parts, and sternum were carefully varnished with yellow vaseline. The following day they were tested with the five oils—peppermint, thyme, wintergreen, clove and bergamot. Thus it was ascertained that they responded nine times more slowly after varnishing than before.

Hindle and Merriman (1912) proved experimentally that Haller's organ is olfactory in function and that it is a means by which ticks are able to recognize their hosts. In *Hæmaphysalis punctata* this organ consists of a minute cavity, containing sensory hairs, and is associated with a specially modified region of the hypodermis. In ticks (Acarina) it is always located on the external dorsal surface of the tarsus of the first pair of legs. Hansen (1893) found a few scattered lyriform organs in acarinids which may also aid in receiving odor stimuli.

SUMMARY OF AUTHOR'S EXPERIMENTS

The following table is a tabulated summary of the author's experiments with spiders and Hymenoptera to determine the location of the olfactory organs. The odors used for the spiders are those from the essential oils of peppermint, thyme, wintergreen, clove, and bergamot. The "three odors" used for the Hymenoptera are those from oil of peppermint, oil of thyme, and oil of wintergreen. The

TABLE II

Summary of author's experiments with spiders and Hymenoptera to determine the location of the olfactory organs

Species.	Experiment.	Average reaction time.		No. of individuals tested.	Average length of life in captivity.	
		for three odors.	for six odors.		Days.	Hrs.
		Sec.	Sec.			
♀ Phidippus....	Unmutilated. Normal in behavior.	5.0	11
♀ "	Pedipalpi pulled off. Normal in behavior.	5.2	11
♀ "	Pedipalpi and maxillæ pulled off. Normal in behavior.	6.0	11
♂+♀ Lycosa....	Unmutilated. Normal in behavior.	7.0	15
♂+♀ "	Lyriiform organs covered with vaseline. Normal in behavior.	61.0	15
♀ Formica.....	Unmutilated. Winged, normal in behavior.	2.12	2.45	25	14	10
♀ "	Funiculi cut off. Abnormal in behavior.	4.38	25	0	19
♀ "	Funiculi glued. Abnormal in behavior.	5.78	25	6	0
♀ "	De'alated. Normal in behavior.	2.50	2.89	4	142	0
♀ "	Wings pulled off. Normal in behavior.	2.32	2.85	25	10	0
♀ "	Bases of wings glued and legs covered with vaseline. Normal in behavior.	4.73	5.21	25	3	0
♀ "	Unmutilated. Winged, normal in behavior.	2.21	2.63	17	Used below.	
♂ "	Wings pulled off. Normal in behavior.	3.00	3.50	7	5	0
♀ Camponotus..	De'alated. Normal in behavior.	2.32	3.25	25	Several months.	
♀ " ..	Glue in wing niches and legs covered with vaseline. Normal in behavior.	5.70	7.94	22	Several months.	
♂ " ..	Winged. Normal in behavior.	2.29	2.74	25	23	9
♂ " ..	Wings pulled off. Normal in behavior.	2.91	3.49	25	7	2
♂ Major Camponotus	Unmutilated. Normal in behavior.	2.32	3.22	25	26	8
♂ Minor Camponotus	Unmutilated. Normal in behavior.	2.27	3.09	25	26	8
♂ Vesputa	Unmutilated. Winged, normal in behavior.	2.43	25	9	7
♀ "	Flagella cut off. Abnormal in behavior.	3.09	25	1	13
♀ "	Wings pulled off. Normal in behavior.	6.35	21	4	8

TABLE II—Continued

Summary of author's experiments with spiders and Hymenoptera to determine the location of the olfactory organs

Species.	Experiment.	Average reaction time.		No. of individuals tested.	Average length of life in captivity.	
		for three odors.	for six odors.		Days.	Hrs.
♂ Apis.....	Unmutilated. Winged, normal in behavior.	2.64	3.40	37	9	3
♂ ".....	Maxillæ and labial palpi cut off. Abnormal in behavior.	3.3	4.0	19	1	0
♂ ".....	Proboscis cut off. Abnormal in behavior.	2.9	22	0	7
♂ ".....	Mandibles cut off. Abnormal in behavior.	3.5	4.8	20	7	0
♂ ".....	Flour paste in mouth. Abnormal in behavior.	2.68	20	7	12
♂ ".....	Wings cut off beyond pores. Normal in behavior.	3.0	17	9	23
♂ ".....	Stings extracted. Normal in behavior.	2.86	20	1	6
♂ ".....	Glue on thorax as control. Normal in behavior.	2.76	19	9	3
♂ ".....	Vaseline on abdomen as control. Normal in behavior.	2.73	18	9	3
♂ ".....	Flagella burned off. Abnormal in behavior.	4.00	7	0	17
♂ ".....	Flagella glued. Abnormal in behavior.	2.90	21	1	0
♂ ".....	Wings pulled off. Normal in behavior.	22.20	27.10	28	9	20
♂ ".....	Bases of wings glued. Normal in behavior.	18.50	28.20	20	9	3
♂ ".....	Pores on legs covered with vaseline. Normal in behavior.	5.20	8.00	20	9	3
♂ ".....	Wings pulled off and pores on legs covered with vaseline. Normal in behavior.	36.90	40.00	20	9	5

"six odors" used for the ants and hornets are those from oil of peppermint, oil of thyme, oil of wintergreen, honey and comb, leaves and stems of pennyroyal, and formic acid. The "six odors" used for the honey bees are the same as those used for ants and hornets, except pollen was employed instead of formic acid.

The preceding table shows the following: (1) When the pedipalpi (slightly comparable to the antennæ of insects) of spiders are pulled off, the arachnids are normal in behavior and the reaction time is practically the same as when unimutilated individuals are

used. (2) But when the antennæ of Hymenoptera are mutilated in the slightest degree, the insects are abnormal, and the reaction times are slower than when unamputated individuals are used, although it is quite possible that the slower reaction times are caused by the abnormal behavior of the insects rather than due to the theory that some of the olfactory organs are prevented from functioning. (3) When the maxillæ of spiders are pulled off, no abnormal behavior results, but the reverse is true for the honey bee. In both cases the reaction time is slightly slower. (4) When the mouth parts of honey bees are mutilated, the insects are abnormal and the reaction times are slightly increased, which may be due to the abnormality of the insects, or to the view that the pores on these appendages are prevented from functioning, or to both of these conditions combined. (5) When the wings are pulled off artificially, most of the pores on these appendages are lost and the reaction times are considerably increased. (6) When the pores on the wings are covered with glue the reaction times are much increased. (7) When most of the pores on the legs are covered with vaseline, the reaction times are greatly increased. (8) When either spiders or Hymenoptera are so mutilated that most of the olfactory pores are prevented from functioning, the reaction times are increased many times, and the mutilated individuals used are absolutely normal in all respects other than their ability to smell.

DISCUSSION

The following criticisms concerning the physiological experiments performed with the antennæ of various insects may be offered. Most of the previous observers have studied the behavior of the insects investigated in captivity for only a short time, while the remainder have paid no attention at all to the behavior of their unamputated insects. They cut off either a few joints of both antennæ, or these entire appendages, or varnished them with paraffin, rubber, etc. When a few joints are severed the sense of smell is apparently weakened. This is true for bees also as ascertained by the author. When both antennæ are amputated or varnished the insects, as a rule, fail to respond to substances which normally affect the olfactory sense. They generally fail to respond to odors held near them and fail to find food in captivity, and do not return to putrid meat and dead bodies when removed from such food. Males so mutilated do not, as a rule, seek females and show no responses when females are placed near them. Such experiments were seriously criticised until Hauser in 1880 presented his apparently conclusive results. Many

of the insects on which he experimented with the antennæ amputated became sick and soon died. Most of them failed to respond when the antennæ were mutilated, although *Carabus*, *Melolontha*, and *Silpha* responded slightly, while all the Hemiptera that he used responded almost as well with their antennæ off as they did with them intact. Only 40 per cent of the ants from which Miss Fielde cut the antennæ recovered from the effect of the shock. Not one of these observers has studied the behavior of the species under observation sufficiently to know exactly how long they live in captivity with their antennæ either intact or mutilated. No one, except Miss Fielde, has kept a record of the death of the mutilated and normal insects accurate enough so that one might know what percentage died from the operation. To cut off some other appendage or even the lower part of the head, as Forel did, is not a fair test, because such operations seldom expose sense cells and never any nerve equal in size to that of the antennæ, unless one pulls off the wings. When the wings are pulled off the large nerve is severed between the masses of sense cells and thorax, and the sense cells are not exposed to the air, as they are when antennæ are cut off. Even if the antennæ are cut through the scape, the large masses of sense cells belonging to Johnston's organs are severed. When the lower part of the head or the tarsi are cut off, as Forel did, no nerves are exposed to the air except ends of small nerves. From the foregoing it is only reasonable to assume that when the antennæ of any insect are injured in the least degree, the insect is no longer normal and if it fails to respond to odors placed near it, this negative response may be caused by the injury.

The following criticisms based on a consideration of the morphology of the antennæ may also be offered. In the honey bee the pore plates can scarcely be considered as olfactory organs, because the drone has almost eight times as many as the queen, and responds to the odors presented in slightly more than one-half the time. It is true that those of the queen are considerably larger, but even on this basis the reaction times are not comparable. The pegs may be entirely eliminated as olfactory organs, because they are absent in the drone, but are abundant in the worker and the queen. Drones, queens and workers have about the same number of Forel's flasks and pit legs. Schenk's view that the pegs receive odor stimuli in the queens and workers, while Forel's flasks and the pit pegs function in this way in the drones is inconsistent, because if the latter two structures function for such a purpose in the drones why should

they not also in the females? Since these two structures are few in number and many times smaller than the pegs, we cannot compare them physiologically. Thus it is seen that not one of these antennal organs of the honey bee offers a solution for the ratios obtained with the use of the various odors. If the reaction time of each caste of the honey bee is compared with the total number of olfactory pores a consistent inverse ratio is obtained. A drone has 2,600 pores and responds in 2.9 seconds; a worker possesses 2,200 pores and responds in 3.4 seconds and a queen has 1,800 pores and responds in 4.9 seconds.

Pore plates are not the olfactory apparatus in all insects, because they are entirely absent in the Lepidoptera. The pegs cannot be the olfactory organs in all insects, for they are absent in many male bees and almost wanting in Lepidoptera, although possibly the end rods in butterflies and moths are homologous. According to Vom Rath, pegs are found not only on the antennæ and mouth parts but also all over the body, and Nagel found them elsewhere than on the antennæ. If the pegs are the olfactory organs and if insects with amputated antennæ are normal, then why do not such insects respond positively at least slightly to odors instead of negatively, as most observers claim?

It is certain that spiders can smell, yet they have no antennæ nor any organs that may be compared to the antennal organs of insects. Hence, this is another argument against the antennæ as being organs of smell. All insects either have antennal organs like those described for the bee, or modifications of them, yet no two authors who have studied them have agreed concerning their function. Such chaos can be replaced by facts, only when the behavior of the insects investigated is thoroughly studied and when experiments are performed in ways other than on the antennæ alone. Then it will be realized that the antennæ can no longer be regarded even as a possible seat of the sense of smell in insects.

In conclusion, it seems that the organs called the olfactory pores by the author are the true olfactory apparatus in Hymenoptera and possibly in all insects and that the antennæ play no part in receiving odor stimuli.

LITERATURE CITED

The authors marked with an * were not accessible to the writer, and their views are cited from the writings of others.

ÆLIAN. 1744. *De Animalibus, quæ Apibus inimica sunt. Natura Animalium*, Londini, t. I, Lib. I, Cap. 58; p. 60.

- ARISTOTLE. The works of Aristotle, translated into English. vol. 4, *Historia Animalium* by Thompson, Oxford, 1910. Book 4, 8, p. 534a.
- BALBIANI, E. G. 1866. Note sur les antennes servant aux insectes pour la recherche des sexes. *Ann. Soc. Ent. France*, t. 6, (4), Bul., p. xxxviii.
- BARROWS, W. M. 1907. The reactions of the pomace fly, *Drosophila ampelophila* Loew, to odorous substances. *Journ. Exp. Zool.*, vol. 4, pp. 515-537.
- BASTER, JOB. 1770. Over het Gebruik der Sprieten by de Insecten. *Hollandische Maatschappye der Weetenschappen te Haarlem*, 12 Deel, pp. 147-182.
- *—— 1798. In *Lehmann's De sensibus externis animalium exsanguinum*, etc. Goettingue.
- BERGMANN UND LEUCKART. 1852. *Anat.-physiol. Uebersicht des Thierreichs*, pp. 453-454.
- BERLESE, ANTONIO. 1906-1909. *Gli insetti*, vol. 1, pp. 610-633.
- BERTÈ, F. 1877. Contribuzione all'anatomia ed alla fisiologia della antenne degli Afanitteri. *Atti Reale Accad. dei Lincei*, vol. 2, serie terza, Roma 1877-1878, pp. 24-29, with 1 pl.
- BONNET, CHARLES. 1781. *Collection des œuvres*, t. 7, pp. 124-125.
- *BONNSDORF. 1792. *De fabrica, usus differentiae palparum in insectis*. Dissertation, Aboæ.
- BÖRNER, CARL. 1902. Ueber das Antennalorgan III der Collembolen. etc. *Zool. Anz.*, Bd. 25, pp. 92-106.
- BREITHAUP, P. F. 1886. Ueber die Anatomie und die Functionen der Bienenzunge. *Arch. f. Naturgesch.*, Bd. 52, pp. 47-112, with 2 pls.
- BRULLÉ. 1840. *Introduction à l'histoire naturelle des Insectes Coléoptères* by Castelnau, t. 1, pp. 78-79.
- BURMEISTER, H. 1836. *Manual of entomology*, translation by W. E. Shuckard, pp. 297-298.
- 1848. Beobachtungen über den feineren Bau des Fühlerfächers der Lamellicornien, als eines muthmasslichen Geruchswerkzeuges. *D'Alton u. Burmeister's Zeitung f. Zool. Zoot. u. Paläozool.*, Bd. 1, pp. 49-56, 67.
- CARUS. 1838. *Traité d'anatomie comparée*, t. 1, paragraph 411, pp. 216-217.
- CHADIMA, JOS. 1873. Ueber die von Leydig als Geruchs-Organen bezeichneten Bildungen bei den Arthropoden. *Mittheil. d. naturwissenschaft. Ver. für Steiermark*, Graz, pp. 36-44.
- CHATIN, J. 1880. *Les organes des sens dans la série animale*, Paris, pp. 274-281.
- CHILD, C. M. 1894a. Beiträge zur Kenntnis der antennalen Sinnesorgane der Insecten. Preliminary communication. *Zool. Anz.*, 17 Jahrg., pp. 35-38.
- 1894b. Ein bisher wenig beachtetes antennales Sinnesorgan der Insekten, mit besonderer Berücksichtigung der Culiciden und Chironomiden. *Zeitsch. f. wiss. Zool.*, Bd. 58, pp. 475-528.
- CLAPARÈDE. 1858. Zur les prétendus organes, auditifs des antennes chez les Coléoptères lamellicornes et autres insectes. *Ann. Sci. Nat., Zool.*, t. 10 (4), pp. 236-250.
- CLAUS, C. 1872. *Grundzüge der Zoologie*, Zweite Auflage, p. 570.
- *COMPARETTI. 1800. *Dinamica animale degli insetti*, 2, Padoue, p. 442.
- CORNALIA. 1856. *Monografia del bombice del gelso*. Memoria dall' I. R. Istituto Lombardo di Scienze, Milan, pp. 304-305.
- COTTREAU, JEAN. 1905. L'odorat chez les insectes. *La Nature*, Ann. 34, Sem. I, p. 39.

- CUVIER. 1805. Leçons d'anatomie comparée, t. 2, p. 675.
- DAILLIGREN ULRIC AND KEPNER, W. A. 1908. Principles of animal histology. New York. MacMillan Co., pp. 264-266.
- *DE BLAINVILLE. 1822. Principes d'anatomie comparée, vol. 1, p. 339.
- DÖNHOFF. 1861. Vom Geruchsorgan der Bienen, Bd. 1, Bienenzeitung, Theoretischer Theil, pp. 507-509.
- DRIESCH. 1839. Odorat des insectes. Journ. l'Institut, Paris, t. 7, No. 294 p. 279.
- DUBOIS, R. 1890. Sur la physiologie comparée de l'olfaction. Comptes Rendus. Acad. Sci. Paris, t. 111, pp. 66-68.
- 1895. Sur le rôle de l'olfaction dans les phénomènes d'accouplement chez les papillons. Assn. France pour l'Avancement des Sci., 24^e session, Bordeaux, pp. 293-294.
- DUFOUR, LÉON. 1850. Quelques mots sur l'organe de l'odorat et sur celui de l'ouïe dans les insectes. Ann. Sci. nat., Zool., t. 14 (3), pp. 179-184.
- DUGÉS. 1838. Traité de physiologie comparée, t. 1. pp. 160-161.
- DUMÉRIL. 1797. Extrait d'une dissertation sur l'organe de l'odorat dans les insectes. Bul. Soc. Philom., Paris, vol. 1, second part, p. 34.
- 1823. Considérations général sur les insectes, pp. 25-30.
- DUPONCHEL. 1840. Réflexions sur l'usage des antennes dans les insectes. Revue Zoologique de M. Guérin Méneville, Paris, pp. 75-79.
- *ERICHSON. 1847. De fabrica et usu antennarum in insectis Berolini, typis fratrum Unger, 4. (15 pag., 1, Kupfertafel).
- FABRE, J. H. 1882. Nouveaux souvenirs entomologiques. Paris, pp. 29-32.
- FABRICIUS, I. C. 1778. Philosophia Entomologica.
- FIELDE, A. M. 1901a. A study of an ant. Proc. Acad. Nat. Sci. Phila., vol. 53, pp. 425-449.
- 1901b. Further study of an ant. *Ibidem*, pp. 521-544.
- 1903a. Artificial mixed nests of ants. Biol. Bul., vol. 5, no. 6, November, pp. 320-325.
- 1903b. A cause of feud between ants of the same species living in different communities. *Ibidem*, pp. 326-329.
- 1904. Power of recognition among ants. Biol. Bul., vol. 7, no. 5, October, pp. 227-250.
- 1905. The progressive odor of ants. Biol. Bul., vol. 10, no. 1, December, pp. 1-16.
- 1907. Suggested explanations of certain phenomena in the lives of ants, with a method of tracing ants to their respective communities. Biol. Bul., vol. 13, no. 3, August, pp. 134-137.
- FOREL, AUGUSTE. 1874. Les fourmis de la Suisse. Ouvrage Soc. Helvétique des Sci. Nat.
- 1878a. Beitrag zur Kenntniss der sinnesempfindungen der Insekten. Mittheil. d. Münchener Ent. Ver., 2 Jahrg., 1 Heft, p. 21.
- 1878b. Der Giftapparat und die Analdrüsen der Ameisen. Zeitsch. f. wiss. Zool., Bd. 30, Supplementary note on p. 61.
- 1885. Etudes myrmécologiques en 1884. Bul. Soc. Vaudoise Sci. Nat., vol. 20 (2), no. 91. p. 334.
- 1902. Die Eigentümlichkeiten des Geruchssinnes bei den Insekten. Verhdlgn. v. internat. zool.-Congr., Berlin, pp. 806-815.
- 1908. The senses of insects. English translation by Yearsley, London, pp. 95-96.

- FREILING, HANS H. 1909. Duftorgane der werblichen Schmetterlinge nebst Beiträgen zur Kenntnis der Sinnesorgane auf dem Schmetterlingsflügel und der Duftpinsel der Männchen von *Danais* und *Euploea*. Zeitsch. f. wiss. Zool., Bd. 92, pp. 210-290 with 17 text figs. and 6 pls.
- GARNIER, M. J. 1860. De l'usage des antennes chez les insectes. Mém. d'Acad. des Sci. d'Amiens, t. 1 (2), pp. 489-501.
- GEGENBAUR, C. 1870. Grundzüge der vergleichenden Anatomie, Zweite Auflage, pp. 387-388.
- GOUREAU. 1841. Ann. Soc. Ent. France, t. 10, Bul. pp. xii-xv.
- GRABER, VEIT. 1878. Ueber neue otocystenartige Sinnesorgane der Insekten. Arch. f. Mikr. Anat., Bd. 16, pp. 36-57.
- 1885. Vergleichende Grundversuche über die Wirkung und die Aufnahme-stellen chemischer Reize bei den Tieren. Biol. Centralblatt, Bd. 5, Nr. 13, pp. 385-398.
- 1887. Neue Versuche über die Function der Insektenfühler. Biol. Centralblatt, Bd. 7, Nr. 1, pp. 13-19.
- GRIMM, O. v. 1869. Beitrag zur Anatomie der Fühler der Insekten. Bul. l'Acad. Imp. des Sci. de St. Pétersbourg, t. 14, pp. 66-74.
- GUENTHER, KONRAD. 1901. Ueber Nervenendigungen auf dem Schmetterlingsflügel. Zool. Jahrb., Anat., vol. 14, pp. 551-572, with 1 pl.
- HANSEN, H. J. 1893. Organs and characters in different orders of arachnids. Entomologische Meddelelser, pp. 136-251.
- HARTING, P. 1879. Reukorgaan der insekten. Album der Natuur, Haarlem. Wetensch. Bijblad, p. 71.
- HAUSER, GUSTAV. 1880. Physiologische und histologische Untersuchungen über das Geruchsorgan der Insekten. Zeitsch. f. wiss. Zool., Bd. 34, Heft. 3, pp. 367-403, with 2 pls.
- HENNEGUY, L. F. 1904. Les insectes, Paris, pp. 138-139.
- HERMESTÄDT, FRIED. 1811. Ueber die Gerüche und die physischen Ursachen ihrer Erzeugung. Der Gesellschaft Naturforschender Freunde zu Berlin, Jahrg. 5, pp. 111-124.
- HICKS, J. B. 1857. On a new organ in insects. Journ. Linn. Soc. London, Zool., vol. 1, pp. 136-140, with 1 pl.
- 1859a. Further remarks on the organs found on the bases of the halteres and wings of insects. Trans. Linn. Soc. London, Zool., vol. 22, pp. 141-145, with 2 pls.
- 1859b. On a new structure in the antennæ of insects. *Ibidem*, pp. 147-154, with 2 pls.
- 1859c. Further remarks on the organs of the antennæ of insects. *Ibidem*, pp. 383-399.
- 1860. On certain sensory organs in insects, hitherto undescribed. *Ibidem*, vol. 23, pp. 139-153, with 2 pls.
- HINDLE, E. and MERRIMAN, G. 1912. The sensory perceptions of *Argas persicus*. Parasitology, vol. 5, no. 3, September, Cambridge Univ. Press, pp. 214-216.
- HOCHREUTHER, RUDOLF. 1912. Die Hautsinnesorgane von *Dytiscus marginalis* L., ihr Bau und ihre Verbreitung am Körper. Zeitsch. f. wiss. Zool., Bd. 103, pp. 1-114.
- HUBER, FRANÇOIS. [Quoted by Jurine L., 1807.] Nouvelle Méthode de classer les Hyménoptères, t. 1. Genève, Introd., pp. 8-9.
- 1814. Nouvelle observations sur les abeilles, t. 2, sec. édit. pp. 375-393.

- JANET, CHARLES. 1904. Observations sur les fourmis. Limoges, pp. 17-22.
- 1907. Anatomie du corselet et histolyse des muscles vibrateurs, après le vol nuptial, chez la reine de la fourmis (*Lasius niger*). Limoges, pp. 46-48.
- 1911. Organes sensitifs de la mandibule de l'abeille. L'Apiculteur, 55^e Année, no. 3, Mars, pp. 107-108.
- JOSEPH, G. 1877. Ueber Sitz und Bau der Geruchorgane bei den Insecten. Ber. 50 Vers. Deutscher Naturf. und Aerzte, München, pp. 174-176.
- KELLOGG, V. L. 1907. Some silkworm moth reflexes. Biol. Bul. vol. 12, no. 3, February, pp. 152-154.
- KIRBY and SPENCE. 1826. Introduction to entomology, vol. 3, pp. 455-456 and vol. 4, pp. 249-255.
- *KNOCH. 1798. In Lehmann's De sensibus externis animalium, etc.
- *KRAPELIN, KARL. 1883. Ueber die geruchsorgane der Gliederthiere, Hamburg.
- KÜSTER. 1844. Zool. Notizen. (Die Fühlhörner sind die Riechorgane der Insecten.) Isis von Oken, pp. 647-655.
- LACORDAIRE. 1838. Introduction à l'entomologie, t. 2, pp. 228-234.
- LANDOIS, H. 1868. Das Gehörorgan des Hirschkafers (*Lucanus cervus*). Arch. f. Mikr. Anat. Bd. 4, pp. 88-95.
- LATREILLE. 1804. Histoire naturelle des crustacés et des insectes, t. 2, pp. 49-51.
- LAYARD, CONSUL E. L. 1878. Smell and hearing in insects. Nature, vol. 18, pp. 301-302.
- *LEE, A. BOLLES. 1855. Les balanciers des Diptères. Rec. Zool. Suisse, t. 2.
- LEFEBVRE, ALEX. 1838. Note sur le sentiment olfactif des antennes. Ann. Soc. Ent., France, t. 7, pp. 395-399.
- *LEHMANN. 1799. De usu antennarum, Leipsig, p. 27.
- LESPE, CH. 1858. Mémoire sur l'appareil auditif des Insectes. Ann. Sci. Nat. Zool., t. 9, (4), pp. 225-249.
- LESSER, P. 1745. Théologie des insectes, translated from the German by Lyonnet, t. 2, pp. 7, 8, 11, 12.
- LEYDIG, FRANZ. 1860. Ueber Geruchs und Gehörorgane der Krebse und Insecten. Arch. f. Anat. und Phys., pp. 265-314, with 3 tables.
- 1886. Die Hautsinnesorgane der Arthropoden. Zool. Anz. 9 Jahrg., pp. 284-291 and 308-314.
- LOWNE. 1870. The organs of hearing and smell in insects. Amer. Naturalist, vol. 4, p. 127.
- LUBBOCK, SIR JOHN. 1877. On some points in the anatomy of ants. Monthly Micr. Journ., vol. 18, pp. 121-142.
- 1882. Ants, bees and wasps. International Scientific Series, New York, pp. 234, 235, 288.
- *——— 1883. Ameisen, Bienen und Wespen. Internat. wiss. Bibl., Bd. 57, p. 197 ff.
- 1899. The senses, instincts and intelligence of animals. International Scientific Series, vol. 65, London, pp. 37, 43, 58.
- LYONNET, P. 1745. In Lesser's Théologie des insectes, t. 2, p. 9 in note.
- MARCEL DE SERRES. 1811. De l'odorat, et des organes qui paroissent en être le siège, chez les Orthoptères. Ann. du Muséum d' Hist. Nat., t. 17, pp. 426-442.

- MAYER, PAUL. 1878. Sopra certi organi di senso nelle antenne dei Ditteri. Reale Accad. dei Lincei, Roma, pp. 3-12, with 1 pl.
- 1879. Zur Lehre von den Sinnesorganen bei den Insecten. Zool. Anz. Jahrg. 2, Nr. 25, pp. 182-183.
- McINDOO, N. E. 1911. The lyriform organs and tactile hairs of araneads. Proc. Phila. Acad. Nat. Sci., vol. 63, pp. 375-418, with 4 pls.
- 1914a. The olfactory sense of the honey bee. Journ. Exp. Zool., vol. 16, no. 3, April, pp. 265-346, with 24 text figs.
- 1914b. The olfactory sense of Hymenoptera. Proc. Phila. Acad. Nat. Sci., vol. 66, pp. 294-341, with three text figs. and 2 pls.
- MÜLLER, H. 1871. Anwendung der Darwinschen Lehre auf Bienen. Leppstadt, pp. 63-68.
- *NAGEL, W. A. 1892. Die neidern Sinns der Insekten. Tübingen.
- 1894. Vergleichend phys. and anat. Untersuchungen über den Geruchs- und Geschmacksinn und ihre Organe. Bibliotheca Zoologica, Heft. 18, pp. 1-207, with 7 pls., two of which are colored.
- 1909. Geruchs- und Geschmacksinn der Insekten. Berliner ent. Zeitsch., Bd. 54, pp. 21-26.
- NEWPORT, GEORGE. 1838. On the use of the antennæ of insects. Trans. Ent. Soc. London, vol. 2, pp. 229-248.
- NOLL. 1869. Feiner Geruch bei Schmetterlingen. Zoolog. Garten, Bd. 10, pp. 254-255.
- OLIVIER. 1789. Article on "Antennes et Antennules." Encyclopédie méthodique, p. 142.
- PAASCH, A. 1873. Von den Sinnesorganen der Insekten im Allgemeinen, von Gehör- und Geruchsorganen im Besondern. Troschel's Arch. f. Naturgesch., 39 Jahrg., pp. 248-275.
- PACKARD, A. S. 1870. Abdominal sense-organs in a fly. Amer. Naturalist, Essex Institute, vol. 4, pp. 690-691.
- PECKHAM, G. W. and E. G. 1887. Some observations on the special senses of wasps. Proc. Nat. Hist. Soc. of Wisconsin, pp. 91-132.
- PERCHERON, A. 1841. Essai sur la valeur relative des organes dans les insectes, pour servir de base à une classification de ces animaux. Comptes Rendus Acad. Sci., Paris, t. 13, p. 1101.
- PERRIS, ED. 1850. Mémoire sur le Siège de l'Odorat dans les Articulés. Ann. Sci. Nat., Zool., t. 14, (3), pp. 149-178.
- PIÉRON, H. 1906. Le rôle de l'olfaction dans la reconnaissance der fourmis. Comptes Rendus Acad. Sci. Paris, t. 143, pp. 845-848.
- PIERRET. 1841. Ann. Soc. Ent. t. 10, Bul. pp. 10-11.
- PLATEAU, FÉLIX. 1885. Expériences sur le rôle des Palpes chez les arthropodes maxillés. Première partie, palpes des insectes broyeurs. Bul. Soc. Zool. de France, vol. 10, pp. 67-90.
- 1886. Une expérience sur la fonction des antennes chez la blatte (*Periplaneta orientalis*). Bul. Comptes Rendus des Séances Ann. Soc. ent. Belgique, t. 30, pp. 118-122.
- PLINY. Histoire naturelle de Pline, traduction nouvelle par M. Ajasson de Grandsagne, t. 7, Paris, 1830, Livre 10, 90 70, p. 351.
- PORTER, C. J. A. 1883. Experiments with the antennæ of insects. Amer. Naturalist, vol. 17, pp. 1238-1245.

- RAMDOHR. 1811. Ueber die Organe des Geruchs und Gehörs der gemeinen Biene. Magazine der Gesellschaft naturf. Freunde zu Berlin, 5 Jahrg., pp. 386-390.
- RÉAUMUR. 1734. Mémoires à l'histoire des insectes, t. 1, Paris.
- REICHENBACH, H. 1879. Allgemeines über Sinnesorgane. Vortrag. Bericht über die Senkenberg, naturf. Ges., p. 136.
- *ROBINEAU-DESVOIDY. 1828. Recherches sur l'organisation vertébrale des crustacés et des insectes.
- 1842. Sur l'usage réel des antennes chez les insectes. Ann. Soc. Ent. France, t. 11, Bul., pp. xxiii-xxvii.
- RÖHLER, ERNEST. 1905. Beiträge zur Kenntnis der Sinnesorgane der Insecten. Zool. Jahrb. Anat., 22, pp. 225-288, with one text fig. and 2 pls.
- ROMANES, G. J. 1877. Smell and hearing in moths. Nature, vol. 17, p. 82.
- RÖSEL und KLEMMANN. 1747. Insecten Belustigung, Theil I, p. 19 under "Geruch in Register."
- *ROSENTHAL. 1811. Ueber den Geruchssinn der Insekten. Reil's arch. f. die Physiologie, T. 10, Halle, p. 427.
- RULAND, FRANZ. 1888. Beiträge zur Kenntnis der antennalen Sinnesorgane der Insekten. Zeitsch. f. wiss. Zool., Bd. 46, pp. 602-628.
- SAMOUELLE, GEORGE. 1819. Entomologist's Compendium, London, pp. 26-27.
- SAZEPIN, BASIL. 1884. Ueber den histol. Bau und die Vertheilung der nervösen Endorgane auf den Fühlern die Myriopoden. Mém. de l'Acad. Impér. d. Sci. de St. Pétersburg, t. 32 (7), no. 9, pp. 1-20.
- *SCHELVER. 1798. Versuch einer naturgeschichte der Sinneswerkzeuge bei den Insekten, in — 8°, Göttinge, p. 46.
- SCHENK, OTTO. 1903. Die antennalen Hautsinnesorgane einiger Lepidopteren und Hymenopteren, mit besonderer Berücksichtigung der sexuellen Unterscheide. Zool. Jahrb. Bd. 17, pp. 573-618, with four text figs. and 2 pls.
- SCHIEMENZ, PAULUS. 1883. Ueber des Herkommen des Futtersaftes und die Speicheldrüsen der Bienen, nebst einem Anhange über das Riechorgan. Zeitsch. f. wiss. Zool., Bd. 38, pp. 71-135, with 3 pls.
- SCHÖN, ARNOLD. 1911. Bau und Entwicklung des tibialen chordotonalorgans bei der Honigbiene und bei Ameisen. Zool. Jahrb. Anat. und Ont., Bd. 31, pp. 439-472, with 9 text figs. and 3 pls.
- SHERMAN, FRANKLIN, JR. 1909. The senses of insects. Journ. Elisha Mitchell Sci. Soc., vol. 25, pp. 78-84.
- SLATER, J. W. 1848. Ueber die Function der Antennen bei den Insecten. Foriep's Notizen, III, no. 155, p. 6.
- 1878. The seat of the sense of smell in insects. Entomologist, vol. 11, p. 233.
- SNODGRASS, R. E. 1910. The anatomy of the honey bee. U. S. Dept. of Agriculture, Bur. of Ent., Tech. Ser. 18, Washington, Gov. Printing Office.
- STRAUS-DURCKHEIM. 1828. Anatomie des Animaux Articulés, pp. 420-422.
- SULZER, J. H. 1776. Abgekürzte Geschichte der Insecten, Erster Theil, p. 16.
- TREVIRANUS. 1816. Ueber den Sitz des Geruchssinns bey den Insekten. Vermischte Schriften anat. und physiol., Bd. 1, Göttingen, pp. 146-155.
- TROUVELOT, L. 1877. The use of the antennæ in insects. Amer. Naturalist, vol. 11, pp. 193-196.
- VARRO. 1735. Scriptores Rei Rusticæ Veteres Latini curante Gesnere, Lipsiæ, Lib. 3, Cap. 16, p. 378.

VIRGIL. Virgil's Georgics, Liber quartus, lines 47-50, 62-64.

*VOGT. 1851. Zool. Briefe, vol. 1, Frankfurt a. M., pp. 516-517.

VOM RATH, O. 1887. Ueber die Hautsinnesorgane der Insecten. Preliminary Communication. Zool. Anz. 10, Jahrg., pp. 627-631 and 645-649.

——— 1888. Ueber die Hautsinnesorgane der Insekten. Zeitschr. f. wiss. Zool. Bd. 46, pp. 413-454, with 2 pls.

——— 1895. Zur Kenntniss der Hautsinnesorgane und des sensiblen Nervensystems der Arthropoden. Zeitsch. f. wiss. Zool., Bd. 61, pp. 499-539, with 2 pls.

WASMANN, E. 1889. Zur Bedeutung der Palpen bei den Insekten. Biol. Centralblatt, Bd. 9, no. 10, pp. 303-308.

WEINLAND, ERNST. 1890. Ueber die Schwinger (Halteren) der Dipteren. Zeitsch. f. wiss. Zool., Bd. 51, pp. 55-166 with 5 pls.

WESCHÉ, W. 1904. Some new sense-organs in Diptera. Journ. Quekett Micr. Club, vol. 9 (2), pp. 91-104.

WITLACZIL, E. 1885. Die Anatomie der Psylliden (Hemiptera). Zeitsch. f. wiss. Zool., Bd. 42, p. 600.

WHEELER, W. M. 1910. Ants. Their structure, development and behavior. New York. Columbia Univ. Press, pp. 509-511.

WOLFF, O. J. B. 1875. Das Riechorgan der Biene nebst einer Beschreibung des Respirationswerkes der Hymenopteren, etc. Nova Acta der Kls. Leop-Carol. Deut. Akad. der Naturf. vol. 38, pp. 1-251, with 8 pls.

WONFOR, T. W. 1874. The antennæ of insects. Science-Gossip, pp. 29-31.