

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 65, NUMBER 14

THE SENSE ORGANS ON THE MOUTH-
PARTS OF THE HONEY BEE

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(PUBLICATION 2381)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
JANUARY 12, 1916

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

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INTRODUCTION AND METHODS

Little experimental work has ever been performed to determine whether insects have a true gustatory sense, although the sense organs on the mouth-parts of various insects have been studied considerably. At least three different kinds of sense organs on the mouth-parts have

been called organs of taste, but no one has ever attempted to prove experimentally the function of these organs. Judging from the fact that insects prefer some foods to others and that certain insects often refuse poisoned foods, it is generally believed that insects can taste, regardless of whether or not they have gustatory organs.

At this place it is desirable to define the human senses of smell and taste, so that we may use the definitions as a basis for interpreting the responses to the same or similar stimuli in the honey bee. The sense of smell is called forth by substances in a gaseous or vaporous condition, although gases dissolved in the liquids of the mouth may give rise to actual tastes. The sense of taste is brought about by substances either in solution when introduced into the mouth, or dissolved by the liquids in the mouth. Parker and Stabler (1913), after experimenting upon themselves, and Professor Parker upon other vertebrates, say:

We therefore definitely abandon the idea that taste and smell differ on the basis of the physical condition of the stimulus, a state of solution for taste, a gaseous or vaporous condition for smell, and maintain that both senses are stimulated by solutions, though in smell, at least for air-inhabiting vertebrates, the solvent is of a very special kind. . . . In air-inhabiting vertebrates the olfactory solvent is a slimy fluid of organic origin and not easily imitated.

From the preceding definitions it is evident that the senses of smell and taste in vertebrates cannot be sharply separated, and the present paper will show that these two senses in the honey bee cannot be separated at all. In the honey bee it will be shown that the sense of taste is only one phase of the olfactory sense. We have not the slightest conception as to how odor and taste stimuli in any animal act upon nerve endings to produce the various sensations of smell and taste; and as shown in the following pages, when bees are fed foods which contain undesirable substances emitting extremely weak odors, they refuse to eat the foods after "tasting" them. In view of the two preceding facts we may call this perception an olfactory-gustatory sense, although the writer will endeavor to show that the gustatory sense plays no part in these responses.

In the investigation herein recorded, two objects which throw considerable light on whether or not bees have a true gustatory sense have been kept in view: (1) To determine whether bees have likes and dislikes in regard to foods, and (2) to make a careful study of the morphology of all the sense organs on the mouth-parts of the honey bee.

To obtain material for the study of the disposition of the sense organs on the mouth-parts, adult specimens were used. In regard to preparing the specimens with caustic potash and to bleaching them with chlorine gas, the reader is referred to the writer's work on Hymenoptera (1914b, p. 295).

To obtain material for the study of the internal anatomy of the sense organs herein discussed, worker pupæ 17 to 21 days old (counting from the time the eggs were laid) were mostly used, but a few adult worker bees were also employed. In regard to fixing this material in Carnoy's fluid and to embedding it in celloidin and paraffin, the reader is referred to the writer's paper on Coleoptera (1915, p. 409). The sections were cut from five to ten microns in thickness, and were stained with iron hematoxylin and eosin, safranin and gentian violet, and with Ehrlich's hematoxylin and eosin.

All the drawings were made by the writer and all are original except the internal anatomy of the mentum (*Mt*) in figure 10, which was copied from Snodgrass (1910). They were made at the base of the microscope with the aid of a camera lucida.

EXPERIMENTS TO DETERMINE WHETHER BEES HAVE LIKES AND DISLIKES IN REGARD TO FOODS

The writer (1914a) made a thorough study of the morphology and physiology of the olfactory pores found on the wings, legs, and sting of the honey bee. At that time the same organs were seen on the mouth-parts, but they were left for future study. Since the olfactory pores are so widely distributed, it is impossible to prevent all of them from functioning either by eliminating them by operations or by covering them with a substance, because the more an insect is mutilated, the more abnormal its behavior becomes. This is particularly true when the mouth-parts are mutilated. When the appendages are covered with liquid glue, vaseline, etc., bees do not eat until the substance is removed. When certain mouth-appendages are removed, bees are not entirely normal and their eating is more or less affected.

Since it is impossible to eliminate the olfactory sense while determining whether bees have a true gustatory sense, and as the various sense organs on the mouth-parts cannot be mutilated without causing considerable abnormality in the behavior of the bees while eating, it was decided to ascertain if bees have likes and dislikes in regard to foods and to make a careful study of the morphology of all the sense organs on the mouth-appendages in order to be able to judge whether or not bees have a true sense of taste.

I. PRELIMINARY EXPERIMENTS IN FEEDING BEES FOODS CONTAINING VARIOUS SUBSTANCES

To determine the behavior of bees toward foods containing various substances under conditions which permitted of their close observation, triangular experimental cases were employed. These were made of three narrow wooden strips, two of which were ten and the third six inches long, each strip being an inch wide. Wire screen served as bottoms and tops for the cases whose apices and bases rested on supports above a table near a window.

Since cane-sugar candy is most conveniently fed to bees in experimental cases, a quantity of this food was made by thoroughly kneading a good quality of confectioner's sugar with a small amount of honey. For convenience in handling it while feeding the bees, a small lump of five grams, placed upon a small piece of cardboard, was put into each case.

Sometimes it was necessary to feed the bees honey. This food was poured into small tin feeders, each one being two and a quarter inches long, one inch wide, and one-fourth inch deep. To prevent the bees from wasting the honey, fine parallel pieces of wire, one-eighth inch apart, were stretched lengthwise over the tops of the feeders.

One drop of oil of peppermint was thoroughly mixed with 25 grams of cane-sugar candy. This mixture was then divided into five equal parts. One hundred milligrams of quinine sulphate were also thoroughly mixed with 25 grams of cane-sugar candy, and the mixture was then divided into five equal parts.

Twenty worker bees from the alighting-boards of various hives were introduced into each of five of the experimental cases, and they were immediately fed the two foods just described and an equal amount of pure cane-sugar candy. The order of placing the foods into the cases was rotated so that case No. 1 received the pure cane-sugar candy first, the candy containing oil of peppermint second and the candy containing quinine third. Case No. 2 received the candy containing oil of peppermint first, the candy containing quinine second and the pure cane-sugar candy third. Case No. 3 received the candy containing the quinine first, the pure cane-sugar candy second, and the candy containing the oil of peppermint third. Cases Nos. 4 and 5 were treated similarly. The order of arrangement of the candies in the cases was also rotated so that no two cases contained the candies in the same arrangement.

When the pure cane-sugar candy was fed first, the bees covered it and ate greedily for several moments. When the candy containing

oil of peppermint was fed first, several bees ate greedily for only a few seconds, and when pure cane-sugar candy was given to them only occasionally was a bee observed eating the candy containing oil of peppermint. When the candy containing quinine was fed first, many of the bees ate greedily until the pure cane-sugar candy was given to them; then they soon deserted the former for the latter. It was soon observed that after eating 10 minutes, the bees were able to select the candy they liked best; therefore the first count was made 10 minutes after giving them the first food and thereafter every 30 minutes. In these experiments, as in nearly all the others performed, 15 or more counts were recorded, but since some of the substances fed cause a greater mortality than others, and in order to obtain a total average as nearly uniform as possible, of the bees eating at any one count, only the first five counts have been considered. To ascertain if the direction of the light was a factor in helping to select the food, the cases were often reversed end for end. After recording the number of bees eating, they were often driven from a certain food by blowing upon them, but they invariably soon returned to the same food. As a general rule for all the experiments performed, the longer the bees were confined in the cases, the smaller was the number observed eating at any given time. Neither the direction of the light nor the arrangement of the food in the cases is a factor in helping to select the foods they like best.

The preceding set of experiments was repeated twice. As an average for the 300 bees for five counts, 35.8 per cent of the bees were seen eating pure cane-sugar candy, none eating candy containing oil of peppermint, and 2.3 per cent were observed eating candy containing quinine, making a total average of 38.1 per cent eating at any one count. Twelve bees in case No. 4 of the first set of experiments began to die when the fifth count was recorded. They had freely eaten the candy containing quinine.

Two days later three grams of chinquapin (*Castanea pumila*) honey were poured into each of five feeders. This food was then given to the bees used in the third set of experiments just described. During the first 15 minutes after introducing the honey, only seven bees ate a little of it. After that they walked over the feeders, but never offered to eat the honey again. This honey has a strong, characteristic, bitter odor. As an average for the 100 bees for five counts, 15 minutes after introducing the honey 24.8 per cent were seen eating pure cane-sugar candy at any one count, but none was noticed eating

the candies containing oil of peppermint and quinine or the chinquapin honey.

The following day honey containing oil of peppermint was substituted for the chinquapin honey. This was had by mixing one drop of the oil of peppermint in 25 cubic centimeters of honey, and the mixture was then divided into five equal parts. It emitted only a faint odor of peppermint, but when eaten by the writer the peppermint attribute was quite pronounced. It no longer tasted like honey. During the first five minutes only a few bees ate a little of it, and after that none offered to eat it. As an average for the 100 bees for five counts, 26.6 per cent were observed eating pure cane-sugar candy at any one count, but none was seen eating the candies and the honey containing oil of peppermint and quinine. Later the pure cane-sugar candy in case No. 1 became exhausted, and instead of the bees selecting either the candy or the honey containing oil of peppermint, they chose the candy containing quinine. For two hours they ate it as freely as they previously had eaten the pure cane-sugar candy, but after the third hour they ceased to eat it. By this time a few were dead and several were sick.

One drop of cider vinegar was mixed with 25 grams of cane-sugar candy and one drop of carbolic acid was mixed with an equal amount of cane-sugar candy. Each one of these mixtures was then divided into five equal parts. Fresh bees were introduced into the cases and were fed pure cane-sugar candy and the mixtures just described. As an average for the 100 bees for five counts, 17.4 per cent were observed eating pure cane-sugar candy, 28.8 per cent eating candy containing vinegar, and 1.4 per cent were seen eating candy containing carbolic acid, making a total average of 47.6 per cent eating at any one count. The vinegar seemed to have brought about a chemical change in the candy and probably inverted the cane sugar. After the fifth count the bees ate this candy more freely than before.

Two days later the candy containing vinegar was removed and candy containing alum was placed in its exact position. The latter candy was composed of one-half powdered alum, and the other half of powdered sugar and honey. At first the bees ran over it, and thereafter only occasionally ate a little of it. As an average for the 100 bees for five counts, 19.2 per cent were seen eating pure cane-sugar candy, 3.8 per cent eating candy containing carbolic acid, and 3.4 per cent were seen eating candy containing alum, making a total average of 26.4 per cent eating at any one count. The candy containing carbolic acid at this time emitted only a faint odor.

The following day mannose (a monosaccharide or simple sugar) candy was given to the bees used in the preceding experiments. This candy was made by kneading pure mannose (crystallized and washed twice) and honey. For a few moments the bees in two cases seemed to like the mannose candy equally as well as the cane-sugar candy, although after a short time they became sick and later several died. As an average for the 100 bees for five counts, 24.2 per cent were observed eating pure cane-sugar candy, 0.2 per cent eating candy containing carbolic acid, none eating candy containing alum and 3.6 per cent were seen eating mannose candy, making a total average of 28.1 per cent eating at any one count.

Fifteen grams of common salt (NaCl) were kneaded in honey. This mixture was then divided into five equal parts. It and chinquapin honey were fed to fresh bees. During the first 15 minutes the bees ate the salt containing honey rather freely, but seldom touched the chinquapin honey and after that seldom ate any of either food. Forty-five minutes after introducing the food, several bees in each case began to die. As an average for the 100 bees for five counts, 2.2 per cent were seen eating chinquapin honey and 2 per cent eating salt containing honey, making a total average of 4.2 per cent eating at any one count.

The following is a tabulated summary of the preceding results obtained by feeding bees foods containing various substances. The figures in the third to tenth columns represent the average per cent or number of bees eating a particular food at any one count.

TABLE I
Preliminary Experiments in Feeding Bees Foods Containing Various Substances

Number of bees used	Number of counts	Average per cent of bees eating foods containing various substances										
		Pure cane-sugar candy	Cane-sugar candy containing oil of peppermint	Cane-sugar candy containing quinine	Chinquapin honey	Honey containing oil of peppermint	Cane-sugar candy containing cider vinegar	Cane-sugar candy containing carbolic acid	Cane-sugar candy containing alum	Mannose candy	Salt containing honey	Total average per cent of bees feeding at any one count
300	5	35.8	0.0	2.3	38.1
100	5	24.6	0.0	0.0	0.0	24.6
100	5	26.6	0.0	0.0	0.0	26.6
100	5	17.4	28.8	1.4	47.6
100	5	19.2	3.8	26.4
100	5	24.2	0.2	0.0	3.6	28.0
100	5	2.2	2.0	4.2

The preceding preliminary experiments clearly show the following: (1) In regard to foods bees have likes and dislikes; (2) before showing preferences between foods bees always eat more or less of them first, unless the foods contain strong repellents; (3) the longer the bees are confined in the experimental cases the less they eat, and (4) some of the substances fed are injurious to them. For the last two reasons only the first five counts are sufficiently reliable for determining the total average per cent of bees eating at any one count. These experiments indicate that bees may have a sense of taste, because neither the direction of the light nor the arrangement of the food in the cases helps in selecting the food they like best, and the olfactory sense may not be the sole factor in selecting foods, for bees must usually eat more or less of them before being able to show preferences between them. It is probable that bees cease eating some foods because their alimentary tracts may be affected, and for this reason alone they may reject the particular food that does not agree with them.

The preceding results suggest five classes of foods to be used in the following experiments. Foods containing strong repellents may be employed to determine the importance of the olfactory sense in causing bees to avoid such substances, and foods containing sweet, bitter, sour, and salty substances may be used to ascertain if bees show preferences between foods having the four attributes of human taste.

2. EXPERIMENTS IN FEEDING BEES FOODS CONTAINING REPELLENTS

Pure cane-sugar and candy containing oil of peppermint (described above, page 4) were fed to fresh bees in the cases as described in the preceding pages. After waiting 10 minutes the first count was recorded, and thereafter every 30 minutes. As an average for the 100 bees for five counts, 35.4 per cent were seen eating the pure cane-sugar candy at any one count, while they never touched the candy containing oil of peppermint.

The preceding was repeated by feeding candy containing carbolic acid (described on p. 6) and pure cane-sugar candy to fresh bees. As an average for the 100 bees for five counts, 41.4 per cent were seen eating pure cane-sugar at any one count, while none touched the candy containing carbolic acid.

The preceding was repeated by feeding pure honey and honey containing whiskey to fresh bees. Four grams of pure honey were

poured into each of five feeders, and the same amount containing three drops of whiskey was likewise poured into each of five other feeders. The odor of whiskey from the latter food was not pronounced to the writer, but the taste of whiskey was quite pronounced. When these foods were introduced into the cases the bees ate one as freely as the other. Five minutes after feeding them the first count was taken and thereafter every five minutes. Since it takes bees confined in these cases only 10 to 15 minutes to fill their honey stomachs with liquid foods, only two counts were taken. As an average for the 100 bees for two counts, 30 per cent were seen eating pure honey and 22 per cent eating honey containing whiskey, making 52 per cent eating at any one count.

A mixture of 25 cubic centimeters of honey and two drops of carbolic acid was divided into five equal parts, each part being fed to 20 fresh bees in the usual manner. For the first 15 minutes after introducing the food, the bees avoided it, but later a few ate it to a limited degree. As an average for the 100 bees for five counts, 3 per cent were seen eating it at any one count. Nine days later this honey did not emit such a strong carbolic-acid odor. It was again fed to bees. Only two counts were taken. As an average for the 100 bees, 27.5 per cent were seen eating at any one count.

The preceding was repeated by feeding honey containing oil of peppermint (described on p. 4) to fresh bees. As long as the mixture emitted a strong odor of peppermint the bees avoided it, but nine days after preparing the mixture the bees ate it rather freely. As an average for the 100 bees, 27.5 per cent were seen eating it at any one count.

Twenty-five cubic centimeters of honey were mixed with two drops of each of the following: formic acid, sulphuric acid, xylol, formaldehyde, kerosene, and lime-sulphur. The bees usually avoided these mixtures, but occasionally one or two offered to eat a little of the food. The first count was recorded 30 minutes after introducing the food and thereafter every hour. As an average for the 100 bees in each set of experiments for five counts, the following numbers represent the bees seen eating at any one count: Formic acid—7.4 per cent, sulphuric acid—4.2 per cent, xylol—5.2 per cent, formaldehyde—3.2 per cent, kerosene—1.6 per cent, and lime-sulphur—1.2 per cent.

The following is a tabulated summary of the preceding results obtained by feeding bees foods containing repellents. The figures

in the third to fourteenth columns represent the average per cent or number of bees eating a particular food at any one count.

TABLE II
Experiments in Feeding Bees Foods Containing Repellents

Number of bees used	Number of counts	Pure cane-sugar candy	Pure honey	Average per cent of bees eating pure foods and foods containing repellents										Total average per cent of bees feeding at any one count		
				Cane-sugar-candy containing carbolic acid	Cane-sugar-candy containing oil of peppermint	Honey containing whiskey	Honey containing formic acid	Honey containing xylol	Honey containing sulphuric acid	Honey containing formaldehyde	Honey containing carbolic acid	Honey containing kerosene	Honey containing lime-sulphur			
100	5	35.4	0.0	35.4
100	5	41.4	0.0	41.4
100	2	30.0	22.0	52.0
100	5	7.4
100	5	5.2
100	5	4.2
100	5	3.2
100	5	3.0
100	5	1.6
100	5	1.2

The preceding results clearly show that when bees are given preferences between pure foods and foods containing strong repellents they freely eat the former and refuse the latter, and when they are fed foods containing repellents without having a preference for pure foods, they eat sparingly. Judging from these experiments we are certainly safe in saying that the bees avoided the foods containing repellents on account of the odors emitted from these substances.

3. EXPERIMENTS IN FEEDING BEES SWEET FOODS

To ascertain if bees show preferences between sweet foods, the following candies were made by using basswood honey with chemically pure potato starch, dextrine and the following sugars: saccharine, mannose, levulose, dextrose, raffinose, lactose and maltose. An equally small amount of honey was kneaded with 15 grams of each of the above nine substances, except that only eight grams of saccharine were used. Each lump of candy was then divided into five equal parts. In the order of the sweetest to the writer, the eight sugars stand as given above. Saccharine, varying from 300 to 500 times as sweet as cane sugar, has a disagreeable sweet-sickening taste.

Mannose, which appears to be almost as sweet as saccharine, has a disagreeable, bitter-sweet taste. Each one of these sugars has its own faint, characteristic odor, but the predominating odor emitted from the candy made of each is that of honey. To the writer the starch candy gave off only one faint odor, that of honey. Dextrine is light yellow and emits a stronger odor than does any one of the sugars.

Twenty fresh bees were introduced into each of five cases. When the preceding nine candies were put into the cases, the bees wandered about considerably and ate a little of each candy, but ate the mannose and levulose most greedily. A short time after eating the mannose, many of the bees began to die. Thirty minutes after feeding the bees, the first count was taken, and thereafter every half hour. The four counts recorded showed that only one bee was seen eating mannose, four eating levulose and none eating any of the other candies. This small number is certainly due to most of the bees soon becoming sick and some dying.

The preceding experiments were repeated by feeding cane-sugar (saccharose), saccharine, mannose and levulose candies to fresh bees. As usual the bees wandered about considerably and ate a little of each candy except the saccharine. An hour later those that had eaten the mannose became sick and ate no more that day, but the next morning most of them had recovered and a few were seen eating a little. As a total for the 100 bees for 17 counts, 10.7 per cent were seen eating cane-sugar, 6 per cent eating levulose, 1 per cent eating saccharine and none eating mannose candy.

To ascertain if bees could be forced to eat saccharine, fresh bees and a lump of the saccharine candy were put into each of the five cases. The bees perched upon and ran over the candy as if it were a piece of wood. It neither repelled nor attracted them, and during an entire hour only five bees licked the candy for a few seconds. The starch candy was next tried alone. During the first ten minutes several bees ate it rather freely, but after that for an hour only occasionally did a bee eat a little of it.

Cane-sugar, dextrose, dextrine and raffinose candies were put into each case, and fresh bees were employed as usual. As an average for the 100 bees for five counts, 41.2 per cent were seen eating cane-sugar, 2.6 per cent eating dextrose, none eating dextrine and 0.2 per cent eating raffinose candy, making a total average of 44 per cent eating at any one count.

Levulose, dextrose and raffinose candies were next used. As an average for the 100 bees for five counts, 20 per cent were seen eating

levulose, none eating dextrose and 1.8 per cent eating raffinose candy, making a total average of 21.8 per cent eating at any one count.

Dextrose, raffinose and dextrine candies were used in the same way. As an average for the 100 bees for five counts, 21 per cent were seen eating raffinose, 12 per cent eating dextrose and 6.8 per cent eating dextrine candy, making a total average of 39.8 per cent eating at any one count.

Dextrine, lactose and maltose candies were used in the same way. As an average for the 100 bees for five counts, 42 per cent were observed eating maltose candy at any one count, but none was seen eating lactose or dextrine candy.

The preferences shown between these candies may have been partially due to the amount of water in them. No two of these candies absorbed the same amount of water vapor from the air, but during the first day the water in any of them was not noticeable, although after that it was quite noticeable. Levulose absorbed the most water vapor and saccharine the least.

Dextrose, raffinose and maltose candies were next used. As an average for the 100 bees for five counts, 16 per cent were seen eating maltose, 12 per cent eating raffinose and 7 per cent eating dextrose candy, making a total average of 35 per cent eating at any one count.

To ascertain if bees show preferences between honeys, an equal amount of light-colored honey and dark-colored honey was poured into each of five feeders. Perhaps most of the light-colored honey came from basswood trees, while the source of the dark-colored honey was unknown. The latter honey was taken in the crystallized form from old combs and was then melted. The odors and tastes of these two honeys were quite different. Fresh bees from the alighting-boards were introduced into the cases, and during the first five minutes after giving them the two honeys, they ate each one greedily. By the time they had eaten five minutes, most of them had selected the honey they liked the better. At this stage the ones eating were counted, and five minutes later were counted again. After this few were seen eating, because nearly all of them by this time had filled their honey stomachs. This set of experiments was repeated twice. As an average for the 300 bees for two counts, 24.3 per cent were seen eating the light-colored honey and 18.8 per cent the dark-colored honey, making a total average of 43.1 per cent eating at any one count.

Fresh bees were placed in the cases, and they were fed light-colored honey and sugar syrup (half sugar and half water) in the same manner as just described. As an average for the 100 bees for

two counts, 37 per cent were seen eating the honey and 4 per cent the syrup, making a total average of 41 per cent eating at any one count.

In the same manner light-colored honey and pollen mixed thoroughly with light-colored honey (1 part pollen to 4 parts honey) were given to fresh bees. As an average for the 100 bees for three counts, 26.3 per cent were seen eating the light-colored honey and 16.3 per cent the honey mixed with pollen, making a total average of 42.6 per cent eating at any one time.

In the same way light-colored honey, and sugar mixed with light-colored honey (half and half) were fed to bees. As an average for the 100 bees for five counts, 30.4 per cent were seen eating the honey and 11 per cent the mixture of sugar and honey, making a total average of 41.4 per cent eating at any one count. Since one of these foods was a thick paste, five counts were recorded before the bees ceased eating, while in the experiments just preceding only three counts were necessary, because the mixture of pollen and honey made a thin paste.

The following is a tabulated summary of the preceding results obtained by feeding bees sweet foods. The figures in the third to fourteenth columns represent the average per cent or number of bees eating a particular food at any one time.

TABLE III
Experiments in Feeding Bees Sweet Foods

Number of bees used	Number of counts	Average per cent of bees eating candies						Average per cent of bees eating liquid foods					Total average per cent of bees feeding at any one count		
		Cane-sugar candy	Levulose candy	Maltose candy	Raffinose candy	Dextrose candy	Lactose candy	Dextrine candy	Light-colored honey	Dark-colored honey	Sugar syrup (1 pt. sugar to 1 pt. water)	Light-colored honey and pollen (4 pt. honey to 1 pt. pollen)		Light-colored honey and sugar (1 pt. honey to 1 pt. sugar)	
100	5	41.2	0.2	2.6	..	0.0	44.0
100	5	20.0	1.8	0.0	21.8
100	5	21.0	12.0	6.8	39.8
100	5	42.0	0.0	0.0	42.0
100	5	16.0	12.0	7.0	35.0
100	2	24.3	18.8	43.1
100	2	4.0	41.0
100	3	26.3	16.3	42.6
100	5	30.4	11.0	41.4

It is evident from the above table that bees show preferences between sweet foods.

4. EXPERIMENTS IN FEEDING BEES FOODS CONTAINING BITTER SUBSTANCES

Two lots of 25 grams of cane-sugar candy each were thoroughly mixed, one with 500 milligrams of finely pulverized quinine sulphate and the other with a like quantity of strychnine sulphate. Each mixture was then divided into five equal parts. To the writer the odor from each mixture was exactly like that from pure cane-sugar candy, although the human nose is able to detect a faint odor emitted from a large quantity of either quinine or strychnine. Strychnine is regarded as the bitterest of all substances. To the writer both of these mixtures were extremely bitter. Equal amounts of pure cane-sugar candy and of these other two foods were fed to fresh bees in the usual manner. Five minutes after introducing the foods, the first count was taken and thereafter every 15 minutes. As an average for the 100 bees for five counts, 47.4 per cent were observed eating pure cane-sugar candy, 5.8 per cent eating candy containing quinine, and 4 per cent eating candy containing strychnine, making a total average of 57.8 per cent eating at any one count.

These experiments were repeated by feeding fresh bees only the candies containing quinine and strychnine. As an average for the 100 bees for five counts, 39.4 per cent were seen eating candy containing quinine and 4 per cent eating candy containing strychnine, making a total average of 43.4 per cent eating at any one count. An hour after introducing the foods, the bees began to die.

Twenty-five grams of cane-sugar candy were mixed with 500 milligrams of liquid picric acid, and then the mixture was divided into five equal parts. This food was almost as bitter as quinine and emitted a faint odor, different from that of pure cane-sugar candy. The preceding experiments were repeated by feeding fresh bees this mixture, candy containing quinine and pure cane-sugar candy. As an average for the 100 bees for five counts, 19.2 per cent were seen eating pure cane-sugar candy, 34.4 per cent eating candy containing picric acid and 2.2 per cent eating candy containing quinine, making a total average of 55.8 per cent eating at any one count.

The preceding was repeated by using the same amount of powdered picric acid instead of the liquid picric acid and by discarding the candy containing quinine. As an average for the 100 bees for five counts, 45 per cent were observed eating pure cane-sugar candy and 1 per cent eating candy containing picric acid, making a total average of 46 per cent eating at any one count.

The experiments just described were repeated by making a candy of powdered picric acid and honey. As an average for the 100 bees for five counts, 45 per cent were seen eating the pure cane-sugar candy at any one count, but none ate the candy made of picric acid and honey. Judging from the three sets of experiments in which picric acid was used, it seems that this acid in the liquid form effects a chemical change in cane sugar, thereby causing bees to prefer candy mixed with it to pure cane-sugar candy.

Chinquapin honey, which has a bitter taste, was next fed to bees as described on page 5. As an average for the 100 bees for seven counts, only 3.4 per cent were seen eating at any one count.

The following is a tabulated summary of the preceding results obtained by feeding bees foods containing bitter substances. The figures in the third to ninth columns represent the average per cent or number of bees eating a particular food at any one count.

TABLE IV
Experiments in Feeding Bees Foods Containing Bitter Substances

Number of bees used	Number of counts	Pure cane-sugar candy	Average per cent of bees eating foods containing bitter substances						Total average per cent of bees feeding at any one count
			Cane-sugar candy containing quinine	Cane-sugar candy containing strychnine	Cane-sugar candy containing liquid picric acid.	Cane-sugar containing powdered picric acid	Candy made of powdered picric acid and honey	Chinquapin honey	
100	5	47.4	5.8	4.6	57.8
100	5	39.4	4.0	43.4
100	5	19.2	2.2	34.4	55.8
100	5	45.0	1.0	46.0
100	5	45.0	0.0	45.0
100	7	3.4

Judging from the above table, it is plain that bees show preferences between foods containing bitter substances.

5. EXPERIMENTS IN FEEDING BEES FOODS CONTAINING SOUR SUBSTANCES.

Twenty grams of honey were thoroughly mixed with 45 drops of lemon juice. The lemon juice made the honey considerably thinner and gave it a slightly different odor and a slightly sour taste. This mixture and an equal amount of pure honey, after being divided into five equal parts, were fed to fresh bees in the usual manner. As an

average for the 100 bees for two counts, 26.5 per cent were observed eating pure honey and 17 per cent eating honey containing lemon juice, making a total of 43.5 per cent eating at any one count.

The preceding was repeated by using three drops of acetic acid (99.5 per cent) in each feeder containing four grams of honey. The acid made the honey quite sour and changed its odor slightly. As an average for the 100 bees for two counts, 28 per cent were seen eating pure honey and 5.5 per cent eating honey containing acetic acid, making 33.5 per cent eating at any one count.

Hydrochloric acid (37 per cent) was used in the same manner. It slightly changed the odor of the honey and gave it a sharp, sour taste. As an average for the 100 bees for two counts, 50 per cent were observed eating pure honey at each count, but none ate the honey containing acid.

Sulphuric acid (95 per cent) was next used in the same manner. This acid gave the honey a less sharp, sour taste than did hydrochloric acid. As an average for the 100 bees for two counts, 28.5 per cent were seen eating pure honey at each count, while none ate the honey containing acid.

Nitric acid (68 per cent) was employed in the same way. This acid gave the honey a sour taste, although not sharp. As an average for the 100 bees for two counts, 33.5 per cent were observed eating pure honey at each count, while none ate the honey containing acid.

The following is a tabulated summary of the preceding results obtained by feeding bees foods containing sour substances. The figures in the third to eighth columns represent the average per cent or number of bees eating a particular food at any one count.

TABLE V
Experiments in Feeding Bees Foods Containing Sour Substances

Number of bees used	Number of counts	Pure honey	Average per cent of bees eating foods containing sour substances					Total average per cent of bees feeding at any one count
			Honey containing lemon juice	Honey containing acetic acid	Honey containing hydrochloric acid	Honey containing sulphuric acid	Honey containing nitric acid	
100	2	26.5	17.0	43.5
100	2	28.0	5.5	33.5
100	2	50.0	0.0	50.0
100	2	28.5	0.0	28.5
100	2	33.5	0.0	33.5

Judging from the above table, it is seen that bees prefer pure honey to honeys containing sour substances.

6. EXPERIMENTS IN FEEDING BEES FOODS CONTAINING SODIUM SALTS

Five lots, each containing 15 grams of cane-sugar candy, were each thoroughly mixed respectively with 500 milligrams of the following finely pulverized and chemically pure salts: sodium chloride (common salt), sodium sulphite, sodium nitrate, sodium carbonate and sodium fluoride. Each one of these mixtures was then divided into five equal parts. Each of the salts used has a faint odor and no two have odors alike, and the odor of each mixture was slightly different from that of pure candy. The taste of the mixture containing sodium chloride was slightly salty and the tastes of the other mixtures were more or less different from that of pure candy; no two were alike and none was exactly salty. Sodium fluoride has a sharp, astringent taste and seems to burn the mucous membrane. Some of the mixtures absorbed more water vapor from the air than others and some changed slightly in color. All five mixtures and pure cane-sugar candy were fed to fresh bees in the usual manner. At first the bees ate a little of each candy, and before having time to select the ones they liked best, many bees became sick and soon began to die.

Pure cane-sugar candy and the candy containing sodium chloride were tried alone. Since all these salts were more or less injurious to bees, the first count was made five minutes after introducing the food and thereafter every 15 minutes. As an average for the 100 bees for five counts, 39.6 per cent were seen eating pure cane-sugar candy and 5.8 per cent eating the candy containing sodium chloride, making a total average of 45.4 per cent eating at any one count.

The candies containing sodium carbonate and sodium sulphite were tried alone. As an average for the 100 bees for five counts, 9 per cent were observed eating the latter mixture, but only 0.6 per cent eating the former mixture, making a total average of 9.6 per cent eating at any one count. A half hour after introducing the food, many bees were sick and a half hour still later several were dead.

The mixture containing sodium nitrate and sodium fluoride were next tried alone. As an average for the 100 bees for five counts, 2.2 per cent were seen eating the latter mixture and 9.6 per cent eating the former mixture, making a total average of 11.8 per cent eating at any one count. A half hour after feeding the bees, many became sick and soon began to die.

Pure cane-sugar candy and the mixture containing sodium carbonate were fed alone. As an average for the 100 bees for five counts, 56.6 per cent were observed eating pure cane-sugar candy at any one count, while none ate the mixture containing sodium carbonate.

Pure cane-sugar candy and the mixture containing sodium sulphite were also fed alone. As an average for the 100 bees for five counts, 52.2 per cent were seen eating pure cane-sugar candy and 3.2 per cent eating the mixture containing sodium sulphite, making a total average of 55.4 per cent eating at any one count. An hour after introducing the food, a few bees became sick.

Pure cane-sugar candy and the mixture containing sodium nitrate were likewise fed alone. As an average for the 100 bees for five counts, 45.6 per cent were seen eating pure cane-sugar candy and 3.8 per cent eating the mixture containing sodium nitrate, making a total average of 49.4 per cent eating at any one count.

Pure cane-sugar candy and the mixture containing sodium fluoride were fed last. As an average for the 100 bees for five counts, 32.2 per cent were observed eating pure cane-sugar candy and only 0.4 per cent eating the mixture containing sodium fluoride, making a total average of 32.6 per cent eating at any one count. A half hour after introducing the food, several bees became sick.

The following is a tabulated summary of the preceding results obtained by feeding bees foods containing sodium salts. The figures in the third to eighth columns represent the average per cent or number of bees eating a particular food at any one count.

TABLE VI
Experiments in Feeding Bees Foods Containing Sodium Salts

Number of bees used	Number of counts	Pure cane-sugar candy	Average per cent of bees eating foods containing sodium salts					Total average per cent of bees feeding at any one count
			Cane-sugar candy containing sodium chloride	Cane-sugar candy containing sodium nitrate	Cane-sugar candy containing sodium sulphite	Cane-sugar candy containing sodium fluoride	Cane-sugar candy containing sodium carbonate	
100	5	39.6	5.8	45.4
100	5	45.6	3.8	49.4
100	5	52.2	3.2	55.4
100	5	32.2	0.4	32.6
100	5	56.6	0.0	56.6
100	5	9.0	0.6	9.6
100	5	9.6	2.2	11.8

Judging from the above table, it is seen that bees prefer pure cane-sugar candy to any one of the above foods containing sodium salts, and that they show preferences between these various mixtures.

7. EXPERIMENTS IN FEEDING BEES FOODS CONTAINING POTASSIUM SALTS

The preceding experiments were repeated by using potassium bromide, potassium carbonate, potassium cyanide, potassium ferrocyanide, potassium iodide, and potassium nitrate. When potassium bromide, potassium ferrocyanide, and potassium nitrate were mixed

TABLE VII
Experiments in Feeding Bees Foods Containing Potassium Salts

No. of bees used	No. of counts	Pure cane-sugar candy	Average per cent of bees eating foods containing potassium salts						Total average per cent of bees feeding at any one count
			Cane-sugar candy containing potassium bromide	Cane-sugar candy containing potassium carbonate	Cane-sugar candy containing potassium cyanide	Cane-sugar candy containing potassium ferrocyanide	Cane-sugar candy containing potassium iodide	Cane-sugar candy containing potassium nitrate	
100	5	36.2	9.6						45.8
100	5	40.2		0.4					40.6
100	5	43.8			0.0				43.8
100	5	24.6				12.4			37.0
100	5	29.8					5.0		34.8
100	5	26.8						5.4	32.2
100	5				0.0	33.4			33.4
100	5		15.6	0.0					15.6
100	5						6.0	3.6	9.6

with pure cane-sugar candy, the mixtures emitted odors and tasted like pure cane-sugar candy as far as the writer could detect. Potassium carbonate and potassium iodide did not change the odor of the cane-sugar candy when mixed with it, but each gave the mixture a slightly bitter taste. The potassium cyanide gave the cane-sugar candy a slightly bitter taste and a comparatively strong odor like cyanogen. It changed the candy from white to a lemon-like color. Three of the other mixtures were also changed slightly in color. The six mixtures were fed, two at a time, to fresh bees, and then each one was fed with pure cane-sugar candy in the manner described for the foods containing the sodium salts. When the bees ate the mixtures containing potassium bromide, potassium carbonate, potassium iodide, and potassium nitrate, they soon became sick and thereafter

almost ceased eating. They wholly refused to eat candy containing potassium cyanide but freely ate the mixture containing potassium ferrocyanide, and this salt apparently did not affect them. A detailed account of these experiments is not necessary, because the results are similar to those when the sodium salts were used.

Table VII is a tabulated summary of the results obtained by feeding bees with foods containing potassium salts. The figures in the third to ninth columns represent the average per cent or number of bees eating a particular food at any one count.

It is evident from the above tabulated results that bees prefer pure cane-sugar candy to the mixtures containing potassium salts, and that they also show preferences between foods containing these salts.

8. SUMMARY OF PRECEDING EXPERIMENTS

The preceding results clearly demonstrate that bees have likes and dislikes in regard to foods, and it seems that their faculty to discriminate between foods is more highly developed than ours, because they can distinguish differences between the foods fed to them better than the writer. The candies containing strychnine and quinine best illustrate this point. Equal amounts of these two bitter salts were used; but when the writer tasted the candies containing them, little or no difference in bitterness could be detected, although, judging from the number of bees that ate them when the two foods were fed alone, the bees distinguished a marked difference between them.

As a general rule, foods agreeable to us are also agreeable to bees, but there are a few marked exceptions. All foods scented with peppermint are pleasant to us, but repellent to bees. The writer does not care for candy containing potassium ferrocyanide, but bees are rather fond of it, and it does not seem harmful to them.

In regard to the repellents used, the few experiments performed do not warrant definite deductions, but the results indicate that lime-sulphur and kerosene are the strongest of the repellents used, while formic acid repels the least and carbolic acid the most among the acids. That the acids as a rule are not better repellents may possibly be explained by the fact that bees are more or less accustomed to the odors from the acids found in their foods and various secretions.

The results obtained demonstrate that bees like honey best of all foods and that they are able to distinguish marked differences between various kinds of honeys. Substitutes for honey as food for bees may be better than honey in a few instances, but these investi-

gations indicate that no substitute can be had which will be liked by bees as well as the best pure honey.

The fact that bees must first eat more or less of the foods before being able to discriminate differences between them, unless they contain repellents, indicates that bees have a true gustatory sense, providing this discrimination is not accomplished by means of the olfactory sense. Since this point cannot be determined experimentally, our only criterion is to make a thorough study of all the sense organs on and near the mouth-parts. This part of the work is given in the following pages.

MORPHOLOGY OF THE SENSE ORGANS ON THE MOUTH-PARTS OF THE HONEY BEE

In the preceding pages it is stated that bees show preferences between foods. In order that they may show preferences between the foods emitting weak odors, it is first necessary for them to eat a little of the foods. This fact indicates that bees may have a true sense of taste. If the mouth-parts possess sense organs which are anatomically fitted for receiving gustatory stimuli, we are safe in saying that bees can taste. In order to find such organs, if possible, it was necessary to make a special study of all the sense organs on and near the mouth-parts. In order to distinguish the sense organs from other structures on the mouth-parts, the internal anatomy of all the structures on the integument was first studied. This was accomplished by making many transverse and longitudinal sections through all parts of the mouth-appendages and even through the entire head. Only two general types of sense organs were found; *viz.*: innervated hairs and innervated pores.

Hairs on the honey bee are of two kinds—branched or barbed hairs and unbranched ones. As far as known the branched ones are never innervated and are never found on the mouth-appendages, but on the head near the mouth-parts and elsewhere. The unbranched hairs not only occur on the mouth-appendages but also on the other parts of the integument, although most abundantly on the mouth-parts and compound eyes. They may or may not be innervated.

All true hairs, whether branched or unbranched, arise from hair sockets (fig. 2 Q, *HrSk*) whose cavities (*SkCav*) communicate with the lumens (*L*) of the appendages and with the cavities (*HrCav*) of the hairs. The long hairlike structures (fig. 3 A, *Hr*¹) on the tongue or glossa may be called pseudo-hairs, because they are merely

prolongations of the chitin. They do not arise from sockets, are not hollow and do not communicate with the lumen (*L*) of the tongue. The spoon-shaped lobe, the labellum (fig. 7, *Lbl*) forming the tip of the tongue, is also covered with pseudo-hairs. These are short and thick and are branched at their tips, while those on the tongue are long and slender and are unbranched. Several minute pseudo-hairs are also present on the dorsal side of the mentum (fig. 7, *Mt*) and elsewhere on various parts of the integument.

The writer in 1914 made a study of the innervated pores (called olfactory pores) found on the wings, legs, and sting of the honey bee.

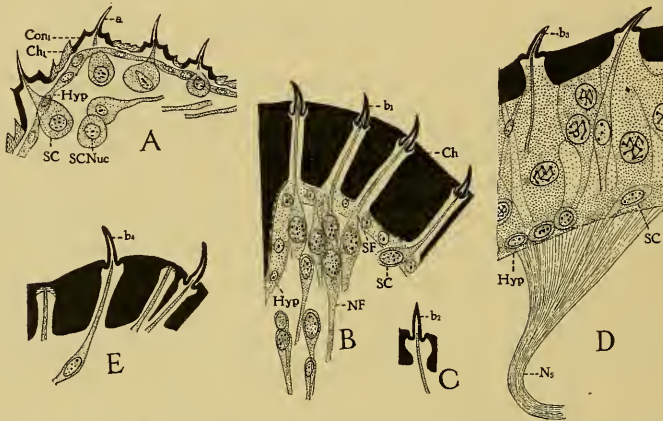


FIG. 1.—Internal anatomy of varieties *a* and *b* of spinelike, innervated hairs of worker honey bees, $\times 580$. A, variety *a* on epipharynx (figs. 9 A and 10, *Ep*). B, C, D and E, variety *b*: b_1 from outer surface at proximal end of mandible (fig. 7, *Md*), b_2 from inner surface at distal end of mandible (fig. 8, *Md*), b_3 from pharyngeal plate (figs. 9 B and 10, *PhPl*), and b_4 from outer surface at tip of mandible (fig. 7, *Md*). C from 17-day-old pupa, B and E from 20-day-old pupæ, and A and D from 21-day-old pupæ. The nerve (*Ns*) in D is taken from a deeper focus than the other parts in the figure. See page 54 for explanation of abbreviations.

At that time he also saw the same pores on the mouth-parts, and since then has seen a few on each antenna near its articulation with the head.

I. STRUCTURE OF THE INNERVATED HAIRS

Innervated hairs may be roughly divided into spinelike and peglike hairs, although there is no sharp dividing line between the two classes. The different varieties of these two classes vary gradually from long, slender hairs to short, stubby ones. For description the varieties may be designated alphabetically.

(a) SPINELIKE HAIRS

Variety a. In describing the spinelike hairs we shall begin with the most delicate ones and then proceed toward the largest, and we shall carefully examine the anatomy of each variety to ascertain if it is anatomically adapted for receiving odor stimuli.

In regard to the thickness of the walls, the most delicate variety is found on the epipharynx (figs. 9 A and 10, *Ep*). These are not typically true hairs, because they do not arise from hair sockets, but from small cones (fig. 1 A, *Con*₁) which, however, might be regarded as another type of sockets. Of all the hairs, these have the thinnest walls. The walls become gradually thinner from the bases to the tips. These hairs are so small and so light in color that they are easily overlooked. Each one arises from the summit of a small cone whose walls are thick and are dark in color, while the chitin (*Ch*₁) between the cones is light in color. Chitin is stained little or not at all with Ehrlich's hematoxylin. Flexible chitin is usually light in color, and when chitin is not flexible it is generally dark in color. For this reason these hairs cannot be bent at their bases but may be bent near their tips; and likewise the cones, which project slightly above the level of the surrounding chitin, are rigid, but since the surrounding chitin is flexible each cone with its hair has considerable freedom of motion.

In most cross-sections through the epipharynx showing these hairs the sense cells are grouped together so closely that each hair seems to be provided with either a multinucleated sense cell or with more than one cell, each having only one nucleus. In extremely thin sections where the sense cells are not piled upon one another, however, it is clearly seen that each hair is innervated by a single sense cell (fig. 1 A, *SC*) having only one nucleus (*SCNuc*). In the 21-day-old pupa the hypodermis (*Hyp*) is comparatively thin.

Wolff (1875) regarded these cones with their hairs as having an olfactory function, and according to their anatomy they are adapted equally as well for gustatory organs, but since chitin after once formed is dead matter and is not porous, it does not seem reasonable to think of either odoriferous particles or liquid foods being able to pass into the hairs in order that the nerves may be stimulated, even if the walls of these hairs are extremely thin.

Variety b. This variety is found on the mandibles (figs. 7, 8, and 6 B, *b*₁, *b*₂ and *b*₄) and on the pharyngeal plate (figs. 9 B and 10, *b*₃). These are short, stout hairs with thick walls. At the proximal end of the mandible (fig. 7, *b*₁) they are usually bent and about a half of each one lies buried in the chitin surrounding the socket (fig. 1 B, *b*₁).

The chitin (*Ch*) at this place is extremely thick, causing the sense fibers (*SF*) to be very long. In all sections passing through this group of hairs the sense cells (*SC*) are discernible, but their fibers are usually severed because an entire cell rarely lies in the same plane in which the section was cut. In the 20-day-old pupa the hypodermis (*Hyp*) is comparatively thin.

On the ventral side of the mandible (fig. 8, *b*₂) these hairs are straight, but have the same structure as the ones just described, except that the sockets (fig. 1 C) are sunk only slightly beneath the outer surface of the chitin.

Those on the pharyngeal plate (fig. 1 D, *b*₃) are slightly larger than the ones just described. These are slightly curved and most of them point toward the mouth. Their sockets stand a little above the level of the chitin, and the walls at their tips are not so thick as at the bases. The sense fibers run nearly all the way to the tips of the hairs. Beneath the pharyngeal plate in the 21-day-old pupæ, the hypodermis (*Hyp*) is extremely thick and its cells are so grouped together that each hair seems to be innervated by a large group of cells, but in all such cases no sense fibers were seen running from the groups to the hairs. After spending considerable time it was ascertained that the sense cells (*SC*) seldom lie in the middle of the hypodermis, but near its inner edge. They are usually cut transversely, and for this reason the fibers are rarely seen connecting with the cell bodies.

The hairs (figs. 1 E and 7, *b*₄) at the distal ends of the mandibles are the longest ones of this variety, and their tips are blunt, while the tips of the others are sharp. In structure they are like those on the ventral side of the mandibles (fig. 1 C, *b*₂), except that they are slightly curved.

Variety c. This variety, found on the head and all the head appendages, varies from the smallest hairs on the antennæ (fig. 2 A) to the largest on the maxillæ (fig. 2 U). Figure 2 A and B represent the smallest and largest on the flagellum of a worker bee, and figure 2 C those on the scape. All of those on the maxillæ are of about the same size (fig. 2 D and E), but when first observed those on the maxillary palpi (fig. 2 E) appear to be the smallest. Those on the labial palpi (fig. 2 F) are slightly larger than those on the maxillæ. Those on the mandibles (fig. 2 G) and paraglossæ (fig. 2 H) are of the same size and are considerably larger than the ones just described. On the cervical plate (fig. 10, *CvPl*) these hairs (fig. 2 I to K) vary considerably in size. Just inside the buccal cavity a few innervated hairs (fig. 2 L) were found; also a few (fig. 2 M) on the head near the

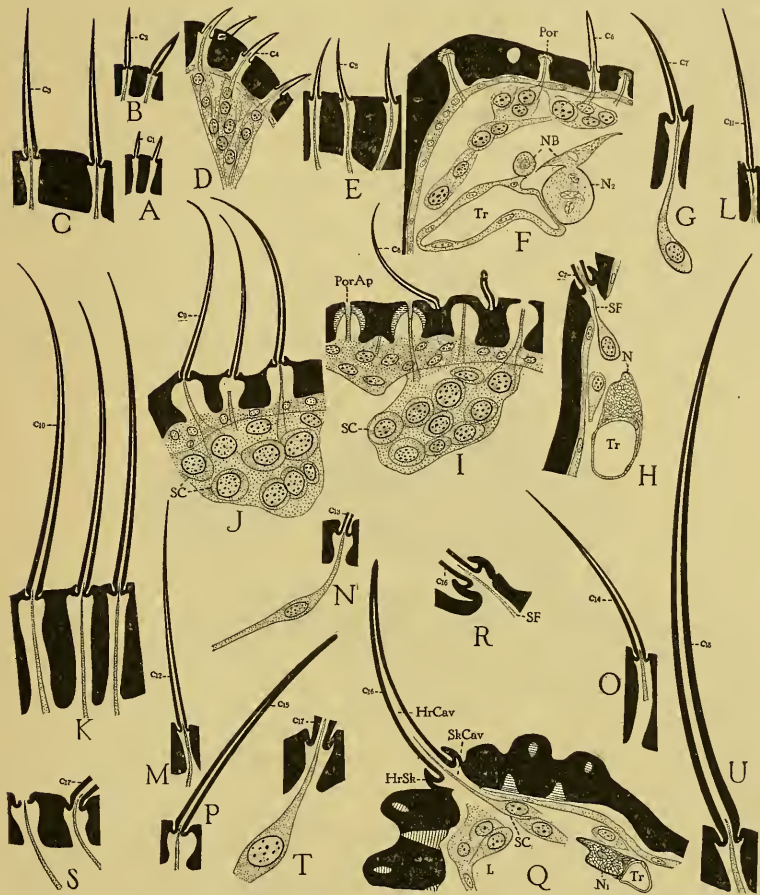


FIG. 2.—Internal anatomy of variety *c* of spinelike, innervated hairs of worker honey bees, $\times 580$. A, smallest and B, largest of these on flagella of antennæ; C from base of scape of flagellum; D from maxilla; E from maxillary palpus; F from labial palpus; G from proximal end of mandible; H from base of paraglossa; I to K from cervical plate; L from just inside buccal cavity; M from side of head, near base of mandible; N from median line on top of head, over pharyngeal plate; O from palpiger; P from side of mentum; Q from middle of glossa, the hair being from a whole mount and the hair socket (*HrSk*) from section; R from tip of glossa; S from dorsal and T from ventral surface of labrum; U from tip of maxilla. All of these hairs, except c_1 to c_3 , may be located by referring to figures 7, 8, 9 C and 10. They were taken from pupa and imago workers of various ages. See page 54 for explanation of abbreviations.

base of the mandibles, and a few (fig. 2 N) on top of the head directly above the pharyngeal plate (fig. 10). The following figures represent the innervated hairs found in sections through the palpigera (figs. 2 O, 7, *Plg*); on the side of the mentum (figs. 2 P, 7, *c*₁₅); on the glossa (fig. 2 Q and R); on the labrum (fig. 2 S and T); and on the labial palpi and maxillæ (fig. 2 U).

In structure these various hairs are all alike in that they have thick walls, sharp points and distinct sockets. The sockets of the smaller hairs usually lie slightly beneath the external surface of the chitin, as shown in figure 2 D, while those of the larger hairs may lie a little beneath the external surface of the chitin, as seen in figure 2 G, or above the surface of the chitin, as shown in figure 2 Q. The chitin connecting the base of the hair with the socket is always more or less

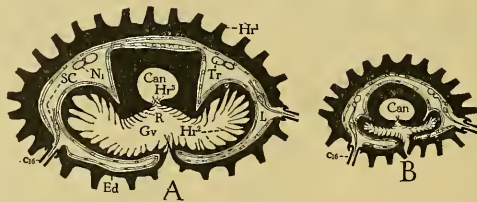


FIG. 3.—Cross-sections through glossa or tongue of a worker honey bee, showing internal anatomy including groove (*Gv*), canal (*Can*) inside rod (*R*), sense cells (*SC*), nerve (*N*₁), trachea (*Tr*); lumen (*L*), and bases of pseudo-hairs (*Hr*¹ to *Hr*²) and innervated hairs (*c*₁₆), x 230. A, through middle and B through tip of glossa.

flexible, so that the least movement of the hair mechanically irritates the end of the sense fiber.

The sense cells belonging to all the hairs drawn were not seen, but the sense fibers were seen as shown. A hair was never regarded a sense organ unless a sense fiber was seen running into it. The sense cells are always spindle-shaped and the sense fibers (fig. 2 H, *SF*) never run far into the hairs.

The hairs at the tip of the tongue of the honey bee (fig. 7, *Gls*) have been regarded as gustatory in function, but as yet no one has ever shown that they are innervated. In cross-sections through the middle of the tongue the sense cells (fig. 2 Q, *SC*) are generally discernible, but owing to the poor fixation only traces of them may be seen in the tip of the tongue, although the sense fibers (fig. 2 R, *SF*) are usually visible. On either side of the tongue a nerve (fig. 2 Q, *N*₁) and a trachea (*Tr*) are always present. They lie side by side and are fastened together with connective tissue. Branches from

the nerve are given off now and then which run toward the sense cells, but the actual connection of them with the cells was not observed. The internal anatomy of the tongue is best understood by referring to the semidiagrammatic figure 3 A and B. Figure 3 A is through the middle of the tongue, while 3 B is through the tip.

(b) PEGLIKE HAIRS

Two varieties of peg-shaped hairs occur on the maxillæ and labial palpi. To compare them with those found on the antennæ, two of the latter have been drawn.

Variety d. Figure 4 A and B represent the smallest and largest pegs seen on the flagellum of a worker bee. The chitin at the tips is about as thick as elsewhere. Other observers state that the chitin at the tips of these hairs is much thinner than elsewhere. This is ap-

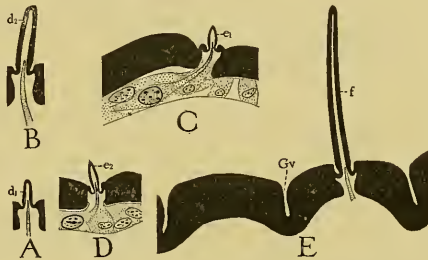


FIG. 4.—Internal anatomy of varieties *d*, *e* and *f* of peglike, innervated hairs of worker honey bees, x 580. A, smallest and B, largest of pegs on flagella of antennæ; C from maxilla; D from labial palpus; E from outer surface near tip of maxilla. These hairs, except *d*₁ and *d*₂, may be located by referring to figures 7 and 8.

parently true when a bright light is used, for the chitin is so nearly transparent at the tip that it appears thinner than where it is darker. When these hairs are carefully observed through the highest lenses and with less light, it is seen that the chitin at their tips is about as thick as at their bases.

Variety e. The peglike hairs on the maxillæ (figs. 4 C, 7 and 8, *e*₁) and labial palpi (4 D and 8, *e*₂) are similar in structure to those on the antennæ. The following slight differences may be pointed out. Those on the mouth-parts are never so large as those on the antennæ. Their tips are less blunt and their sockets project slightly above the surface of the chitin, while the sockets of those on the antennæ lie a little below the external surface of the chitin.

Variety f. These are found on the distal ends of the maxillæ and labial palpi (figs. 7 and 8, *f*). They are long and slender, usually

slightly curved, and have blunt tips (fig. 4 E). The chitin of the distal half of the maxilla contains many long longitudinal and deep grooves (fig. 4 E, *Gv*). These grooves cause the wide maxillary lobe to be quite flexible, thus enabling the bee to fold the maxillæ around the other mouth-parts.

Judging from the anatomy of all the spinelike and peglike hairs described in the preceding pages, it does not seem possible that they can serve either as gustatory or as olfactory organs because the odoriferous particles in the air and the liquids carrying substances in solution could not pass through the hard and thick walls of the hairs to stimulate the ends of the nerves. Since insects cannot feel weak mechanical stimuli through their chitinous integuments without some kind of a sensory organ, it seems that all of these innervated hairs are well adapted to serve as tactile organs. The sense of touch is further discussed on page 39.

2. STRUCTURE OF THE OLFACTORY PORES

Olfactory pores were found on the mandibles (figs. 7 and 8, *Md*, *Por*), maxillæ (fig. 8, *Mx*), labial palpi (fig. 7, *LbPlp*), tongue (fig. 7, *Gls*), side of head, in the buccal cavity, on the cervical plate and on the bases of the scapes of the antennæ. In structure all of these are similar, and they are identical with those which have already been found on the legs, wings and sting.

Figure 5 A represents one of the largest olfactory pores found on the mandibles. The chitin (*Ch*) of the mandibles is always very thick, making the necks (fig. 5 E, *NkFl*) of the small pores long and slender. A chitinous cone (fig. 5 A, *Con*) is always present. In pupæ these cones are usually connected with a hypodermal secretion (*HypS*), but in adults this secretion is never seen. Sometimes this secretion fills the entire pore, and it generally contains streaks running from the hypodermis (*Hyp*) to the cone. Unless all stages of these organs are critically studied, it is easy to imagine that this secretion is a permanent structure of the pores. This explains why Janet (1911) regards this substance as a part of the organ, and why he thinks that the cavity of the pore is filled with two or three concentric cylinders. In studying the same organs in Coleoptera, the writer (1915, p. 422) shows that the cones are a later formation than the chitin surrounding them and that the hypodermal secretion does not begin to form the cones until the sense fibers have connected with the pore apertures. The writer has also shown

that the sense cells begin to differentiate when the hypodermal cells begin to form the chitin. It is thus seen that by the time the chitin is of considerable thickness, the sense fibers have united with the pore apertures and the formation of the cones has begun. There are two possible functions of the cones: (1) to strengthen the chitin forming the bottoms of the flask-shaped pores, and (2) to insure firm attachments for the peripheral ends of the sense fibers. The latter function

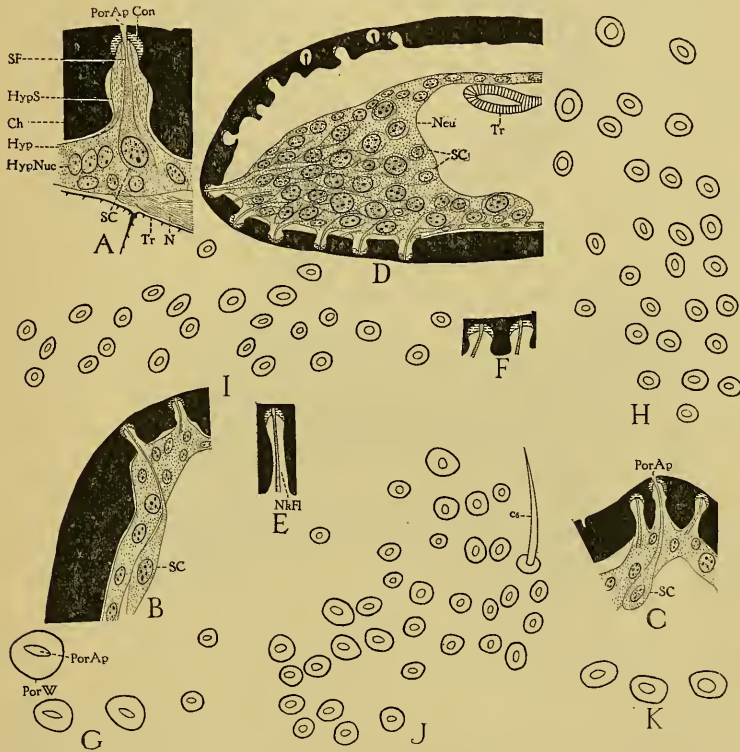


FIG. 5.—Internal anatomy and superficial appearance of olfactory pores on mouth-parts, head and cervical plate of worker honey bees, x 580. A to F, cross-sections; A, one of largest olfactory pores on mandible of a 20-day-old pupa, showing sense cell (SC), pore aperture (PorAp), and hypodermal secretion (HypS) forming the cone (Con); B, two olfactory pores and one sense cell from base of glossa; C, three olfactory pores and one sense cell from mandible; D, a group of olfactory pores and sense cells in labial palpus; E, an olfactory pore from side of head; F, two olfactory pores from buccal cavity; G to K, superficial appearances: G, three of largest olfactory pores on mandible; H, one of the two groups of olfactory pores on base of tongue; I, group of olfactory pores on maxilla; J, group of olfactory pores on labial palpus; K, three of largest olfactory pores on cervical plate. These pores may be located by referring to figures 7, 8, 9 C and 10. See page 54 for explanation of abbreviations.

seems absolutely necessary for the following reason. In adult bees the hypodermis is quite thin and in certain places has practically disappeared. It no longer is firmly fastened to the chitin and it can no longer hold the sense cells in their proper places. If the sense fibers were fastened to the chitin only by the ends of their walls and not by the entire peripheral ends being surrounded by the chitinous cones, the sense fibers would break loose from the pore apertures. Firm attachments for the sense fibers in spiders (McIndoo, 1911) are not necessary, because the sense cells lie in a thick hypodermis which persists throughout the lives of the spiders; and furthermore, cones are not formed, because the pore apertures pass entirely through the cuticula, so that the sense fibers join the apertures on the internal surface of the integument.

The olfactory pores on the base of the tongue (fig. 5 B), maxillæ (fig. 5 C), labial palpi (fig. 5 D), and the smallest on the mandibles, are of about the same size as those on the wings. The spindle-shaped sense cells are easily seen; but owing to the small size of the pores, the pore apertures are rarely discernible. Beneath the group of pores on the labial palpus, the sense cells (fig. 5 D, *SC*) occupy about a half of the space in the appendage. Fig. 5 E and F represent, respectively, the sizes of the pores found on the side of the head near the base of the mandible, and just inside the buccal cavity. A nerve (N_2) and a trachea (fig. 2 F, *Tr*) run near the group of sense cells through the labial palpus. Figure 2 I shows the structure of the largest olfactory pores on the cervical plate. These are equally as large as the largest ones on the mandibles, but the smallest ones are never so small as the smallest on the mandibles.

Under the microscope with transmitted light the olfactory pores appear as bright spots. Each bright spot is surrounded by a dark line, the pore wall (fig. 5 G, *PorW*). Outside this line the chitin is generally dark in color, while inside of it the chitin is almost transparent, and at the center there is an opening, the pore aperture (*PorAp*).

Figure 5 G to K represent, respectively, the sizes of the superficial appearances of the pores on the mandible, tongue, maxilla, labial palpus, and cervical plate.

To learn how well the mandibles are provided with sense organs, the reader is referred to figure 6 A. This is a semidiagrammatic drawing taken from one cross-section through the middle of a mandible of a 20-day-old worker pupa. The details of the hypodermis

(*Hyp*) were taken from another section in which the hypodermal cells were better fixed. Any section through the middle of a mandible invariably shows from two to four large pores, from one to three small pores, and one or more innervated hairs. The nearer the distal end of the mandible a section is taken, the fewer the large pores and

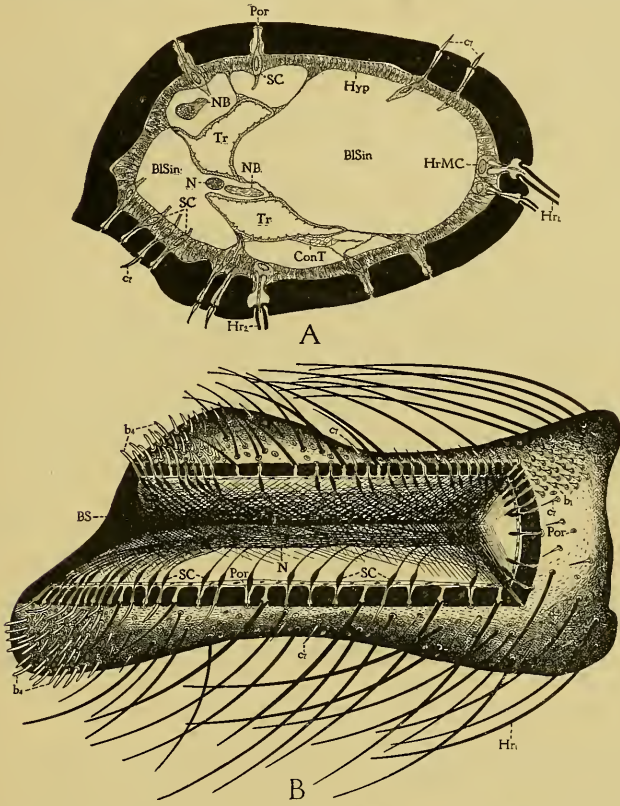


FIG. 6.—Internal anatomy of mandible of a worker honey bee, showing how well this appendage is innervated. A, semidiagram of cross-section through middle of mandible, showing innervation of olfactory pores (*Por*) and tactile hairs (*cr*), blood sinuses (*BISin*), nerve (*N*), nerve branches (*NB*), tracheæ (*Tr*), etc. The details of the hypodermis (*Hyp*) were taken from another section, $\times 185$. B, diagram of transverse-longitudinal view of mandible, showing innervation of olfactory pores (*Por*) and tactile hairs (*b₁*, *b₄* and *cr*), and superficial appearances of these sense organs. The hairs in solid black are not innervated, while all the others are connected with sense cells (*SC*). See page 54 for other abbreviations.

the greater the number of small pores and innervated hairs it shows. Large hypodermal cells, called hair-mother cells (*HrMC*), are often seen beneath the largest hairs on the mandibles. They send processes

into the hairs through which the cellular secretion passes to form the hairs. At first sight these cells resemble sense cells, but a further study shows that they are quite different. The tracheæ (*Tr*) are suspended to the hypodermis by connective tissue (*ConT*) and the nerves (*N*) are suspended to the tracheæ in the same manner. All the space not occupied by the enumerated structures may be called blood sinuses (*BISin*).

A still better idea of how well the mandibles are innervated is gained by referring to figure 6 B. This is a transverse-longitudinal diagram showing the main nerve (*N*) sending off branches to the sense cells (*SC*) belonging to the olfactory pores (*Por*) and the three varieties of innervated hairs (b_1 , b_4 and c_7).

3. DISPOSITION OF THE INNERVATED HAIRS

In the preceding pages the distribution and number of the sense organs on the mouth-parts have been briefly discussed in connection with their anatomy. Now since we have classified these organs on the basis of their structure, their disposition will be given in detail. In counting the number of sense organs herein discussed, five individuals each of workers, queens and drones have been used. Owing to some of the parts being mutilated and concealed, a few of the groups of hairs and olfactory pores could not be counted; so it was necessary to estimate the number in such groups. It was not possible to count all the sense organs on the mandibles on account of the opaqueness and rotundity of these appendages; therefore, only estimates of all the sense organs on the mandibles except variety b_1 of the hairs will be given.

(a) SPINELIKE HAIRS

Variety a. This variety is found only on the epipharynx. The epipharynx is a large three-lobed appendage (fig. 9 A, *Ep*) depending from the roof of the preoral cavity (fig. 10, *Ep*) just in front of the mouth (*Mo*). It is movable up and down and serves to close the mouth opening. These hairs (fig. 9 A, *a*) are arranged in two groups at the base of the epipharynx, a group lying on either side of the high, vertical, keel-shaped median lobe (*K*) of the so-called dorsal tongue. For workers, the number of hairs in a single group varies from 41 to 79; in a pair of groups, from 83 to 147, with an average of 104 hairs for one worker. For queens, the number of hairs in a single group varies from 24 to 92; in a pair of groups, from 55 to 176, with an average of 103 hairs for one queen. For drones, the number of hairs

in a single group varies from 40 to 74; in a pair of groups, from 82 to 134, with an average of 101 hairs for one drone. It is thus seen that each caste possesses virtually the same number of hairs on the epipharynx.

Variety b. Hairs marked b_1 are found only at the proximal end of the mandible on the outer, dorsal corner (fig. 7, b_1). There are about 85 in each group.

Hairs marked b_2 occur only on the inner surface of the mandible, on an elevated ridge (figs. 8 and 10, Rg) just posterior to the biting surface (BS). Each mandible has a single row of these organs, consisting of about five hairs.

Hairs marked b_3 are present only on the pharyngeal plate. This plate is a strong chitinous structure forming the anterior part of the floor of the pharynx (fig. 10, $PhPl$). It has two terminal points (figs. 9 B and 10, TP) hanging downward over the lower rim of the mouth and two long chitinous rods which are attached to the sides of the plate. These rods ($PhPlR$) run around the sides and to the top of the pharynx (Ph), where they are fastened to muscles which in turn are attached to the chitin on the top of the head. The posterior part of the pharyngeal plate is arched upward, forming two large domes, with a deep groove between the domes. The hairs under discussion are grouped on these domes. Some of the hairs point forward, some backward and others toward the roof of the pharynx. The number of hairs in the groups varies only slightly. As an average for workers, there are 90 hairs on a pharyngeal plate; for queens, 74 hairs; and for drones, 66 hairs. It is thus seen that these hairs in the three castes vary considerably in number.

Hairs marked b_4 (fig. 7) are found only on the outer surfaces of the mandibles at the tips. They are arranged irregularly, except that one row follows the contour of the biting edge. The hairs in this row project slightly beyond this edge and often curve over it. There are probably 100 of these hairs on each mandible.

Variety c. Hairs marked c_1 are present on the flagella of the antennæ where there are no pore plates. Those marked c_2 are usually found between the pore plates. Those marked c_3 occur only on the scapes of antennæ.

Only a few hairs marked c_4 (figs. 7 and 8) occur on each maxilla. Twenty-five marked c_5 are found on the base of each maxillary palpus. Only a few marked c_6 are present among the olfactory pores on the inner surface of the labial palpus. About 75 marked c_7 occur on each mandible, the most of them being on the outer surface, and about 40

of the same kind are found at the base of each paraglossa on the dorsal side. About 35 hairs are present on each cervical plate, the most of them being the ones marked c_{10} . This plate is a heavy chitinous structure on the "throat" of the bee (figs. 9 C and 10, *CvPl*), and the writer has called it the "cervical" plate on account of its

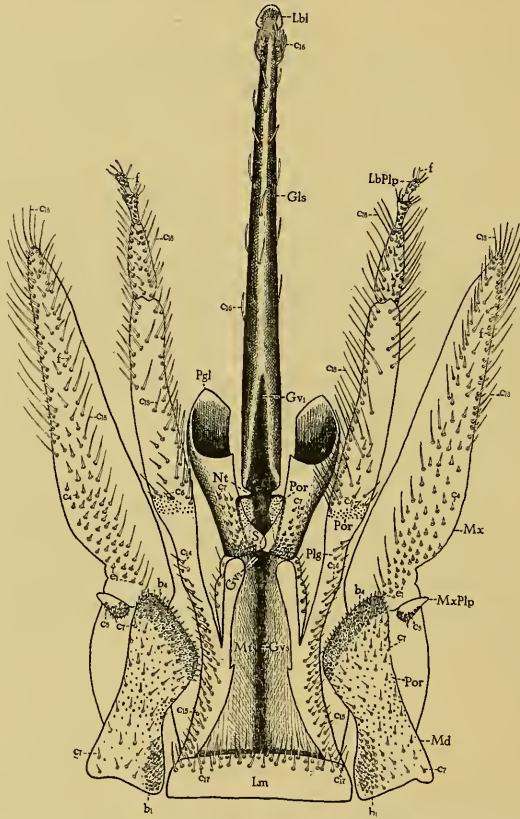


FIG. 7.—Diagram of mouth-parts of a worker honey bee spread out flat, showing disposition of innervated hairs (b_1 , b_2 , c_1 to c_7 , c_{14} to c_{18} , e_1 and f) and olfactory pores (*Por*), on dorsal surfaces of glossa (*Gls*), paraglossa (*Pgl*), palpigers (*Plg*), mentum (*Mt*), and labrum (*Lm*), on inner surfaces of labial palpi (*LbPlp*), and on outer surfaces of maxillæ (*Mx*) and mandibles (*Md*), x 25. All the hairs shown are innervated, and the pseudo-hairs on the glossa have been omitted. See page 54 for other abbreviations.

position. It has two deep folds, in the anterior one (fig. 9 C and 10, *F*) of which may be seen the tactile hairs (c_8 to c_{10}) and olfactory pores (*Por*). A few scattered, innervated hairs were found just inside the buccal cavity, a few on the side of the head and a few on

TABLE VIII
Disposition of Immolated Hairs herein Discussed

Caste	Spine-like Hairs										Peg-like Hairs						
	Variety b				Variety c						Variety e		Variety f on maxillae and labial palpi				
	b ₁ on mandibles	b ₂ on mandibles	b ₃ on pharyngeal plate	b ₄ on mandibles	c ₁ to c ₈ on antennae	c ₄ on maxillae	c ₅ on maxillary palpi	c ₆ on labial palpi	c ₇ on mandibles and paraglossae	c ₈ to c ₁₀ on cervical plate	c ₁₁ to c ₁₃ in buccal cavity; on sides and top of head	c ₁₄ to c ₁₅ on palpi- gerts and mentum		c ₁₆ on glossae	c ₁₇ on labrum	c ₁₈ on maxillae and labial palpi	d ₁ on maxillae
Drone...	101	101	66	200	Many	Few	50	Few	230	35	Few	Several	83	Several	Many	100	Many
Worker...	104	170	90	200	Many	Few	50	Few	230	35	Few	Several	83	Several	Many	100	Many
Queen...	103	170	74	200	Many	Few	50	Few	230	35	Few	Several	83	Several	Many	100	Many

TABLE IX
Disposition of Olfactory Pores herein Discussed and Those previously Found elsewhere on Honey Bee

Caste	Number of pores on wings	Number of pores on legs	Number of pores on sting	Number of pores on mandibles	Number of pores on glossa	Number of pores on labial palpi	Number of pores on maxillae	Number of pores on cervical plate	Number of pores in buccal cavity	Number of pores on sides of head	Number of pores on scapes of antennae	Total number of pores
Drone.....	1998	606	204??	31	46	40	23	Few??	Few??	Few??	2948+
Worker.....	1510	658	100	300?	48	68	56	26	Few	Few	Few	2706+
Queen.....	1310	450	100	210??	32	48	40	24	Few??	Few??	Few??	2214+

top of the head (fig. 10, c_{13}). Several were seen on each palpiger (figs. 7 and 8, c_{14}) and several, marked c_{15} , on the ventral surface and sides of the mentum. Eighty-three hairs marked c_{16} were counted on the tongue. The most of these lie on the ventral side. Several innervated hairs marked c_{17} were seen on each side of the labrum near the anterior edge. All the large hairs marked c_{18} on the maxillæ and labial palpi seem to be innervated.

(b) PEGLIKE HAIRS

Variety d. Those marked d_1 and d_2 are found only on the flagella of the antennæ.

Variety e. Those marked e_1 are found on both sides of the maxillæ near the maxillary palpi. There are perhaps 50 on each maxilla. Only a few marked e_2 are present on the base of each labial palpus.

Variety f. Several marked f occur at the distal end of each maxilla and labial palpus.

In conclusion under this heading it is seen that all the true hairs on the tongue are innervated, while practically all on the maxillæ, labial palpi, palpigers, paraglossæ and mentum are connected with nerves. All of those near the anterior edge of the labrum and all on the mandibles, except two varieties of large hairs (figs. 6 B, Hr_1 and 10, Hr_2), are also connected with sense cells.

Table VIII is a tabulated summary of the disposition of the innervated hairs herein discussed. The blank spaces mean that hairs were not looked for on the appendages recorded.

4. DISPOSITION OF THE OLFACTORY PORES

Olfactory pores (figs. 7 and 8, *Por*) were found irregularly distributed over the entire surface of the mandibles (*Md*), except on the biting surfaces (*BS*) and between the two ridges (*Rg*). Very few occur on the proximal half of this appendage, while they are quite abundant on the distal half. There are at least 150 on each mandible of the workers.

On the tongue (fig. 7, *Gls*) olfactory pores were found only on the dorsal side at the base. These are arranged in two groups, each group being located on a prominence just posterior to the notch (*Nt*). A groove (Gv_2) connecting with the two notches runs between the two prominences and continues as a shallow depression (Gv_3) to the base of the mentum (*Mt*). The number of pores in either group on any given tongue is almost constant, and the individual variations

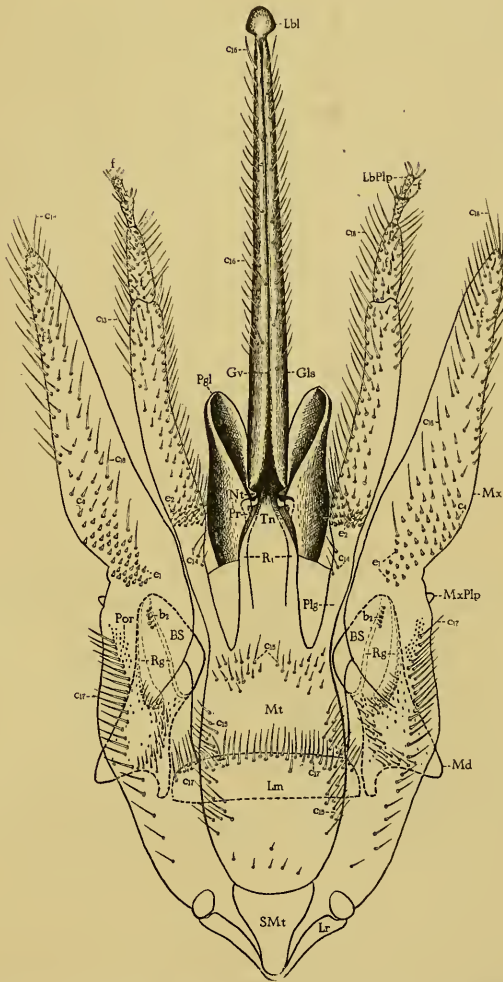


FIG. 8.—Diagram of mouth-parts of a worker honey bee spread out flat, showing disposition of innervated hairs (b_2 , c_4 , c_{14} to c_{18} , e_1 , e_2 , and f) and olfactory pores (*Por*) on ventral surfaces of glossa (*Gls*), palpigers (*Plg*), mentum (*Mt*) and labrum (*Lm*), on outer surfaces of labial palpi (*LbPlp*), and on inner surfaces of maxillæ (*Mx*) and mandibles (*Md*), $\times 25$. The mandibles and labrum are seen by looking through the other appendages. All the hairs shown are innervated, and the pseudo-hairs on the glossa have been omitted. See page 54 for other abbreviations.

are insignificant, but the caste variations are sufficiently large to indicate that queens and drones do not have as strong likes and dislikes for foods as do workers. As an average for workers, there are 48 pores on each tongue; for queens, 32 pores; and for drones, 31 pores.

On the inner surface of each labial palpus (fig. 7, *LbPlp*) a group of olfactory pores (*Por*) extends entirely across the base of this appendage. These groups are always present and the individual variations are slight. As an average for workers, there are 34 pores on each labial palpus; for queens, 24 pores; and for drones, 23 pores.

On the inner surface of each maxilla (fig. 8, *Mx*) near the maxillary palpus (*MxPlp*) there is a group of olfactory pores (*Por*). This group is never absent and the individual variations in number of pores in it are slight. As an average for workers, there are 28 pores on each maxilla; for queens, 20 pores; and for drones, 20 pores.

A group of olfactory pores (figs. 9 C and 10, *Por*) is always present on the cervical plate (*CvPl*). As an average for workers, this group contains 26 pores; for queens, 24 pores; and for drones, 23 pores.

A few olfactory pores were seen in each of the following places: just inside the buccal cavity, on each side of the head, and on the base of the scape of each antenna.

Table IX is a tabulated summary of the disposition of the olfactory pores herein discussed and those previously found elsewhere on the honey bee by the writer. The plus sign, "+," means that there were more than the number recorded. The single question mark, "?," means that the pores were estimated; and the double question mark, "??," means that the numbers recorded were computed by using the ratios of the total number of pores on the other mouth-parts as a basis.

It is thus seen that drones as an average have a few more than 2,948 olfactory pores; workers a few more than 2,766, and queens a few more than 2214 olfactory pores.

In various papers the writer has shown experimentally that the olfactory pores on the legs and wings of hymenopterous and coleopterous insects receive odor stimuli, and it is only reasonable to suppose that the same organs on the mouth-parts perform the same or a similar function, although we have no way of knowing whether the sensation produced is that of smell or that of taste. Judging from the anatomy of the organs, we are inclined to call the sensation smell, but judging merely from the experiments to determine whether

bees have likes and dislikes in regard to foods, the indications are that bees have a sense more or less similar to our sense of taste.

To ascertain whether the elimination of the olfactory pores on the wings would produce any effect upon the ability of bees to discriminate between foods, the wings of 20 workers were pulled off at their articulations. Such an operation eliminates all the sense organs on the wings, and the writer has previously shown that bees without wings behave normally in all respects except that they respond more slowly to odor stimuli. These 20 bees were fed pure cane-sugar candy and cane-sugar candy containing strychnine, as described on page 14. At first a few ate a little of the poisoned candy, but after that not a single bee was seen eating it, but they ate the pure cane-sugar candy normally. This indicates that when the 1500 pores on the wings are prevented from functioning, the remaining 1200 pores found elsewhere on a worker are sufficient to enable the bee to distinguish the candy containing strychnine from the pure candy. These experiments showed that further experimentation along this line was useless.

5. THE TACTILE SENSE OF THE HONEY BEE

Since the innervated hairs herein discussed certainly cannot serve either as olfactory or as gustatory organs, there still remain only two known senses which we might consider in connection with these hairs. (1) An auditory function has never been attributed to any of these hairs, but similar hairs on spiders have been called auditory hairs. We need not consider the sense of hearing further. (2) The tactile sense seems to be the most plausible function to attribute to them, although no experiments were performed to test this view.

If we call these innervated hairs tactile hairs, we can easily explain many of the activities of bees. Since bees are covered with a hard chitinous integument, a person often wonders how it is possible that they can perform their many duties of caring for the brood, building comb, etc., unless they have an acute sense of touch. They certainly cannot feel weak mechanical stimuli through the integument as we do through the skin, and for this reason various kinds of hairs have become innervated.

Instead of the innervated hairs on the tongue being gustatory in function, they are certainly used chiefly in examining food as to whether it is solid or liquid. If the food should be solid and must be dissolved before being eaten, these hairs perceive stimuli which cause a copious flow of saliva. If the food should be a solid and

not to be dissolved, it is first probably examined by the maxillæ and labial palpi before being seized by the mandibles. By means of the many sense hairs covering the mandibles, these appendages are able at any moment to perceive the size, shape and firmness of the food; and when the food particles are sufficiently small to be swallowed, they are placed upon the dorsal side of the mentum (fig. 7, *Mt*). While watching a bee eat, it is easily observed by using a pair of binoculars that the mentum (fig. 10, *Mt*) may be moved in three directions. The forward and backward movement is most noticeable. The second movement is up and down and the third is a sidewise

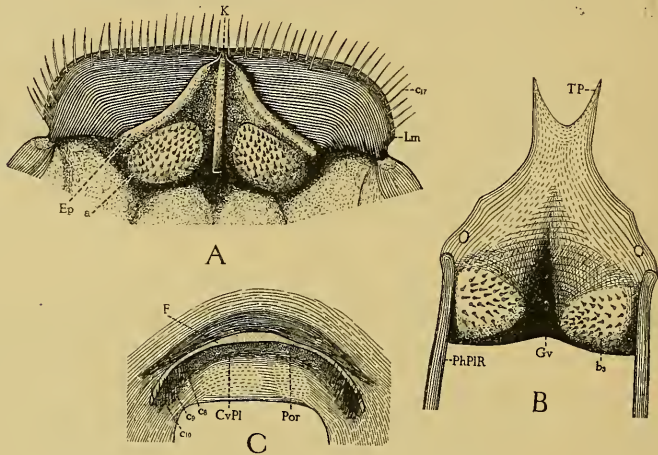


FIG. 9.—Superficial appearances of the innervated hairs (*a*, *c*₁₇, *b*₃, *c*₈ to *c*₁₀) on the epipharynx, labrum, pharyngeal plate and cervical plate, and of the olfactory pores (*Por*) on the cervical plate of worker honey bees. A, ventral surfaces of labrum (*Lm*) and epipharynx (*Ep*), showing two groups of variety *a* of innervated hairs on prominences at base of epipharynx, x 45. B, inner surface of pharyngeal plate, spread out flat, showing two groups of variety *b* of innervated hairs (*b*₃) on dome-shaped prominences at posterior end of this plate, x 45. C, outer surface of cervical plate (*CvPl*), spread out flat, showing a group of variety *c* of innervated hairs (*c*₈ to *c*₁₀) on either side of this plate with a long group of olfactory pores (*Por*) between them, x 50. For other abbreviations see page 54.

one. The mentum, including the appendages attached to it, acts like a small crane which may be moved backward and forward, up and down, and from side to side to a limited degree. The mentum is moved forward when the food particles are to be conveyed from the mandibles to the mouth. After these particles have been placed upon the mentum posterior to the paraglossæ, the mentum is moved backward and upward through the buccal cavity (*BCav*) until the particles are at the mouth opening (*Mo*). The tactile hairs inside

this cavity may be stimulated by the particles touching them, thereby informing the bee that the food is ready to be swallowed. The presence of the food in the mouth is made known to the bee by means of the hairs on the epipharynx (*Ep*) coming in contact with it. The act of swallowing is facilitated by means of the epipharynx pushing the food into the mouth. This act is explained by the fact that the fleshy-like epipharynx may be moved up and down by a set of longitudinal muscles (M_3), and it is also capable of completely closing the mouth opening by the longitudinal (M_3) and transverse muscles (M_{10}) working in unison.

Should a particle of food, too large to pass through the narrow œsophagus (fig. 10, *E*), be swallowed, it would be stopped when it reached the hairs (b_3) on the pharyngeal plate (*PhPl*) by means of the transverse muscles (M_{10}) contracting, thereby forcing it to the exterior. It is thus seen that the hairs on the pharyngeal plate act as a safety device to prevent pieces of solid food, too large to go through the œsophagus, from passing into the pharynx (*Ph*).

The tactile hairs on the maxillæ and labial palpi are of the utmost importance to workers while caring for the brood and in examining the comb, etc. The hairs marked b_4 on the mandibles perhaps play their greatest rôle while these appendages are being used for building comb. Regarding these as tactile hairs, it is easy to understand how bees are able to mold the walls of all the cells of uniform thickness.

6. HOW BEES EAT LIQUID FOODS

While watching a bee eat honey under a simple microscope, it will be observed that the maxillæ remain almost stationary while the mentum, carrying the tongue, paraglossæ and labial palpi, is being moved forward and backward, up and down through the buccal cavity between the maxillary bases as if the honey were being either pumped or sucked up into the mouth. It is now generally believed that liquid foods pass up the glossa or tongue by capillary attraction and are then sucked into the mouth. This view seems to be the only plausible one, and after completely understanding this method it is seen that Nature could not have devised a better plan. If a bee ate only liquid foods, a proboscis connecting directly with the mouth would be a better apparatus, but we well know that bees eat more or less of solid food in the form of pollen.

As a typical example to serve all purposes, let us suppose that a bee is about to eat candy containing a small amount of quinine, and let us suppose that the bee cannot smell the quinine in the candy.

The bee probably first recognizes the candy as food by smelling it before touching it. After smelling the candy the first reaction of the bee is to move toward it, to extend the tongue and to examine the food with the sense hairs on the tip of the tongue. The extending of the mentum (fig. 10, *Mt*) is accomplished by muscles not shown in figure 10. The tongue is unfolded from beneath the mentum by the contraction of a pair of muscles (M_2), attached to a pair of hard chitinous processes (*Pr*). The tongue is folded beneath the mentum by means of two muscles (fig. 10, M_1) pulling on a pair of chitinous rods (R_1) which are the two forks of the chitinous rod (*R*) extending the full length of the glossa through the center. When the tongue is extended and as quickly as the bee recognizes that the food must be dissolved, the salivary syringe (*SS*) forces its supply of saliva to the exterior, at the point marked *S* in figures 7 and 10. The saliva runs forward along the groove between the two groups of olfactory pores (fig. 7, *Por*) and passes around the notches (*Nt*) to the ventral side of the tongue, where it enters the proximal end of the groove (fig. 8, *Gv*) which extends the full length of the glossa. The extreme proximal end of the groove is wide and shallow, and at this place there is no distinction between the groove (fig. 3 A, *Gv*) proper and the canal (*Can*) formed by the rod (*R*). Not far from the notches the wide groove becomes narrow and deep and the canal is distinctly separated from the groove. A portion of the ventral surface of the mentum extends as a fleshy tongue (fig. 8, *Tn*) along the roof and through the center of the wide groove. The end of this tongue terminates where the canal is separated from the groove. Now the saliva, in traveling from the external opening of the salivary syringe on the dorsal side of the tongue to the ventral side of the tongue by capillary attraction, is guided into the canal by means of the fleshy tongue just described. From this place to the tip of the tongue the canal is completely separated from the groove by minute interlocking pseudo-hairs (fig. 3 A, *Hr^s*) which point toward the tip of the tongue. According to the law of capillarity the saliva, aided by the pseudo-hairs, passes through the canal as rapidly as oil climbs a wick. The saliva, after reaching the tip of the tongue, spreads over the surface of the spoon-shaped labellum (fig. 8, *Lbl*) which is used for scraping the candy. The scraping and changing of the sugar to liquid is facilitated by the many forked pseudo-hairs on the labellum. When the food is dissolved, it enters the groove at the tip of the tongue, passes through the entire length of the groove to the base of the tongue, where it then passes through the notches to the dorsal side of the tongue and

then along the groove (fig. 7, *Gv*₂) to the place marked *X* on the dorsal surface of the mentum (fig. 10).

While eating honey and syrup greedily, the distal half of the groove may be opened widely to the exterior so that the liquid may enter more rapidly. Since there are no muscles in the glossa, the only way to explain the opening of the groove is by supposing that the blood rushes

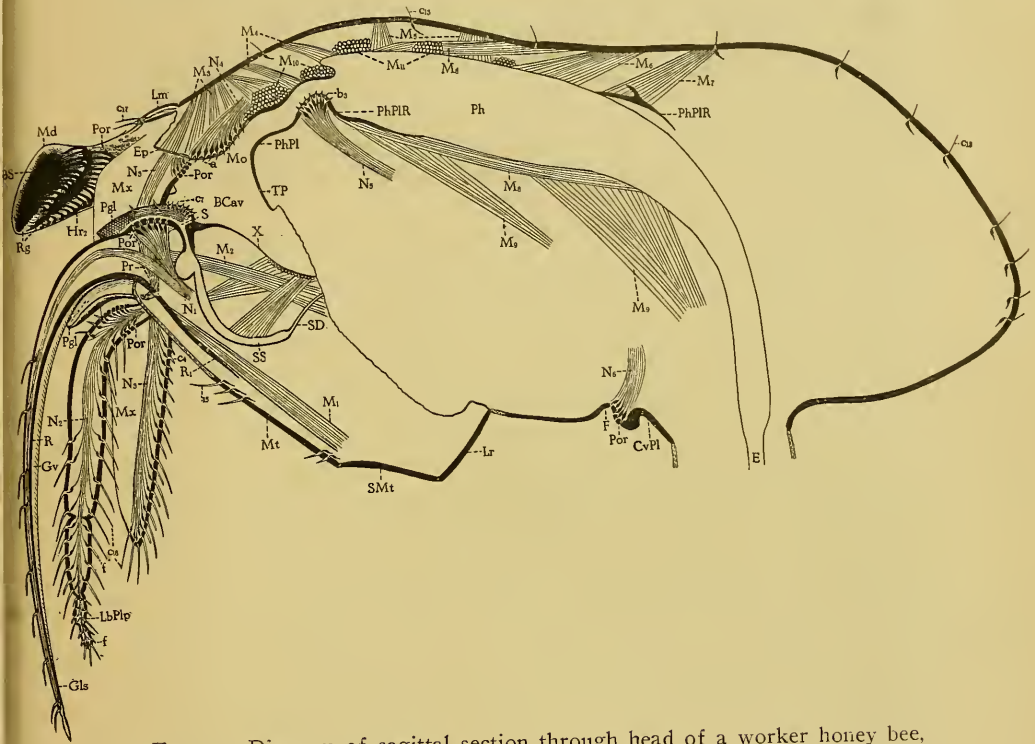


FIG. 10.—Diagram of sagittal section through head of a worker honey bee, slightly lateral to median line of head, pharyngeal plate (*PhPl*), epipharynx (*Ep*), labrum (*Lm*), cervical plate (*CvPl*), mentum (*Mt*), paraglossa (*Pgl*), and glossa (*Gls*). Diagrams of longitudinal sections of maxilla (*Mx*) and labial palpus (*LbPlp*), and of inner surface of right mandible (*Md*), are drawn in their approximate positions. This diagram is meant to show chiefly innervation of glossa by nerve marked *N*₁, labial palpus by nerve marked *N*₂, maxilla by nerve marked *N*₃, epipharynx by nerve marked *N*₄, pharyngeal plate by nerve marked *N*₅ and cervical plate by nerve marked *N*₆, and to show how foods are swallowed when elevated to mouth (*Mo*) at point marked *X* on mentum (*Mt*) by means of various combinations of contracting and relaxing of muscles (*M*₂ to *M*₁₁) attached to epipharynx, pharyngeal plate and walls of pharynx. Muscles marked *M*₁ and *M*₂ fold and unfold glossa respectively. For other abbreviations see page 54.

into this part of the tongue and the edges of the groove (fig. 3 *A*, *Ed*) are widely separated by blood-pressure. In sections the rod (*R*) is often everted to the outside of the tongue.

According to the law of capillarity the height to which a liquid rises in a tube varies inversely with the diameter of the tube. In other words, the smaller the tube the higher a liquid rises in it. Using a tube four times as long as the glossa and with the diameter equal to that of the average diameter of the groove in the glossa, water would rise to the top of the tube merely by capillary attraction. This demonstrates that liquids quickly pass through the groove, and the movement of them is increased by the aid of the many pseudo-hairs (fig. 3 A, Hr^2) lining the groove and by some of them interlocking at the extreme edges of the groove to exclude the outside air. These hairs point toward the base of the tongue, making the groove as capable of carrying liquids as a wick is of lifting oil from the bottom of a tall bottle.

At the proximal end of the groove the liquid is turned to either side of the glossa by the fleshy tongue (fig. 8, Tn), and is prevented from traveling further on the ventral side of the mentum by the shoulder which is formed by the two chitinous processes (Pr) projecting below the ventral surface of the glossa. The shallow groove (fig. 7, Gv_1) on top of the tongue probably serves to hold the excess of liquid when it has difficulty in following its proper course.

As soon as saliva mixes with the food, a chemical or physical change is effected, and this change perhaps liberates odors that were not smelled by the bee before the food was eaten. Again, the saliva might so affect the quinine in the food described on page 14 that the faintest odor imaginable could be detected by the pores on the base of the tongue, and also probably by those on the labial palpi and maxillæ. It must be remembered that while the liquids are passing from the ventral side to the dorsal side of the tongue, and *vice versa*, the paraglossæ close around the tongue, making a perfect tube, and the labial palpi close tightly against the paraglossæ, and the maxillary lobes are folded around all of these appendages. It is thus seen that the olfactory pores on the glossa, labial palpi and maxillæ are almost against the liquid as it passes to the base of the mentum, for, as already pointed out, the pores on the labial palpi and maxillæ lie on the inner surfaces of these appendages.

This closes the description of the rôle played by capillary attraction in carrying liquids from the tip of the tongue to the base of the mentum. The entire process is clear to the writer except where the saliva and liquid food pass around the base of the tongue. It is strange that both liquids can travel in opposite directions along the same route by no force other than capillarity. This is partially

elucidated by the fact that the paraglossæ, in closing tightly around the base of the tongue, make a perfect tube which connects the groove on the ventral side of the glossa with the one on the dorsal side of the same appendage, and perhaps most of the liquid food is sucked into the mouth from the cavity formed by the paraglossæ.

We are now ready to explain how the liquid is sucked into the mouth. Cross-sections through the head of the bee show that the pharynx (fig. 10, *Ph*) assumes various shapes, but the shape shown in figure 10 is the most typical. Just posterior to the hairs (b_3) on the pharyngeal plate, it expands into a large, saclike body, while its posterior end gradually becomes smaller and is called the œsophagus (*E*) where it enters the thorax. The walls of the alimentary tract, from the mouth to the honey stomach, were examined to see if they contain sense organs, but none was found other than those already described. Nerves running to the cervical plate (N_6), pharyngeal plate (N_5) and the epipharynx (N_4) were seen, but no other nerves were observed connected with the pharynx, although several muscles were traced from the pharynx to their places of attachment. A study of these muscles shows that the pharynx may be moved in at least six different ways as follows: Muscles marked M_4 pull it forward; M_5 , upward; M_6 and M_7 , upward and backward; M_8 , directly backward; M_9 , downward and backward; and M_{10} and M_{11} change the diameter of it. It will be seen that M_7 is attached to the pharyngeal plate rod (*PhPIR*) and M_8 is fastened to the pharyngeal plate. The contraction of either one of these muscles would enlarge the tube leading from the mouth to the pharynx. From the preceding description it is easily understood that by various combinations of these muscles the pharynx works like a powerful pump, and when the liquid food on the dorsal surface of the mentum is raised to the mouth opening, the suction from the pharynx draws it into the mouth as easily as a person draws into his mouth water held in the palm of the hand.

7. SUMMARY OF SENSE ORGANS

Only two general types of sense organs were found on the mouth-parts of the honey bee. They are innervated hairs and innervated pores, called olfactory pores by the writer (1914a). Judging from their anatomy, the innervated hairs can serve only as tactile organs, and none of them are anatomically adapted to function either as olfactory organs or as gustatory organs. The writer has divided them into spinelike and peglike hairs. Both types vary considerably in size and structure. In size the spinelike hairs vary from the smallest

ones on the antennæ to the largest ones on the maxillæ and labial palpi; the peglike hairs, from the short and thick ones on the maxillæ to the saber-shaped ones on the labial palpi and maxillæ. The spine-like hairs were found on all the mouth-parts, pharyngeal plate, antennæ, in the buccal cavity, all over the head and on the cervical plate. The peglike hairs were observed only on the antennæ, maxillæ and labial palpi.

Judging from the disposition and innervation of the hairs under discussion, the tactile sense in the honey bee is highly developed. The application of this perception easily explains how bees are able to perform their many duties, such as caring for the brood, building comb, etc.

The act of eating liquid foods is accomplished by capillary attraction, and by the pumping force of the pharynx.

Olfactory pores were found at the bases of the tongue and labial palpi, on the maxillæ near the maxillary palpi, widely distributed over the mandibles, on the cervical plate, in the buccal cavity, on the sides of the head and on the scapes of the antennæ. Their structure is identical with that of the olfactory pores on the legs, wings and sting, and therefore their function should be the same.

DISCUSSION OF LITERATURE

A review of the literature pertaining to the sense organs on the mouth-parts and to the gustatory sense of insects shows so much confusion in regard to the names of the various sense organs and their probable functions that it is impossible to classify the various structures correctly. The present writer has separated all the sense organs on the mouth-parts of the honey bee into olfactory pores and innervated or tactile hairs, the latter group being divided into spinelike and peglike hairs. Other writers have called the hairs setæ, pegs, cones, bristles, or just "hairs," and the few who have seen the olfactory pores have called them taste-pits, taste-cups, taste-papillæ or beaker-shaped organs, etc. Let us consider the olfactory pores first.

Meinert (1861) seems to be the first to suggest that insects have gustatory organs. He described a row of chitinous canals on the maxillæ and base of the tongue of ants. He thought they were innervated and might serve as gustatory organs. Forel (1873) saw the same or similar structures on the maxillæ and tongue of *Formica*, and he called them gustatory papillæ.

Wolff (1875) first described the olfactory pores on the base of the tongue of the honey bee. He called them taste-beakers in analogy

to the gustatory organs at the base of our tongues, and he thought that the secretion of the salivary glands, always present inside the glossal covering, kept the beakers constantly moist and gustatory stimuli were effected by the saliva changing the honey which passes through the groove in the glossa.

Joseph (1877) saw taste-pits on the bases of the tongues of specimens belonging to nearly all the insect orders, and especially on those of plant-eating insects.

Kraepelin (1883) thought that he found gustatory organs on the proboscides of flies. These were seen on the inner surface of the cushion of the labellum. From his description they may be the same as the olfactory pores under discussion.

Will (1885) described the olfactory pores on the tongue, maxillæ and labial palpi of the honey bee and various other insects in much the same manner as depicted by the present writer. He called them beaker-shaped organs and imagined that they receive gustatory stimuli because the peripheral ends of their nerves come in direct contact with the food. He saw two groups of them on the base of each tongue, and the number of organs in each group varies as follows: *Apis* (worker), about 25; *Osmia*, 14 to 16; *Bombus*, 20 to 24; and Ichneumonidæ, 12 to 14. About 40 organs were seen in each group on the maxillæ of the Apidæ, but very few in the Tenthredinidæ. Will failed to understand the internal anatomy of these organs. He thought the sense cells are multinucleated and that their sense fibers pierce the thin membranes covering the beakers in order to come in contact with the external air.

Breithaupt (1886) describes the pits or pores found on the base of the tongue of the honey bee. Being unable to make thin sections through these organs, he constructed a schematic drawing of a single pore which shows the sense fiber of the spindle-shaped sense cell running to the extremely thin and transparent membrane which covers the pore.

Vom Rath (1886) seems to have found organs similar to the olfactory pores in the labium of millipedes (*Chilognatha*). Each organ is porelike and is two-thirds filled with a pear-shaped bundle of nerve fibrillæ which pass through the fine pore aperture and come in contact with the external air. The same author (1887, 1888) seems to have seen the same organs on the palpi of beetles.

Janet (1904) found a constant group of olfactory pores on each labial palpus, two rows on the tongue, and some on the pharynx of ants. Those seen by him on the pharynx perhaps really lie on the

cervical plate, as already described by the present writer, because either in sections or in whole mounts of the integuments of the heads it is often difficult to determine whether the pores lie on the pharyngeal plate or on the cervical plate. Janet (1911) saw the same organs widely distributed over the integument of the mandibles of the honey bee. According to him, all the pores, whether on the mouth-parts or on the legs, have a similar structure, and they resemble the structure of the olfactory pores described by the present writer; 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. Janet thinks that 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. He imagines that they are special olfactory organs, but different from the olfactory organs on the antennæ. In regard to those on the mandibles, he believes that they aid in building comb and in collecting pollen and propolis.

Hochreuther (1912) found a few olfactory pores 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 and many on the legs of *Dytiscus marginalis*. He called them dome-shaped organs and describes and gives drawings of them in a manner somewhat similar to that of Janet.

We shall now discuss the innervated hairs only briefly, because, as already pointed out, they probably serve neither as olfactory organs nor as gustatory organs.

Wolff (1875) was the first to describe the hairs on the epipharynx. In the honey bee he described each organ as a small cone with a pit in the summit bearing a small hair. He thought that each hair is connected with a sense cell group and that these organs receive olfactory stimuli.

Künkel and Gazagnaire (1881) found innervated hairs on the paraglossæ, on the epipharynx and on the pharyngeal plate of Diptera. They imagined that these hairs receive gustatory stimuli.

Becker (1882) found sense hairs on the ventral side of the labrum of certain Diptera. He believed that they serve as gustatory organs.

Haller (1882) says that the small hairs and pegs on the dorsal side of the labium of *Hydrodroma rubra* probably serve as gustatory organs.

Kraepelin (1882, 1883) attributes a gustatory or olfactory function to certain innervated hairs on the proboscides of Hymenoptera and Diptera.

Kirbach (1883) calls certain small hairs in Lepidoptera gustatory papillæ.

Briant (1884) regards the innervated hairs on the tongue of the bee as merely tactile organs and not as gustatory structures as generally believed.

Sommer (1885) found innervated hairs on the legs, palpi, labrum and labium of *Macrotoma plumbea* (Thysanura), but he says nothing about their function.

Will (1885) gives a drawing of a hair from the tip of the tongue of *Vespa*, but none from *Apis* nor *Bombus*. The sense cell is multinucleated, and the sense fiber stops in the base of the hair, whose walls are thick.

Breithaupt (1886) described papillæ with very short hairs on the mouth-parts of *Bombus*. He thinks that some serve as gustatory organs while others serve as tactile organs, the function being determined by the location of the hairs.

Gazagnaire (1886) says that the gustatory organs in Coleoptera should be found in the buccal cavity in the form of hairs.

Vom Rath (1887, 1888, 1894, 1896) has made a comprehensive study of the morphology of all kinds of hairs on the mouth-parts belonging to various insect orders. All his drawings are good, and each sense hair, peg or cone is usually innervated with a sense cell group, but sometimes with a single sense cell.

Reuter (1888) describes cone-shaped sense hairs on the palpi of Lepidoptera. These are connected with sense cell groups.

Packard (1889, 1903) studied the epipharynx in various insect orders. He almost invariably found hairlike sense organs on each epipharynx examined. These organs are setæ associated with sense pits, cups and rods. Packard seems to think that some of the setæ are used merely to guard the sense cups while the others aid the sense cups in receiving gustatory stimuli.

Nagel (1892, 1894, 1897) has made a special study of the morphology of the olfactory and gustatory organs of insects. He divides

the organs receiving gustatory stimuli into inner gustatory organs and outer ones. The inner ones found inside the buccal cavity are located on the epipharynx as minute pit-pegs or cones. The outer ones are found outside the buccal cavity on the various mouth-parts. They are cones and pit-pegs of various sizes and shapes.

Röhler (1906) found various kinds of sense hairs on the mouth-parts of the grasshopper, *Tryxalis*. He thinks that some of these serve mechanically to examine the food, while the others function as gustatory organs.

The following is a brief discussion of the experimental work pertaining to the sense of taste.

Forel (1873, 1908) was apparently the first to determine experimentally that insects show preferences between foods. When morphine and strychnine are mixed with honey, he says that ants do not at first recognize these substances by smell, but after eating a little honey containing these substances, they immediately leave it. Ants do not always know how to distinguish foods containing injurious substances, because when he fed them honey containing phosphorus, they gorged themselves with it and many of them soon died. In repeating the experiments of Plateau (1885) and Will (1885), Forel amputated the antennæ and the four palpi of several wasps. When he fed them honey containing quinine, they soon left it after eating a little of it, but greedily ate pure honey not containing quinine. From this he concludes that the gustatory faculty is independent of the antennæ and palpi, and that it resides in the mouth. He agrees with Plateau and Will that the amputation of the palpi in no way modifies the olfactory, gustatory or masticatory faculties. He thinks that the palpi serve as special tactile organs.

Will (1885) carried on a series of experiments to demonstrate the sense of taste in insects. He ascertained that wasps, bees, and bumblebees soon leave foods containing alum, quinine, and salt after eating a little of them. He thinks that the gustatory perception lasts a rather long time, because insects, after eating foods containing these substances, clean their mouths for several minutes and then, when given pure honey, "taste" it several times before definitely beginning to eat. As a general rule, Will found that the larvæ are more "difficult to please" in the choice of their foods than the imago insects.

Lubbock (1899) noticed that some individual ants seem to possess a finer sense of taste than others, and he thinks this is partially explained by the fact that the number of taste-pits is not the same in all individuals. He concludes "that the organs of taste in insects are

certain modified hairs situated either in the mouth itself or on the organs immediately surrounding it." "But though the lower animals undoubtedly possess the sense of taste, it does not, of course, follow that substances taste to them as they do to us. I have found by experiment that sugar and saccharine, which are so similar to us, taste very differently to ants and bees."

In conclusion under this heading, the results obtained by the preceding authors are less satisfactory in explaining that insects have a true gustatory sense than the results obtained by the present author in showing that insects do not have a true gustatory sense, because the preceding authors have found no organs anatomically adapted for receiving gustatory stimuli. Even if the antennæ are amputated, the olfactory organs are not eliminated, because olfactory pores are widely distributed over the integument, and for this reason the olfactory sense cannot be eliminated while testing for the sense of taste. The present writer's opinion is that insects do not have a sense of taste, because their highly developed olfactory organs are sufficiently capable of receiving the odors, however weak, from any and all substances. Whenever the odors are extremely weak, it is then necessary for the insects to eat a little of the foods containing the undesirable substances before being able to smell these substances. For this reason the present writer has called this faculty an olfactory-gustatory sense, although according to the definition of the sense of taste in vertebrates the gustatory perception plays no part in the responses.

GENERAL DISCUSSION

The present writer, and the few other authors who have fed insects foods containing undesirable substances, have observed that the insects sooner or later refuse such foods after eating more or less of them. Judging from this behavior, the other authors have concluded that insects can taste, regardless of knowing whether or not they have sense organs, anatomically adapted for receiving gustatory stimuli, and without considering the rôle played by the olfactory sense in these responses. As Parker has already said for vertebrates, and as we well know for ourselves, it is almost impossible to determine whether we taste or smell certain substances when we eat them. To us sometimes a food, before being eaten, emits only a faint odor or no odor at all; but when we eat it, we perceive a pronounced odor. In such a case the odorous particles are not given off until the food is taken into the mouth and mixed with saliva. The same principle is certainly applicable when bees eat candies which contain undesirable

substances emitting extremely weak odors. As quickly as the saliva has dissolved the candy and has had time to effect a chemical or physical change, the odorous particles are given off, and since the olfactory pores on the mouth-parts are nearest the food, they are the first ones to receive the odorous particles. For this reason the so-called gustatory sense in insects is only a phase of the olfactory sense.

That we cannot smell certain substances is no proof that insects cannot smell them, for the many experiments performed by the present writer during the past four years cause him to believe that the olfactory sense in the honey bee is much more highly developed than ours.

It is reasonable to think that many foods and chemicals emit odors, although we may not be able to perceive all of them; but judging from the experiments herein discussed, it is not impossible for bees to discriminate between them better than we can. If they are not able to do this without eating them, only a few "tastes" are necessary to demonstrate their preferences. In a few instances the present writer was not able to discriminate differences between candies containing certain chemicals by using both senses of smell and taste, but the bees were able to distinguish marked differences. It therefore seems evident that this faculty in the honey bee is more highly developed than in man.

In all probability bees have no other means of chemically discriminating between foods than by smelling them, because no sense organs were found connected with the alimentary tract between the pharyngeal plate and the honey stomach, and because the innervated hairs described are not anatomically adapted for this purpose. The walls of the alimentary canal certainly cannot serve such a function except when corrosive or caustic substances are eaten.

After once refusing foods which contain undesirable substances emitting weak odors, bees seem to know these foods and seldom eat any more of them unless forced to partake of them by the removal of the foods they like better.

In conclusion it may be said that the olfactory sense in the honey bee is highly developed and that it serves as an olfactory and gustatory perception combined.

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ABBREVIATIONS

avariety <i>a</i> of innervated hairs
b ₁ to b ₄variety <i>b</i> of innervated hairs
c ₁ to c ₁₈variety <i>c</i> of innervated hairs
d ₁ and d ₂variety <i>d</i> of innervated hairs
e ₁ and e ₂variety <i>e</i> of innervated hairs
fvariety <i>f</i> of innervated hairs
BCavbuccal cavity
BSinblood sinus
BSbiting surface of mandible
Cancanal in rod of glossa
Chchitin
Ch ₁flexible chitin
Concone of olfactory pore
Con ₁cone of innervated hair on epipharynx
ConTconnective tissue
CvPlcervical plate
Eesophagus
Ededge of groove on glossa
Epepipharynx
Ffold in cervical plate
Glsglossa, tongue or proboscis
Gv, Gv ₁ to Gv ₃	...groove
Hr ₁ and Hr ₂non-innervated hairs on mandible
Hr ¹ to Hr ³pseudo-hairs on glossa
HrCavhair cavity
HrMChair-mother cell
HrSkhair socket
Hyphypodermis
HypNuchypodermal nucleus
HypShypodermal secretion

K	keel-shaped lobe of epipharynx
L	lumen
Lbl	labellum of glossa
LbPlp	labial palpus
Lm	labrum
Lr	lorum
M ₁ to M ₁₁	muscles
Md	mandible
Mo	mouth
Mt	mentum
Mx	maxilla
MxPlp	maxillary palpus
N, N ₁ to N ₆	nerves
NB	nerve branch
Neu	neurilemma
NF	nerve fiber
NkFl	neck of flask-shaped pore
Nt	notch at base of glossa
Pgl	paraglossa
Ph	pharynx
PhPl	pharyngeal plate
PhPIR	pharyngeal plate rod
Plg	palpiger
Por	olfactory pore
PorAp	olfactory pore aperture
PorW	olfactory pore wall
Pr	chitinous process in base of glossa
R	rod in glossa
R ₁	fork of rod in glossa
Rg	ridge on inner side of mandible
S	external opening of salivary syringe
SC	sense cell
SCNuc	sense cell nucleus
SD	salivary duct
SF	sense fiber
SkCav	cavity in hair socket
SMt	submentum
SS	salivary syringe
Tn	fleshy tongue on ventral surface of mentum
TP	terminal tip of pharyngeal plate
Tr	trachea
X	place on dorsal surface of mentum to which liquid foods perhaps travel before being swallowed