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THE OLFACTORY SENSE OF LEPIDOPTEROUS LARVÆ.

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INTRODUCTION.

A thorough investigation of the above subject will undoubtedly throw some light upon how plants attract insects, because as yet no one has shown experimentally that lepidopterous larvæ can smell and the olfactory organs have never been described. Whenever it is proved that insect larvæ respond to chemical stimuli, and whenever organs suitable for the reception of these stimuli have been found, then we can intelligently ask why do the cotton caterpillar (*Alabama argillacea* Hübr.) and cotton boll weevil (*Anthonomus grandis* Boh.) feed exclusively on the cotton plant?; or why does the silkworm (*Bombyx mori* L.) feed almost exclusively on mulberry-tree leaves?. Many more similar examples could be given by any entomologist, but why is it that some larvæ are very selective in regard to their food while others show little or no preference between members of a large list of plants. Also, how does a female lepidopteron distinguish the best or only suitable host plant for her progeny so that she can deposit her eggs on this particular plant? The only plausible answer for all of these questions is to suppose that plants, as well as animals, emit odors, and that insects in searching for food, either for themselves or for their young progeny, are guided by the odors emitted by the plants. In order that the odors of plants may differ, it may also be assumed that the various chemical constituents of plants emit particular odors and that the odor emitted from a plant may be a combination of all the odors from the various constituents, or possibly one odor might be so strong that it masks all the others.

Upon this hypothesis, the odors from plants would vary according to the number, combination and quantitative percentages of the various constituents. Reasoning along this line of thought, we may be able to explain why a few insects have only one host plant; why many have a preferred host plant, but will eat other allied plants; and why others eat a large number of plants. If we could positively answer the above questions, we might be able to devise practical methods for the control of certain insects, as by trap baits, etc.

The present investigation will show that lepidopterous larvæ respond to chemical stimuli and that they have organs suitable for receiving these stimuli; and the following review of the literature will indicate how insects are attracted by certain host plants.

Verschaffelt (1910), experimenting with the cabbage-butterfly larvæ, *Pieris brassicæ* and *P. rapæ*, found that they are very fond of the cultivated species of the Cruciferæ and that in captivity they ate leaves from 15 indigenous species, representing 14 genera, of the same family. They did not eat all of these species, however, equally readily, and refused to eat species belonging to 17 other families, but did attack *Tropæolum* and *Reseda* which belong to two other families. Chemists have determined that all of the plants eaten by the above larvæ contain mustard oils. To determine whether these larvæ could be induced to eat leaves not ordinarily attacked, leaves of *Apios tuberosa* were smeared with the juice from the leaves of a crucifer (*Bunias orientalis*); these leaves were at once attacked and in a short time devoured. Wheat flour and corn starch, which when dry or moistened with water are rejected by both *Pieris-larvæ*, are eaten with avidity when soaked with *Bunias*-juice. The larvæ behave in a similar manner toward filter paper saturated with *Bunias*-juice.

To ascertain the exact constituent in the plants and juices which attracted the larvæ, Verschaffelt wet leaves of *Apios tuberosa* and *Rosa* (two species not containing mustard oil) with a fairly strong solution of pure sinigrin (potassium myronate), the glucoside of black mustard; these leaves were eagerly eaten by the larvæ. He says: "It is clear that *Pieris*-caterpillars seek out various mustard oils, just like the various glucosides derived from them. They are clearly attracted by the whole group of substances."

RESPONSE TO CHEMICAL STIMULI.

While feeding silkworms it is easy to determine that they can smell; this is done by placing fresh mulberry-tree leaves near them so that they can neither see nor touch the leaves; immediately the silkworms move their heads, work their mouth parts and begin crawling toward the leaves, and sometimes a hungry silkworm for several minutes will follow a leaf dragged slowly just in front of its head and the writer believes that the larva is guided solely by means of the odors emitted from the leaf rather than by seeing the leaf. Silkworms may also be induced to eat other leaves which they will not ordinarily even "taste." This was proved by the following test: Leaves from peach trees, cherry trees, plum trees, and apple trees were dipped into the juice from mulberry-tree leaves and were then fed wet to silkworms; all of these leaves were eaten, although some of them apparently were not really relished. When other leaves of the same trees were dipped into water, the silkworms did not even "taste" them.

To test the responses to other chemical stimuli the various larvæ used were confined in small observation cases and the sources of the odors were usually kept in small vials which were held directly beneath the larva in the case. The following larvæ were used in the experiments: Tent caterpillars, fall webworms, tussock-moth larvæ, army worms and larvæ of a butterfly (*Papilio polyxenes*). The following sources of odors were employed and the average reaction time of the above larvæ to them are: Oil of peppermint, 14.6 seconds; oil of thyme, 9.5 seconds; oil of wintergreen, 17.6 seconds; dried leaves of pennyroyal, 20.1 seconds; dried leaves of spearmint, 22.9 seconds; wild cherry-tree leaves, 42.5 seconds; fresh grass, 19.1 seconds, old honey and comb, 51.5 seconds; protruded thoracic glands of above Papilio larvæ, 22.8 seconds; and as a control—a clean and empty vial, 60 seconds (totally negative). The details pertaining to these experiments are as follows:

In each set of experiments 10 larvæ were used, one larva being confined in a case. As a rule, the more the larvæ were handled the more satisfactorily they responded to odors, but generally speaking these larvæ were the most unfavorable insects that the writer has ever used for testing the responses to odors. When placed in the experimental cases, all of them,

except the army worms, had the habit of crawling into the corners and lying there more or less dormant and in such a position would never respond to odors; therefore, before testing a larva it was first necessary to see that it was lying flat on the bottom of the case, and in order to insure, if possible, a response to another odor after an interval of 15 minutes, it was usually touched with a pencil to "awaken it from its stupor." Caterpillars in their webs rarely responded to the odors used. The following records include only the first responses and their reaction times.

MEDIUM SIZED TENT CATERPILLARS (*Malacosoma americana* Fab.).

Oil of peppermint:
6 moved head slightly. 1 raised head and crawled away.
1 moved away slowly. 1 moved head and worked mouth parts.
1 raised head quickly.
Reaction time 3 to 15 seconds, average 7.5 seconds.

Oil of thyme:
6 moved head slightly. 1 raised head and moved away slowly.
3 moved away slowly.
Reaction time 3 to 15 seconds, average 5.4 seconds.

Oil of wintergreen:
5 moved head slightly. 2 raised head and moved away slowly.
2 showed no response. 1 moved away slowly.
Reaction time 4 to 60 seconds, average 20.6 seconds. In all cases 60 seconds was regarded totally negative.

Dried leaves of pennyroyal:
5 moved away slowly. 1 moved head sidewise.
3 moved head slightly. 1 showed no response.
Reaction time 3 to 60 seconds, average 22.2 seconds.

Dried leaves of spearmint (odor very weak):
5 showed no response. 2 moved head slightly.
2 moved away slowly. 1 moved leg back and forth.
Reaction time 5 to 60 seconds, average 38.3 seconds.

Wild cherry tree leaves cut into small pieces (their favorite food):
4 showed no response. 1 moved away slowly.
4 moved head slightly. 1 raised head slowly.
Reaction time 5 to 60 seconds, average 42.5 seconds.

Old honey and comb (odor very faint):
6 showed no response. 4 moved head slightly.
Reaction time 20 to 60 seconds, average 51.5 seconds.

Empty and odorless vial (used as a control):
10 showed no response.

SMALL FALL WEBWORMS (*Hyphantria cunea* Dru.)

Oil of peppermint:
3 moved slightly. 1 moved head sidewise.
2 raised head and thorax quickly. 1 turned around.
2 worked mouth parts. 1 raised head.
Reaction time 2 to 40 seconds, average 11.8 seconds.

Oil of thyme:
4 raised head quickly. 1 moved away quickly.
3 moved head and worked mouth parts. 1 raised thorax quickly.
1 moved slightly.
Reaction time 2 to 10 seconds, average 4.5 seconds.

Oil of wintergreen:
3 moved head slightly. 1 worked mouth parts.
2 raised head quickly. 1 moved head sidewise.
2 moved away quickly. 1 raised head and thorax slowly.
Reaction time 2 to 30 seconds, average 7.5 seconds.

Dried leaves of pennyroyal:
5 moved slightly. 1 moved head slightly.
2 raised head and thorax slowly. 1 moved head and thorax sidewise and bit wire-screen bottom of case.
1 moved away slowly.
Reaction time 2 to 25 seconds, average 7.4 seconds.

Dried leaves of spearmint (odor very weak):
4 moved slightly. 2 moved away quickly.
2 raised head quickly. 1 moved head slightly.
1 moved slightly.
Reaction time 3 to 15 seconds, average 6.4 seconds.

LARGE TUSSOCK-MOTH LARVAE (*Hemerocampa leucostigma* S. and A.)

Oil of peppermint:
6 moved slightly. 1 showed no response.
2 moved away. 1 raised head and thorax quickly.
Reaction time 2 to 60 seconds, average 17.3 seconds.

Oil of thyme:
8 moved slightly. 1 showed no response.
1 raised head.
Reaction time 2 to 60 seconds, average 13.1 seconds.

Oil of wintergreen:
3 raised head. 1 moved head sidewise.
2 moved slightly. 1 moved away slowly.
2 jerked head backward. 1 showed no response.
Reaction time 2 to 60 seconds, average 16.3 seconds.

Dried leaves of pennyroyal:
4 moved away slowly. 2 raised head.
3 moved slightly. 1 showed no response.
Reaction time 2 to 60 seconds, average 23.2 seconds.

Dried leaves of spearmint (odor very weak):
6 moved away. 2 showed no response.
2 moved slightly.
Reaction time 5 to 60 seconds, average 30 seconds.

Protruded thoracic glands of larvæ (*Papilio polyxenes*).
5 moved slightly. 2 showed no response.
2 moved away slowly. 1 raised head.
Reaction time 2 to 60 seconds, average 22.8 seconds.

LARGE ARMY WORMS (*Cirphis unipuncta* Haw.)

Oil of peppermint:
5 raised head quickly. 3 raised head quickly and waved it sidewise.
2 raised head slowly.
Reaction time 2 to 5 seconds, average 2.9 seconds.

Oil of thyme:
4 raised head quickly and moved sidewise. 3 raised head quickly.
3 raised head slowly.
Reaction time 2 to 5 seconds, average 2.5 seconds.

Oil of wintergreen:
5 raised head quickly and moved it sidewise.
2 raised head quickly and moved backward.
2 raised head slowly.
1 raised head quickly.
Reaction time 2 to 10 seconds, average 2.9 seconds.

Dried leaves of pennyroyal:
8 raised head slowly.
1 raised head quickly.
1 moved away slowly.
Reaction time 2 to 10 seconds, average 4.2 seconds.

Dried leaves of spearmint (odor very weak):
6 raised head slowly.
3 raised head quickly.
1 raised head slowly and waved it sidewise.
Reaction time 2 to 4 seconds, average 2.7 seconds.

Fresh grass in vial (food of these larvæ):
2 raised head slowly.
2 moved slightly.
2 showed no response.
2 moved backward slowly.
1 moved forward quickly.
1 raised head and bit screen-wire bottom of case.
Reaction time 2 to 60 seconds, average 19.1 seconds.

BUTTERFLY LARVAE (*Papilio polyxenes* Fab.)

Oil of peppermint:
5 raised head.
5 showed no response.
Reaction time 3 to 60 seconds, average 33.2 seconds.

Oil of thyme:
5 raised head.
2 moved quickly.
2 showed no response.
1 moved caudal end of body.
Reaction time 2 to 60 seconds, average 22.1 seconds.

Oil of wintergreen:
5 moved slightly.
5 showed no response.
Reaction time 7 to 60 seconds, average 40.7 seconds.

Dried leaves of pennyroyal:
4 showed no response.
3 raised head.
3 moved slightly.
Reaction time 10 to 60 seconds, average 43.5 seconds.

Dried leaves of spearmint (odor very weak):
5 showed no response.
3 raised head.
2 moved slightly.
Reaction time 3 to 60 seconds, average 37.3 seconds.

In comparing the preceding reaction times, no conclusion can be drawn in regard to the comparative sensitiveness of the five species tested, because the responses depended more on the behavior of the larva tested than on its ability to perceive chemical stimuli. Of the five species used, only the army worms were favorable for experimental purposes; these were usually active, never failed to respond when tested, and the responses were generally quick and pronounced ones. Of the five species used, the butterfly larvæ were the most sluggish and their reaction times are the slowest of all.

MORPHOLOGY OF OLFACTORY PORES OR PUNCTURES.

The preceding pages show that lepidopterous larvæ respond to chemical stimuli, and the following pages will show that these larvæ have organs suitable for the reception of chemical stimuli, but no experiments were performed to determine the function of these organs which were first called olfactory pores by the writer (1914a). The same type of organs seems to be common to all adult insects and the writer has proved experimentally that they receive chemical stimuli in Hymenoptera (1914b) and Coleoptera (1915). They have also proved to be common to all of the coleopterous and lepidopterous larvæ yet examined by the writer, and now for several years systematists have known them in lepidopterous larvæ as "punctures." The writer (1918) has recently described the external and internal anatomy of them in a coleopterous larva of the 'fig-eater,' *Allorhina* (*Cotinis*) *nitida* L.

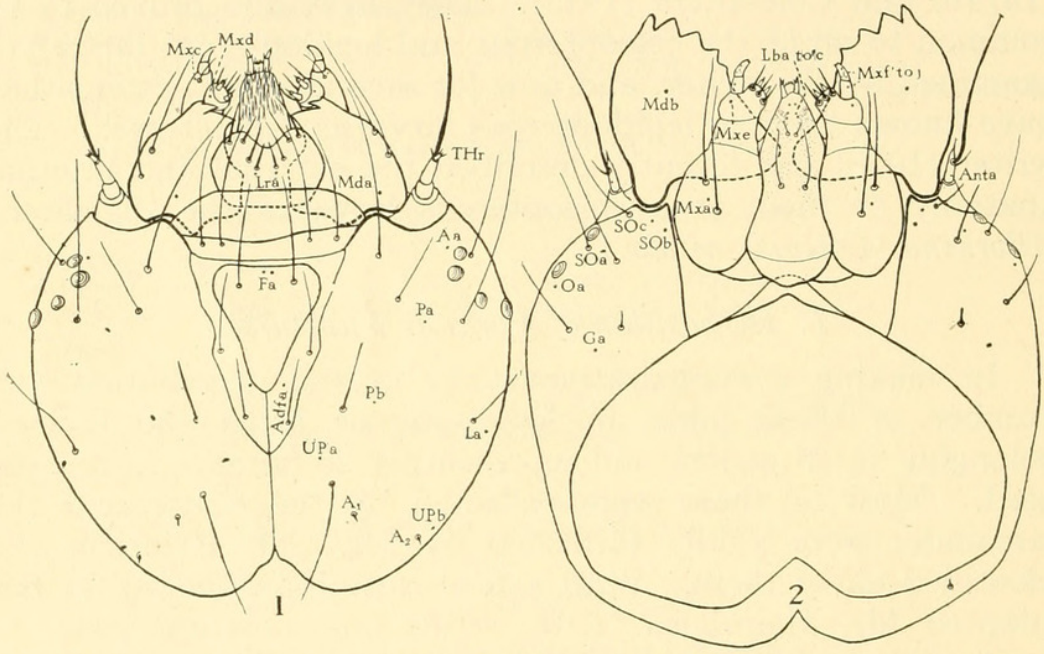
1. Disposition of Pores or Punctures.

In making a comparative study of the distribution and number of these pores in lepidopterous larvæ, 30 species, belonging to 28 genera and representing 20 families have been used. Most of these were collected by the writer and the remainder were kindly furnished by Mr. Carl Heinrich who identified all of them. With a few exceptions, the writer has adopted Mr. Heinrich's (1916, 1918) nomenclature given to most of the punctures present on the head capsule and at the suggestions of Messrs. Heinrich and Busck he has formulated new names for those pores not already named. The various parts of the anatomy on which these pores occur were verified by Dr. Adam Böving; the three foregoing mentioned men also belong to the Bureau of Entomology.

In most cases only one specimen of each species was examined, and consequently, owing to unfavorable mounts and the lack of sufficient material, the total number of pores recorded can not be regarded as accurate. Since the army worm was the most favorable material at hand, several specimens of it were treated with caustic potash and the pores on it have been studied and drawn in detail.

The description of them will be given first and then will follow a brief account of those in other species.

Army Worm: Upon examining the head capsules of lepidopterous larvæ under a low-power lens, several minute circular light spots were seen; these spots resemble hair sockets from which the hairs have been removed, but former studies dealing with similar spots at once suggested that they might be the olfactory pores, so common to adult insects and coleopterous larvæ. Upon examining them under a high-power lens, it was soon observed that their external anatomy is different from that of hair sockets and sections through them proved that they are really olfactory pores.



FIGS. 1 AND 2.—Disposition of the pores or punctures and setæ on the head of a small army worm (*Cirphis unipuncta* Haw.), only the pores being here named, × 20. Fig. 1, dorsal view and Fig. 2, ventral view. Frontal pore (*Fa*); adfrontal pore (*Adfa*); anterior pore (*Aa*); posterior pores *a* (*Pa*) and *b* (*Pb*); lateral pore (*La*); ultraposterior pores *a* (*UPa*) and *b* (*UPb*); labral pore (*Lra*); mandibular pores *a* (*Mda*) and *b* (*Mdb*); maxillary pores *a* (*Mxa*), *c* (*Mxc*), *d* (*Mxd*), *e* (*Mxe*), and *f* to *j* (*Mxf* to *j*); labial pores *a* to *c* (*Lba* to *c*); antennal pore (*Anta*); genal pore (*Ga*); ocellar pore (*Oa*); subocellar pores *a* (*SOa*), *b* (*SOb*) and *c* (*SOc*); secondary setæ (A_1 and A_2); and Nagel's so-called olfactory pegs on antennæ (*THr*).

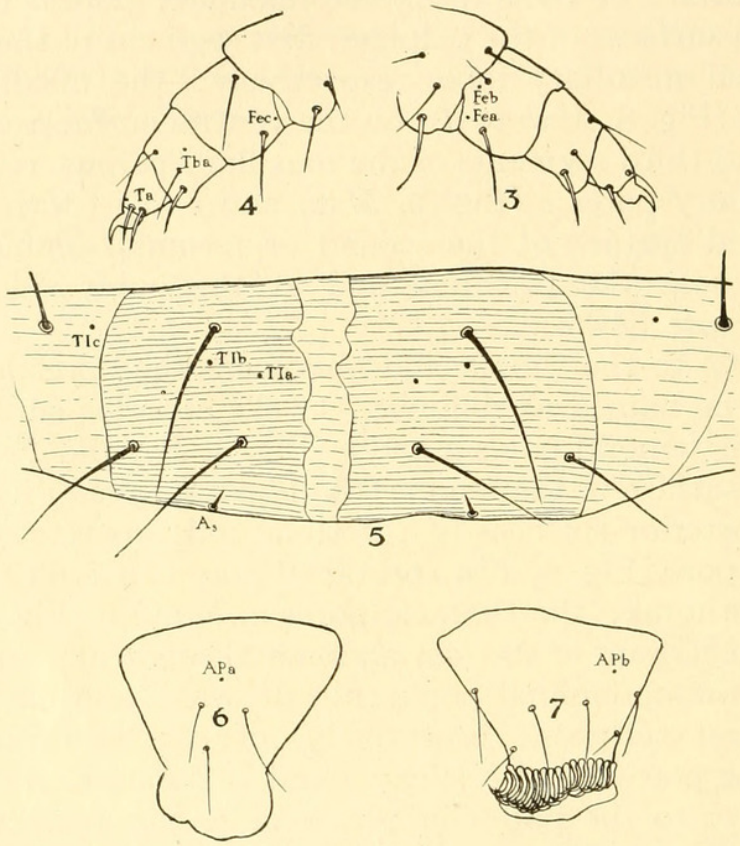
Referring to Figures 1 and 2, it is seen that they are always paired and they are located and named as follows: On the front: the frontal pore (*Fa*); on the adfrontal piece: the adfrontal pore (*Adfa*); on the dorsal sureface of the epicranium: the anterior pore (*Aa*), posterior pores *a* (*Pa*) and *b* (*Pb*), lateral pore (*La*), and ultraposterior pores *a* (*UPa*) and *b* (*UPb*); on the ventral surface of the epicranium: the genal pore (*Ga*),

ocellar pore (*Oa*), and subcellar pores *a* (*SOa*), *b* (*SOb*) and *c* (*SOc*); on the dorsal and ventral surfaces, respectively, of the mandible: the mandibular pores *a* (*Mda*) and *b* (*Mdb*); on the ventral surface of the labium: the labial pores *a*, *b* and *c* (*Lba* to *c*); and on the dorsal surface of the labrum: the labral pore (*Lra*). Relative to the maxilla they are as follows: On the ventral surface of the stipes: the maxillary pore *a* (*Mxa*); on the dorsal surfaces of the palpiger, first segment of the maxillary palpus and maxillary lobe, respectively: the maxillary pores *b*, *c* and *d* (Fig. 8, *Mxb* to *d*); on the ventral surfaces of the first, second and third segments of the maxillary palpus, respectively: the maxillary pores *e* (Fig. 2, *Mxe*) and *f* to *j* (*Mxf* to *j*). On the ventral surface of the second or terminal segment of the antenna, near the proximal end at the outer side, lies the antennal pore (*Anta*).

Relative to the thorax and abdomen, the pores are located and may be named as follows: On the anterior surface of the femur: the femoral pores *a* and *b* (Fig. 3, *Fea* and *Feb*); on the posterior surface of the femur: the femoral pore *c* (Fig. 4, *Fec*); on the posterior surfaces of the tibia and tarsus, respectively: the tibial pore (Fig. 4, *Tba* and tarsal pore (*Ta*); on the tergum of the prothorax: the thoracic pores *a*, *b* and c (Fig. 5, *TIa* to *c*); on the tergum of the last abdominal segment: a single pair of pores, the abdominal pores (not drawn); and on the dorsal and ventral surfaces, respectively, of the anal proleg: the anal-proleg pores *a* and *b* (Figs. 6 and 7, *APa* and *APb*).

Relative to the pores on the head of the army worm, the subocellar pores (Fig. 2, *SOb* and *SOc*) and mandibular ones (*Mdb*) are the most difficult to be found. While the former lie in almost transparent chitin, the latter one lies in very dark chitin; all of these, as well as the pair (Fig. 1, *Mda*) on the dorsal side of the mandibles, seem to have been overlooked by other observers. The ultraposterior ones (Fig. 1, *UPa* and *UPb*) are easily mistaken for the secondary setæ (A_1 and A_2) and can only be distinguished from them by aid of a high-power lens. Perhaps all of the pores on the labium and maxillæ have been seen by systematists, but it seems that the third labial pair (Figs. 2 and 20, *Lbc*), and maxillary pores *b*, *g* to *j* (Figs. 8 and 9, *Mxb*, *g* to *j*) have never been drawn. As far as known to the writer, those on the legs, last abdominal segment and on the anal prolegs are here reported for the first time.

The location and total number of the pores on various parts of the army worm are as follows: front, 2; adfrontal piece, 2; epicranium, 22; antennæ, 2; mandibles, 4; labium, 6; labrum, 2; maxillæ, 20; trochanters, 18; tibiæ, 6; tarsi, 6; prothorax, 6; last abdominal segment, 2; and anal prolegs, 4; making 102 pores in all.



FIGS. 3 TO 7.—Disposition of pores or punctures on leg, first thoracic segment and on anal proleg of a small army worm, × 20. Figs. 3 and 4, anterior and posterior surfaces, respectively, of left prothoracic leg. Fig. 5, most of tergum of prothorax; the shield or strongly pigmented stripes are more heavily shaded than are the lightly pigmented portions. Figs. 6 and 7, dorsal and ventral surfaces, respectively, of same anal proleg. Femoral pores *a* (*Fea*), *b* (*Feb*) and *c* (*Fec*); tibial pore (*Tba*); tarsal pore (*Ta*); thoracic pores *a* (*TIa*), *b* (*TIb*) and *c TIc*); anal-proleg pores *a* (*APa*) and *b* (*APb*); and secondary seta (A_3).

Other species. The integuments of other species examined were not studied as critically as were those of the army worm, and consequently, some of the pores have certainly been overlooked, particularly the ones most difficult to be found. Some of the preparations had to be bleached with chlorine gas before they could be studied, but most of them were so light in color that it was difficult to find some of the pores, and the butterfly

larvæ were the least favorable of all, owing to their almost total lack of pigment and to the fact that the hairs on the epicranium arise from large tubercles.

The following table gives the larger variations concerning the disposition of these pores and now the smaller variations may be briefly stated. For sake of brevity, instead of using the long scientific names of the larvæ examined, the species will be numbered from 1 to 30, and those interested in associating the names of the species with the variations described may do so by referring to the names and numbers of the species in the table on page 76. For each of the 30 species examined, the pores are constant in number on the following parts of the integument: Front, 2; each antenna, 1; each stipes, 1; each maxillary lobe, 1; each second segment of the maxillary palpus, 1; and each third or terminal segment of the maxillary palpus, 4. The number of pores found on the epicranium (including the adfrontal piece) varies as follows: On each of 14 species, 10 pores (Nos. 1, 3, 6, 10, 12, 14, 16–18, 21, 24, 25, 29, 30); on each of 4 species, 12 pores (Nos. 2, 4, 5, 22); on each of 9 species, 14 pores (Nos. 9, 11, 13, 15, 19, 20, 23, 27, 28); on each of 2 species, 18 pores (Nos. 7, 26); and on 1 species, 24 pores (No. 8, the army worm).

If all of the pores on each epicranium had been found, perhaps 20 would be a common number for nearly all of the species. One pore was found on each mandible of 29 species, but had this appendage been examined more carefully two pores might have been found on each mandible as already shown for the army worm. The number of pores found on the labium varies as follows: On each of 12 species, 4 pores (Nos. 1, 12, 13, 15–21, 23, 26); and on each of 18 species, 6 pores (Nos. 2–11, 14, 22, 24, 25, 27–30). The number of pores found on the labrum varies as follows: On each of 5 species, 2 pores (Nos. 7–10, 16); on each of 11 species, 4 pores (Nos. 6, 11, 14, 17–19, 21, 23, 25–27); and on each of 14 species, 6 pores (Nos. 1–5, 12, 13, 15, 20, 22, 24, 28–30). The first segment of each maxillary palpus has 1 pore, except 2 were found on each one of 4 species (Nos. 3–5, 8). Three pores were found on each femur, except 2 on each one of 10 species (Nos. 14, 15, 17–19, 21, 22, 24, 25, 29). One pore was found on each tibia, except 2 pores on each of 1 tibia of 2 species (Nos. 9, 14) and 3 pores on 1 tibia of 1 species (No. 30). One pore was found on each tarsus, except

TABLE I.

Disposition of the pores or punctured found on *lepidopterous larvæ.*

Family and Number and Name of Species	Number of Pores on					Total No. of pores found
	Head		Thorax		Abdomen	
	Head capsule	Head appendages	Legs	First thoracic segment	Last segment and anal prolegs	
SPHINGIDÆ—						
1. *Phlegothontius sexta* Joh	12	30	30	...	...	72
2. *Ceratomia catalpæ* Bvd	14	32	30	...	...	76
SATURNIIDÆ—						
3. *Antomeris io* Fab	12	36	30	...	...	78
ARCTIIDÆ—						
4. *Hyphantria cunea* Dru	14	34	30	...	...	78
NOCTUIDÆ—						
5. *Apatela(Acronycta)americana*Harr	14	34	30	...	1	79
6. *Prodenia ornithogalli* Guen	12	30	30	...	...	72
7. *Feltia* sp	20	28	30	6	2	86
8. *Cirphis unipuncta* Haw	26	34	30	6	6	102
NOTODONTIDÆ—						
9. *Datana integerrima* G. & R	16	28	31	3	...	78
10. *Datana ministra* Dru	12	28	30	2	...	72
LIPARIDÆ—						
11. *Hemerocampa leucostigma* S.& A.	16	30	30	...	...	76
LASICAMPIDÆ—						
12. *Malacosoma americana* Fab	12	30	30	2	2	76
BOMBYCIDÆ—						
13. *Bombyx mori* L	16	30	30	...	3	79
GEOMETRIDÆ—						
14. *Alsophila pometaria* Harr	12	30	19	...	...	61
PSYCHIDÆ—						
15. *Thyridopteryx ephemeræformis* Haw	16	30	18	...	...	64
COCHLIDIIDÆ—						
16. *Sibine stimulea* Clem	12	26	30	...	...	68
MEGALOPYGIDÆ—						
17. *Lagoa crispata* Pack	12	28	24	...	...	64
18. *Megalopyge opercularis* S. & A.	12	28	24	...	...	64
ZYGÆNIDÆ—						
19. *Harrisina americana* Guér-Mén.	16	28	24	...	...	68
PYRALIDÆ—						
20. *Diatræa saccharalis* Fab	16	30	30	4	...	80
21. *Achroia grisella* Fab	12	28	24	...	...	64
22. *Dioryctria abeitella* D. & S	14	32	24	4	1	75
OLETHREUTIDÆ—						
23. *Laspeyresia pomonella* L	16	28	30	3	1	78
24. *Laspeyresia molesta* Busck	12	32	24	2	...	70
YPONOMEUTIDÆ—						
25. *Atteva aurea* Fitch	12	30	24	...	...	66
GELECHIIDÆ—						
26. *Pectinophora gossypiella* Saund.	20	28	30	2	...	80
BLASTOBASIDÆ—						
27. *Valentinia glandulella* Riley	16	30	30	2	...	78
PAPILIONIDÆ—						
28. *Papilio polyxenes* L	16	32	30	...	...	78
PIERIDÆ—						
29. *Pontia rapæ* L	12	32	24	...	...	68
NYMPHALIDÆ—						
30. *Basilarchia archippus* Cram	12	32	32	...	...	76
Variation	12-26	26-36	18-32	0-6	0-6	61-102

none on the tarsi of 2 species (Nos. 14, 15). The number of pores found on the first thoracic segment varies as follows: Six on each of 2 species (Nos. 7, 8); 4 on each of 2 species (Nos. 20, 22); 3 on each of 2 species (Nos. 9, 23); and 2 on each of 5 species (Nos. 10, 12, 24, 26, 27). Two pores were found on each of the last abdominal segment of 3 species (Nos. 7, 8, 13). The number of pores on both anal prolegs varies as follows: One for each of 3 species (Nos. 5, 22, 23); 2 for each of 2 species (Nos. 12, 13); and 4 for the army worm (No. 8).

The total number of pores found varies from 61 to 102, but no conclusion in regard to the comparative sensitiveness of the various species can be drawn, owing to the fact that only one of the species listed was critically studied.

In these examinations no attention has been paid to the size or age of the larva being examined and at first thought one might think that the disposition of the pores would vary according to the instars, but Mr. Busck informs me that he has found no such variations.

Discussion. According to the earlier papers concerning lepidopterous larvæ, some of the entomologists have observed the more conspicuous pores on the heads of these larvæ; they have called these organs sensory pits and punctures, but knew nothing about their internal anatomy. Within the past few years, systematists have been making comparative studies of the setæ and punctures present on the integuments of lepidopterous larvæ and have used these characters successfully for classifying the larvæ.

Forbes (1910) seems to have presented the first comparative paper on this subject. He appears to have found some punctures on all of the larvæ examined; he has mapped the frontal punctures on 33 species and adfrontal ones on 28 species, but represents only a few of those present on the epicranium and mouth parts. The same author (1911) mapped 3 pairs of punctures on the labrum each of 4 sphingids.

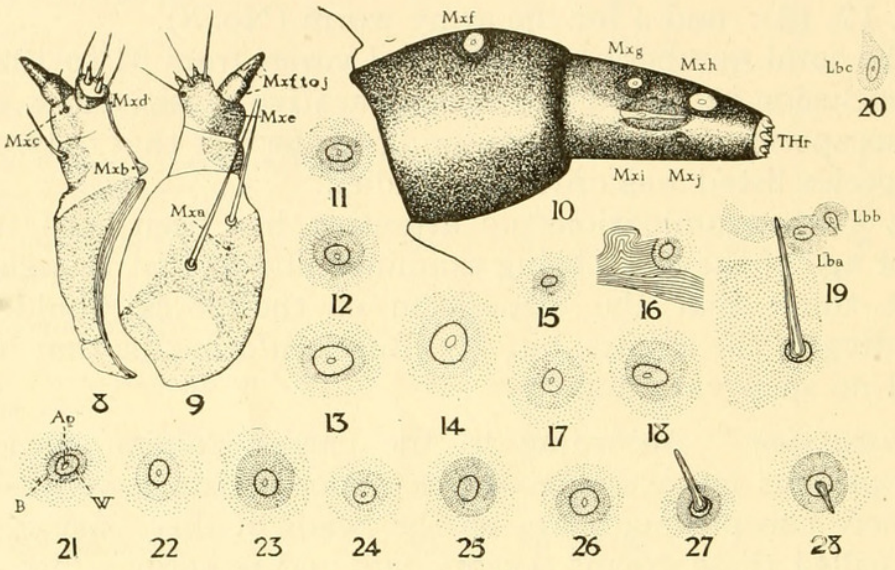
Tsou (1914) mapped 2 pairs of punctures on the dorsal surface of the prothorax of two genera.

Fracker (1915) mapped the frontal and adfrontal punctures of several species.

Heinrich (1916) named and mapped most of the punctures present on the head capsule of a micro-lepidopteron, and the

same author (1918) continued this study using the genus *Opostega*.

Busck (1917) mapped most of the punctures present on the head capsules of the pink bollworm (*Pectinophora gossypiella* Saund.) and the scavenger bollworm (*Pyroderces rileyi* Wals.). He found 22 punctures on each capsule, while the present writer found 20 on the former capsule; in all probability there are 26 on each capsule.



FIGS. 8 TO 28.—Disposition and external view of pores or punctures on same army worm as represented in Figs. 1 to 7. Figs. 8 and 9, disposition of pores on dorsal and ventral surfaces, respectively, of left maxilla, × 50. Maxillary pores *a* to *j* (*Mxa* to *j*). Figs. 10 to 28, external structures of pores and setæ, × 320. Fig. 10, ventral surface of second and third segments of maxillary palpus, showing maxillary pores *f* to *j* (*Mxf* to *j*) and tactile hairs (*THr*) at tip of palpus. Fig. 11, tibial pore; Fig. 12, thoracic pore *c;* Fig. 13, abdominal pore; Fig. 14, anal-proleg pore *b;* Figs. 15 and 16, maxillary pores *d* and *b*, respectively; Fig. 17, labral pore; Fig. 18, mandibular pore *a;* Figs. 19 and 20, labial pores *a* to *c*, drawn in proper relation to each other; Fig. 21, frontal pore; Fig. 22, adfrontal pore; Fig. 23, lateral pore; Fig. 24, subocellar pore *c;* Fig. 25, ultraposterior pore *b;* Fig. 26, antennal pore; Fig. 27, secondary seta (Fig. 5, A_3) on prothorax; and Fig. 28, secondary seta (Fig. 1, A_2) on head. Pore aperture (*Ap*); pore border (*B*); and pore wall (*W*).

2. External Anatomy of Pores or Punctures.

Under a high-power lens it is observed that a pore usually has a dark border (Fig. 21, *B*) which may be round, oblong or occasionally almost diamond-shaped, and it may show indications of radial streaks. Inside the border lies the wall (*W*) which is usually dark and heavy; it is the most conspicuous part of the organ and may be round or oblong. Inside the wall the chitin is lighter in color and at the center may be seen an

aperture (*Ap*) which appears as a transparent spot; the aperture is a minute opening passing through the thin chitin inside the wall.

Sometimes it is almost impossible to distinguish a secondary seta from a pore, but in almost all cases the chitin inside the wall of such a seta is lighter in color than that inside the wall of a pore, and this fact may help to distinguish a seta from a pore in case the seta has been pulled out; this comparison may be seen by referring to Figures 25 and 28, both of which structures come from the same region on the epicranium.

In size the pores do not vary greatly, as may be observed by looking at Figures 10 to 28. The smallest one (Fig. 10, *Mxj*) lies on the terminal segment of the maxillary palpus and the largest one (Fig. 14) in the army worm lies on the anal proleg; the former is scarcely discernible and seldom has a border. The one (Fig. 10, *Mxi*) nearest it is always slit-shaped and also in some species can scarcely be seen. The other two (*Mxg* and *Mxh*) on this segment are easily seen in good mounts, and have distinct borders.

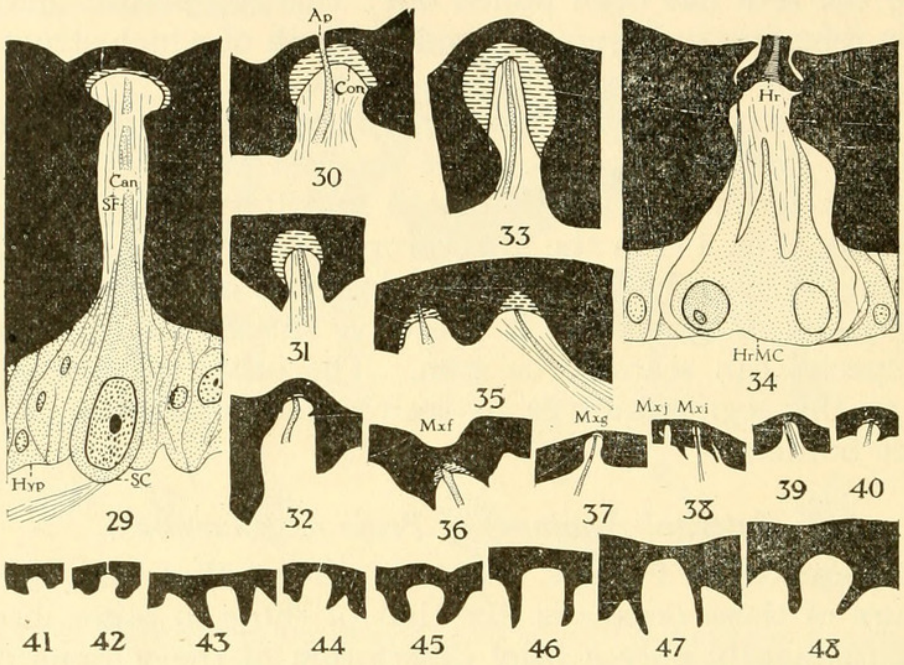
3. Internal Anatomy of Pores or Punctures.

A reference to Figures 29 to 48 shows that the internal structure of these organs is like that of those in other insects, and consequently only a brief description of the various parts of them will suffice here. Lying in the thick hypodermis (Fig. 29, *Hyp*) is the large sense cell (*SC*) whose peripheral end (*SF*) passes through the pore canal (*Can*), pierces the chitinous cone (Fig. 30, *Con*) and then stops in the bottom of the pore aperture (*Ap*) where it seems to come in direct contact with the external air. The chitin covering the cone may be dome-shaped, with the dome either lying in a depression (Fig. 29) or elevated above the surrounding chitin(Fig. 33); or it may form a depression whose bottom is pierced by the pore aperture (Fig. 36); or it may lie on the same level with the surrounding chitin (Fig. 31).

Since the chitin was so thick, not a single section showed all the details of one of these organs, because the microtome knife never passed properly through the structure; but Figures 29 and 30 combined give a good idea of their anatomy, which is very different from the internal anatomy of a large hair (Fig. 34) which is formed by a large hair-mother cell (*HrMC*) sending

forth processes through the pore canal to the base of the hair (*Hr*). Should both the base of the hair and the hair-mother cell be missing, the hair socket itself in sections serves well to distinguish this structure from a pore.

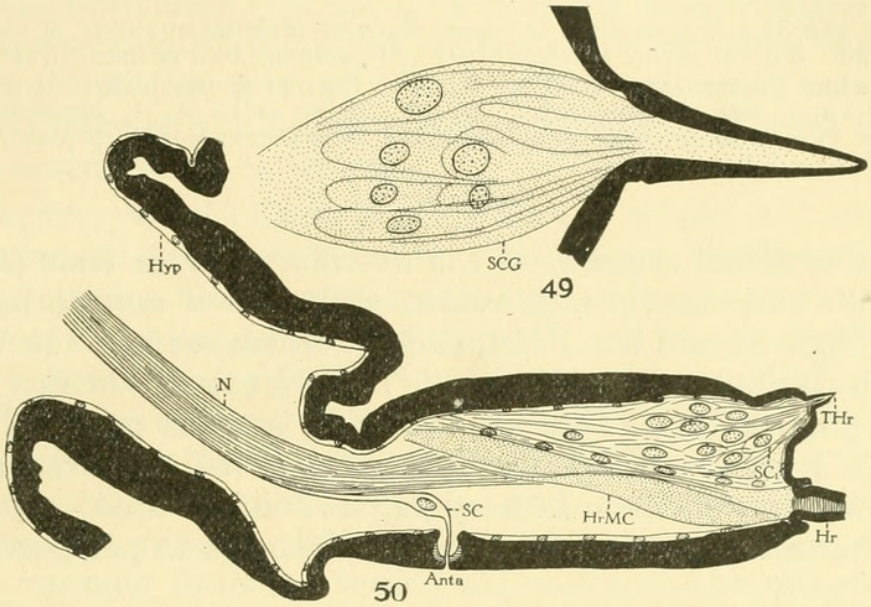
To determine whether all of the structures recorded as pores are really pores or hair sockets, thin sections made through the various parts of the integuments bearing these structures were



FIGS. 29 TO 48.—Sections, showing internal anatomy of pores or punctures and of one hair from various lepidopterous larvæ, × 500. Figs. 29, 31 to 34 are pores from *Ceratomia catalpæ*; Fig. 29, being from epicranium; Fig. 31, from antenna; Fig. 32, from palpiger; Fig. 33, from labium; and Fig. 34 is internal structure of a large hair on epicranium. Fig. 30 is a pore from labrum of *Telea polyphemus* and Fig. 35, two pores from labrum of silkworm (*Bombyx mori*). Figs. 36 to 38, maxillary pores *f* (*Mxf*), *g* (*Mxg*), *j* (*Mxj*) and *i* (*Mxi*), respectively, of tomato worm *Phlegothontius sexta*). Fig. 39, pore from labrum and Fig. 40, pore from antenna of cabbage-butterfly larva (*Pontia rapæ*). Figs. 41 to 48, sections from material, treated with caustic potash. Fig. 41, pore from terminal segment of maxillary palpus of codling moth (*Laspeyresia pomonella*). Figs. 42 to 48, pores from army worm (*Cirphis unipuncta*); Fig. 42, from tibia; Fig. 43, from antenna; Fig. 44, from maxillary lobe; Fig. 45, from femur; Fig. 46, from mandible; Fig. 47, from front; and Fig. 48, from anal proleg. Sense cell (*SC*); hypodermis (*Hyp*); sensory fiber (*SF*); pore canal (*Can*); chitinous cone (*Con*); pore aperture (*Ap*); hair-mother cell (*HrMC*); and base of hair (*Hr*).

carefully studied; in every case the suspected pore proved to be a real pore. Since most of these are so scattered, they are easily overlooked in sections made from fixed material, but were found much more easily in sections made from material treated with caustic potash (Figs. 41 to 48).

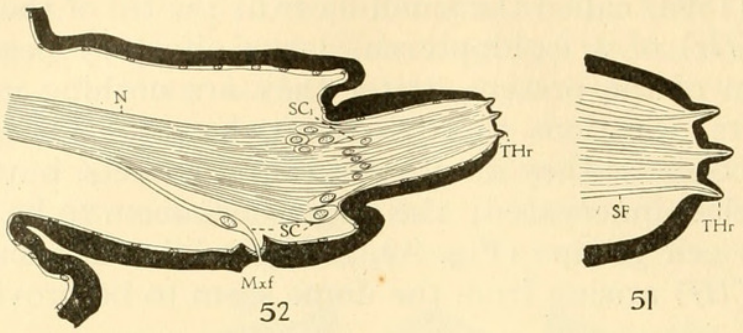
Nagel (1894) called the small hairs at the tip of the antennæ (Fig. 1, *THr*) of a lepidopterous larva olfactory pegs, but in the opinion of the present writer they are nothing more than tactile hairs. Sections through them show that they are not true hairs, because they do not arise from sockets, but each one is nevertheless innervated; the larger ones seem to be provided with sense cell groups (Fig. 49, *SCG*), while the smaller ones (Fig. 50, *THr*) arising from the dome seem to be provided with



FIGS. 49 AND 50.—Longitudinal sections, showing internal anatomy of antenna of tomato worm. Fig. 49, the larger type of one of Nagel's so-called olfactory pegs at tip of antenna, × 500; sense-cell group (*SCG*). Fig. 50 shows how well antenna is innervated; semidiagrammatic, × 100. Hypodermis (*Hyp*); nerve (*N*); antennal pore (*Anta*); probably hair-mother cell (*HrMC*); sense cell (*SC*), connected with pore; sense cell (SC_1), connected with peg; smaller type of one of Nagel's so-called olfactory pegs (*THr*) arising from dome; and base of large true hair (*Hr*).

single sense cells (SC_1). The large hair (*Hr*) at the tip of the antenna is a true hair, but it does not appear to be sensory, although lying at its base there are one or two large cells (*HrMC*) which resemble hair-mother cells more than sense cells.

One author draws the antennæ of lepidopterous larvæ as if they were composed of 3 or 4 segments, but sections show only two distinct segments in each, although sometimes the basal one is so folded that indications of two more segments are visible, as shown in Figure 50, which also gives a good idea of how well the antenna is innervated.



FIGS. 51 AND 52.—Longitudinal sections, showing internal anatomy of maxillary palpus. Fig. 51 shows sensory fibers (*SF*) running to 3 of hairs (*THr*) at tip of palpus of *Ceratomia catalpæ*, × 500. Fig. 52 shows how well palpus is innervated; semidiagrammatic, × 190. Sense cells (SC_1), connected with hairs (*THr*); sense cells (*SC*), connected with pores; maxillary pore *f* (*Mxf*); and nerve (*N*).

The terminal segment of the maxillary palpus ends bluntly (Fig. 53) and the tip is provided with 8 or 9 minute pseudo-hairs (Figs. 51 and 52, *THr*), each of which seems to be innervated by a single sense cell (SC_1). These sense cells lie in a group at the proximal end of the segment near another group of sense cells (*SC*) which evidently belong to the pores. Figures 52 and 53 show how well the maxillary palpus is innervated; a portion of the terminal segment in Figure 53 is shown in perspective.

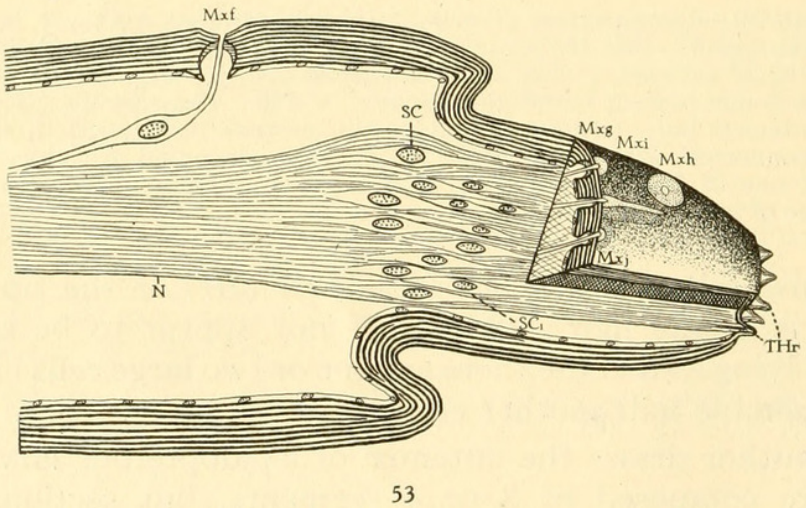


FIG. 53.—Schematic drawing of maxillary palpus of tomato worm, showing innervation of maxillary pores *f* to *j* (*Mxf* to *j*) and tactile hairs (*THr*); a portion of terminal segment is in perspective.

SUMMARY.

To determine whether lepidopterous larvæ respond to chemical stimuli, tent caterpillars, fall webworms, tussock-moth larvæ, army worms and larvæ of *Papilio polyxenes* were tested by using the following sources of odors: Oils of peppermint, thyme and wintergreen, dried leaves of pennyroyal and spearmint, wild cherry-tree leaves, fresh grass, old honey and comb, and the protruded thoracic glands of the above Papilio larvæ. The larvæ usually responded to the exhalations from these substances, but the average reaction times obtained seemed to depend more on the degree of sluggishness of the larvæ than on their sensitiveness to odors.

Organs, called olfactory pores by the writer, but known as punctures to systematists, were found widely distributed on the head capsule, head appendages, legs, dorsal surfaces of the prothorax and last abdominal segment, and on the anal prolegs. It is believed that a few of those on the head and all of those found on the legs and abdomen are here reported for the first time. Their internal structure is like that of those in adult insects and coleopterous larvæ, and consequently are well adapted to receive chemical stimuli, because their sensory fibers running from the sense cells pass into the minute pores or punctures and seem to come in direct contact with the external air. No experiments, however, were performed to determine their function.

Verschaffelt determined experimentally that cabbage-butterfly larvæ are attracted by the various mustard oils contained in the host plants, and this explains why these larvæ refuse plants not containing such oils; he also thinks that the larvæ smell the odors from the mustard oils before they begin to eat the food. If we knew more about the chemotaxis of insects, we might be able to devise practical methods for the control of certain insects, as by trap baits, etc.

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