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TROPISMS AND SENSE ORGANS OF  
COLEOPTERA

(WITH TWO PLATES)

BY

N. E. McINDOO

Senior Entomologist, Deciduous-Fruit Insect Investigations,  
Bureau of Entomology, U. S. Department of Agriculture



(PUBLICATION 3113)

CITY OF WASHINGTON

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#### INTRODUCTION

This paper is a continuation of a series of studies dealing with the tropisms and sense organs of insects, suggested by Dr. A. L. Quaintance, Associate Chief of the Bureau of Entomology. It is written as a complement to the writer's former paper (47) entitled "Tropisms and Sense Organs of Lepidoptera," and contains practically no information found in the former one, although, of course, the information which deals with the Coleoptera alone, is of a similar nature.

In the paper on Lepidoptera the original work dealt mostly with the codling moth, but since this species was not a favorable insect on which to experiment in the laboratory, the original plan for conducting tests was much curtailed. In the present study the experimental work has been expanded and the Mexican bean beetle (*Epilachna corrupta* Muls.), which first appeared in Takoma Park and Sligo, Md., in 1927, was selected to represent the Coleoptera, owing to its abundance and great economic importance. When tested to odor stimuli alone it also was found to be an unfavorable insect; but when the adults were allowed to come in contact with the substances to be tested as foods, the beetles clearly demonstrated their likes and dislikes; and when tested to light and gravity in a dark-room, the adults proved to be almost ideal for this purpose.

In order to obtain comparative results which could be treated statistically, new technique and apparatus were devised, and the more important experiments were repeated over and over under controlled conditions.

## A. TROPISMS

The tropisms of Coleoptera will be discussed first and then the sense receptors.

### I. PHOTOTAXIS, GEOTAXIS, AND THIGMOTAXIS

#### I. REVIEW OF LITERATURE

Information concerning the phototaxis, geotaxis, and thigmotaxis of beetles is limited. Publications pertaining to light traps are numerous, but papers concerning the geotaxis, thigmotaxis, and other phases of phototaxis are scarce. In regard to the reactions of beetles to wave length and intensity of light, the field is practically unexplored.

#### (A) GENERAL REMARKS

Loeb (37, p. 20) remarked that an imago animal may respond to light in one way, its larva in a different way. For example, an adult June beetle moves toward light and is called photopositive, whereas its larva moves away from light and is thus photonegative. He further said (p. 70-73) that mealworms (larvae of *Tenebrio molitor*) are photonegative and behave under red glass as they do in the dark; but under blue glass, just as they do in the light. They adhere closely to objects, being positively stereotropic or thigmopositive. They flee from moisture and seek dry spots. He believed that positive thigmotaxis (stereotropism) and negative phototaxis determine the habits of these insects, which live in flour, protected from the light. The behavior of cockchafer (*Melolontha vulgaris*) under red and blue glass is similar to that of mealworms. Loeb believed that negative phototaxis may cooperate, but that thigmotaxis is doubtless the chief factor concerned in causing the larvae of cockchafers to burrow in the ground. The same writer (p. 85-86) put coccinellid beetles in a wooden box which was then placed in a dark closet. After repeated tests these lady-beetles were always found at the top of the box, proving that they were geonegative.

Weiss (94) placed three species of lady-beetles at the base of a 15-foot pole, which they soon climbed. He believes that this behavior demonstrates negative geotaxis.

Woodsdalek (97) has demonstrated that the phototactic responses of certain dermestids vary at different life-history periods. The larvae of *Trogoderma tarsale* immediately after hatching are photonegative. Negative phototaxis persists throughout the larval period, and even for a short time after the adults mate. Soon after ovipositing, the females become gradually indifferent to light and later become photopositive.

Breitenbecher (7) experimented with potato beetles, under dry and moist conditions, to ascertain what their tropic responses would be in a desert. When the beetles were confined in a moist medium, they were found to be photopositive and geonegative; but when desiccation resulted in a dry medium, they were photonegative and geopositive.

Rimmer (69, p. 25) tested tobacco beetles with color screens or ray filters which transmitted practically monochromatic light rays. He remarks that these beetles, in common with other insects, reacted most strongly to colors of shortest wave length. The movement toward blue or blue-violet was most pronounced, and the movement toward red least of all. These beetles, like other insects reacting negatively toward intense sunlight, were only slightly sensitive to light at the lower end of the spectrum, and rays of longer wave length, limited to red and orange, seemed to act on them in much the same manner as darkness. Beetles exposed to bright sunshine under color screens of red and blue were observed to collect under the red screen almost as readily as they did when an opaque screen was used instead of the red, although the apparent intensity of light under the two screens was the same.

Smith (75) remarks that the larvae of the Japanese beetle are thigmopositive to living roots, and if these are not available, they adhere to stones, sticks, or the bottom and sides of the breeding cage. The adult beetles apparently can see colors, particularly green. This is taken advantage of by painting the bait traps green and by using green lead arsenate (78).

Moore and Cole (56) report that Japanese beetles collect in great numbers at the tops of trees, bushes, and weeds. This is caused by two tropic responses—positive phototaxis and negative geotaxis, which determine the head-tail orientation of the body. In the field and laboratory certain degrees of heat and light are necessary to cause active movements. These writers further say that since a geotactic response is shown by the beetles only when they are illuminated, it therefore follows that their movement in a lighted field is the result of three factors—negative geotaxis, photokinesis, and positive phototaxis. The first is constant, while the other two factors are functions of the



intensity of the illumination. Moore and Cole conducted many tests by confining Japanese beetles in a specially constructed wire-screen cage. Five light intensities were used in securing the reaction time of the beetles. The results obtained are presented in tables and graphically. Their summary is about as follows. Light and temperature above 23° C. are necessary to cause activity in the Japanese beetle. The effect of light as indicated by the rate of locomotor responses was related to light intensity according to Fechner's expression of Weber's law.

Richmond (67) devised an apparatus to determine the value of color and intensity of light. Over 100 tests were conducted, using Japanese beetles, but no definite conclusions were drawn from the results obtained.

Crozier (12) states that when creeping mealworms are tested to light rays, a definite intensity of white light (about 136 m. c.) is required to produce negative orientation away from contact with a vertical glass surface. This gives a measure of stereotaxis in terms of phototaxis, or vice versa. The effectiveness of light for the suppression of stereotaxis varies with the wave length. By determining the minimum energy required to inhibit stereotaxis with the different regions of the spectrum, it was found that the maximum effectiveness was sharply localized in the neighborhood of 535 millimicrons. The same author (11) conducted other experiments to show that mealworms, while creeping, exhibit homostrophic responses and stereotropic orientation to lateral contacts. Crozier finally concludes that stereotropism is truly a tropic character.

• (B) LIGHT TRAPS FOR BEETLES

Artificial light as a control measure was probably first used in 1787 for attracting vine moths in Europe. Since that date light traps have been gradually developed and improved until today there are many types and varieties of gasoline, kerosene, acetylene, and electric lamps used for this purpose. Most of these have been devised primarily for catching Lepidoptera, but many beetles also are caught in them, and other traps are designed primarily for Coleoptera. It seems that none, however, has given complete satisfaction as a control measure.

Since 1914 Jarvis and his co-workers (28, 33, 35) have been devising light traps to catch sugarcane beetles in Queensland, Australia. Their object has been to develop a trap so simple that it might come into general use in sugarcane-growing regions. A very successful trap has finally been developed. It consists of a large pan about a yard square, with sides about 4 inches high, and of an ordinary acetylene

lamp. In Cuba, Barreto (5) reports that light traps are an effective means of dealing with other species of sugarcane beetles.

For many years light traps have been used for catching May beetles (*Lachnosterna*), but it is still doubtful whether this method, as a control measure, is really worthwhile. Sanders and Fracker (70) in Wisconsin used gasoline lantern traps to collect May beetles. Results were obtained concerning the distribution of species over a comparatively limited area, the optimum temperature for flights, and the most favorable location and arrangement of the light traps. Seventeen out of the 19 species known to occur in Wisconsin were caught in the traps. Van Zwaluwenburg (91) reports that in Porto Rico large numbers of May beetles were caught by means of a 400-candlepower gasoline lamp, and that the use of light traps should constitute a valuable means of control. Harned (22) reports that, in pecan orchards in Mississippi, where trapping May beetles at night by lanterns placed over tubs of oil and water has been practiced for many years, their numbers have been considerably reduced, and they appear to have caused less damage there than in previous years.

Runner (69, p. 49-51) reports that the tobacco beetle may be attracted to light traps in tobacco factories or warehouses and large numbers of them destroyed. An efficient trap can be made quickly and easily by pinning sheets of sticky fly paper around an electric light. Other types of light traps are discussed. One consists of a large globe connected with a cyanide jar; another, of a light and a shallow pan of oil; another, of a suction fan and a light; and another method is to collect the beetles at windows. Some of the beetles caught were examined for the purpose of determining their sex; nearly two-thirds proved to be females.

Smith (77) reports that light traps, placed over large funnels, have proved effective against the adults of the Asiatic garden beetle (*Aserica castanea* Arrow). In one instance as many as 157,774 beetles were caught in one trap during a period of 30 days.

For several years Williams (96) has been developing and improving light traps for insects. At last he has perfected one which has been proved successful. The source of the light is acetylene or electricity, and the killing agent is carbon tetrachloride or potassium cyanide.

In New York State, Collins and Nixon (9) have just published a second report concerning an investigation conducted on a large scale, in which 105 water-pan electric-light traps were installed in an orchard. Most of the insects caught were Lepidoptera, but incidentally many beetles were trapped. The method recently employed by Hermes

(23) in California is also recommended to future investigators. He used large electric lights in an orchard to attract codling moths.

Gourdon (20) states that ultra-violet rays have been found to attract both diurnal and nocturnal insects. The rays appear to produce in the insects a sensation which is at first agreeable, but which soon becomes dangerous, if not fatal; in certain cases they are immediately blinded. A trap for use in vineyards, orchards, or fields is described, to which insects are attracted by means of ultra-violet rays, and are either drawn by the suction of an electric fan into a metal basket or fall blinded outside the trap, where they become an easy prey to birds.

Many more references on light traps are cited in "The Review of Applied Entomology, Series A," but perhaps enough has been said to convince the reader that this method of control is worth further investigation.

## 2. ORIGINAL WORK ON MEXICAN BEAN BEETLE

### (A) RESPONSES OF LARVAE AND ADULTS TO DAYLIGHT

When the sun is shining brightly on warm days, larvae and adult bean beetles are rarely seen exposed to the direct sunshine in bean patches. During cloudy days and early in the morning many may be seen on the upper surface of the leaves, but most of them at all times live and feed on the under surface.

When brought into the laboratory most of them move toward the windows, being photopositive, while occasionally one moves away from the light, thus being photonegative. When tested in a phototactic box, 18 inches long, 12 inches wide, 12 inches high, and lined with a dead-black cloth (fig. 1), their responses were similar to those of codling-moth larvae, recently described by the writer (47, pp. 12-13). This box lay on a table by a south window in bright light, although not in direct sunshine. Dozens of insects were placed in it and the tracks of most of them were traced with a lead pencil. Larvae of the first and second instars were found to be weakly photopositive or indifferent to light. Many moved slowly, bending to the right and left, in any direction as if searching for food, while a few moved in circles toward the light (fig. 1, *a* and *b*).

Most of the larvae of the third instar were strongly photopositive (fig. 1, *c*), while the remainder were weakly photopositive or indifferent to light. The more active larvae of the fourth instar were usually strongly photopositive, but a few were indifferent. The less active ones were usually strongly photonegative (fig. 1, *d*). It was

later ascertained that most of the larvae, when about ready to pupate, became photonegative. These were sluggish in action, were deeper yellow in color, and their intestines usually were not visible through the integument as they are in the more active larvae.

Hundreds of adult bean beetles, including the overwintering ones, those of the second and third broods, and many ready to hibernate, were tested in one way or another. Practically all were found to be photopositive, most of them being strongly so (fig. 1, *e*). At no time were photonegative beetles observed. The nearest approach to this

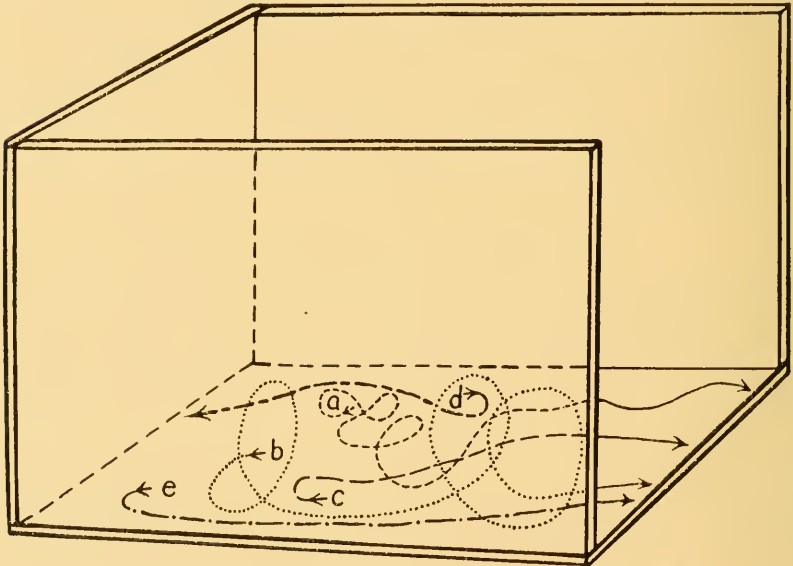


FIG. 1.—Diagram of phototactic box and tracings of tracks of Mexican bean beetle, illustrating responses to light of this insect. The tracings are as follows: *a*, larva just hatched; *b*, larva of second instar; *c*, larva of third instar; *d*, larva of fourth instar; and *e*, adult ready to hibernate.

condition was found among old ones of the second brood, but when repeatedly tested it was decided that they too were still photopositive.

#### (B) DESCRIPTION OF DARK-ROOM AND APPARATUS

Since it is often difficult to separate phototactic responses from geotactic ones, special apparatus is then necessary. Not having a dark-room whose temperature and relative humidity could be controlled, an attempt was made to construct one by using a room, 10 feet long, 9 feet wide, and 9 feet high. It was made totally dark as follows: Boards were nailed to the wooden shutters which closed

snugly, and then a dark green window shade (fig. 2, A) was pulled to the bottom of the window. The door (B) was made light-proof by fastening strips of black cloth around all its edges, and its transom

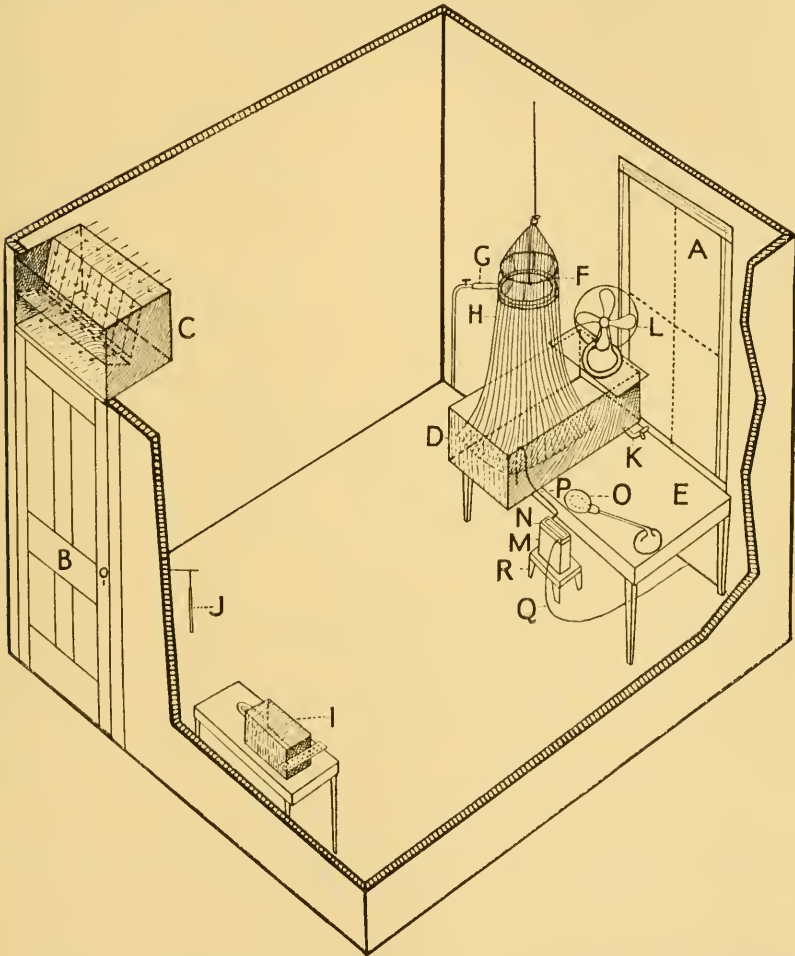


FIG. 2.—Diagram of a constant temperature and humidity dark-room, showing parts of room and apparatus used in testing photo-geotactic responses of Mexican bean beetle. The parts and apparatus are as follows: A, window shade; B, door; C, ventilator; D, box; E, table; F, lawn sprayer; G, garden hose; H, bath towels; I, hygromograph; J, thermometer; K, outlet water pipe; L, electric fan; M, photo-geotactic box; N, water screen; O, electric lamp; P, siphon running to water screen; Q, siphon running from water screen; and R, stool.

was changed into a ventilator (C) through which air passed freely, but no light. The temperature and humidity were partially controlled by the following means. A box (D), 40 inches long, 24 inches wide,

and 12 inches high, lay on a table (*E*) by the window at the south end of the room. A wire frame-work, supporting a circular lawn sprayer (*F*), was suspended from the ceiling directly over the box; and a garden hose (*G*), running to a water spigot, was connected with the sprayer. Two large bath towels (*H*), put around the frame-work above the sprayer reached half-way to the bottom of the box, which was kept two-thirds full of water. A hygrothermograph (*I*) lay on another table at the north side of the room, and near this table there was a centigrade thermometer (*J*) the scale of which was marked in fifths of degrees. Before starting an experiment in this dark-room, water was turned on at the spigot, passed upward and outward from the spray, struck the bath towels, ran down them into the box, and finally passed through a pipe (*K*) to the outside of the room. In order to have good ventilation and a more humid atmosphere, air from an electric fan (*L*) was directed against the wet towels and water in the box. If the temperature and relative humidity could not have been satisfactorily controlled for the tests planned, the original idea was to use ice and water in the box for cooling the air, and a stove for heating it. Since small variations in temperature and relative humidity did not seem to affect the responses of the bean beetle, the ice and stove were not used.

Experience showed that the temperature and relative humidity inside the dark-room were influenced only slightly by outside climatic conditions. During the forenoons the temperature was often held nearly constant, and never varied more than two degrees centigrade, but during the afternoons the variation was usually larger. Table 1 shows that the greatest variation of temperature, between 9:00 o'clock a. m. and 4:30 o'clock p. m., was  $4.2^{\circ}$  C. and the smallest variation was  $1.8^{\circ}$  C. When the outside relative humidity was exceedingly high, water was not run through the sprayer, because it made the inside humidity too high.

The testing apparatus consisted of a tall box (fig. 2, *M* and fig. 3), a shallow water screen (*N*), and a lamp (*O*). The inside dimensions of the box (fig. 3, *A*), called a photo-geotactic box, were 12 inches by 5.5 inches by 1.75 inches. It had two sets of shutters, one of glass (*a*) and the other of wood (*b*), which fitted snugly in slots. The four sides inside the box were covered with a dead-black cloth, while one of the glass shutters was covered with cheesecloth. The inside of the box was marked with white lines into ten equal sections, numbers 1 to 10. When all four shutters were in place it was almost totally dark in the box.

The inside dimensions of the water screen (fig. 3, B) were 6 inches by 2 inches by 0.25 inch. The two pieces of glass (*c*) were held securely one-fourth inch apart by a strong wooden frame (*d*). The running water passed through a siphon (fig. 2, *P*) and a glass tube (fig. 3, B, *e*), having a bore of one-eighth inch, into one end of the water screen and out again at the other end through another tube and siphon (fig. 2, *Q*, fig. 3, B, *f*).

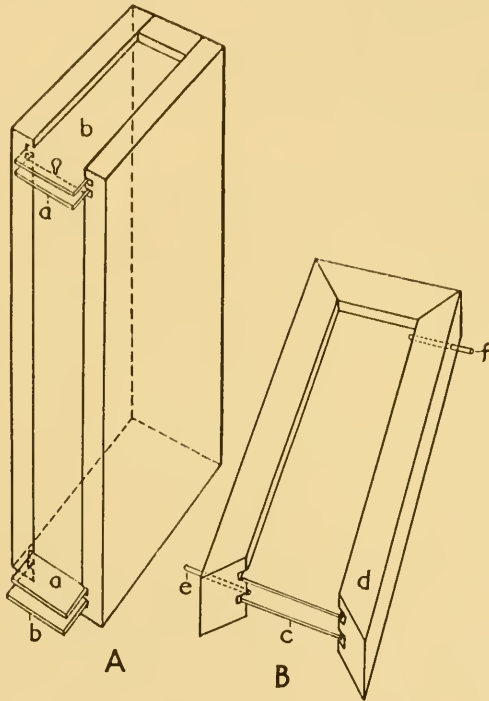


FIG. 3.—Diagrams of photo-geotactic box (A) and water screen (B), showing following parts of them: *a*, glass shutter; *b*, wooden shutter; *c*, piece of glass; *d*, wooden frame; *e*, inlet glass tube; and *f*, outlet glass tube.

The lamp (fig. 2, *O*), consisting of a blue daylight bulb 100 W, 110 V, rested on the table (*E*), or on a box, while the photo-geotactic box and water screen lay on a stool (*R*).

(C) RESPONSES OF ADULT BEETLES AND THEIR LARVAE IN DARK-ROOM

Since the writer was not able quickly and accurately to separate the live bean beetles according to sex, sex was disregarded in all the tests conducted. The beetles, otherwise, were selected so that those in each set were of practically the same age and responded to daylight readily.

After the temperature and relative humidity in the dark-room had become nearly constant, both shutters at the bottom of the photo-geotactic box were inserted and 25 adult beetles were then put in the box on the cloth-covered glass shutter, after which the glass shutter at the top of the box was inserted, and finally the testing apparatus was assembled as shown in figures 2 and 3. The blue electric light bulb was then placed 10 inches directly above the water screen, which prevented the infra-red or heat rays from the light from reaching the insects. After a period of 15 minutes the wooden shutter was removed and the box was gently raised and turned toward the light so that the observer could see through it from end to end. The position of the beetles in the ten sections was then quickly noted and recorded in a table.

In test number 2 the beetles were again put in the bottom of the box on the cloth-covered shutter, but this time the box was gently turned upside-down and rested on the water screen, 10 inches below which was the light. In this case the beetles clung to the cloth and did not fall when turned upside-down. During the same forenoon tests number 1 and 2 were repeated alternately three times, and finally the results obtained in the two sets, each consisting of four tests, were treated statistically and recorded in table 1.

To secure a frequency distribution the responses were given values ranging from 1 to 10, corresponding to sections 1 to 10 in which the 25 insects were counted at the end of a test. If all 25 insects remained in section 1, the total value would be 25, or 1 as an average; and if all moved to section 10, the total value would be 250, or 10 as an average; but neither one of these extremes was actually observed, because the insects were always counted in two or more sections. To secure the arithmetic mean, which in each test lay somewhere between 1 and 10, the total value was divided by 25, and since each set of experiments consisted of four tests the frequency curve was represented by only four means. Owing to the small number of statistical items, Bessel's formula

$$\left( P. E. m = \pm 0.6745 \sqrt{\frac{\sum d^2}{n(n-1)}} \right)$$

was used to calculate the probable errors.

The values were accurate for those insects counted in sections 2 to 10, but not so for those counted in section 1, because they may have responded little or none, although most of them had left the cloth-covered shutter on which they were put. Consequently, the mean positions given in table 1 under the headings "up" and "down"



TABLE 1.—*Tests to determine differences between phototactic and geotactic responses of Mexican bean beetle, with and without use of light*

Stage of insects tested	Phototactic and geotactic responses combined (100 watt light used)			Geotactic responses alone (No light used)			Num-ber of tests	No. of set	Tempera-ture C°	Relative humidity	Date
	Mean position of insects forced		Difference	Mean position of insects forced		Difference					
	Up	Down		Up	Down						
Over-wintering beetles...	8.21 ± 0.041	5.81 ± 0.113	2.40 ± 0.120	8.05 ± 0.156	2.78 ± 0.083	5.27 ± 0.177	4	4	26.4-29.0	89-93	June 17
	7.75 ± 0.224	4.92 ± 0.337	2.83 ± 0.405	7.49 ± 0.309	2.01 ± 0.113	5.48 ± 0.329	4	5	26.0-29.2	90-93	June 20
	9.42 ± 0.065	6.98 ± 0.176	2.44 ± 0.188	7.98 ± 0.062	2.35 ± 0.108	5.63 ± 0.124	4	6	26.0-30.2	92-95	June 21
General average of above.	8.46 ± 0.072	5.90 ± 0.120	2.56 ± 0.140	7.84 ± 0.106	2.38 ± 0.055	5.46 ± 0.119	12	5			
Old beetles of 2nd brood...	7.41 ± 0.188	6.48 ± 0.029	.93 ± 0.190	6.31 ± 0.688	2.25 ± 0.173	4.06 ± 0.709	4	15	24.5-26.6	93-96	Aug. 19
Larvae of third instar....	2.24 ± 0.087	2.14 ± 0.059	.10 ± 0.105	2.28 ± 0.118	1.41 ± 0.098	.87 ± 0.153	4	4	24.0-25.8	86-88	June 26
Larvae of fourth instar...	9.05 ± 0.177	6.42 ± 0.192	2.63 ± 0.261	2.25 ± 0.149	1.47 ± 0.151	.78 ± 0.212	4	5	23.0-27.0	84-87	June 27

are slightly too high for those insects which did not respond readily; but the figures given under the heading "difference" are practically the same as those when all the insects counted in section 1 were eliminated.

Usually during the afternoon similar tests were conducted four times, using the same beetles, but no light was used. In this case, without the use of light, the geonegative response was  $5.27 \pm 0.177$  more than the geopositive one, while with the use of light it was only  $2.40 \pm 0.120$  more (table 1), 10.00 being equal to a 100 per cent response.

On later dates the preceding tests were again repeated, using two other sets of overwintering beetles. The general average and probable errors of the three series were therefore obtained by using the 12 means and the mean of them. Thus, for active, overwintering beetles the geonegative response, when light was used, was  $2.56 \pm 0.140$  more than the geopositive one; but when no light was used, it was  $5.46 \pm 0.119$  more, indicating that when the beetles were forced downward by the light this stimulus overcame about one-half of the geotactic one. In two of these series of tests the light was used during the forenoon, but in the third series during the afternoon. The sequence in which these insects were tested, therefore, had little or no effect on the results obtained.

The preceding tests were repeated by using one set of old beetles of the second brood. These insects were not so active as they were when younger and did not respond so readily to light and gravity as did the more active overwintering beetles. Their lower responses were due mostly to the fact that the insects soon became tired of being forced to respond.

Two sets of larvae were likewise tested in the photo-geotactic box and were found to be photopositive and geonegative (table 1). Compared to the adults they were sluggish and three times in four did not respond as readily to light and gravity. Larvae of the third instar reacted weakly to light and gravity, while the larvae of the fourth instar responded strongly to light but weakly to gravity.

The reader has doubtless noted that the writer has designed his experiments and discussed his results from the point of view that rate of movement is a measure of tropic response. After an animal is oriented, some writers claim that the rate of its movement toward or away from the source of excitation is not a measure of its tropic response. If a tropic response includes nothing more than the mere act of orienting, the preceding results then have little to do with the subject of tropisms. The writer in various publications has dis-

cussed the subject of tropisms from a broad point of view, and has not yet accepted any definition nor does he know exactly what a tropic response includes, but he believes that it includes more than orienting in a certain direction.

In conclusion, bean beetles and their larvae are usually found on the upper portions of their host plants, because they are photopositive and geonegative; but since direct sunshine in warm weather is harmful to them, they are usually found on the lower surface of the leaves.

## II. CHEMOTAXIS

### I. REVIEW OF LITERATURE

Most of the information regarding chemotaxis found in the widely scattered literature pertains to the subject of baits. Scores of references have been consulted, but only the more important ones will be cited.

#### (A) BAITS FOR WIREWORMS AND TENEBRIONIDS

It is not known when the practice of using baits for beetles was first begun, although this is an old control method. The Japanese growers, according to Treherne (85), were probably the first ones to use baits for catching wireworms, the larvae of elaterid beetles. After roasting dry rice shorts or rice bran, the Japanese then moistened the roasted material with water and made it into small balls, which had a strong odor said to be attractive to wireworms. The Japanese claimed that a single ball would catch 100 or more wireworms, but when this method was tested by Treherne a single bait buried in heavily infested soil never yielded more than 90 larvae.

Treherne (86) also tells about the old-fashioned way of attracting wireworms, which is still recommended as one of the few control measures. Pieces of cut potatoes, to which white wires have been attached, are buried in the infested soil. Upon visiting the infested area the potatoes are pulled from the ground by means of the wires, the wireworms are removed and destroyed, and then the potatoes are buried again. In Canada attractive baits, consisting of potatoes, balls of dough, shorts, meal, or rice bran, are set in the soil. The addition of molasses or other attractant ("attractant") in these bran baits does not improve their attractiveness, nor has the inclusion of arsenicals been of any practical value.

Weldon (95) reports that small pieces of potatoes were planted between rows of beans in California. This bean crop was saved, while 30 acres of beans nearby, not thus protected, were entirely destroyed.

Borodin (6) reports that in Russia the best remedies for wireworms are various baits, consisting of sliced potatoes, carrots, beets, oil cakes, cabbage stalks, etc., buried 3 or 4 inches in the soil. Those poisoned with Paris green or arsenic need no further attention. The unpoisoned ones must be inspected weekly. Poisoned maize baits are also recommended.

French (15) says that in Australia poisoned baits consisting of cut-up turnips, carrots, etc., soaked in lead arsenate, have given good results.

Lovett (38) states that in Oregon poisoned-bran mash may be placed under stones or boards in the fields as a control measure for wireworms.

Masaitis (39) reports that in Siberia baits of horse dung, poisoned with sodium arsenite, appeared to be considerably more effective than those of poisoned linseed or hempseed cake.

More recently special attractants have been given serious attention. Comparative tests, conducted in Washington State by Spuler (83), in which rice flour, graham flour, graham flour and sugar, bran, graham flour and oranges, graham flour and lemons, potatoes, carrot roots, carrot tops, and apples were used as baits gave a descending order of attractiveness as listed. Other tests, in which baits consisting of germinating Alaska peas, beans, corn, graham flour, and potatoes were used, indicated that the seeds and flour were about equal in attractiveness, but that the potatoes were far inferior. For practical control work use baits, particularly germinating seeds, to allure the wireworms to definite spots, and then the worms may be easily killed with a soil fumigant, such as calcium cyanide. When the worms have gathered around the bait, spaced about four feet apart, to partake of the feast prepared for them, all that remains to be done is to bury a little of this granular fumigant near the bait. Shortly the deadly fumes send the banqueters to their happy hunting ground and all is ended.

Federal entomologists (1) at Clarksville, Tenn., have recently made an interesting discovery in connection with poisoned-bran bait fed to tobacco wireworms, which have hitherto stubbornly resisted all efforts at direct control. These worms were easily attracted to bait flavored with ordinary nitrobenzene. In five series of large-scale experiments in tobacco fields these worms were reduced from 50 to 60 per cent by the use of this chemical as a bait flavoring. Other entomologists (2) at the Florida experiment station remark that a flavoring of nitrobenzene added to poisoned-bran bait is very attractive to a variety and large range of insects, and they found it quite

attractive to the celery leaf-tier. If it is attractive to such diverse insects as wireworms and caterpillars it is quite possible that it will be found of value against a large number of insects.

Melander (50) states that a dough made of flour or bran proved very attractive to wireworms, but the addition of sugar, oranges, lemons, etc., added little to the drawing power of the baits.

Since the larvae of certain tenebrionid beetles are destructive, why not attack the evil at the source by destroying their parents? This was the way Wakeland in Idaho reasoned during the season of 1921. After discovering that these beetles feed greedily for a month before egg-laying time, he next found out that they could be easily killed during this period by feeding them poisoned-bran bait, thus largely eliminating them before they had a chance to start a new generation. The following season he (93) continued his experiments and states that the bait used consisted of bran, Paris green, amyl acetate, and water. It was distributed broadcast or in the bottom of furrows, plowed at regular intervals, over an area of 18,000 acres. This method is said to be practical and economical, because the beetles were effectively killed at a cost of about two and a half cents per acre for materials, and the labor involved was not a large item.

In 1920 Jack (29) in Rhodesia poisoned the adults of certain tenebrionids by using the bait recommended against cutworms.

Swenk (84) remarks that a promising remedy against the adults of *Elcodex opaca* is a bait prepared by mixing, dry, 25 pounds of coarse wheat bran and 1 pound of Paris green, to which is added  $\frac{3}{4}$  ounces of amyl acetate in enough water to make a stiff mash. This quantity is sufficient for several acres when put in furrows.

Other species of tenebrionids in the United States (8), Russia (73), and Rhodesia (30) are more or less controlled by poisoned baits. In Southern Rhodesia several formulas have been used (31) successfully against so-called wireworms (tenebrionids). One of them is made of chopped green stuff, dipped in a solution consisting of 1 pound of sodium arsenite, 8 pounds of cheap sugar or 1 gallon of molasses, and 10 gallons of water. This bait may be broadcast or applied like bran bait.

#### (B) BAITS FOR STRAWBERRY-ROOT WEEVILS

During the past 25 years strawberry growing in the western parts of Washington, Oregon, and British Columbia has been handicapped by strawberry-root weevils. For 20 years or more many efforts have been made to develop a remedy for this serious pest, but not until recently has a satisfactory control measure been discovered. An

attractive poisoned bait was developed by M. J. Forsell of Seattle, Washington, who, at the suggestion of the present writer, attacked the problem through the weevil's sense of smell. In the preliminary experiments dried ground apples were found to be the most attractive substance tested, and magnesium arsenate was the most satisfactory poison. It is further claimed that the discovery and perfection of this bait marks an important horticultural step in the fruit industry of the State of Washington, as these weevils had become so serious in many places that the strawberry-growing industry seemed doomed.

Melander and Spuler (51) report their results concerning the poison-bait remedy for the strawberry-root weevils in Washington. They say that these destructive weevils can be satisfactorily, economically, and practically controlled by the distribution of a poisoned bait immediately at the close of the berry harvest. This bait consists of sun or oven dried sliced apples, ground into pulp or granules, to which an arsenical is added, magnesium arsenate being the most satisfactory. The bait is broadcast over the strawberry plants at the rate of about 70 pounds per acre.

Mote and Wilcox (57) tell about the bait method used in Oregon. They remark that a homemade bait consisting of 95 pounds of ground dried apple waste, mixed with 5 pounds of calcium arsenate, kills the strawberry-root weevils. A commercial bait is also reported to be efficient.

Downes (13) further experimented with baits for strawberry-root weevils. He states that apple waste containing about 20 per cent of moisture was found more attractive than super-dried bait, and that sodium fluosilicate was the most suitable poison to use with apples containing that percentage of moisture. Two applications of the bait are recommended, the first in April and the second in June.

#### (c) BAITS FOR THE JAPANESE BEETLE

A study of the chemotaxis of the Japanese beetle was begun in 1922 at the Japanese Beetle Laboratory in New Jersey, and since that date several persons have worked on it, but some of them have never received credit in the published papers on this subject. This is particularly true of F. J. Brinley, who did the work in 1923 and discovered that geraniol was the most important attractant used. Richmond and the present writer continued the work in 1924, the former doing the field-work and the latter the laboratory work. Some of Richmond's results have been published, but since those of the writer were only preliminary they still remain unpublished.

The first authentic report on this subject is by Smith (76), who states that in chemotactic studies it has been found that Japanese beetles are strongly attracted by geraniol, and nearly 50,000 beetles in 1924 were collected from baits containing this substance. Bait mixtures, containing bran, molasses, and geraniol retain the odor for a long time if protected from the rain. Eugenol, citral, and citronellol as attractants, and tar oil as a repellent, appear to have some value.

Richmond (66) gives a detailed report on this subject and tells about the earliest experiments conducted. Since the beetles were known to have favored food plants and were strongly attracted to ripening fruit, various chemicals were tested in 1922 to ascertain if the fruit odors might be imitated. To determine whether beetles could be attracted to the sources of odors, a number of essential oils were sprayed on foliage. The results indicated that the oils of sassafras, hemlock, mustard, and lemon, and iso-amyl valerate were somewhat attractive. More detailed experiments were conducted in 1923 and a large number of compounds were studied. Bran-bait mixtures, put in cans which hung in trees, were used. Among the oils, sassafras and clove were easily the leaders, while ethyl alcohol, geraniol, and eugenol proved to be the most important constituents. In 1924 greater detailed studies were undertaken. The adult beetle was found exceedingly susceptible to the influence of color, odor, temperature, humidity, and light. The six leading chemicals tested are geraniol, eugenol, citronellal, citral, citronellol, and diphenyl ether. Geraniol proved to be far superior to the other five. In other experiments emulsions were tested. When cloths (1 foot square) were dipped in a 10 per cent emulsion of geraniol and suspended in orchards (pl. 1, A), beetles were drawn as if by a magnet and 13,000 beetles were collected on 12 cloths over a period of 5 successive days. In 1925 and 1926 this project was much expanded so that it included the testing of various types of bait cans and bait traps. The best type of trap devised was cylindrical in shape. A single one of these caught over 13,000 beetles in 8 hours. Richmond's summary follows:

Geraniol is clearly the primary attractant of the Japanese beetle but its combination with eugenol materially lowers the cost and increases its effectiveness. During the summer of 1924 over 65,000 beetles were actually collected from the bait can experiments. Nearly 50,000 of these beetles were present on geraniol baits alone. The results of experimentation in 1925 and 1926 were in keeping with these remarks, but, inasmuch as more extensive tests were conducted, the number of beetles collected was proportionately greater. The activities of the adult varied with temperature, humidity and vapor pressure. Females are attracted approximately one-third more frequently than males when geraniol and most other chemicals are employed. Molasses has only a slight attractive

value. Satisfactory traps have been evolved and it seems possible that they will have considerable value in reducing the number of beetles in a given orchard. Bran retains odors over long periods if protected from the rain. Geraniol has been satisfactorily incorporated in poison sprays although its odor is not retained for a long enough period. To this end experiments on the absorption of this chemical on charcoal, clays, etc., are under way. The value of geraniol, when used in connection with a contact spray, has been demonstrated. Eugenol, citral, citronellol and citronellal follow geraniol as attractive agents.

It is further stated (3) that methods have been devised whereby geraniol may be used to concentrate the beetles in a relatively small area. It was found that by spraying less than an acre of orchard with geraniol, beetles could be drawn on the leeward side of the orchard for a distance of nearly one-half mile within the first 15 minutes after the spray had been applied. This makes it possible to destroy large numbers of beetles with a comparatively small quantity of a contact spray.

Van Leeuwen and others (87, 90) determined that acetic acid, an accumulation of beetles, geraniol, and fermented apple juice attract these beetles. It was discovered that the beetles would gorge themselves upon foliage sprayed with a mixture of lead arsenate and refined sugar, on trees to which they had been attracted by geraniol (pl. 1, B). More beetles fed on this foliage than on unsprayed leaves, and consequently the mortality was greater than ever before obtained. Smith (78) more recently reports that a combination of lead arsenate and refined cane-sugar sirup has been found useful as a spray on non-economic plants. The beetles are strongly attracted to it and eat it readily. He says that this preparation is probably one of the most effective lethal sprays yet devised for the Japanese beetle. Owing to its tendency to injure foliage it is not recommended for use on economic plants.

Metzger (52) and Richmond and Metzger (68) describe various types of traps, one being called the standard bait trap. Each kilogram of the standard bait contains 500 grams of bran, 455 grams (350 cc.) of molasses (refiners' sirup 75 per cent), 44 grams (40 cc.) of glycerine, and a quantity of an attractant. With geraniol as the attractant making 5 per cent of the prepared bait, the bran-glycerine-molasses mixture does not deteriorate to any marked degree when exposed to the weather, and its attractive odor has been retained more than three years in some traps. In practice, baits were renewed twice a month, 150 grams of the prepared bait being put in each trap. The best bait, however, was found to be a technical geraniol, 58.8 per cent pure, used in the proportion of 2.5 per cent with eugenol in the proportion of 0.25 per cent of the total material. The total number of



beetles caught in 39 traps in 1926 was about 2,000,000, one trap catching 13,476 in one day. These traps were used also in connection with ecological investigations, and to obtain data on the degree of infestation at different points in different years. Beetles are caught in the traps before any are observed in the immediate neighborhood. As a result of these investigations various types of traps have been put on the market by commercial firms. In the 1929 report on the Japanese beetle, Smith (78) has the following to say about geraniol and traps:

Several years ago chemotropic investigations revealed that geraniol, one of the higher alcohols, was extremely attractive to the Japanese beetle. Few, if any, other insects have been found to be attracted to any degree by this chemical and it is apparently a specific for this insect. In commerce it is commonly used as an ingredient in the cheaper perfumes. Geraniol has been utilized in several ways in the control of the beetle; these include combining it with poisoned baits, as a means of concentrating the beetles in a small area where they may be killed with contact sprays, or more often as a constituent of baits used in mechanical traps. The Japanese beetle traps have come into wide use by residents in the suburban area around Philadelphia. In conjunction with spraying, the traps are useful in capturing large numbers of beetles. During the summer of 1929, 500 traps were placed on a 15-acre estate in the heavily infested district near Roxborough, Pennsylvania. The record of collections in these traps during the period between July 9 and August 23 gives a total of 1,874½ pounds of adult beetles and represents approximately 10,000,000 individuals. Many types of beetle traps are now on the market, ranging in price from 10 cents upward. The traps have not yet become sufficiently effective to warrant their use on farms. In fact, the presence of large numbers of traps may attract many beetles which are not captured, with the result that the grub population in the soil, in the vicinity of the traps, is greatly increased over what it would have been had the traps not been used.

During the past few years traps have come into general use for catching large numbers of Japanese beetles, but for various reasons a large percentage of the insects attracted to the traps are not caught; therefore, Mehrhof and Van Leeuwen (49) devised and perfected an electric trap (pl. 2) which not only attracts the beetles but kills practically all of them that come to it. This trap, in the form of a hollow cube, is 3 feet on each side, with parallel wires,  $\frac{5}{8}$  inch apart, on all four sides and on the top. The most effective bait was geraniol emulsion, sprayed on peach foliage which was suspended in the center of the trap. By this method beetles were at times attracted from a distance of one-fourth mile.

Siegler and Brown in 1927 (74) first published on the idea that attractive baits might be used advantageously in scouting for injurious insects. During the season of 1929 the Federal Plant Quar-

tine and Control Administration made practical use of this idea by installing bait traps along the edges of the Japanese-beetle infested zones. So far little has been published on this particular phase of the work. According to the report of Secretary of Agriculture Hyde (27) the use of beetle traps at Baltimore and Washington, and in Alexandria County, Virginia, has resulted in the collection of great numbers of beetles. The possibility of substantial control at such isolated points by this method will thus be given. It has already been demonstrated that enormous quantities of beetles can be collected by trapping. In fact, on a single property in Pennsylvania (not New Jersey as reported) nearly a ton of beetles were thus collected in 1929. In the heavily infested areas, such trapping is of little value unless the employment of this method is general. Van Leeuwen (88) states that 25,000 of the Government standard traps, which he illustrates, were used by the Plant Quarantine and Control Administration during 1929 in its scouting work to determine the presence of beetles. Rex (65) illustrates and briefly discusses these traps and gives the bait formula recommended by the Japanese Beetle Laboratory in New Jersey. Van Leeuwen and Metzger (89) give the very latest information about traps for the Japanese beetle. They recommend the following formula for one baiting of a standard trap.

Geraniol (at least 58 per cent pure).....	15	grams (4 teaspoonfuls)
Eugenol (U. S. P.).....	1.5	grams ( $\frac{1}{2}$ teaspoonful)
Bran .....	75	grams ( $1\frac{1}{2}$ cups)
Water .....	13	cc. (1 tablespoonful)
Molasses .....	39	cc. ( $2\frac{1}{2}$ tablespoonfuls)
Glycerine (C. P.).....	6	cc. ( $1\frac{1}{2}$ teaspoonfuls)

Figure 4 was drawn by the present writer and illustrates the various parts of one of the standard traps.

At this place a few more remarks concerning the attractiveness of geraniol should be made. The effort is usually made to correlate attractive odors either with the food or opposite sex of an animal; but in some cases it is questionable whether food, or sex, or some unknown factor, is involved. For example, why should the banana-like odor of amyl acetate attract grasshoppers, or certain beetles? And why does the odor from the catnip plant attract members of the cat family? In regard to the attractive power of geraniol, a food odor is probably involved, although we know little about it. Smith (76, p. 59) and Smith and Hadley (79, p. 58) in two of their earlier reports remark that several of the essential oils were found to be highly attractive to the Japanese beetle, and that on studying these oils, it was discovered that one of the higher alcohols, geraniol, was

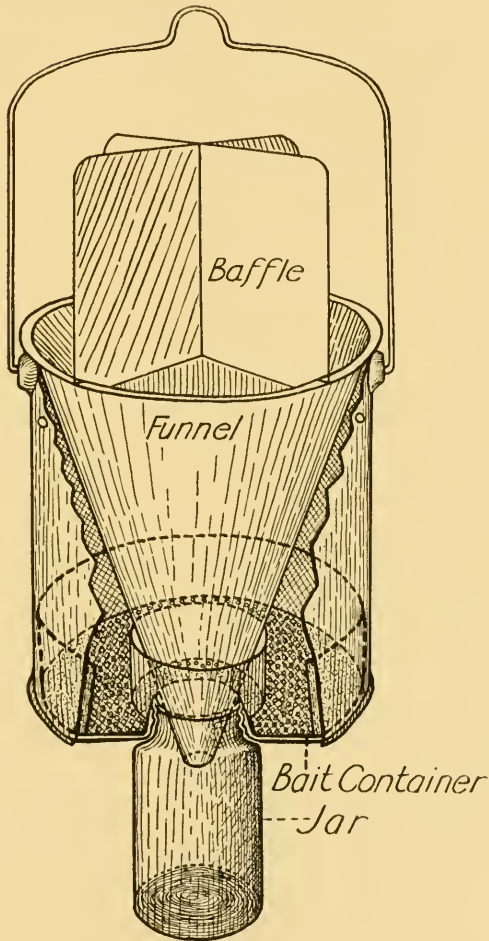


FIG. 4.—Japanese beetle trap, used by the Federal Plant Quarantine and Control Administration, showing parts of it in a cut-out perspective view. It is one-fourth natural size and was drawn by the writer by using a 1929 trap and a drawing of a 1930 trap, the latter being furnished by Mr. Courtney. The beetles, attracted by the odor from the bait in the bait container, fly directly into the funnel or strike the baffle and then fall down through the funnel into the fruit jar, where they cannot escape because they can neither fly out nor climb the walls of the jar.

a constituent of all the oils found to be distinctly attractive. Tests were made of a series of the preferred food plants, and in all cases these plants contained geraniol in varying quantities. The present writer has seen no report by a chemist concerning the last statement; but as regards fruit, Power and Chesnut (61) found geraniol in apples. They used only the parings of the McIntosh, one of the most fragrant varieties of apples, and say that geraniol, either in the free state or in the form of esters, is probably contained in varying quantities in all the numerous varieties of apples, although to the greatest extent in those which possess its distinctive odor. Power and Kleber (62) tell us that the two oils, one from sassafras bark and the other from sassafras leaves, are fundamentally different in regard to their chemical compositions. Oil from sassafras bark contains eugenol but no geraniol, while oil from sassafras leaves contains geraniol but no eugenol. There are also other differences. The fact that Japanese beetles were observed to be fond of sassafras leaves led to tests in which the oil of sassafras was used; after learning that oil from sassafras leaves contains geraniol it was only natural to continue using geraniol in bait mixtures.

A popular impression is that Japanese beetles are fond of geraniums and that our supply of geraniol comes from these plants, but this is far from the truth. Ballou (4) informs us that these beetles do feed upon the flowers and to a limited extent upon the foliage of cultivated geraniums (*Pelargonium* spp.), but with deleterious effects to themselves, because this food is toxic to them. Most of our commercial supply of geraniol is said to be derived from the oil of citronella, but in perfumery much of it also comes from the oil of palmarosa or Turkish geranium. Geraniol also occurs in the oils of lemon-grass, geranium, rose, sassafras leaves, and other essential oils.

#### (D) BAITS FOR OTHER BEETLES

Since 1916 it has been reported in numerous publications that certain sugarcane cockchafers in Australia can be attracted by odors from various chemicals and by the aromas distilled from their food plants, but it seems that so far no practical results have been obtained. Other reports by Jarvis (34, 36), however, indicate that poisoned baits have a practical value in helping to control the grubs of these beetles.

For years it has been known that poisoned-bran baits are of considerable value against the common May beetles and more recently Vickery and Wilson (92) used a bait consisting of 20 pounds of

wheat bran, 1 pound of Paris green, 1 quart of sirup, and the juice of 3 lemons or 1 teaspoonful of anise oil successfully against a wingless May beetle.

McKinney and Milam (48) and Gilmore and Milam (19) have successfully used a poisoned-bran bait against the grubs of the green June beetle in tobacco-plant beds and in a tobacco field.

A large white grub of a dynastid beetle is the most serious pest of sugarcane in St. Croix. The control recommended in 1916 by Smith (80) was a poisoned bait.

Poisoned-bran mash was the best control used by Cooley (10) in 1917 against the spinach carrion beetle.

Using a poisoned-bran bait in 1916 Scholl (71) destroyed the striped blister beetle on alfalfa and tomatoes.

Newman (59) in 1929 reports that a poisoned-bran bait gave excellent results against a subterranean clover weevil.

Jack (32) in 1928 reports that over 95 per cent of certain weevils in a maize field were killed by one application of a bait consisting of 1 pound of sodium arsenite, 8 pounds of sugar, and 10 gallons of water on chopped fodder.

During the seasons of 1926, 1927, and 1928, over 1,000 traps, containing fermenting sugar or molasses, were used in a peach orchard in Pennsylvania for the purpose of trapping oriental fruit moths. Frost and Dietrich (16) report that incidentally 40 families of beetles, including 188 genera and 258 species, were also caught in these traps.

Snapp and Swingle (81) have recently tested a large number of aromatics, including various steam distillates and other odorous materials derived from the food of peach insects. A large number of chemicals were found, under orchard conditions, to be slightly attractive to various peach insects, as well as to the plum curculio, but none showed much promise of being valuable from the standpoint of control.

Garman and Zappe (18) have also recently conducted many tests, trying to find attractants and repellents for the plum curculio. They remark that curculios are very sensitive to odors. Acetaldehyde and malic acid were the only substances used in the laboratory which showed much attractive power, but when these substances were tested in the field no curculios were trapped.

In conclusion under this heading a few remarks may be made about the present writer's (45) results obtained when testing potato beetles in an olfactometer. In this study no baits were actually used, but it was proved for the first time that plants (not flowers) attract insects

by emitting odors. Since odors from the steam distillates and emanations from 4 or 5 species belonging to the potato family attracted potato beetles, it was then suggested that the chemist tell us what constituent or constituents, common to these plants, did the attracting. If we had this information, we might be able to use these substances in poison baits.

(E) REPELLENTS USED AGAINST BEETLES

Under this heading many repulsive substances are regarded as repellents, but for some of them a more appropriate word would be deterrents; nevertheless, there is little distinction between these two words. Let us define a repellent as an odorous substance, which by means of its unpleasant exhalations repels insects before they have touched it; and a deterrent as an inodorous substance which repels insects after they have touched it. Thus defined, a deterrent repels mostly, if not entirely, through the sense of touch; while a repellent operates either through the sense of smell or, if its exhalations are poisonous, then through the breathing pores. These definitions are easily made, but it is perhaps almost impossible to have a deterrent which is totally inodorous to insects; and furthermore, other factors are often involved. These terms have been used loosely by various writers, and since this subject is yet confused, the present writer will still continue to use them without attempting to explain how the enumerated substances repel, deter, or otherwise keep insects away from plants. The following remarks by the writer's reviewers help to elucidate the subject.

In regard to the Japanese beetle, Doctor Van der Meulen and Mr. Van Leeuwen believe that there should be another subdivision of repellents to include those substances which mask attractive odors; for example, those from geraniol. We might call these "maskers" or "neutralizers," because they repel from a short distance merely by covering up or neutralizing the attractive odors. Relative to "inodorous" materials, Japanese beetles may also be repelled before touching dusted or sprayed food by means of the sense of sight. In regard to the repellency of the arsenates, the subject of toxicity should also be considered; but at present we are not able to evaluate the various factors, including the senses of sight, smell, touch, taste, and probably a general sense connected with the digestive system.

After reading the preceding definitions, Dr. F. L. Campbell proposed that attractants, now usually called attractants, should be divided. The odor from geraniol causes the Japanese beetle to orient and to move toward this substance; therefore, geraniol is a true

attractant. In the course of random movements certain other insects may come upon sugar, for example, which holds them after they have touched it. In this case, Campbell says that sugar might be called a true "arrestant." If insects have true senses of smell and taste, an attractant then attracts through the sense of smell and an arrestant arrests through the sense of taste.

Since entomologists already know much of the following information, only the more important references consulted will be cited here. The substances inodorous or slightly odorous to us, which have been found repulsive to insects, may be briefly discussed as deterrents. Whitewash may be considered the first deterrent used. White-washing the bases of fruit trees has been practiced for years. It is still questionable whether such a practice is of any real economic importance, but its advocates claim that the lime in it has a tendency to drive away noxious insects and may be slightly injurious to insect eggs. The most improved and best mixture of whitewash, as recently recommended in France, consists of lime, calcium arsenate, lime sulphur, and water. In this case the lime might act as a deterrent and the lime sulphur, which has a strong disagreeable odor, as a repellent. One of the most efficient deterrents used in the United States is air-slaked lime, which is employed extensively for dusting melons and cucumbers to prevent the attacks of the striped cucumber beetle. It is also said to prevent injury to stored beans by the bean weevil. In Germany a mixture of white sand and hydrated lime has recently been used to deter flea-beetles. Paints, particularly white-lead paint, are recommended for preventing boring beetles from entering wounds on fruit trees. The coat of paint covering the fresh wound preserves the wood and also acts as a mechanical barrier to the beetles. Lead arsenate, when sprayed or dusted on foliage, deters a number of insects, including the Japanese beetle, western cabbage flea-beetle, desert corn flea-beetle, and striped cucumber beetle. Most of the arsenicals deter the Mexican bean beetle. Bordeaux mixture sprayed on the leaves of eggplant and potatoes deters flea-beetles and the potato leafhopper, which causes the disease called "hopperburn."

In regard to repellents used against beetles, the first ones used were probably decoctions of certain poisonous plants. As early as 1848 leather waste from tanneries, when put among plants in Germany, was found to be a repellent against flea-beetles, and more recently in France sawdust coated with coal tar when placed among the plants repelled these insects. The most successful repellent used against these tiny insects and the striped cucumber beetle in the United States

is nicotine dust. Since it is almost impossible to kill flea-beetles by using arsenicals or other insecticides, the repellent method is an important control measure.

In Europe there has been considerable experimenting with repellents to keep beetle larvae, particularly white grubs, from attacking the roots of plants. The odorous substances were usually worked into the soil around the bases of the plants, but it is doubtful whether much protection ever resulted. In France and Belgium crude naphthalene mixed with sand was used. In France three other repellents were found more or less effective—first, residue of glue; second, naphthalene and kerosene mixed with sawdust; and third, crude oil mixed with lime, plaster of Paris, and feces. In Germany sulphur was worked into the ground around strawberry plants. In England naphthalene was successfully used against wireworms in gardens, and in Australia crude naphthalene was effective against wireworms injuring sugarcane.

McColloch and Hayes (40) have recently reviewed the methods and enumerated the repellents used to protect germinating seeds and roots and to prevent the invasion of the soil by underground insects, particularly beetles. Numerous substances have been recommended as repellents, including crude carbolic acid, turpentine, naphthalene, paradichlorobenzene, creosote, coal tar, oils of lemon and tansy, kerosene, and phenol. They state that no satisfactory repellent has yet been found which can be depended upon under varying conditions existing in the soil. They believe that this subject needs further investigation.

Since the Japanese beetle is fond of ripening fruit, particularly apples and peaches, and since it is not advisable to spray early fruit with arsenicals, ripening fruit should be protected by other means. Therefore, much experimental work has been done to develop an effective repellent to take the place of the arsenicals. Metzger and Grant (54) have developed smudge candles, which, when lighted and hung in peach trees, give off ill-smelling smoke for a period of five to eight hours. The mixture, to be burned slowly without producing a flame, was put in a wire-screen cylinder, 31 inches long and 2.25 inches in diameter. In conclusion they say that wood flour and potassium nitrate, when properly mixed, form a satisfactory base for smudges. The fumes from pine-tar oil, Dippel's oil (bone oil), and a commercial mixture of chloronaphthalenes, when given off from burning smudge candles, are definitely repellent to Japanese beetles. Air currents in the orchard, however, prevented the repellent smoke from giving satisfactory control of beetles on early peach trees.



Metzger (53) describes five methods used in testing 430 materials, alone and in combination, as repellents for the Japanese beetle. Under method 1, "testing material in comparison with a known attractant," 306 materials were tested, and 45 of them decreased the attraction of the geraniol-eugenol combination. Beginning with the one most repellent, the first ten in the list are o-cresol, pine-tar oil, phenol, Dippel's oil, high boiling tar acids, coal-tar neutral hydrocarbon oil, trichlorobenzene, crude dichlorobenzene No. 1, alpha chloronaphthalene, and crude dichlorobenzene No. 2.

Another difficult test has been to find a successful repellent for wood-boring beetles. The first object is to prevent them from entering the living trees, lumber, or manufactured wooden articles, and the second object is to kill them or drive them out of their burrows after they have once entered. Little success has yet been accomplished along this line, but it is easier to prevent their entrance than to control them later. In Brazil a mixture consisting of crude carbolineum 1 part, quicklime 10 parts, and water 40 parts is painted on the trunks of citrus trees to prevent the entrance of borers. In the United States carbolineum and creosote are often applied to the trunks of aspen trees in forests to prevent the entrance of the aspen borer. A successful repellent has recently been recommended by Pettit (60) against flat-headed borers which do considerable damage to apple trees. Following a special procedure a thick solution is prepared by using 50 pounds of laundry soap, 3 gallons of water, 25 pounds of flake naphthalene, and 2 pounds of flour. After warming and thinning this mixture to the consistency of heavy cream, it is applied several times with a brush to the trees.

The *Lyctus* powder-post beetles, which cause much damage to hardwood lumber, implement handles, furniture, etc., throughout the world, may be deterred and repelled by several substances. In the United States, according to Snyder (82), the usual method recommended is to immerse the lumber, already infested or liable to infestation with these borers, in vats of kerosene, or in a mixture of creosote and kerosene, or in one of creosote and naphtha. The writer has recently been told that these beetles may be repelled by using coal-tar creosote and orthodichlorobenzene. The lumber and handles which can not be treated by the vat method may be stored in closed sheds and close-fitting houses and then sprayed at intervals with these chemicals. In Great Britain lumber stacked in the open is often treated with cold paraffin mixed in equal parts with oil of cedar, linseed oil, or a heavy mineral oil. To lumber stored in sheds orthodichlorobenzene is applied with a brush or sprayer, or paradichlo-

robenzene is scattered on top of the stacks and suspended in bags from the roofs of the sheds.

Carpet beetles, also called "buffalo moths," often do considerable damage to carpets, woolens, furs, feathers, and upholstered furniture. One of the control measures is to prevent them from coming in contact with these articles by using repellents, such as naphthalene in the form of flakes and moth balls, paradichlorobenzene, or camphor, or by the use of red cedar chests.

## 2. ORIGINAL WORK ON MEXICAN BEAN BEETLE

In 1928, Mr. J. E. Graf, Assistant Chief of the Bureau of Entomology, handed the writer a manuscript entitled "Some chemotropic responses of the Mexican bean beetle," by Wallace Colman, who tested over 200 materials, but found only a few to be attractive while a larger number were repellent. According to the results in this unpublished manuscript, which deals with the sense of smell alone, the following seemed to be attractive: banana peel, amyl acetate, vanillin, coumarin, corn sirup, honey, and molasses of the higher grades; while certain lead and arsenic compounds, including lead arsenate, seemed to be repellent. Using different methods the present writer tested all of the above supposed attractants, but found only the corn sirup and molasses to be attractive, while lead arsenate proved to be repellent.

### (A) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING AN OLFACTOMETER

Using the writer's (45) olfactometer, with the plant chamber disconnected, no important results were obtained, but the following remarks may have some theoretical interest. On several occasions fresh bean leaves were put in the small bottle, used for holding the odorous substance to be tested. In each test in which only a few leaves were used the odor or exhalation from the leaves was attractive to the bean beetles, although the highest attraction was only 57.9 per cent. In two other tests the bottle was filled full of leaves. The results (61.8 per cent and 72.5 per cent), instead of showing attraction, showed repulsion, indicating that attractants when concentrated become repellents. The odors from table molasses (1 part molasses and 1 part water) and the water extract (diluted juice) of bean leaves were also found to be slightly attractive.

The following, used in minute quantities, were repellent: oil of peppermint, creosotum, nicotine sulphate, banana peel, amyl acetate, and geraniol.

## (B) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING FEEDING METHOD

A search for attractants and repellents was begun in 1928, but during that year no important results were obtained. The following remarks, however, may be of some interest. A liquid, highly scented with skatol, when sprayed on bean foliage in the laboratory did not delay the eating of the leaves. A piece of cotton, scented with oil of peppermint, was put among some bean leaves. The leaves were eaten as usual. Four odorous powders were prepared with the aid of heat by using (1) nicotine sulphate and lead arsenate; (2) nicotine sulphate and lime; (3) tar and lead arsenate; and (4) tar and lime. When these powders were mixed with soap solution and sprayed on bean foliage in the laboratory the sprayed leaves were eaten almost as readily as were the untreated leaves nearby.

A wire-screen cage, 4 feet long, 3 feet wide, and 3 feet tall, containing hundreds of adult beetles, was put in the insectary. A pan containing bran bait was suspended in each corner. The first bait was flavored with black-strap molasses; the second, with amyl acetate; the third, with vanillin; and the fourth contained only bran and water. The second and third baits each attracted only a few beetles; the fourth, many; while the first, more than twice as many as the fourth. It thus seems that the molasses bait was slightly attractive.

The preceding test was repeated by putting a pan containing black-strap molasses and water in each corner, an aromatic being put in each of three pans. The pans containing coumarin and vanillin attracted practically the same number of beetles; the pan containing amyl acetate, several more; and the pan containing only molasses and water, a few more, but the attraction was not significant.

The foregoing test was repeated by putting three pans in the cage. One contained the juice from bean leaves; the second, the remaining pulp of the leaves and diluted table molasses; and the third, diluted table molasses. The first and third attracted beetles in equal number, while the second attracted three times as many, not a sufficient number to appear significant.

A pan containing fermenting table molasses was next put in the center of the cage. For five days the beetles in it were counted, but no striking attraction was noticed at any time.

Not yet having found any substance which seemed promising as an attractant, the writer in 1929 decided to test a large number of materials. After spending much time, 104 aromatic chemicals, 3 brands of molasses, 2 varieties of canesugar, and 1 highly scented honey were tested. The method consisted of testing 8 substances at one time in a small wire-screen cage. This method was found to be

faulty, yet the writer believes that if a strong attractant in the proper concentration had been used striking results could have been obtained quickly. No important results were really obtained, but the following remarks may be worth recording. Using water as a control, methyl anthranilate, benzaldehyde, methyl benzoate, terpinyl acetate, dibenzyl ether, tertiary amyl alcohol, and ethyl iso-valerate seemed to be more or less attractive, but not sufficiently so to be significant. The most promising chemical, methyl anthranilate, was tried in the bean patch but attracted no beetles. In the preliminary tests while using water and portions of bean leaves as controls, a good grade of table molasses diluted with water was nearly always preferred to the controls. Fermenting table molasses was attractive up to the vinegar stage of fermentation, after that its attractiveness ceased. During warm weather when the beetles were thirsty, a long series of tests was conducted to ascertain their preferences when given water, molasses, sugar, and honey. The final results showed their preferences to be: (1) water alone; (2) corn sirup and granulated sugar, practically the same; (3) table molasses and sugar sirup, the same; (4) brown sugar; (5) honey; and (6) black-strap molasses. The sugar sirup consisted of boiled brown sugar and water (about 1 to 1). The brown sugar was a saturated solution. Each of the others was half sweet substance and half water. On August 5 and 12, pans containing table molasses, corn sirup, and black-strap molasses were put between rows of beans in the garden. Observations were taken thereafter for several days, but not a bean beetle was seen in the pans, although many moths and certain other insects were caught in the baits.

(C) SEARCH FOR ATTRACTANTS AND REPELLENTS, USING AN IMPROVED  
FEEDING METHOD

In order to obtain comparative results which could be treated statistically, four cages were constructed. Each cage was 8.75 inches square, 0.75 inch deep (inside dimensions), and had a wooden bottom and a top of wire-screen and glass (fig. 5, A). The substances to be tested were put on pieces of cardboard (W, X, Y, and Z), 1.75 inches square, which were arranged in a row, being equally spaced between themselves and the sides of the cage. From left to right the positions of the cardboard were numbered 1, 2, 3, and 4. In the first series of tests the substances were arranged in the four cages as indicated by the first row in the four diagrams (B, C, D, and E); in the second series, as indicated by the second row; in the third series, as indicated by the third row; and in the fourth series, as

indicated by the fourth row. According to this arrangement of food, no two rows in the same cage were exactly alike; likewise, no two rows of all 16 rows were identical, although the distribution of food was not so complete. These four series of tests were conducted during the forenoon, and then usually repeated in the afternoon. Each

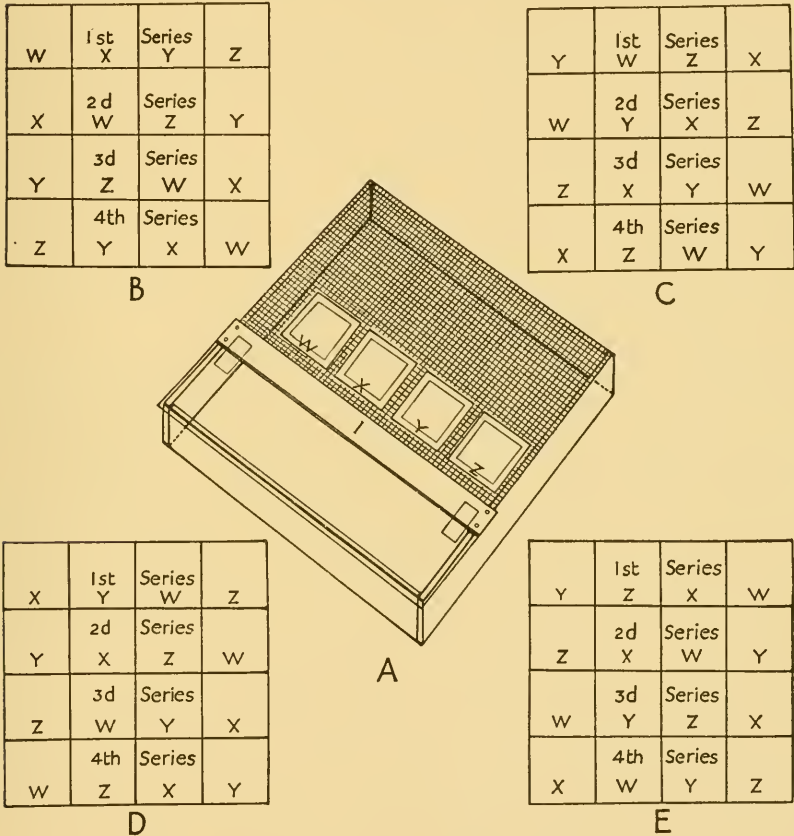


FIG. 5.—Diagrams of wire-screen cage (A) and arrangement of substances (B, C, D, and E) to be tested by bean beetles. See text, p. 32, for further explanation.

individual substance used was therefore tested 16 times in the forenoon and usually 16 times in the afternoon.

It was difficult to decide whether tests of this kind should be conducted in the dark-room or in the well-lighted laboratory. After trying the dark-room it was observed that the bean beetles did not eat freely either in artificial light or in total darkness. So it was decided to place the cages on a table by a south window, but not in the

direct sunshine. As suspected under these conditions, the number of beetles counted in the four positions varied greatly. More beetles were always counted in the outer positions (Nos. 1 and 4) than in the inner ones (Nos. 3 and 4). This was caused largely by the beetles following the sides of the cage while moving toward the window. In 40 series of tests, selected at random, 67.04 per cent of the beetles were counted in the outer positions and 32.96 per cent in the inner positions. The following percentages were counted in the four positions: 37.06 per cent in position 1; 17.01 per cent in position 2; 15.95 per cent in position 3; and 29.98 per cent in position 4. Since each substance used lay in all four positions during any one series of tests, these large differences did not supposedly change the arithmetic mean, but they greatly affected the probable error, because each number of beetles counted on a substance was considered a statistical item. Since the beetles ate more freely during the forenoon than during the afternoon, the probable errors were further affected.

In addition to the preceding statements, the general plan in conducting these tests was to put 60 beetles of approximately the same age and physiological condition in each cage. The number of beetles on (or touching) the food was counted at intervals of 45 minutes, and this number was considered a statistical item. The food was renewed whenever necessary to keep it in an appetizing condition, and to prevent contamination it was usually put on unused pieces of cardboard. Since the beetles had a tendency to congregate at the ends of the cages nearest the window, the cages were often turned end for end, thus causing the insects to scatter more evenly. The daily temperature and relative humidity in the laboratory were recorded, and a record of the outside climatic conditions was also kept. In brief, everything possible was done to obtain reliable data which could be treated statistically. The arithmetic mean and probable error are stated in tables 2 to 11 for reference in connection with the following discussion. Since the statistical items were never less than 16, the following formula for calculating the probable error was used—

$$P. E. m = \pm 0.6745 \frac{\sigma}{\sqrt{N}}$$

(1) *Beetles can distinguish differences between water and salty liquids.*—To determine whether Mexican bean beetles “like” or “dislike” the four classes of substances which produce the four human attributes of taste, many series of tests were conducted. The results obtained are given in tables 2 to 5.

To ascertain whether these insects “like” salty water, sodium chloride, potassium nitrate, and magnesium sulphate (epsom salts)

TABLE 2.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and salty liquids*

Methods of feeding salty liquids	Total number of beetles on cotton	Mean and probable error	Relative value of beetles on cotton	Number of set of beetles	Date	Number of tests
Water on cotton (control) .....	106	$3.31 \pm 0.44$	1.00	} 16	Aug. 29-30	32
Sodium chloride on cotton .....	13	$0.41 \pm 0.12$	0.12			
Potassium nitrate on cotton .....	30	$0.94 \pm 0.28$	0.28			
Magnesium sulphate on cotton .....	56	$1.75 \pm 0.27$	0.53			

TABLE 3.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and sour liquids*

Methods of feeding sour liquids	Total number of beetles on cotton	Mean and probable error	Relative value of beetles on cotton	Number of set of beetles	Date	Number of tests
Water on cotton (control) .....	150	$9.38 \pm 1.12$	1.00	} 16	Aug. 31	16
Acetic acid on cotton.	36	$2.25 \pm 0.61$	0.24			
Hydrochloric acid on cotton .....	31	$1.94 \pm 0.47$	0.21			
Lemon juice on cotton.	27	$1.69 \pm 0.44$	0.18			

TABLE 4.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and bitter liquids*

Methods of feeding bitter liquids	Total number of beetles on cotton or leaves	Mean and probable error	Relative value of beetles on cotton or leaves	Number of set of beetles	Date	Number of tests
Water on cotton (control) .....	171	$10.69 \pm 0.84$	1.00	} 14	Aug. 16	16
Strychnine on cotton.	102	$6.38 \pm 0.78$	0.60			
Quinine on cotton....	83	$5.19 \pm 0.72$	0.49			
Picric acid on cotton.	46	$2.88 \pm 0.26$	0.27	} 20	Sept. 14	32
Leaves, sprayed with water (control) ..	198	$6.19 \pm 0.29$	1.00			
Leaves, sprayed with beetle extract .....	172	$5.38 \pm 0.39$	0.87			

were used at the rate of 1 gm. of salt to 25 cc. of water (table 2). Pieces of cotton of equal size were wet with tap water and with the three salty solutions, and then they were put on the pieces of cardboard, as already described.

(2) *Beetles can distinguish differences between water and sour liquids.*—To ascertain whether the above statement is true, three

TABLE 5.—*Tests to determine whether Mexican bean beetles can distinguish differences between water and sweet substances*

Methods of feeding sweet substances	Total number of beetles on cotton or leaves	Mean and probable error	Relative value of beetles on cotton or leaves	Number of set of beetles	Date	Number of tests
Water on cotton (control) .....	34	1.06 ± 0.23	1.00	16	Aug. 29-30	32
Cane sugar on cotton..	307	9.60 ± 0.75	9.03			
Grape sugar on cotton.	87	2.72 ± 0.35	2.56			
Saccharine on cotton..	15	0.47 ± 0.12	0.44	20	Sept. 13	32
Leaves, sprayed with water (control) ....	141	4.41 ± 0.36	1.00			
Leaves, sprayed with cane sugar .....	254	7.94 ± 0.41	1.80			
Leaves, sprayed with grape sugar .....	202	6.31 ± 0.44	1.43			
Leaves, sprayed with saccharine .....	113	3.53 ± 0.27	0.80			
Leaves, sprayed with water (control) ...	108	3.38 ± 0.33	1.00	21	Sept. 16	32
Leaves, sprayed with table molasses .....	261	8.16 ± 0.51	2.42			
Leaves, sprayed with corn sirup .....	174	5.44 ± 0.40	1.61			
Leaves, sprayed with black-strap molasses.	203	6.34 ± 0.41	1.88			

sour liquids were used, each of two being prepared at the rate of  $\frac{1}{2}$  cc. of glacial acetic acid (99.5 per cent) or hydrochloric acid (85.9 per cent) to 25 cc. of water, and the third at the rate of 4 cc. of lemon juice to 21 cc. of water (table 3).

(3) *Beetles can distinguish differences between water and bitter liquids.*—To determine whether the above statement is correct, four bitter liquids were used, each of three being prepared at the rate of



50 mg. of picric acid, quinine sulphate, or strychnine sulphate to 25 cc. of water. The fourth was prepared by adding 25 cc. of water to the macerated bodies of 20 live bean beetles. The resulting liquid, when filtered, was yellowish and to the writer had a bitter taste and an unpleasant odor. It was sprayed upon bean leaves, which when dry were cut into pieces, one inch square, then put on the pieces of cardboard, and finally fed to the beetles (table 4).

TABLE 6.—*Tests to determine whether bean foliage sprayed with sweetened arsenicals is more attractive to Mexican bean beetles than unsprayed foliage*

Leaves: un-sprayed and sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control)..	74	2.31 ± 0.35	1.00	18	Sept. 5	32
Calcium arsenate and sugar .....	106	3.31 ± 0.31	1.43			
Magnesium arsenate and sugar .....	131	4.10 ± 0.33	1.77			
Lead arsenate and sugar .....	132	4.12 ± 0.30	1.78			
Unsprayed (control)..	131	4.10 ± 0.38	1.00	22	Sept. 25	32
Magnesium arsenate and table molasses..	194	6.06 ± 0.40	1.48			
Magnesium arsenate and corn sirup.....	157	4.90 ± 0.49	1.20			
Magnesium arsenate and black-strap molasses .....	113	3.53 ± 0.40	0.86			

(4) *Beetles can distinguish differences between water and sweet liquids.*—To determine whether the above is correct, 24 series of tests were conducted by using six sweet solutions, each of five of them being prepared at the rate of 1 gm. or 1 cc. of granulated cane sugar, grape sugar (dextrose), a high quality table molasses, corn sirup, or black-strap molasses to 25 cc. of water; and the sixth at the rate of 20 mg. of saccharine to 25 cc. of water (table 5).

From the information given in tables 2 to 5, with additional notes, it may be concluded that Mexican bean beetles exhibit "likes" and "dislikes" when fed substances which produce the four human at-

tributes of taste. They "disliked" water containing salts, acids, bitter materials, and saccharine, but "liked" the other sweet substances, including cane sugar, grape sugar, table molasses, corn sirup, and black-strap molasses, and even showed preference between them. To the writer the saccharine solution was sweetest, but distasteful; the cane sugar, less sweet, and tasteful; and the grape sugar, least sweet, and less tasteful. The beetles showed "dislikes" and

TABLE 7.—*Tests to determine whether bean foliage sprayed with arsenicals, is repellent to Mexican bean beetles*

Leaves: un-sprayed, and sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control) .	191	5.97 ± 0.49	1.00	} 17	Sept. 3	32
Calcium arsenate ....	160	5.00 ± 0.62	0.84			
Magnesium arsenate..	177	5.53 ± 0.56	0.93			
Lead arsenate .....	111	3.47 ± 0.40	0.58			
Unsprayed (control)..	275	8.59 ± 0.67	1.00	} 17	Sept. 4	32
Calcium arsenate ....	177	5.53 ± 0.50	0.64			
Magnesium arsenate..	122	3.81 ± 0.42	0.44			
Lead arsenate .....	122	3.81 ± 0.48	0.44			
Unsprayed (control)..	172	5.38 ± 0.46	1.00	} 24	Sept. 27	32
Calcium arsenate ....	159	4.97 ± 0.35	0.92			
Magnesium arsenate..	104	3.25 ± 0.25	0.60			
Lead arsenate .....	101	3.16 ± 0.22	0.59			
SUMMARY of above:				} .....	.....	above 96
Leaves, unsprayed (controls) .....	638	6.64 ± 0.33	1.00			
Calcium arsenate ....	496	5.17 ± 0.29	0.78			
Magnesium arsenate..	403	4.20 ± 0.26	0.63			
Lead arsenate .....	334	3.48 ± 0.22	0.52			

"likes" in somewhat the same order. To the writer the picric-acid solution was most bitter, the quinine less bitter, and the strychnine least bitter. The insects "disliked" these solutions in about the same order. To the writer the solutions containing acetic acid and hydrochloric acid had practically the same degree of sourness, while the diluted lemon juice was sourer. The beetles also showed only slight differences between them. In regard to the salty solutions, the writer disliked only the magnesium sulphate solution, but the beetles preferred it to the other two.

(5) *Bean foliage sprayed with sweetened arsenicals is more attractive than unsprayed foliage.*—To ascertain whether the above is correct, 16 series of tests were conducted. The arsenicals were prepared as stated on the following page, then 1 gm. of granulated cane

TABLE 8.—*Tests to determine whether bean foliage sprayed with sweetened magnesium arsenate is more attractive to Mexican bean beetles than foliage sprayed with non-sweetened magnesium arsenate*

Leaves sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Magnesium arsenate (control) . . . . .	71	2.22 ± 0.26	1.00	} 23	Sept. 26	32
Magnesium arsenate and table molasses (2 to 50) . . . . .	192	6.00 ± 0.61	2.70			
Magnesium arsenate and corn sirup (2 to 50) . . . . .	114	3.56 ± 0.39	1.60			
Magnesium arsenate and black-strap molasses (2 to 50) . . . . .	122	3.81 ± 0.43	1.72			
Magnesium arsenate (control) . . . . .	82	2.56 ± 0.28	1.00	} 25	Sept. 30	32
Magnesium arsenate and black-strap molasses (2 to 50) . . . . .	132	4.12 ± 0.36	1.61			
Magnesium arsenate and black-strap molasses (1 to 50) . . . . .	115	3.59 ± 0.29	1.40			
Magnesium arsenate and black-strap molasses (½ to 50) . . . . .	134	4.19 ± 0.32	1.63			

sugar or 1 cc. of a high quality table molasses, corn sirup, and black-strap molasses was added to 25 cc. of the spray mixture (table 6).

According to the results given in table 6, it is again shown that these beetles like their food sweetened.

(6) *Bean foliage sprayed with arsenicals is repellent.*—To determine whether bean foliage sprayed with arsenicals is eaten as readily as are unsprayed bean leaves, 24 series of tests were conducted. The

leaves were sprayed with calcium arsenate, magnesium arsenate, and lead arsenate at the rate of 1 pound of powder to 50 gallons of water. The calcium-arsenate mixture also contained lime at the rate of 1.5 pounds to 50 gallons of water (table 7).

The results given in table 7 clearly show that arsenicals are repellent, but not sufficiently so to prevent the foliage from being eaten. Lead arsenate was most repellent, magnesium arsenate was less so, and calcium arsenate was least repellent. The word "deterrent" is probably the better expression in this case.

TABLE 9.—*Tests to determine whether water extract and steam distillate of bean leaves are attractive to Mexican bean beetles*

Methods of feeding leaves and liquids	Total number of beetles on leaves or cotton	Mean and probable error	Relative value of beetles on leaves or cotton	Number of set of beetles	Date	Number of tests
Leaves, unsprayed (control) . . . . .	190	5.94 ± 0.39	1.00	} 21	Sept. 18	32
Water on cotton . . . . .	28	0.87 ± 0.14	0.15			
Water extract on cotton . . . . .	167	5.22 ± 0.40	0.88			
Water extract and cane sugar (1 to 25) on cotton . . . . .	677	21.16 ± 0.82	3.56	} 21	Sept. 19	64
Water on cotton (control) . . . . .	415	6.48 ± 0.41	1.00			
Distillate on cotton . . . . .	436	6.81 ± 0.43	1.05			

(7) *Bean foliage sprayed with sweetened magnesium arsenate is more attractive than foliage sprayed with non-sweetened magnesium arsenate.*—To determine whether the above is true 16 series of tests were conducted by using magnesium arsenate (1 pound to 50 gallons water) with molasses added at the rate of 2, 1, and  $\frac{1}{2}$  gallons to 50 gallons of the spray mixture (table 8).

The results given in table 8 once more show that sweetened food is preferred to non-sweetened food.

On September 30 four small bean plants, each bearing six leaves, were sprayed. Two of these were sprayed with magnesium arsenate alone and the other two with a mixture of magnesium arsenate and black-strap molasses (1 to 50). One plant sprayed with the non-sweetened mixture and one with the sweetened mixture were put to

gether in one end of a cage, and the other two sprayed plants were arranged likewise at the other end of the cage. Soon after placing 100 beetles in the cage the insects climbed upon the sprayed foliage, paying apparently no more "attention" to the sweetened leaves than to the non-sweetened ones, but after a few hours and thereafter until October 3, when the experiment was ended, the sweetened leaves bore the more beetles and were the more eaten. The final result

TABLE 10.—*Tests to determine whether chemotaxis or phototaxis is more important in the finding of food by Mexican bean beetles*

Methods of feeding leaves and liquids	Total number of beetles on leaves or cotton	Mean and probable error	Relative value of beetles on leaves or cotton	Number of set of beetles	Date	Number of tests and remarks
Bean leaves, not sprayed (control).	68	2.12 ± 0.31	1.00	} 22	Sept. 23	32 tests. Beetles in direct sunshine.
Apple leaves not sprayed . . . . .	4	0.12 ± 0.02	0.06			
Green water on cotton . . . . .	196	6.12 ± 0.76	2.88			
Green sugar water (1 to 25) on cotton..	635	19.84 ± 0.99	9.34			
Bean leaves, not sprayed (control).	116	3.62 ± 0.24	1.00	} 22	Sept. 24	32
Mulberry leaves not sprayed . . . . .	19	0.59 ± 0.11	0.16			
Mulberry leaves, sprayed with sugar water (1 to 25)...	73	2.28 ± 0.30	0.63			
Bean leaves, sprayed with sugar water (1 to 25).....	221	6.91 ± 0.42	1.90			

showed that the sweetened leaves bore 69.7 per cent of all the beetles counted on the four sprayed plants.

(8) *Water extract and steam distillate of bean leaves tested.*—To test the diluted juice of bean foliage, a water extract was prepared by adding 50 cc. of water to 10 gm. of leaves, cut into small pieces. After macerating the pieces and decanting the liquid through cheesecloth, 50 cc. of a greenish liquid was secured. To test the steam distillate of bean foliage, 100 cc. of water was added to 30 gm. of leaves, cut into small pieces, and then 50 cc. of a clear and odorous distillate was collected (table 9).

The results given in table 9 show that when water extract of bean leaves was compared to unsprayed leaves it was about equally attractive, while sweetened water extract was about 3.56 times as attractive. Steam distillate from bean leaves was not attractive, but gave practically the same result as did water, indicating that its faint odor had no attractive influence.

(9) *Chemotaxis more important than phototaxis in the finding of food.* Sixteen series of tests were conducted to ascertain whether phototaxis or chemotaxis, or possibly thigmotaxis, is the more important in the finding of food. Squares of bean leaves, apple leaves,

TABLE 11.—*Tests to determine whether repellents would protect beans from the Mexican bean beetle*

Leaves: un-sprayed and sprayed with:	Total number of beetles on leaves	Mean and probable error	Relative value of beetles on leaves	Number of set of beetles	Date	Number of tests
Unsprayed (control) ..	226	7.06 ± 0.49	1.00	} 19	Sept. 9	32
Tar and lime.....	216	6.75 ± 0.53	0.96			
Nicotine sulphate and lime .....	196	6.12 ± 0.47	0.87			
Derris product .....	120	3.75 ± 0.47	0.53			
Unsprayed (control) ..	256	8.00 ± 0.64	1.00	} 19	Sept. 10	32
Cresol .....	251	7.84 ± 0.49	0.98			
Nicotine sulphate ....	219	6.84 ± 0.56	0.85			
Beta naphthol .....	142	4.44 ± 0.47	0.55			

and mulberry leaves, all of the same shape and size (1 in. square), but some bearing a film of cane sugar, represented practically the same color, form, and texture, but differed chemotactically. Cotton wet with green water and with green sugar water (a green dye being used) also somewhat resembled the leaves in color but differed in other respects (table 10).

The results given in table 10 show that sweetened food is preferred to non-sweetened food and that chemotaxis is more important than phototaxis in bringing about the results obtained.

(10) *Repellents would probably not protect beans.*—To ascertain whether certain substances, usually known as repellents, would keep the beetles away from the treated leaves in the four small cages, bean foliage was sprayed with the following: Tar and lime, combined as a dust; nicotine sulphate and lime, combined as a dust, a com-

mercial Derris product, consisting mostly of pyridine; cresol, U. S. P. (1 cc. shaken in 400 cc. water); 40 per cent nicotine sulphate in water (1 to 400); and beta naphthol (1 gm. powder in 400 cc. water; powder not all in suspension) (table 11).

The results given in table 11 show that the repellents more or less protected the leaves, but not sufficiently so to prevent them from being eaten. The Derris product and beta naphthol were the only ones which might be considered promising, yet their protective value was about equal to that of lead arsenate, as already shown in table 7.

### III. THERMOTAXIS

After having searched the literature for references on other tropisms not yet discussed, the writer found a few more concerning Coleoptera, but only two of these references pertain to the orientation of beetles to temperature. Much experimental work on various temperatures, particularly as control measures, has been done, but very little of it can be discussed from the tropic point of view.

#### I. REVIEW OF LITERATURE

Fulton (17) devised a crude temperature gradient with which he determined that the choice of temperature of adult click beetles is much below the usual maximum temperature in open fields during summer. He also says that negative phototaxis causes the beetles to seek dark hiding places during the day. Wireworms, or the larvae of these beetles, were found more resistant to heat than were the adults, but they did not voluntarily seek higher temperatures. Seasonal movements of the larvae may be closely correlated with changes in soil temperature.

Grossman (21) tried three methods to determine the orientation of cotton boll weevils to heat stimuli, but decided that only the results obtained by using a new apparatus were reliable. This apparatus was constructed by using 16 copper bars  $\frac{1}{8}$  inch wide and  $\frac{1}{16}$  inch thick, with  $\frac{1}{4}$  inch insulating space between each two bars. Using only two variables, temperature and light, 126 boll weevils were tested 1,993 times. The average temperatures to which they reacted definitely were 130° F. at the hot end of the apparatus and 26° F. at the cold end.

#### B. SENSORY RECEPTORS

Since tropic responses are brought about largely by external stimuli affecting either the special sense organs or others not definitely known and localized, called the general sense organs, it is only natural to discuss the tropic responses and sensory receptors in the same paper.

## I. PHOTORECEPTORS

According to the phototactic responses of the Mexican bean beetle and its larva, already discussed, the compound eyes and ocelli in this species are normally developed and seem to function adequately, so far as beetles are concerned. It is recalled that the adults are always photopositive and that the larvae up to the time of pupation are photopositive, too, but when ready to pupate they become photonegative. Whether the negative reaction is caused by a change in the structure of the ocelli is not known.

Since the morphology of insects eyes has often been discussed and as the writer (46, 47) has recently cited reviews on this subject, no further discussion is needed here. Also, the other sense organs and senses of beetles will be discussed only briefly.

## II. CHEMORECEPTORS

Chemoreceptors include both olfactory and gustatory organs, but we are not absolutely sure that insects have true chemoreceptors, although their organs certainly belong to the same category.

### I. SO-CALLED OLFACTORY ORGANS

#### (A) ANTENNAL ORGANS

The organs on the antennae of the Mexican bean beetle are comparatively few; that is, these antennae are nearly bare in comparison to most antennae (fig. 6). Only four types of sense organs were found on them. They are as follows: (1) Two groups of tiny hairs (*St*); and (2) three or four pores (*P*), called olfactory by the writer, lie on the base of the first antennal segment; (3) the Johnston organ (*J*) lies at the distal end of the second segment; and (4) five areas of thin-walled hairs (*OHR*) were found on the distal ends of the ninth, tenth, and eleventh segments. All of these structures are sense organs, because sense cells were found connected with them, while the larger hairs (*Hr*), usually called sense bristles, were found to be non-innervated.

Of these four types of sense organs only the olfactory pores and thin-walled hairs may be regarded as so-called olfactory organs. The thin-walled hairs are numerous and most of them lie on the dorsal surface of the antennae (fig. 6, *OHR*). Under a high-power lens they appear long and slender, have thin, almost transparent walls (*C, OHR*), and are connected with sense cells.

From the preceding it is evident that pore plates, found only on the antennae of aphids, bees, wasps, and on some beetles, are totally absent on the antennae of the Mexican bean beetle. The pore plates,



when present, are considered the olfactory organs by most writers. Figure 7 illustrates the antennal organs of a water beetle, copied from Hochreuther (25). The pore plates (*PP*), hollow pit pegs (*HPPg*), and massive pit pegs (*MPPg*) might be called olfactory organs, but Hochreuther regarded only the hollow pit pegs as probably olfactory in function. If they really act as olfactory organs, then the mouth parts, thorax, legs, and sexual organs must aid in receiving odor stimuli, because Hochreuther found them also on these parts of the anatomy.

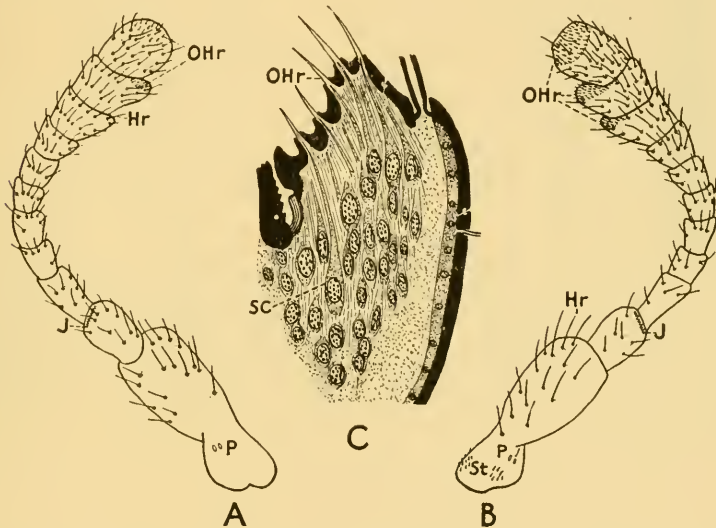


FIG. 6.—Drawings of antennae of adult Mexican bean beetle, showing organs on them. A, ventral surface, and B, dorsal surface, showing location of following: *Hr*, noninnervated hairs; *J*, Johnston organs; *P*, pores called olfactory by the writer; *OHR*, so-called olfactory hairs; and *St*, tactile hairs. C, a semi-diagrammatic drawing from a section through tenth segment, showing structure of so-called olfactory hairs (*OHR*) and their sense cells (*SC*). A and B,  $\times 53$ ; and C,  $\times 500$ .

#### (B) OLFACTORY PORES

The writer (46, p. 1105) in 1926 cited references pertaining to these organs in beetles and in 1929 he (47, p. 27) stated why they were called "olfactory pores." In 1915 (41) he made a comparative study of them in 50 species of beetles belonging to 47 genera and representing 34 families. In that study only the legs, elytra, and wings were examined for these pores. A group of pores (fig. 8, A and B, 1) was always found on the peduncle of each elytron. The number of pores in it ranged from 12 to 310, and the more pores in the group the smaller they were and the closer they were together. Of the 47

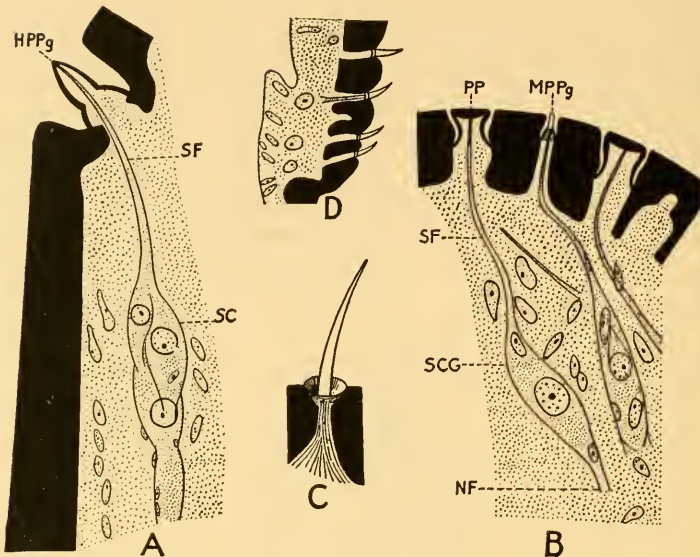


FIG. 7.—Antennal organs of a water beetle, *Dytiscus marginalis*, copied from Hochreuther (25). A, longitudinal section through a hollow pit peg (HPPg); B, longitudinal section through a small massive pit peg (MPPg) and 2 pore plates (PP). This drawing is a combination of Figs. 32 and 58 from Hochreuther, slightly modified. C, a small tactile hair from first segment, total preparation; and D, portion of Fig. 12 from Hochreuther, showing 4 small sense bristles from second segment. NF, nerve fiber; SC, sense cell; SCG, sense cell group; and SF, sense fiber.

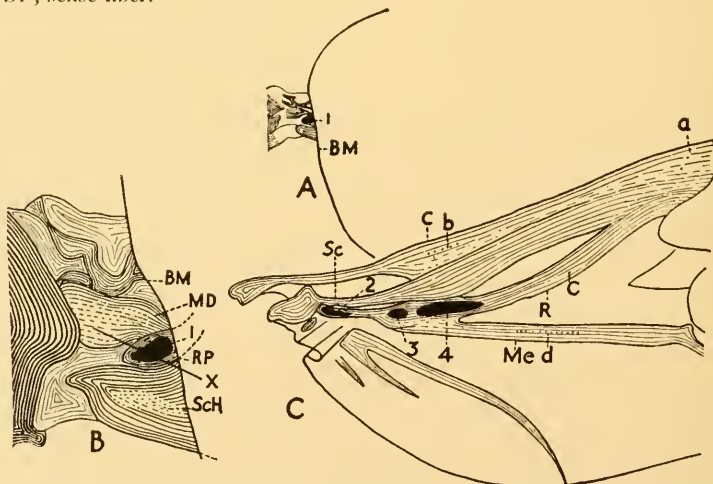


FIG. 8.—Portion of left elytron (A and B) and left wing (C) of Mexican bean beetle, showing position of olfactory pores as indicated by numbers 1 to 4 and letters a to d on dorsal surfaces. A shows relative sizes of peduncle of elytron and group 1 when compared with size of basal margin (BM) of elytron; A and C,  $\times 12$ ; and B,  $\times 67$ . The lower side of A and B is the outer margin of the elytron. C, costa; MD, muscle disk; Me, media; R, radius; RP, radial plate; Sc, subcosta; ScH, subcostal head.

winged species examined, 11 had only one group of pores on each wing, 21 had two groups on each wing, 12 had three groups on each wing (C, 2, 3, and 4), and 3 had four groups on each wing. The

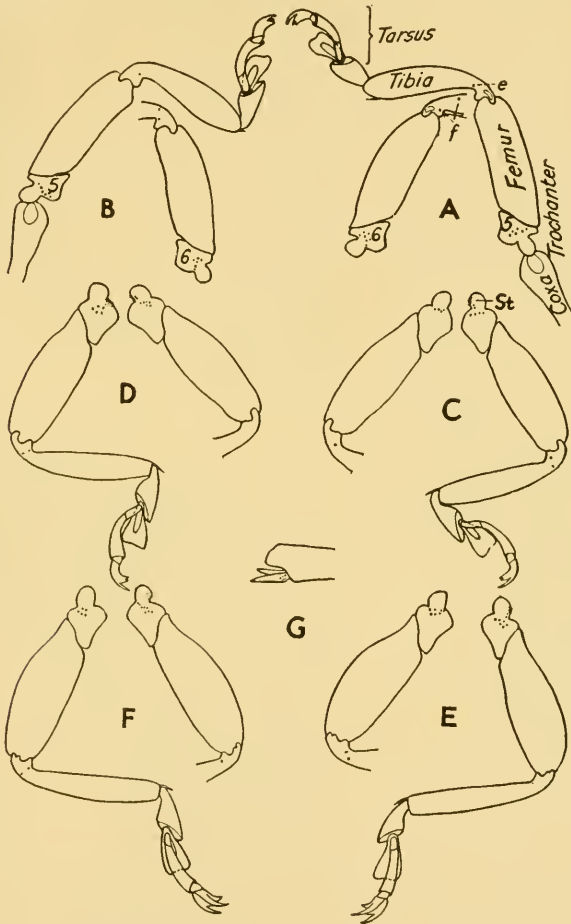


FIG. 9.—Position of sense organs on legs of adult beetles; dots, marked 5 and 6, and *e* and *f*, being olfactory pores; and *St*, tactile hairs. A to F, legs of Mexican bean beetle,  $\times 12$ ; and G, distal end of tibia from front leg of *Epicauta marginata*, showing 5 olfactory pores on tibial spine. The drawing of each leg in which the tarsus is shown represents the outer surface and the portion of leg without tarsus represents the inner surface of the same leg. A, right front leg; B, left front leg; C, right middle leg; D, left middle leg; E, right hind leg; and F, left hind leg.

number of pores on a pair of wings ranged from 130 to 982. The number of pores counted on all six legs of an individual ranged from 49 to 341. There were usually two groups of pores on each trochanter (fig. 9, 5 and 6). Sometimes a pore was found at the proximal end of

the femur. A few pores were always found at the proximal end of each tibia (*e* and *f*), and sometimes pores were found in the tibial spines (*G*) and on the tarsi.

In regard to water beetles, the better the legs are adapted for locomotion in water, the fewer pores they have. The smallest winged species examined had 273 pores, which is the smallest number counted of all the species, and the largest species had 1,268 pores which is the largest number of all the species examined. The wingless species had more pores on the legs than usual. As a rule, the smaller the species, the fewer its pores and the larger they are, comparatively speaking. As a rule, no generic and specific differences were found, except variations in number of pores, the amount of variation depending on the sizes of the individuals compared. There were no individual and sexual differences other than slight variations in number of pores.

The pore apertures or pits are round, oblong, slitlike, or club-shaped. On the elytra and wings (fig. 10, *A* and *B*, *Ap*) they are always round or oblong. On the legs (*C*) they have all four of the enumerated shapes.

The spindle-shaped sense cells (fig. 10, *C*, *SC*) of most beetles lie in the lumens of the appendages outside the pore cavities. A small chitinous cone (*Co*) is always present. It is formed by the hypodermal cell at the mouth of the pore after the insect has emerged from the last pupal instar, and at the same time when the chitinous integument is being considerably thickened. The sense cells are fully developed when the insect emerges into the imago. The sense fiber pierces the cone, and comes in direct contact with the outside air. This statement is denied by other writers. In the legs of the lady-beetle *Epilachna borealis* the pore apertures lie in the center of domes (fig. 10, *C*) above the general surface of the legs.

A large nerve and a large trachea run into each elytron (fig. 10, *A*, *N* and *Tr*) and wing. In the peduncle of the elytron they run through the radial plate just beneath the group of olfactory pores. Branches from the nerve are given off which connect with the sense cells. The large nerve and trachea passing into the wing soon divide so that a smaller nerve and a smaller trachea (*B*, *N* and *Tr*) run through each main vein. The largest trachea passes through the subcosta, and the largest nerves pass through the veins bearing the olfactory pores. These nerves give off branches which connect with the sense cells. The sense cells (*C*, *SC*), wherever found, are always surrounded by blood (*Bl*).

In a study of the sense organs of the cotton boll weevil, the writer (46) found the olfactory pores common to both the adult and larva ;

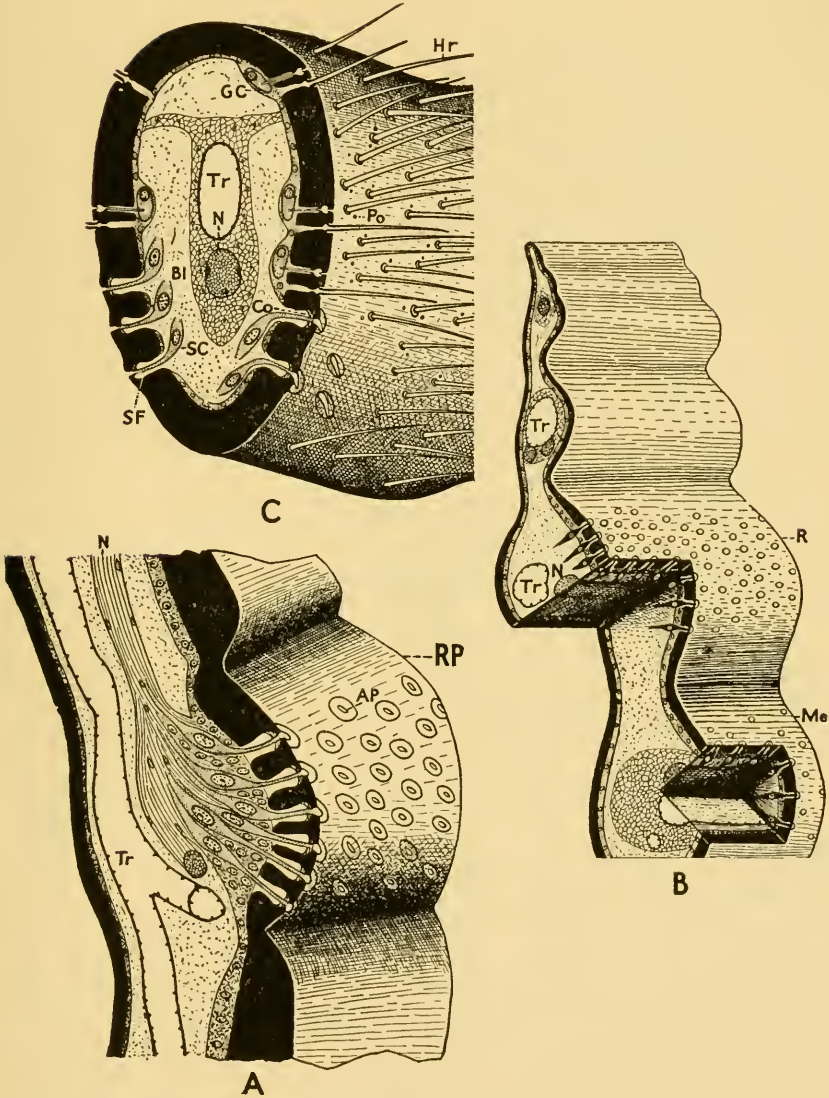


FIG. 10.—Diagrams showing portions of elytron, wing, and leg of adult beetles, to illustrate internal and external anatomy of these appendages and of olfactory pores and hypodermal glands. A, oblique transverse-longitudinal view of portion of peduncle of *Epilachna borealis*. The transverse portion passes through group 1 of the olfactory pores and radial plate (RP) in the direction of the line marked X in figure 8 B. B, transverse-longitudinal view of portion of wing of *Orthosoma*, passing through pores on radius (R) and media (Me). C, transverse-longitudinal view of proximal end of trochanter belonging to right hind leg of *E. borealis*, passing through group 6 of olfactory pores (4 pores on right) and group 5 (3 pores at left). Ap, pore aperture, BI, Blood; Co, chitinous cone; GC, hypodermal gland cell; Hr, noninnervated hair; N, nerve; Po, pore of hypodermal gland; SC, sense cell; SF, sense fiber; and Tr, trachea.

but the other so-called olfactory organs, which are nothing more than ordinary innervated hairs, are common only to the antennae of the adult, although similar innervated hairs are also found on other parts of both adult and larva. In the adult the olfactory pores were found on the head capsules, legs, elytra, wings, and mouth parts, and at the base of the antennae; in the larva, on the head capsule, base of antennae, mouth parts, clypeus, and second thoracic segment. The individual and sexual variations found in the pores were small, although the females have 13.7 per cent more pores than have the males.

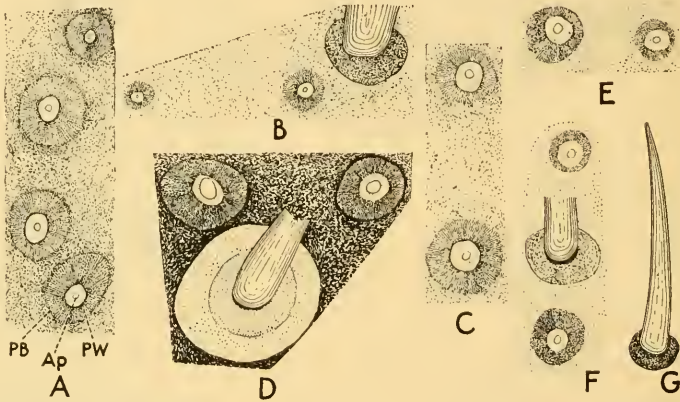


FIG. 11.—External view of single olfactory organs and noninnervated hairs on larva of *Cotinis nitida*,  $\times 320$ . A, 4 organs from trochanter, showing pore border (*PB*), pore aperture (*Ap*), and pore wall (*PW*). B, 2 organs and a hair from hypopleural region; C, 2 organs from maxilla; D, 2 organs and a hair from labium; E, 2 organs from labium; F, 2 organs and a hair from epicranium; and G, a hair from first antennal segment.

On the larva of the green June beetle (*Cotinis nitida* L.) the writer (44) found the olfactory pores unusually numerous and consisting of two types. The single olfactory organs are isolated pores, not arranged in groups. They were found on the antennae, all mouth parts, head capsule, thorax, and legs, and average 1,359 pores per individual larva. This number is slightly more than the total number of pores found on the elytra, wings, and legs of an adult of the same species. Their external anatomy is unusual in that the pore border (fig. 11, *PB*) is radially striated, while the border around the hairs never shows striae. The compound olfactory organs (fig. 12) are variously shaped plates, each of which bears many apertures. They were found only on the distal halves of the last antennal segments. Figure 13 illustrates the internal anatomy of the single and compound organs.

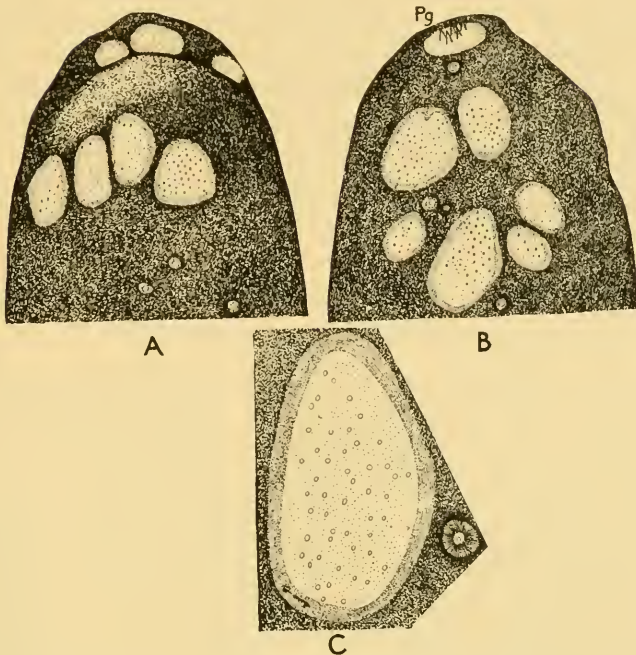


FIG. 12.—External view of compound and single olfactory organs and olfactory pegs on distal half of last antennal segment of larva of *Cotinis nitida*. A, 9 compound organs and 3 single ones on ventral side of antenna, viewed from a flat surface,  $\times 100$ ; 2 of the compound organs at extreme tip are not shown. B, 6 compound organs, 4 single ones, and 1 group of olfactory pegs (*Pg*) on dorsal side of antenna, viewed from a flat surface,  $\times 100$ . C, external view of a compound and a single organ,  $\times 320$ ; the small circles represent pore apertures.

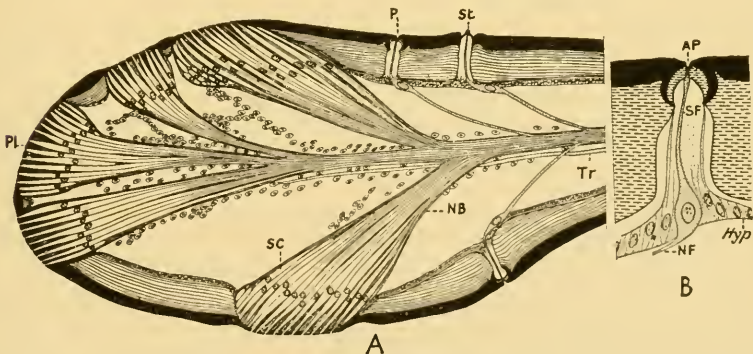


FIG. 13.—Internal anatomy of sense organs on antenna of larva of *Cotinis nitida*. A, longitudinal section through tip of antenna, showing innervation of compound (*Pl*) and single olfactory organs (*P*), and tactile hair (*St*); two-thirds diagrammatic,  $\times 100$ . (At this magnification the pore apertures are never discernible). B, cross section through single olfactory organ from antenna,  $\times 500$ . *Ap*, pore aperture; *Hyp*, hypodermis; *NB*, nerve branch; *NF*, nerve fiber; *SC*, sense cell; *SF*, sense fiber; and *Tr*, trachea.

The olfactory pores on several males and females of the Mexican bean beetle were examined, but they were actually counted on only one female, and these are illustrated in figures 6, 8, 9, 14, and 15. In this study only one totally new fact was learned. In all the previous studies on beetles, no olfactory pores were seen on the ventral side of the peduncles of the elytra, but in this position on the bean beetle 7 pores were seen on one elytron and 6 pores on the other. The groups

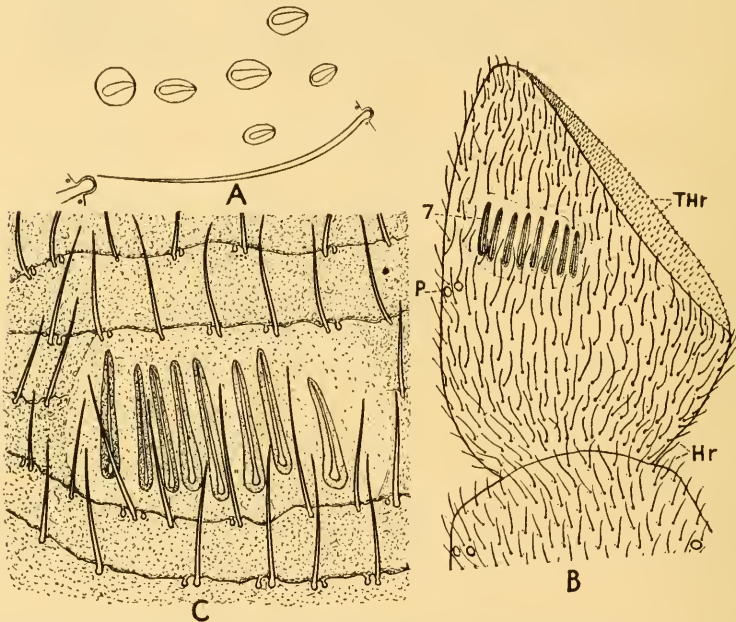


FIG. 14.—External view of chemoreceptors of adult Mexican bean beetle. A, noninnervated hairs and group 5 of olfactory pores on trochanter of front leg,  $\times 500$ . B, ventral surface of distal end of maxillary palpus, showing numerous noninnervated hairs (*Hr*) with their gland pores, isolated olfactory pores (*P*), group 7 of olfactory pores (*7*), and a plate bearing numerous so-called taste hairs (*THr*),  $\times 100$ . C, group 7 of olfactory pores, markings on chitin, hairs, and gland pores,  $\times 500$ .

of pores are numbered, as usual, from 1 to 7, and small letters are used to indicate the position of some of the isolated pores. Group 1 on the elytra (fig. 8, A) contains 58 pores on the left peduncle and 65 on the right one. Groups 2, 3, and 4 on the dorsal surface of the wings (C) have as follows: Group 2, 58 and 64 pores; group 3, 43 and 38 pores; and group 4, 70 and 64 pores. Isolated pores on the wings are as follows: At *a*, 2 on the ventral side; at *b*, 8 on the dorsal side; at *c*, 1 on the dorsal side; and at *d*, 12 on the dorsal side and 8 on the ventral side. The number of pores in groups 5 and 6 and at *e*



and *f* on the legs (fig. 9) can be counted by inspection. Group 7, consisting of 8 slit-shaped pores, lies on the ventral surface of the terminal segment of the maxillary palpus. All the remaining pores counted are isolated ones found on the antennae and mouth parts. The total number of pores on all appendages of the same bean beetle are as follows: Wings 397, elytra 136, legs 95, maxillae 32, labium 14, antennae 8, mandibles 6, and labrum 4, making 692 in all. The

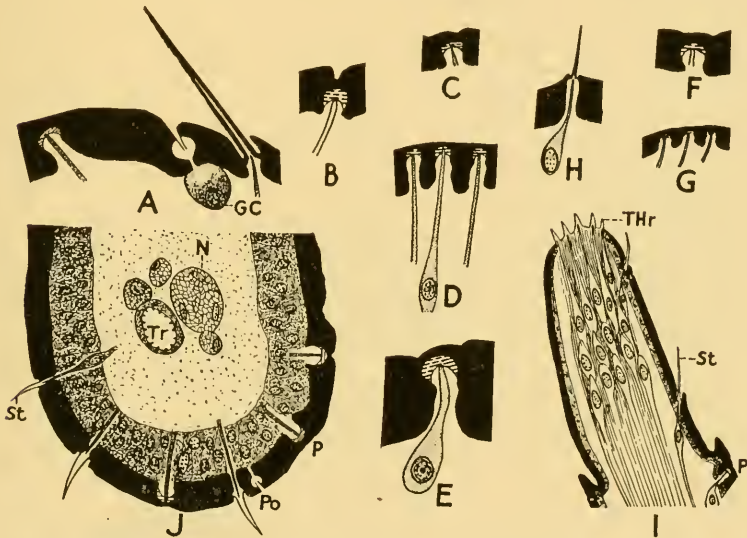


FIG. 15.—Internal structure of sense organs on adult Mexican bean beetle,  $\times 500$ . A, an olfactory pore, gland cell (GC), and sense hair from dorsal surface of labrum. B to G, olfactory pores; B, from mandible, C, from maxilla; D, from elytron; E, from trochanter; F, from tibia; and G, from wing. H, sense hair from trochanter. I, drawing, two-thirds diagrammatic, from longitudinal sections of distal end of labial palpus, showing innervation of so-called taste hairs (THr), tactile hairs (St), and olfactory pore (P). J, semidiagrammatic drawing from 3 cross sections through base of first antennal segment, showing tactile hairs (St), gland pore (Po), olfactory pore (P), trachea (Tr), and nerve (N).

fact that this number is small for an adult insect might be correlated with the fact that the bean beetle is "stupid" when the olfactory responses are considered.

The olfactory pores on several individuals of all four instars of bean-beetle larvae were examined. Since no differences in number and position were observed, the pores were carefully studied on only individuals of the fourth instar. They are illustrated in figure 16. The total number of pores on all appendages and the head are as follows: Legs 30, maxillae 12, head capsule 6, antennae 4, labrum 4,

labium 4, and mandibles 2, making 62 pores in all. The fact that this number is extremely low for any insect may help to explain why these larvae did not respond readily to odor stimuli.

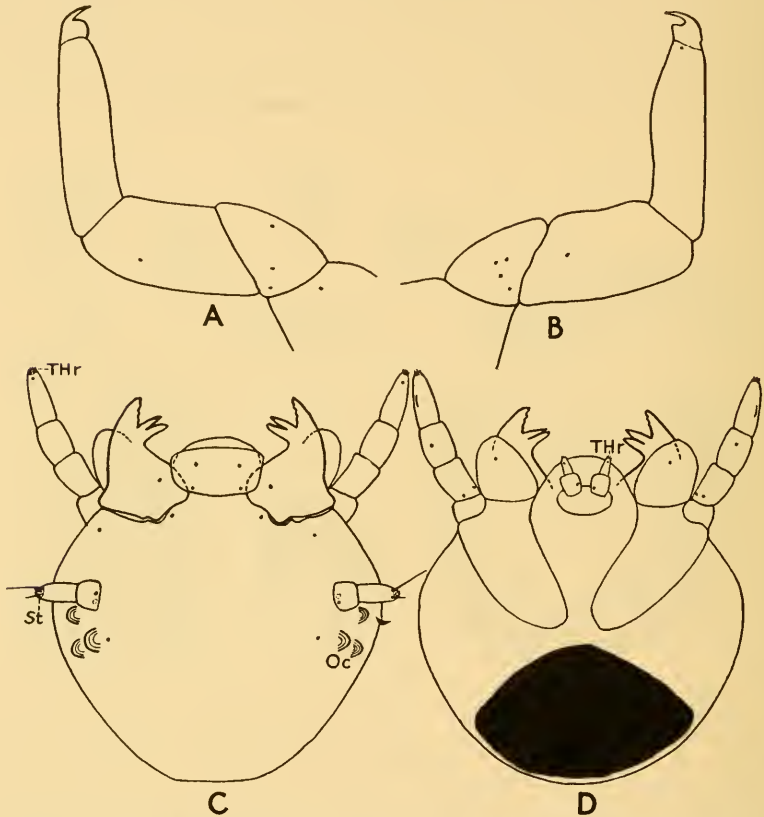


FIG. 16.—Position of olfactory pores (dots), 12 to 15 so-called taste hairs (*Thr*) at tip of each maxillary palpus, 8 tactile or so-called olfactory hairs (*St*) at tip of each antenna, and ocelli (*Oc*) on larva of bean beetle,  $\times 32$ . A and B, inner and outer sides respectively of right front leg. The number of pores on the legs is nearly constant, and they shift only slightly in position. C and D, dorsal and ventral surfaces respectively of the head and head appendages. On the base of each antenna one pore is on the dorsal side and one on the ventral side. On each terminal maxillary segment there is a slit-shaped pore.

## 2. SO-CALLED TASTE ORGANS

Several writers, particularly Nagel (58), have described certain tiny peglike hairs on the mouth parts of insects as taste organs, but no one has ever demonstrated that they perform such a function. Hochreuther (25) found many "Tast- und Geschmackszäpfchen" on the maxillary and labial palpi of the water beetle *Dytiscus margi-*

*nalis*. The earlier papers concerning the chemoreceptors of Coleoptera are reviewed by Deegener (see Schröder (72, pp. 150-151). Since Minnich's papers on the taste organs of butterflies and flies have recently been reviewed by the writer (47, pp. 36-39), they will not be discussed here. The reader should know, however, that according to the experiments conducted by Minnich certain butterflies bear so-called taste organs in their tarsi, and certain hairs on the proboscis of the blowfly serve as gustatory organs. The most recent paper by Minnich (55) discusses the chemical sensitivity of the legs of a blowfly.

The writer (46) described and illustrated many tiny peglike hairs found on the cotton boll weevil, but did not attribute a gustatory

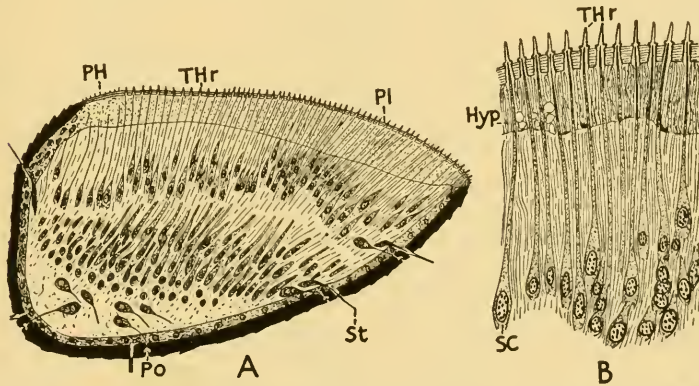


FIG. 17.—Internal anatomy through tip of maxillary palpus of adult Mexican bean beetle, showing following: *Hyp*, thick hypodermis; *PH*, pseudohairs; *PI*, soft plate; *Po*, gland pore connected with gland cell, which lies some distance from pore; *SC*, sense cells; *St*, tactile hairs; and *THR*, so-called taste hairs. A, drawing, two-thirds diagrammatic,  $\times 300$ ; and B, semidiagrammatic,  $\times 500$ .

function to any of them. According to position, and possibly to structure, the ones on the tips of the labial and maxillary palpi are best suited to be taste organs. The same type of hairs was also found at the same place on both adult and larva of the Mexican bean beetle (figs. 14-17, *THR*). The ones at the tip of the maxillary palpus of the adult (fig. 14, B) are the most numerous and most conspicuous of any yet observed by the writer, and consequently they would appear to have some function other than that of touch. These tiny, thin-walled, and transparent hairs arise from a slightly convex plate, which is soft, flexible, and transparent. The number of hairs on the organ illustrated in figure 17 is about 447. An oblique cross section through the fourth or terminal maxillary segment is represented by figure 17,

A. The transparent plate (*Pl*) is bordered by tiny pseudo-hairs (*PH*) and the hypodermis (*B*, *Hyp*) just beneath the plate is very thick. Each hair is connected with a sense cell (*SC*) and these cells almost fill the lumen of the segment. The sense cells are very long and slender and have conspicuous nuclei.

Now, if aqueous solutions can pass quickly through the walls of these sense hairs in order to stimulate the nerves inside, these structures would be excellent taste organs. Or, if air can pass quickly to the nerves, they would then be olfactory organs. The fact that the bean beetle possesses two of these highly developed sense organs helps to explain how these insects were able to distinguish so readily between the various aqueous solutions and insecticides fed to them.

### III. AUDIRECEPTORS

Since the writer (46, p. 1119; 47, p. 39) has already reviewed the literature on the sense of hearing in insects, no further review is necessary here, other than to cite the recent book by Eggers(14).

#### I. JOHNSTON ORGANS

In caustic-potash preparations of the antennae of the adult bean beetle the location of the Johnston organs may be determined by focusing downward with the microscope when looking at the distal end of the second antennal segment. A serrated structure (fig. 6, A and B, *J*) will be observed to encircle the segment. The distal ends of the sense cells are attached to this structure. In longitudinal sections the Johnston organs appear about as shown in figure 18, A. At the base of the second segment the nerve divides into two branches, which run directly to the sense cells (*SC*). Formerly the Johnston organs were assumed to be auditory in function, but more recently they have been called muscular receptors or statical-dynamic organs to register the movements of the antennae.

#### 2. CHORDOTONAL ORGANS

Chordotonal organs very often accompany the Johnston organs, as illustrated by the writer in the cotton boll weevil; but none was found in the Mexican bean beetle. Many sections through the larvae were also made and studied, but no chordotonal or Johnston organs were found.

Since the writer has never reviewed the literature on the so-called auditory organs in larvae, the reader is referred to the paper by Hess (24) who gives a brief history of the chordotonal organs and de-

scribes them in cerambycid larvae. Hess determined that the pleural discs in these larvae are the points of attachment of abdominal chordotonal organs. Two of Hess's drawings (fig. 18, B and C) were copied to illustrate the internal structure of these organs in coleopterous larvae.

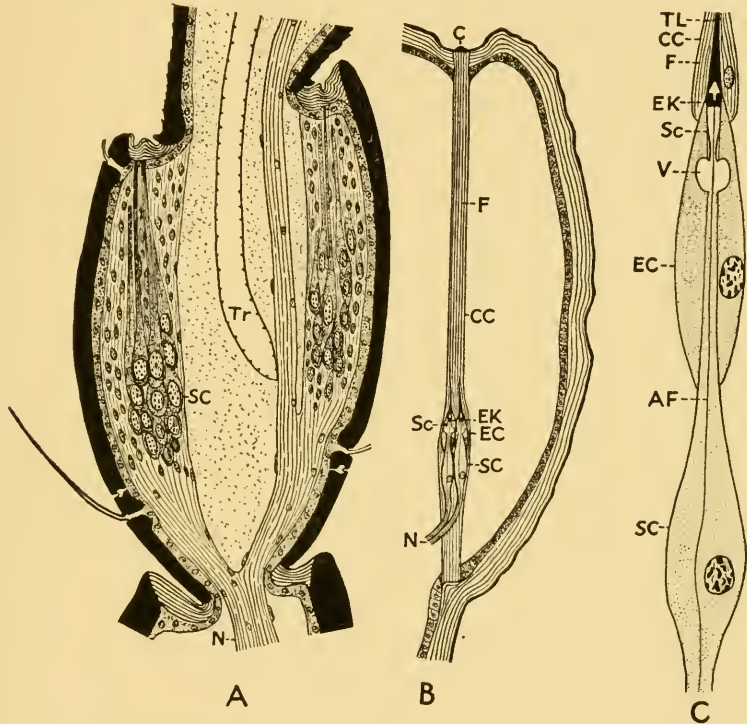


FIG. 18.—Internal anatomy of so-called auditory organs of beetles. A, drawing, two-thirds diagrammatic, from longitudinal sections through second antennal segment of an adult Mexican bean beetle, showing Johnston organs consisting of groups of sense cells (*SC*),  $\times 500$ . B and C (after Hess), longitudinal-vertical section of the pleural zone and chordotonal ligament from a larva of *Ergates spiculatus*, showing following: *AF*, axis fiber; *C*, chitinous cap; *CC*, cap cell; *EC*, enveloping cell; *EK*, end knob; *F*, fibrils of cap cell; *N*, chordotonal nerve; *Sc*, scolopale; *SC*, sense cell; *TL*, terminal ligament; and *V*, vacuole.

#### IV. THIGMORECEPTORS

##### I. TACTILE HAIRS

Hochreuther (25) made a thorough study of the sense hairs on a water beetle (*Dytiscus marginalis*). On the basis of external structure, he separated them into five divisions. Vom Rath (63, 64) found sense cells connected with all the small hairs on the maxillary palpi of *Coccinella septempunctata*, *Melolontha vulgaris*, and *Tenebrio*

*molitor*, and also with all the small hairs on the labial palpi of the last species. The present writer (46) found tactile hairs on the cotton boll weevil as follows: Sense hairs (*Sensilla trichodea*) on the head capsule, antennae, mouth parts, thorax, legs, wings and abdomen; sense bristles (*S. chaetica*) on nearly the same parts; and sense pegs (*S. basiconica*) on the head capsule, mouth parts, and genitalia.

In regard to tactile hairs on the Mexican bean beetles, all parts of the integument were not searched for them, but practically all the innervated hairs already discussed might be considered as touch hairs; however, the sense hairs (*Sensilla trichodea*) are considered to have no function other than that of touch. On the base of each antenna lie two groups of these hairs (figs. 6, B, and 15, J, *St*) and each trochanter bears one or two groups (fig. 9, C, and 15, H, *St*). They were also found on the maxillary and labial palpi (fig. 15, I, *St*) of the adult and on the head (fig. 16, C, *St*) of the larva.

### C. SCENT-PRODUCING ORGANS AND REFLEX "BLEEDING"

The study of scent-producing organs follows as a corollary to that of tropisms and sensory receptors, and reflex "bleeding" is closely related to them. Since the sense of smell is such an important means of communication among insects, it is probably true that all insects have structures for producing odors. In fact these structures have already been described for most insect orders, and particularly for Coleoptera.

The writer (43) in 1917 reviewed the literature on this subject. A brief summary of that review concerning beetles follows: The simplest type of a scent-producing organ in beetles is composed of unicellular glands distributed over the entire body surface. In some beetles these unicellular glands are grouped and thus form glands varying considerably in complexity. In *Malachius* two pairs of caruncles serve as the scent-producing organs; unicellular glands lie in the walls of these structures. In *Dytiscus*, *Gyrinus*, and *Acilius* two different kinds of liquids issue from unicellular glands situated in the articular membranes between the thoracic segments. The liquid emitted at the femoro-tibial articulation during reflex "bleeding" of certain beetles seems to be secreted by two types of unicellular glands at this location. The highest type of scent-producing organ among insects is the anal glands of beetles. These have been found in several families.

In regard to the Mexican bean beetle, no careful search was made for the purpose of finding scent-producing organs other than the

unicellular glands distributed over the entire body surface. In fact this type of scent organ is the only one in lady-beetles known to the writer. The bean beetle, like other coccinellids, is well supplied with these glands. All parts of the body surface are covered with comparatively large hairs. Near the base of each hair there is usually one and sometimes two gland pores (figs. 6, 10, 14, 15, 17-19, *Po*). The large gland cells (figs. 10, C, and 15, A, *GC*) are variously constructed, but are always connected with reservoirs lying in the integument. In some of the smaller appendages, for example the maxillary palpi, where the available space is limited, the gland cells lie some distance from their pores and often nearly fill the lumen of the appendage.

The writer (42) in 1916 reviewed the literature on reflex "bleeding" in beetles and added further information by using the squash lady-beetle, *Epilachna borealis*. When disturbed certain coccinellid and meloid beetles fold the antennae and legs against the body, eject small drops of liquid from the femoro-tibial articulations, and feign death. There has been a controversy as to how the liquid is expelled so quickly and as to whether the liquid is blood or is a glandular secretion. The writer has now shown that in regard to the squash lady-beetle and the Mexican bean beetle (*E. corrupta*) the phenomenon is a true reflex, but that instead of the liquid being blood, it is a secretion from two types of hypodermal glands and that it passes to the exterior through innumerable tubes opening near and in the articular membrane. The gland pores of the first type, with reservoirs, lie in groups on the tarsi and around the femoro-tibial articulations. Two groups of these are located at the extreme proximal end of the tibia and two at the distal end of the femur around the articular membrane (fig. 19, A, *Po*). The gland pores of the second type, without reservoirs, lie in the articular membrane, marked *a* in figure 19. The discharge of the amber-colored secretion is accomplished by putting the gland cells under a high blood pressure. This is made possible by a muscular contraction in the femur whereby the blood is forced into a specially devised chamber containing the gland cells which belong to the pores in and near the femoro-tibial articulation. The glandular secretion is bitter and has an offensive odor. Its chief purpose is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species.

Hollande (26) in 1911 wrote a large paper in which he reviewed the literature on the phenomenon of discharging "blood" in insects and on the toxicity of this substance. He also added new information on these subjects. He reports that self-bleeding has been found in

Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera. Under his general conclusions he states that some authors believe that the discharged liquid is blood, while others think it is a glandular secretion. The manner in which the liquid is discharged is little known, except in a few cases. In general it is admitted that the blood is discharged by a reflex action, being a means of defense. He discusses four methods in which the blood is discharged and gives

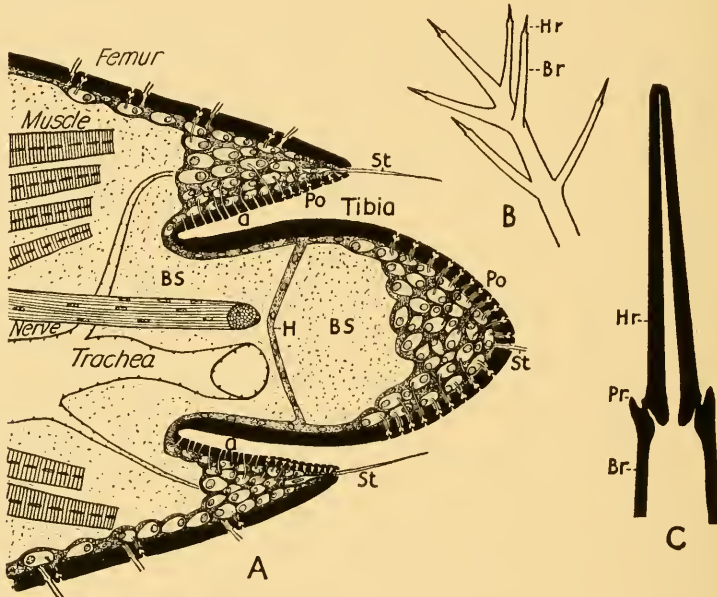


FIG. 19.—Drawings, illustrating reflex “bleeding” in lady-beetles. A, diagram of a section through femoro-tibial articulation of *Epilachna borealis*, showing following: *a*, pores of gland cells without reservoirs; *BS*, blood sinus; *H*, membrane dividing lumen of leg into two chambers; *Po*, pores of gland cells having reservoirs; and *St*, sense hairs. B and C, portion of tubercle on larva of bean beetle; B, distal end of tubercle having 6 branches (*Br*), each of which is terminated with a hair (*Hr*),  $\times 32$ ; and C, distal end of a branch, showing hair arising from a socket, which is surrounded by 5 processes (*Pr*), only 2 being shown,  $\times 320$ .

examples of insects for each method. He further remarks that the ejected blood is usually very toxic.

While discussing coleopterous larvae, Hollande shows how coccinellid larvae protect themselves by discharging blood. As an example he used *Epilachna argus*, whose body is covered with chitinous tubercles, which in turn bear many smaller branches, each of which is terminated by a hair. The discharged blood is accomplished by a rupture of the chitin near the base of the hair. When one seizes the



larva with the fingers, the hairs pierce the epidermis on the fingers and are then broken off, causing the blood of the larva to exude as small drops.

The larvae of the bean beetle are likewise covered with hairlike tubercles (fig. 19, B), which bear many branches (*Br*); each of which is terminated by a hair (*Hr*). While picking up the larvae the writer observed a yellowish liquid on his fingers. This liquid was bitter and very distasteful. After carefully examining the larvae under a binocular, it was learned that the bitter liquid came from the tips of the branches (*C, Br*). Using a needle it was possible to touch the hairs (*Hr*) lightly, so that they broke at their weakest point; that is, at the socket which is surrounded by five processes (*Pr*).

#### SUMMARY

This paper is written as a complement to the writer's (47) former one entitled "Tropisms and Sense Organs of Lepidoptera," and contains information of a similar nature, but dealing with Coleoptera alone. A large mass of literature on the sense organs and tropisms of beetles, including papers on light traps, attractive baits, and repellents, has been consulted; but only the more important information found has been briefly summarized.

The Mexican bean beetle was selected to represent the Coleoptera. When tested to odor stimuli alone this beetle was found to be an unfavorable insect; but when the adults were allowed to come in contact with the substances to be tested as foods, the beetles clearly demonstrated their "likes" and "dislikes"; and when tested to light and gravity in a dark-room, the adults proved to be almost ideal for this purpose. In order to obtain comparative results which could be treated statistically, new technique and apparatus were devised, and the more important experiments were repeated many times under controlled conditions. The more important results obtained are as follows:

When tested in a phototactic box, which lay on a table by a south window in bright light, although not in direct sunshine, larvae of the first and second instars were weakly photopositive or indifferent to light. Most of the larvae of the third instar and the more active ones of the fourth instar were strongly photopositive. As a rule, the larvae up to the time of pupation were found to be photopositive, but when ready to pupate they became photonegative. Whether the negative reaction is caused by a change in the structure of the ocelli is not known. Hundreds of adult bean beetles were also tested and all proved to be photopositive, most of them being strongly so.

In a dark-room in which the temperature and relative humidity were fairly constant many tests were conducted to determine the difference between the phototactic and geotactic responses of adult bean beetles and their larvae, with and without the use of light. The insects were confined in a photo-geotactic box, just above or below which lay a water screen to prevent the infra-red or heat rays from reaching the beetles. Under these conditions the following results were obtained. For active, overwintering adult beetles the geonegative or upward response, when light was used, was  $25.6 \pm 0.20$  per cent stronger than the geopositive or downward one; but when no light was used, it was  $54.6 \pm 0.17$  per cent stronger, indicating that when the beetles were forced downward by the light this stimulus overcame about one-half of the geotactic one. Old beetles of the second brood did not respond so readily, yet their geonegative responses were stronger than their geopositive ones. Larvae of the third instar did not respond readily and they went up only slightly more than down. When light was used, active larvae of the fourth instar reacted as readily as did the overwintering adults; but when no light was used, they did not respond so readily, although they went up more than down.

While searching for attractants and repellents an improved feeding method was devised. The adult bean beetles were confined in four small wire-screen cages, each of which contained a row of the same four foods, but differently arranged. This series of tests, with the foods differently arranged each time, was then repeated three times in the forenoon, and usually the four series were again repeated in the afternoon. Each individual food used was therefore tested 16 times in the forenoon and usually 16 times in the afternoon. According to the arrangement of food, no two rows in the same cage were exactly alike; likewise, no two rows of all 16 rows were identical, although the distribution of food was not so complete. This plan was adopted in order to equalize the number of beetles counted on the same food which lay in all four positions during any one series of tests; and furthermore, everything possible was done to obtain reliable data which could be treated statistically. Using this plan the following results were obtained.

To determine whether bean beetles "like" or "dislike" the four classes of substances which produce the four human attributes of taste, many series of tests were conducted. It was soon learned that they have "likes" and "dislikes" in regard to food. They "disliked" water containing salts, acids, bitter materials, and saccharine; but "liked" the other sweet substances tested, including cane sugar,

grape sugar, table molasses, corn sirup, and black-strap molasses, and even showed preferences between them.

Bean foliage, sprayed with arsenicals, was repellent, but not sufficiently so to prevent the leaves from being eaten. Lead arsenate was most repellent; magnesium arsenate was less so; and calcium arsenate was least repellent. Bean foliage sprayed with sweetened arsenicals was more attractive than unsprayed foliage. Bean foliage sprayed with sweetened magnesium arsenate was more attractive than foliage sprayed with nonsweetened magnesium arsenate. This would indicate that it might be of economic importance to use sweetened arsenicals in control measures, particularly to poison the overwintering beetles early in the season.

In regard to the tropic receptors of the bean beetle, the following may be stated. The structure of the compound eyes and ocelli was not studied, but these organs are normally developed and seem to function adequately, so far as beetles are concerned.

Two kinds of so-called smelling organs—certain hairs on the antennae, and pores, called olfactory by the writer—are fully described. These hairs appear long and slender, have thin, almost transparent walls, and are connected with the sense cells. They are numerous and lie in five groups on the distal ends of the ninth, tenth, and eleventh segments. The olfactory pores on the adult beetle were found as usual on the elytra, wings, legs, mouth parts, and antennae. The total number counted was only 692. The pores on the larva lie on the head, antennae, legs, and mouth parts. The total number found was only 62. The fact that the total number of pores on both adult and larva is comparatively small might be correlated with the fact that this species is "stupid" when olfactory responses are considered.

A so-called taste organ was found at the tip of the maxillary palpus of the adult. It is a soft plate which bears about 447 tiny, thin-walled sense hairs. The fact that the bean beetle possesses two of these highly developed sense organs helps to explain how these insects were able to distinguish so readily between the various aqueous solutions and insecticides fed to them.

The only so-called auditory organ found in the bean beetle lies in the second antennal segment. These structures, called Johnston organs, were formerly assumed to be auditory in function, but now are believed to be muscular receptors to register the movements of the antennae.

The remaining receptors described are the tactile hairs, which are widely distributed over the surface of the beetle.

In connection with the receptors the scent-producing organs and the phenomenon of reflex "bleeding" were studied. The only scent-producing organ found was the unicellular glands, which are distributed over the entire body surface. The bean beetle, like other coccinellids, is well supplied with these hypodermal glands. The chief purpose of the secretion is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species. When disturbed the adults eject small drops of a glandular secretion from the femoro-tibial articulations. This is called reflex "bleeding." The larvae of the bean beetle also protect themselves in a similar manner. When they are handled or even touched the yellowish and bitter "blood" exudes from ruptures at the bases of the hairs, which terminate the branches on the tubercles.

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## EXPLANATION OF PLATES

### PLATE 1

Photographs taken at the Japanese Beetle Laboratory in New Jersey, showing hundreds of Japanese beetles attracted by geraniol; 1, loaned by the Japanese Beetle Laboratory, and 2, by Van Leeuwen *et al.*

1. When cloths (1 foot square) were dipped in a 10 per cent emulsion of geraniol and suspended in orchards, beetles were drawn as if by a magnet. Some of the attracted beetles, shown in the photograph, are on the cloth, but most of them lie on the peach tree.
2. It was discovered that the beetles would gorge themselves upon foliage, sprayed with a mixture of lead arsenate and sugar, on trees to which they had been attracted by geraniol.

### PLATE 2

Photographs taken at the Japanese Beetle Laboratory, showing an electric trap which attracts and kills Japanese beetles. (After Mehrhof and Van Leeuwen.)

1. The trap rests on supports 4-1/2 feet high. A 250-Watt step up transformer, a resistance coil, and a condenser lie in the box under the trap. Several dead beetles may be seen below the trap. The danger sign was placed on the trap to prevent outsiders from molesting it.
2. Near view of the trap, showing its construction and the bait inside. The most effective bait was geraniol emulsion, sprayed on peach foliage which was suspended in the center of the trap.

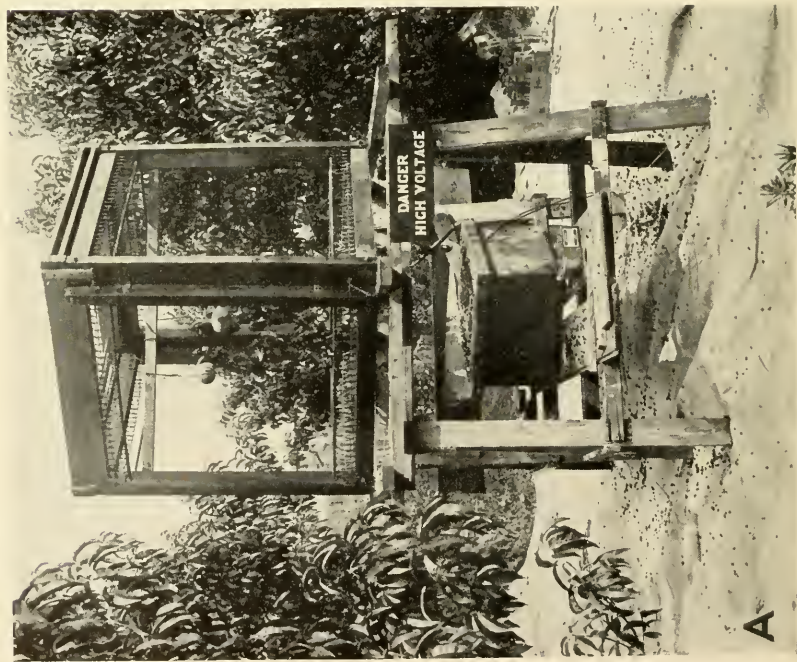


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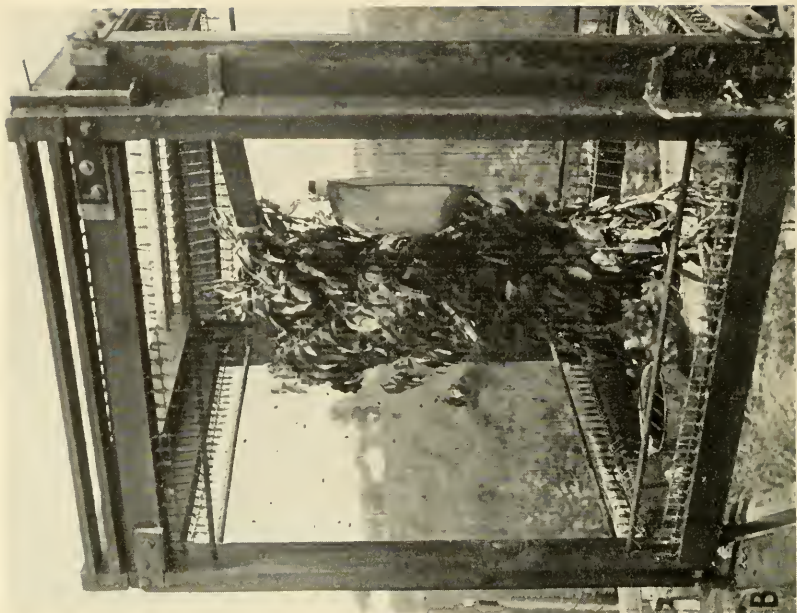


2

For explanation, see page 70.



1



2

For explanation, see page 70.