TROPISMS AND SENSE ORGANS OF LEPIDOPTERA

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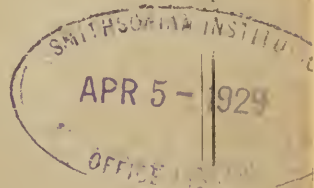# TROPISMS AND SENSE ORGANS OF LEPIDOPTERA

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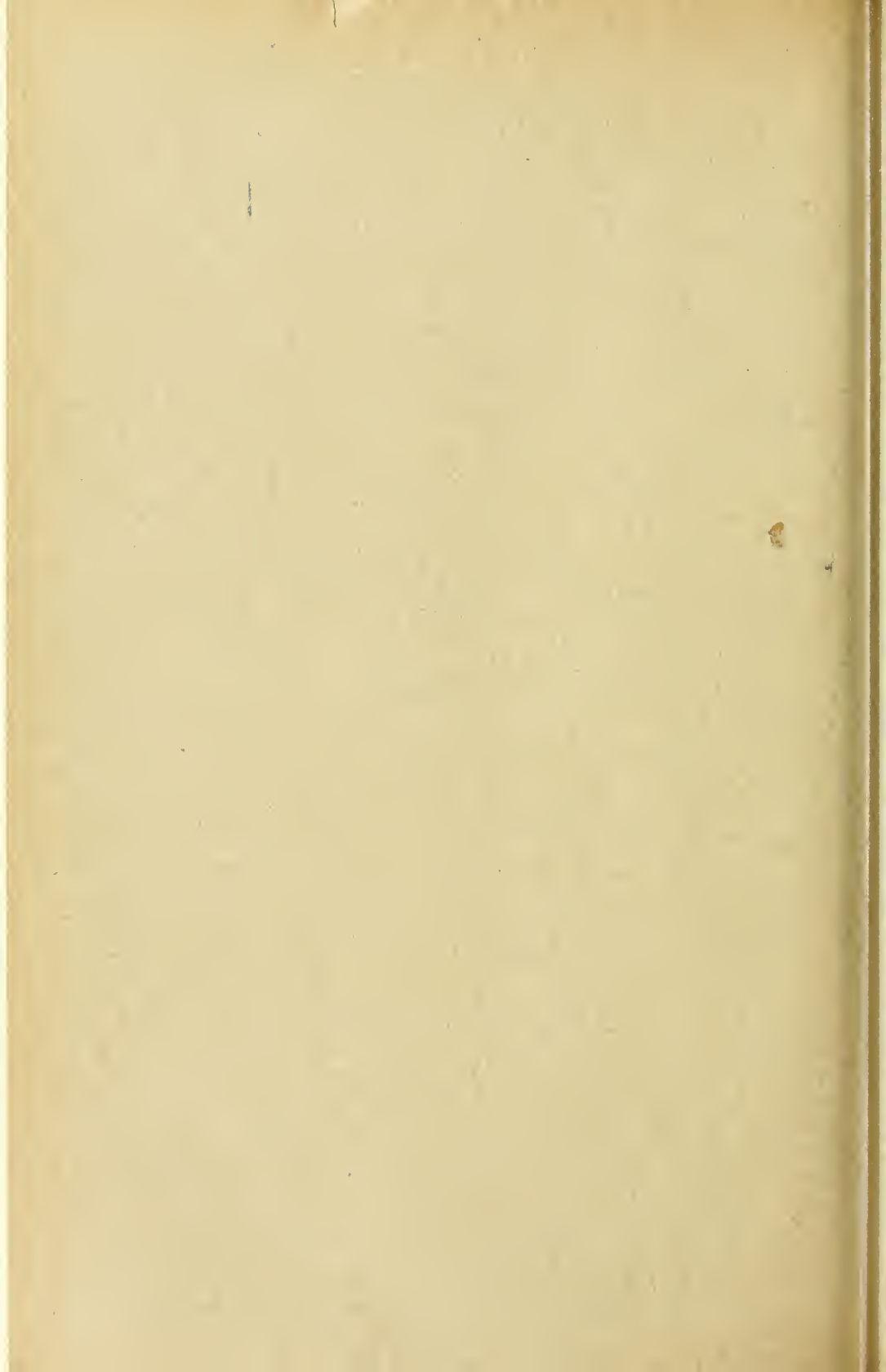
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INTRODUCTION

Entomologists know considerable about the behavior of insects, but are still unable to explain many of their activities. Since insects are cold-blooded animals and their anatomical organization is entirely different from that of higher animals, their responses to environmental conditions are different. For this reason their activities are not so easily understood. Most of their reactions are tropic responses to external stimuli. We know considerable about some of our own external stimuli, such as light, sound, and heat, and how they affect us; but we know very little about the external stimuli which cause responses in insects, and we know still less about the sensory impressions which are produced in them by these stimuli.

When it is desired to control an insect, the first step is to study its life history, which is largely a study of its behavior, and in turn behavior is largely a result of tropic responses. A study of tropisms is, therefore, a basic one, but economic entomologists in their haste to obtain practical results usually overlook this fact. The late Jacques Loeb was our greatest advocate of the study of tropisms, and as a result of his indefatigable efforts there has arisen a much broader and more important subject—general physiology. If entomologists would study tropisms more seriously, using the best equipment obtainable, they would certainly obtain much information which could be used in insect control.

The object of this paper is to bring together the available information on the tropisms and sense organs of Lepidoptera, hoping that this information will encourage a more serious study of tropic responses. At the suggestion of Dr. A. L. Quaintance, Associate Chief of the Bureau of Entomology, the writer began a series of studies dealing with the tropisms of various insects, particularly those of the codling moth. The results herein discussed include those obtained by the writer in his studies on Lepidoptera and a review of the literature, most of which pertains only to butterflies and moths.

A. TROPISMS

The term tropism comes from the Greek word meaning "turn." According to Mast (56, p. 53) it was first used in 1832 by DeCandolle, who called the bending of plants toward light heliotropism. Later the word heliotropism came to signify both the bending and the explanation of the process. Verworn and Loeb, in 1886 and 1887, as cited by Mast, using tropisms as a basis for investigation, were the first to study animal behavior from the physico-chemical point of

view. Loeb attempted to show that the behavior in plants and animals is practically alike, and concluded that the behavior in animals is largely controlled by external agents, and is influenced by internal factors. He and his followers described reactions in animals in terms of tropisms.

There has been a controversy among various classes of scientists in regard to the proper terminology to be used in connection with tropic responses. Couch (6) proposes that the generic name, tropism, be retained for all the classes, but that biologists and biochemists use the words phototaxis, geotaxis, chemotaxis, etc., leaving the " isms " to be used by chemists and physicists, and particularly the word phototropism by the photochemist.

Mast (57) informs us that the term tropism has been defined in some 20 different senses. Since there is so much confusion about its meaning, he proposes that we cease using it altogether, using instead terms with more precise meanings as (p. 261) : " negative or positive orientation or reaction to light, gravity, etc. ; photo-, geo-, etc., negative or positive ; or merely negative or positive reactions to light, gravity, chemicals, etc." In the following discussions these suggestions will be frequently followed, and instead of saying that an insect is negatively or positively phototropic or phototactic, it will be said to respond or react negatively or positively to light, or to be photonegative or photopositive.

I. PHOTOTAXIS

1. REVIEW OF LITERATURE

(a) *Definitions and problems in the study of light reactions.*—The terms heliotropism and phototropism have been generally used by both botanists and zoologists, but as already mentioned, Couch proposes that biologists use the word phototaxis, leaving the former terms for the photochemist. Botanists still insist on using them, but recommend that zoologists should say phototaxis and phototactic. According to Mast (56, p. 253) the botanists are correct, because

Organisms which orient and move toward or from a source of light are usually termed phototactic, those which orient but do not move as phototropic, and those which do not orient but still react have been termed photopathic.

Loeb, discussing both plants and animals, used the word heliotropism in his original German publications, in their English translations, and even in his latest papers. For our purpose here Loeb's definition of phototaxis will suffice. He says (43, pp. 135, 139) :

Heliotropism covers only those cases where the turning to the light is compulsory and irresistible, and is brought about automatically or mechanically by

the light itself. . . . If the current curves of radiating energy, *e. g.,* light rays, strike an animal on one side only, or on one side more strongly than on the symmetrical side, the velocity or the kind of chemical reactions in the symmetrical photosensitive points of both sides of the body will be different. The consequence will be in a positively heliotropic animal a stronger tension or tendency to contract in the muscles connected with the photosensitive points of the one side of the body than in those connected with the opposite side.

Mast (56, pp. 57, 58) points out several problems in the study of light reactions which entomologists should carefully consider. They are discussed with others as follows:

(b) *Are light reactions adaptive?*—No, according to Loeb's definition. He says that animals go toward light neither because it is useful for them to do so nor because they enjoy it, but because they are photopositive. Mast strongly refutes this explanation by saying (56, pp. 298, 237):

Reactions to light are in general adaptive. There are, however, certain reactions which are clearly injurious and often fatal; as, for example, the flying of insects into a flame and the positive reactions of organisms which live in darkness. But the positive reactions of insects are ordinarily advantageous. It is only under artificial conditions that they prove fatal, and the ancestors of many animals which now live in darkness lived in the light. Positive reactions were probably advantageous to them, and the power to respond thus was probably inherited by the offspring, in which it is useless. . . . Negative response to light tends to keep these creatures [blowfly larvae] buried in cadavers where they find food. It is ordinarily only under artificial conditions that the reactions of organisms to light prove fatal. Positive reactions to candle, lamp and lighthouse destroy untold numbers of moths and flies and bees and beetles and birds, but who has seen such fatalities under natural conditions? Under such conditions the responses to light direct these animals to the advantage of their well-being.

Loeb's (43, p. 160) explanation of the origin of adaptive light reactions follows:

The fact that cases of tropism occur even where they are of no use, shows how the play of the blind forces of nature can result in purposeful mechanisms. There is only one way by which such purposeful mechanisms can originate in nature; namely, by the existence in excess of the elements that must meet in order to bring them about.

Mast (56, p. 368) adds that light reactions are variable, modifiable, and in general adaptive, and that regulation constitutes perhaps the greatest problem of life. Loeb (43, p. 125) believes there is a phototactic difference between the sexes of Lepidoptera, for male moths are more apt to fly into candle flames than are the females. It is well known, however, that both sexes are attracted to strong electric lights. It was assumed long ago that moths fly into flames because they are fond of light, but Loeb assures us that this is a purely mechanical

response, comparable to the turning of a plant toward light. In reply to the question as to why moths fly toward a candle at night and not toward the moon, Mast (p. 227) replies that in moonlight there are large illuminated areas all about, whereas in candle light the objects are so faintly lighted that moths do not react to light reflected from them. In reply as to why mourning-cloak butterflies fly toward a large illuminated patch of flowers rather than toward the sun which is much brighter, Parker (69) says it is because the patch of flowers makes a larger " spot on the retina." All of these responses Mast considers adaptive regardless of the explanations given.

(c) *Is orientation accomplished by selection of trial movements?*— Loeb (42, p. 57) exposed blowfly larvae in front of a window. He found them to be photonegative and to crawl with mathematical precision. Other investigators have repeated these tests, but they failed to find that blowfly larvae, or in fact any other insects, respond to light with mathematical precision. Mast (56, p. 196) says that blowfly larvae are excellent examples of animals which are guided fairly directly on their courses by successive trial movements.

Loeb (42, p. 24) tested caterpillars of *Euproctis* (*Porthesia*) *chrysorrhoea* and he found them to be strongly photopositive, creeping in a straight line toward the light. Lammert (40) in 1925 tested three other species of caterpillars which were also photopositive, but crawled in wavy lines. The present writer's results (p. 13) with codling-moth larvae agree with those of Lammert.

(d) *How do light rays bring about orientation?*—Loeb in 1888, according to Mast (56, pp. 54, 57, 228-235), claimed that orientation in animals is controlled by the direction in which the rays pass through the tissue. In 1889 he further said that symmetrically located points on the photosensitive surface must be struck by light at the same angle. Later he abandoned the idea of the importance of the angle between the sensitive surface and the light rays and substituted the view that orientation is brought about by absolute difference of intensity of the light on symmetrically located points on the sensitive surface. Jennings, Mast, and others claim that orientation is accomplished by changes of intensity on the sensitive surface. Loeb believed that light acted constantly as a directive stimulation similar to the action of a constant current of electricity, while Jennings and Mast believe that it acts only when the animal turns out of its course so as to produce changes of intensity.

(e) *Do circus movements support Loeb's theory?*—Mast (56, pp. 215-218) states that several workers have found that if one of

two symmetrically located sense organs has been prevented from functioning, the animal no longer orients but turns toward one side when stimulated. Certain flies with one eye blackened turned toward the functioning eye. Parker (69) obtained similar results with a butterfly (*Vanessa antiopa*). Loeb (44, pp. 52-61) cites the results of several writers, who conducted similar tests on insects, as giving " direct proof of the muscle tension theory of heliotropism in motile animals." Dolley (10) experimented with *Vanessa antiopa* and concluded that his results contradicted Loeb's " continuous action theory." According to this view the tension of the muscles of the appendages on both sides of the body is controlled through direct reflex arcs by the photochemical changes produced by light in the two retinas. Dolley says that these butterflies with one eye blackened can orient and can turn under certain conditions toward either side, all of which indicates that orientation in them is not wholly dependent upon the relative intensity of light on the two eyes. The same author (11) determined that *Vanessa antiopa* moves faster in weak light than in strong light. This behavior is not in accord with the above theory. Dolley also determined that these butterflies move faster in intermittent light than in continuous light, which indicates that orientation in them is " due to the time rate of change of intensity."

(f) *What wave lengths stimulate insects most?*—The determining of this is perhaps the most difficult of all the problems encountered in a study of tropisms, and much confusion has arisen while trying to solve it. Many erroneous conclusions have been derived ; first, because the investigators, as a rule, have had a poor knowledge of the physics of color ; and second, because in most cases they have not been properly equipped with apparatus to study the effects of various wave lengths on insects.

Loeb (42, p. 18) remarks that all authors who have studied the behavior of plants behind screens have usually concluded that only the more refrangible rays are heliotropically active. Using two colored screens (red and blue), he concluded that the more refrangible rays of the visible spectrum are more effective than the less refrangible rays in causing orientation in animals (p. 82). He tested the caterpillars of *Euproctis chrysorrhoea* (pp. 29-31) with these screens, which had been examined spectroscopically, and determined that they reacted most decidedly to the shorter wave lengths.

Mast (56, pp. 302-365) in 1911 reviewed the entire subject of wave lengths or colors and discussed insects in particular (pp. 343-355). He reviewed Loeb's work on animals and fails to understand how the

latter could have made such positive statements since only two colors were used. It is easy to ascertain that animals can distinguish wave lengths that we call colors, but it is difficult and perhaps impossible to determine whether the responses are brought about by the quality or quantity of the wave lengths, that is, by actual color or by brightness. Our only recourse is to test them and to judge their responses from the human point of view, which proves little or nothing in regard to insects. On this point Mast (p. 362) says:

> Bees and fishes can undoubtedly distinguish different regions in the spectrum. They can be trained to select any of the primary colors of the spectrum by associating these colors with food. That is, they are positive to (or select) one color at one time and another at a different time. Just what mechanism is involved in this power of selection is unknown. Whether it is on the basis of brightness or on the basis of color vision or neither is a matter concerning which experimental evidence does not warrant a definite conclusion. Many organisms react to ultraviolet much as they do to visible rays. This is in harmony with the following quotation from Schäfer referring to man (1898, p. 1055): "The invisibility of the infra-red rays is probably due to insensitiveness of the retina, while the ultra-violet rays fail to be seen, partly, at any rate, owing to absorption by the ocular media."

Washburn (90, pp. 144-159) discusses the problem of visual qualities in invertebrates. Certain authors believe that vision as far as color is concerned in the lower animals, particularly insects, is similar to that in totally color-blind people. On this point Washburn (pp. 145, 147, 148, 157) says:

> It is therefore of some importance to the problem of color vision in the lower animals to find *how strongly* the light rays of various wave-lengths affect them. But we must bear in mind that for the lower animals it is impossible to conclude color-blindness from the fact that the brightness values, that is, the effective intensities, of the different colors are what they would be for a color-blind human being. Just this unsafe inference is, however, drawn by certain authorities. . . . It is thus clear that when an animal discriminates between rays of different colors, the discrimination may be based merely on the intensity of the rays, either in themselves or in the effect which they have on the organism, rather than on their wave-length or color. . . . He [Hess] found that the yellow and green rays produce much more effect than the red and violet rays. Since this is true also of the color-blind human eye, he argues that the animals tested are totally color-blind. He holds, in fact, that all invertebrate animals are totally color-blind, on the same evidence. . . . But again we may remind ourselves that it does not follow that because a human being who finds the yellow-green, rather than the yellow, the brightest spectral region, is totally color-blind, therefore an animal, especially an invertebrate animal, the chemical substances in whose eye may have no resemblance to those in the human eye, is color-blind if it shows these reactions to the different regions of the spectrum.

Mayer and Soule (59) in 1906 determined that the caterpillars of the milkweed butterfly are photopositive to ultraviolet rays, but barely respond to the rays which man sees in the spectrum.

Lutz (46) in 1924 used colored filters as windows in a box and determined that insects can readily distinguish ultraviolet rays. Certain individuals, particularly Lepidoptera, stubbornly refused to respond to any condition of illumination, even clear sunshine, when they were placed in the box. Certain others responded only when urged to do so by jarring the box, but then their reactions were definite. The skipper *Epargyreus tityrus,* when put in the box " went to sleep," but when touched it went to the ultraviolet filter and tried to get out.

Other recent workers, whose apparatus and procedure are recommended to research students, have obtained results showing that insects respond to the color of certain wave lengths. Thus Abbott (1) determined that a certain ant responds most readily to yellow, and Bertholf (3) ascertained that red does not stimulate honeybees as much as it does humans, but that violet stimulates them more.

Besides consulting the references already cited students are advised to consult others, particularly Parsons (71) and Luckiesh (45).

One of the most recent papers on this subject is by Peterson and Haeussler (74), who studied the responses of the oriental fruit moth (*Laspeyresia molesta* Busck) and the codling moth (*Carpocapsa pomponella* L.) in 1925, 1926, and 1927. Several thousand individuals of each species were tested after dusk at Riverton, N. J., where an abundance of material could be secured. Two types of apparatus were used, but the most satisfactory one is what they call a " four-way light apparatus." The colored screens and lights used were submitted to Dr. P. A. van der Muelen of Rutgers University, who examined them spectroscopically. Their summary in part is as follows: Oriental fruit moths and codling moths seek the light side of containers in which they are placed. This indicates that they are photopositive under ordinary conditions. When tested under laboratory conditions in the four-way light apparatus, with the four compartments equally lighted with white lights, practically the same number of moths went into each compartment. When the compartments were unequally lighted, the largest number of moths went to the strongest light. When the moths were given the choice of lights varying in color from red to violet and the ratios of relative intensities of the colored lights were approximately equal, practically all of the moths went to blue and violet lights. Few or none were attracted to the red light. Orange and yellow lights, when compared to bluish ones, were also unattractive. Green light, possessing no blue rays, was likewise unattractive. Violet light was preferred to blue, and ultrapurple wave lengths appeared to be more attractive than violet. Ultraviolet light

was probably perceived by oriental fruit moths and they were probably attracted by it. Codling moths seemed to be more strongly photopositive to blue and violet lights than were oriental fruit moths. The responses of males and females of both species to colored lights appeared to be similar. Experiments in which ordinary electric lights were installed in a peach orchard were unsuccessful, only a few of the oriental fruit moths being caught in traps. Codling moths were not tested in orchards.

There is considerable difference of opinion regarding the apparatus to be used in light experiments. Yerkes and Watson (91, p. 3) say that simpler and more conveniently manipulated apparatus may be used in preliminary work, but emphatically recommend that such apparatus be abandoned as soon as possible. They recommend a very complicated piece of apparatus for thoroughgoing, intensive, and quantitative work.

(g) *Light traps are not yet considered successful.*—Dewitz (9) in 1912 briefly discussed the practical side of phototaxis as applied in economic entomology, but regretted that this subject had never been seriously studied from a scientific point of view. To his knowledge only one investigator spectroscopically examined the various lights used. This man projected a large spectrum on a screen in a dark room and then observed certain moths collect on the different colors of the spectrum. He found that the less refractive colors (red to green) exercised by far the strongest attraction. It is also stated that experiments were conducted in vineyards in Germany in which lamps provided with glass covers of various colors were used. The lamps with green glass attracted the largest number of moths.

According to Dewitz, artificial light as a control measure was first used in 1787 for attracting vine moths to lighted candles on window sills and to wood fires in vineyards. Since that date light traps have been gradually developed and improved until to-day there are many types and varieties of kerosene, acetylene, and electric lamps used for this purpose. It seems that none, however, has given complete satisfaction as a control measure. The present writer does not know of a single authentic report that this method has been successful on a large scale, although he has a recent newspaper report stating that along the German-Polish frontier powerful searchlight traps have been used successfully against a nocturnal moth whose larvae ravage the pine forests. Millions of moths are said to have been cremated by being attracted to flames near the searchlights.

At last an investigation on a large scale, in which up-to-date scientific methods are being used, has been started by the New York (Geneva) State Agricultural Experiment Station and the Empire State Gas and Electric Association. So far only a progress report of this work has been presented by Parrott (70), who regards a study of tropic responses of insects as one of the most promising fields of entomological inquiry, and who believes that when the more important facts about light attraction for insects are known we may, perhaps, be able to change some of our present practices on insect control. Experiments in orchards in which various kinds and colors of electric light bulbs were used gave a total catch of 65,000 insects, of which 29.6 per cent were Lepidoptera and 52.5 per cent were Diptera. All of the Lepidoptera, most of the Coleoptera and Hemiptera, and a smaller percentage of the Diptera and Hymenoptera caught were injurious species. Among the Lepidoptera were the codling moth, fruit-tree leaf-roller, cutworm moths, and several other species. This method was also found useful for trapping codling moths and other injurious insects in cold storage houses. In a dairy barn clear and white frosted bulbs attracted more flies than did the other colors, and red attracted the least of all. Tests in which colored glass filters were used with several species of moths including codling moths and European corn-borer moths showed that these insects did not respond to the red end of the visible spectrum, but the light yellow, light blue-green or daylight, red-purple, and blue-purple filters proved the most attractive.

2. PHOTOTACTIC EXPERIMENTS ON CODLING-MOTH LARVAE

The writer, like other observers, has found the adult codling moth an unfavorable insect on which to experiment in the laboratory. These moths are extremely erratic in behavior. They are very quiet and usually non-responsive during the daytime, but at dusk and later they are more active and readily respond the first time, although thereafter their responses are irregular and not fully reliable. Since the same individuals cannot be repeatedly tested with satisfaction and as the writer's supply of them was limited, he was not able to conduct the experiments as originally planned.

Having failed to obtain definite results by testing a small number of the adults, the writer spent much time in 1927 on the larvae, which proved to be more favorable material for tropic tests. In all 154 larvae, belonging to the two broods at Silver Spring, Md., were tested in the laboratory under various conditions. Most of them had been reared from eggs in the laboratory. The wormy apples

were kept in battery jars and drinking glasses, and an accurate record of the age, size, color, and behavior of the infesting larvae was recorded. The instars were determined by use of Dyar's (14) method of head measurements, the live larvae being rendered inactive by laying them upon a piece of ice on the microscope stage. Temperature and humidity records were obtained from centigrade thermometers and a hygrothermograph. Notes pertaining to the date, time of day, character of sky and wind, degree of brightness of sunshine, and rainfall were recorded, but unfortunately it was difficult and sometimes impossible to correlate climatic conditions with the tropic responses obtained. For this type of work more refined methods and apparatus are badly needed.

Since it was not possible to carry on phototactic tests among the trees in orchards in the natural environment of these insects, the next best condition was to use daylight in the laboratory. Daylight, however, was unsatisfactory because the intensity varied daily and even from hour to hour, so that comparative quantitative results were impossible. Artificial light with a 100-watt " daylite " bulb was tried. The larvae usually responded to it only after being touched and then very feebly. For these experiments a simple and quick method for determining daylight intensities was badly needed, but none seemed available.

Relative to ecological photometry and means of measuring light, Klugh (39) presents a critical review of the entire subject and then describes a new instrument, called an ecological photometer. There are already three kinds of instruments of high precision for measuring radiation. Two of them, the pyrheliometer and spectrobolometer, are used by the astrophysicist and the third, the spectrophotometer, is employed by the physicist. The new instrument is said to meet the needs of the ecologist, but in order to operate it one should be considerably experienced in photography. Using the new instrument Klugh obtained very interesting results. As an example to show the great variations in daylight intensity, he selected an open habitat on a bright clear day, July 26. Letting the intensity at noon equal 100 per cent, he then determined the following percentages of intensities: At 9 a. m., 90 per cent; at 5 p. m., 83 per cent; at 6 p. m., 66 per cent; and at 7.45 p. m., 5.2 per cent. On another bright sunshiny day he found the intensity to be only 2 per cent in a woods while in the open it was 100 per cent, but on a cloudy day it was 10 per cent in the same woods as compared to 100 per cent in the open. The intensities on clear and cloudy days vary greatly. Filmy clouds over the sun

reduce the intensity, whereas white clouds in the sky but not over the sun increase it by reflection from 10 to 40 per cent over that of a cloudless day.

In view of the varying light values and other conditions involved in phototactic experiments, the reader can appreciate the experimenter's difficulties and can understand why it is so difficult to interpret the results correctly.

In bright light, although not direct sunshine, codling-moth larvae of the first instar were found to be weakly photopositive, and their reactions agreed in general principles with those described by other investigators. None was found, however, to orient and to move with mathematical precision as was stated by Loeb for certain insects.

Larvae of the first instar, confined in an uncovered box in which most of the light was reflected from the ceiling, moved in all directions. Recently hatched larvae placed on a table by a south window and six feet from an east window, instead of moving directly toward the south window, deviated toward the left (fig. 1, A). This reaction agrees with those described by other writers, for example Dolley (12), when two sources of light at right angles are employed.

In order to eliminate side lights a box, 18 inches long, 12 inches wide, 12 inches high, and lined with a dead-black cloth, was constructed. One end and the top were left open. The open end faced the south window while the experimenter, from above, traced the tracks of the insect with a pencil. Since there was apparently no difference between white paper and black paper as to effects of reflected light on the insect, all tracings were made on white paper. The pencil was moved gently a few millimeters behind the insect and this usually did not affect the behavior of the larva, although in tracing the path of photonegative insects care had to be exercised not to allow shadows from the pencil to fall upon the insect. Recently hatched larvae, when put in this phototactic box on either bright sunshiny days or on cloudy days, oriented themselves and tended to move toward the direct rays of light as illustrated in figure 1, B, in which those tested before noon deviated toward the left (No. 96) while those tested after noon deviated toward the right (Nos. 98, 99). Many exceptions to this tendency, which the writer cannot explain, were recorded, so no definite rules can be stated. In order to be reasonably certain about the light reactions of all the larvae tested, it was necessary to test each one two or more times before drawing conclusions.

Larvae of the second, third, and fourth instars were found to be weakly photopositive to weak light (fig. 1, C, Nos. *112a, 113a, 124a*), but indifferent to strong light (Nos. *112b, 113b, 124b*).

Larvae of the fifth instar sometimes acted indifferently to light (fig. 1, D, No. *108*) but generally were weakly photonegative (Nos. *102, 118, 126, 129*). Larvae of the sixth instar were either weakly (fig. 1, E, No. *100*) or strongly photonegative (Nos. *54, 68, 72, 73, 78*), the degree depending on their age. In all cases they oriented quickly and moved hurriedly from the light as illustrated in figure 1, E.
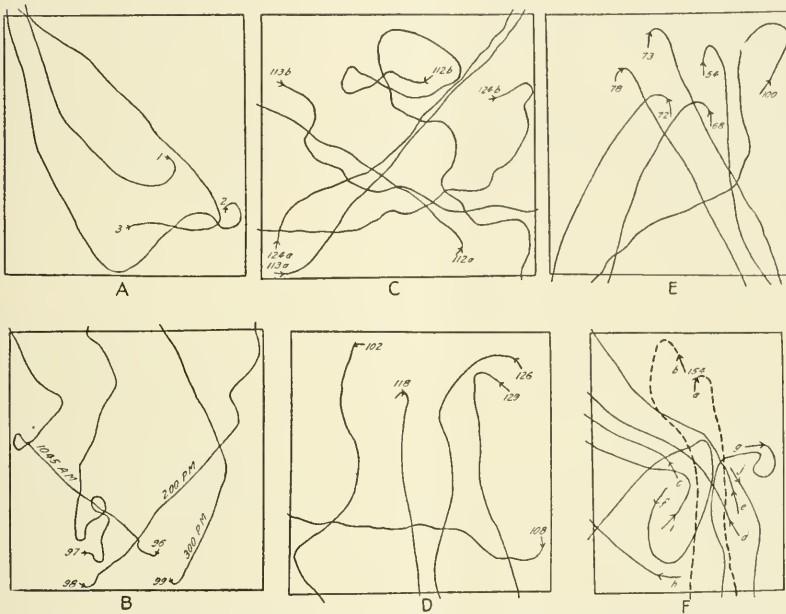
Fig. 1.—Tracings of phototactic responses of codling-moth larvae (see p. 12 for further explanation). A, Movements of recently hatched larvae of first brood tested on table between an east and a south window at 3.45 P. M. B, Recently hatched larvae of second brood tested in phototactic box. C, Larvae of second brood; Nos. *112 a* and *b*, fourth instar; Nos. *113 a* and *b*, third instar; and Nos. *124 a* and *b*, second instar. D, Larvae of second brood, fifth instar. E, Larvae of second brood, sixth instar, fully grown. F, Fully grown larva, No. *154*, ready to spin; *a* and *b*, normal; *c* to *j*, ocelli blackened.

Normal larvae of the sixth instar, ready to spin cocoons, were strongly photonegative (fig. 1, F, No. *154a* and *b*), but when their ocelli were covered with a mixture of glue and lamp black they became indifferent to light as illustrated in figure 1, F, *c* to *j*.

One of Loeb's early observations indicated to him that lepidopterous larvae do not generally react to geotaxis, but that this tropism is replaced by phototaxis. According to Lammert (40), Schmitt-Auracher, after finding a migration of pigment in the ocelli of insects, supported this view and then assumed that the ocelli were capable of

two adaptive conditions, which are distinguished morphologically by different pigment deposits and that phototaxis depends on these deposits; that is, a dark deposit of pigment causes a dark adaptation and negative phototaxis, while a light deposit brings about a light adaptation and positive phototaxis. Lammert does not support this hypothesis because he failed to find a migration of pigment in the ocelli of certain insects, but his tests in which the ocelli were blackened caused him to believe that lepidopterous larvae have two kinds of photoreceptors—the ocelli and others lying in the body integument. He believes, therefore, that these larvae have a skin sensitive to light. The present writer's few experiments on this subject do not indicate that codling-moth larvae have photoreceptors in their integument, and· these larvae do not appear to be suitable material in which to search for a migration of pigment in their ocelli.

II. CHEMOTAXIS

1. REVIEW OF LITERATURE

Much was learned about chemotaxis long before the term chemotropism was first applied to it. Among the earliest publications are those of Fabre (20, pp. 179-216) and Forel (21, p. 76), who established the fact that male moths are attracted from long distances to their mates apparently by means of odors emitted by the females. Mayer (58) in 1900 carried on tests with promethea moths and established the fact beyond doubt that the males are attracted by emanations from scent-producing organs of the females. Later Mayer and Soule (59), Kellogg (37), Freiling (23), and others corroborated the view that the emanations are emitted from scent-producing organs. Prüffer (75, 76) more recently has supported this view in regard to the gipsy moth. He assures us that the attraction between the sexes is accomplished by means of aromatic substances which are secreted by the females and the odors of which are perceived by the males. To determine whether or not the attraction is similar to the radiation from radioactive material, he confined the females in a lead cylinder which would reduce the supposed radiation to a minimum and then allowed the emanations from the cylinder to escape by means of a specially constructed column of mercury. Using this apparatus he soon determined that the females thus confined attracted the males in the same manner as do the females in the open air, but that the males were not attracted when the females were confined in a hermetically sealed glass container. Dead females were also able to attract males, but to a lesser degree. Prüffer furthermore tells us that the radiation from a

living insect, which when laid upon a photographic plate leaves an impression, plays no part in this attraction.

Loeb (43, p. 155) in 1889 seems to have been the first one to use the term chemotropism in connection with the responses of Lepidoptera that have just been discussed and with the attractiveness which meat has for blowflies and their larvae.

As the writer (54, 55) has recently reviewed the literature dealing with chemotaxis in economic entomology, only a short discussion need be given here.

Chemotaxis, like the other tropisms, has two divisions. Attrahents, usually called " attractants," induce positive chemotaxis and repellents induce negative chemotaxis. For our purpose here Trägårdh's (85) definition will suffice. He says (p. 113):

> By the term " chemotropism " is meant, as well known, the automatic orientation of the animals to any olfactory sensation in such a manner that both sides of the body are struck by the lines of diffusion at the same angle. Theoretically, when a substance diffuses an odour, fine particles are ejected in straight lines, but in reality the air currents cause the lines to deviate from their straight track.

In the control of Lepidoptera many practical applications of chemotaxis have been made. Attractive poisoned bran baits are used as control measures against armyworms and cutworms. As early as 1896 baited traps were used by collectors to catch large numbers of fertilized, egg-laying female moths. Many years ago the common control method against grapevine moths in Europe was the use of attractive baits; but more recently the use of insecticides has supplanted this method as a control measure, so that now it seems to be used only as an indicator of the approximate number of moths present. With this information the grower knows when to apply the insecticides.

A molasses-yeast bait was placed by Peterson (72) in a peach orchard in New Jersey, and it was observed that large numbers of the oriental fruit moth came to the bait pans. This observation was a stimulus for more extended work with attractive baits, but this particular bait when fermenting proved to be the most attractive one tested. Frost (24) used weak acids, volatile oils or their constituents, sugars, and molasses as attractants. The fermenting sugar baits attracted the most moths. Peterson (73) tested about 250 aromatic chemicals as possible attractants for the oriental fruit moth. Terpineol and several essential oils were somewhat attractive, but not so attractive as several fermenting sugar-producing products. Fermenting fruits (dried fruit in water), particularly prunes, pears, and apricots, attracted large numbers of moths. By using dried fruits, sugars, and

2

sirups in Maryland peach orchards in 1926, Siegler and Brown obtained results similar to those of Peterson. Apricots were the most attractive of the dried fruits used. A late report about baits for the oriental fruit moth is by Frost (25), who discusses comparative tests with various baits, factors affecting the catches of moths, and the value of bait pails as a means of control. He believes that this method may find a definite place in the control of this moth. The latest report consulted on this subject is by Stear (83), who says that bait pans offer little hope in practical control.

Supposing that the codling moth was attracted to fruit trees by odors, Yetter (92) conducted a large series of experiments in Colorado, using 35 aromatic chemicals. Of these only five attracted moths in sufficient numbers to give promising results. These five are isobutylphenyl acetate, diphenyl oxide, bromo styrol, benzyl benzoate, and safrol. He firmly believed that, if trapping were systematically carried out by all the growers in the Grand Valley and for the entire season, much could be accomplished in checking the damage done by this pest.

Yetter and Yothers each seem to have begun testing baits in 1923, but the latter did not publish his results until 1927. Yothers' (93) summary follows in part: Cooked, fermented apple juice, containing some of the apple pulp, proved more attractive than did vinegar or cider. A molasses ferment proved much more effective than did apple ferment, honey ferment, or any one of two dozen essential oils. Of the essential oils only three—clove, citronella, and sassafras—proved attractive to codling moths. About 55 or 60 per cent of the moths caught were females, and 95 per cent of these were gravid. The baits gave a good indication of the beginning and end of the codling-moth season, the appearance of each brood, and the maximum abundance of each. This information may be used to advantage in arranging spray dates for moth control. In bait tests final counts of fruit showed an increase of from 12 to 16 per cent of fruit over similar plots without traps. Yothers believes than an attractive bait may yet be discovered which will be so attractive that this method may then be recommended as a satisfactory supplementary control measure.

Yetter's first report encouraged others to try this supplementary control measure. Spuler (82) found codling moths to be attracted in large numbers to a fermented bait consisting of one gallon of apple cider, one-half pound of brown sugar, and one yeast cake. Approximately 60 per cent of the moths caught were females. It was concluded that the bait traps will reduce the number of moths in an orchard, thus serving as an important supplement to spraying, and will furnish infor-

mation as to the time of appearance of the moths. Other similar reports on this subject are by Headlee (30) and by List and Yetter (41). According to Fowler (22), baits are also being used in South Australia as an aid in codling-moth control. This writer says that large numbers of moths can be caught in suitable traps properly baited, and that it is profitable to put out a number of traps from the last week in October until the end of November, and again from the end of January to the middle of February, which intervals cover the periods of maximum emergence and give the best results. Baits are likewise being used in South Africa.

After experimenting with a large number of aromatic substances for several years at Clarksville, Tenn., Morgan and Lyon (67) have recently reported that amyl salicylate incites a decided feeding response in tobacco hornworm moths (*Phlegethontius carolina*), inducing an attraction to artificial flowers. Sixteen species of Sphingidae were caught in traps baited with the chemical besides the two species frequenting tobacco. In field experiments a number of female moths sufficient to have deposited 8.1 eggs per tobacco plant were caught in traps. Amyl benzoate was also found very attractive.

Attractants and repellents have been used in control measures against other species of moths, and a further discussion is perhaps not necessary to convince the reader that this new line of research merits further serious consideration.

2. CHEMOTACTIC EXPERIMENTS ON CODLING-MOTH LARVAE

The preliminary results which follow were obtained by testing codling-moth larvae with attractants and repellents. As an example of the procedure in the tests, a recently hatched larva was put in the phototactic box described on page 12 to be sure that it responded normally to light. After tracing its tracks (fig. 2, A, *a*) a sheet of white paper was laid on the table by the south window. Twelve cubes of green apple, each 4 or 5 millimeters in size, were placed an inch or more apart on the paper inside a circle having a diameter of 5 inches (fig. 2, A). The larva was then placed inside the circle and allowed to search for the pieces of apple while slowly moving toward the light. It was given 10 chances and each time it touched a piece of apple or the circle that particular chance ended. Pieces of cork of the same size as those of the apple and squares equally large, drawn with a pencil inside the circle, were used as controls.

Several larvae recently hatched went to the pieces of apple, on an average, in 65 per cent of the chances offered to them; several larvae

of the second instar in 50 per cent; one larva of the third instar in 60 per cent; and one larva of the sixth instar in 85 per cent. Several recently hatched larvae went to the pieces of cork in 40 per cent of the chances offered to them and others passed over the squares in 30 per cent of the chances.

These results indicate that smell and sight aid in locating objects, the former being the more important in perceiving odorous objects. Therefore, since larvae of the first instar have photopositive eyes, they remain in the open on apple-tree foliage and search freely for food, apparently not being aided by their senses until within a few millimeters of the food, because in these tests they wandered about
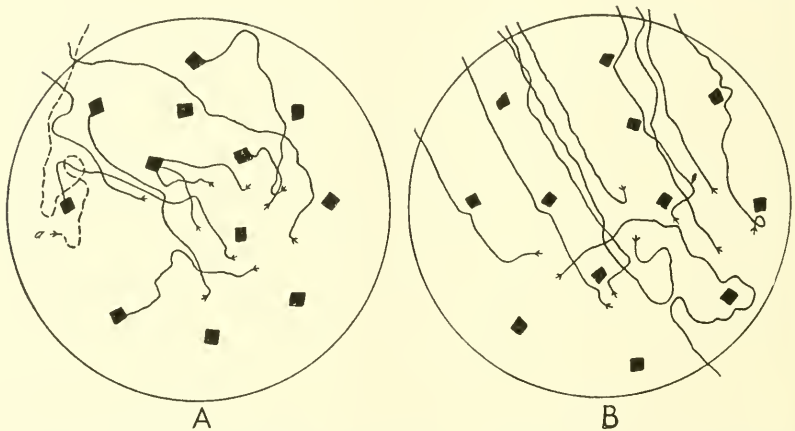
Fig. 2.—Tracings of chemotactic responses of recently hatched codling-moth larvae (see p. 17 for further explanation). A, Positive responses to small cubes of green apple; B, negative responses to synthetic apple oil on small cubes of cork.

aimlessly and did not perceive the pieces of apple and cork until near them, when they often turned and went directly to them.

Two tests were conducted with a repellent. Pieces of cork, after being dipped into concentrated synthetic apple oil, were laid inside the circle, and within a few moments the oil had spread on the paper around the cork. A recently hatched larva was given 10 chances to touch the cork, but not once was it touched. When approaching a piece of cork the larva often circled around the margin of oil on the paper. The following day the same pieces of cork were tested with another recently hatched larva. To the writer the cork was highly scented, but it did not wet the paper. In 10 chances this larva was turned 12 times from its course by the repellent odor (fig. 2, B).

III. GEOTAXIS

1. REVIEW OF LITERATURE

Frank in 1870, according to Mast (56, p. 12), invented the term geotropism to designate the reactions of parts of plants to gravity. Loeb (42, p. 85; 43, p. 125) in 1888 claims to be the first to call attention to the influence of gravity on the orientation of animals. Caterpillars of *Bombyx neustria* were found to be geonegative, for, when confined in a wooden vessel with the opening at the bottom, they crept upward. Loeb says that " geotropism," like " heliotropism," is evident only at certain epochs in the life of an animal, for the result of the geotactic tests were not at all times consistent in the same animals. Loeb (42, pp. 33, 44) confined caterpillars of *Euproctis chrysorrhoea* in test tubes in a dark room and found them to be geonegative. He remarks that strongly negative geotaxis is no isolated phenomenon in insects at the hatching time and immediately after the adults have emerged from the pupa cases. Caterpillars of butterflies, like freshly emerged moths, are also geonegative, though not so markedly. Immediately after emerging geotaxis is much stronger than phototaxis in the butterfly, but later these reactions are usually reversed.

Mayer and Soule (59) found three species of caterpillars to be geonegative. Geonegative and photopositive reactions serve to maintain the caterpillars of the milkweed butterfly near the upper part of their food and to lessen the risk of their wandering down the stem and starving before being able to find another milkweed. Two species of moth caterpillars were geonegative when about to pupate, but they always pupated head downward.

Dewitz (9) remarks that geotaxis may frequently combine with phototaxis, thereby forcing the animals to locate themselves on the extreme ends of tree branches and on the crowns of trees (negative geotaxis), or to descend into the soil (positive geotaxis).

Lammert (40) used an electric light beneath a special apparatus and found all the caterpillars tested to be geonegative with the light turned off. When the stimuli from light and gravity were simultaneously tested the light stimuli were the stronger.

The latest paper known to the writer which deals with geotaxis in insects is by Crozier and Stier (7). Their tests were conducted in a ventilated dark room the temperature of which ranged from 21° to 24° C. A weak nondirective red light was used and the observer's breathing currents were excluded by a screen. Tent caterpillars (*Malacosoma americana*) were tested and each was caused to creep diagonally across an inclined plane, which rested on a horizontal one.

They call the acute angle between the two planes a and the acute one between the track of the caterpillar and the horizontal plane θ. The angle a was changed for each series of tests, and in order to have an average angle θ a caterpillar was repeatedly tested, first with one side and then the other side downward. The results obtained are quantitatively described in terms of trigonometry. The summary in part is about as follows: The geotactic orientation of tent caterpillars while creeping upon a surface inclined at angle a to the horizontal is such that the path makes an average angle θ upward on the plane, of a magnitude proportional to *log sin a*. This is attributed to the fluctuation of the pull of the head region upon the lateral musculature of the upper side during the side-to-side swinging brought about in creeping.

A review of the literature by Crozier and Stier (7) shows that neither the mechanical theory nor the statolith theory is sufficient to explain geotaxis, because neither accounts " for the quantitative relationships between gravitational pull and the amplitude of orientation. There is left the appeal to the proprioceptive results of muscle tensions, already suggested to account for certain features of geotropism among insects and molluscs."

2. GEOTACTIC EXPERIMENTS ON CODLING-MOTH LARVAE

Recently hatched codling-moth larvae do not seem to be influenced by gravity either in the laboratory or on the foliage of apple trees. They avoid bright sunshine as much as possible, and if there are no interfering factors they crawl in all directions, as if hunting for food. Seventy-five larvae belonging to the fourth, fifth, and sixth instars were subjected to phototactic and geotactic tests in the laboratory. A branch of an apple tree, 30 inches long and bearing leaves, a small apple, and small twigs, was suspended from a chandelier. At the extreme top and bottom of the branch twine was wound loosely around the twigs to furnish a cocooning place for the larvae being tested. After receiving the phototactic test a larva was laid horizontally in one of the forks of the branch, and in such a position the light was not an interfering factor. The results obtained follow.

The light reactions were found to be a crude index for judging the responses to gravity. Those individuals which were weakly photonegative or were indifferent to light were generally not yet ready to make cocoons and consequently were not geopositive; but when ready to spin, or later, they were nearly always strongly photonegative and geopositive. When larvae ready to spin were put on the branch, they

wandered up and down, but finally went as a rule to the bottom where many made cocoons in the twine, while a few dropped by threads to the floor. This shows that larvae of the sixth instar at cocooning time are strongly geopositive, but shortly before this they were usually indifferent to gravity. The younger instars were either indifferent or geonegative. Therefore, at cocooning time negative phototaxis and positive geotaxis are closely correlated, and when one is known the other can be correctly assumed. In a case of this kind why assume the presence of geotaxis? Instead, why not say: " They go up owing to a hunger urge, and down because of a cocooning urge?" To the writer it seems that they " know " up from down at all times.

While ascending the branch a few of the larvae seemed to perceive the small apple when within an inch of it. They stopped crawling and reached as far as possible in the direction of the apple. These and others after finally reaching it ceased to wander farther.

IV. THIGMOTAXIS

I. REVIEW OF LITERATURE

Dewitz in 1885, according to Loeb (42, p. 23; 43, p. 156), first called attention to a contact-irritability exhibited by spermatozoa of a cockroach. Three years later Loeb noticed the same tropism in Infusoria and gave the name " stereotropism " to the peculiarity, which some animals have of orienting their bodies in a definite way toward the surfaces of solid bodies. Since this tropism in those animals having tactile organs is brought about through the sense of touch, the term thigmotaxis (touch arranging) seems to be more appropriate.

Loeb (43, p. 158; 44, p. 167) believes that positive thigmotaxis is second to chemotaxis in bringing about the union of the sexes. The holding of the female during mating is evidently a thigmotactic sense, and since only males and females of the same species mate, he believes that thigmotaxis plays a part in the selection of the proper species. The same author (42, pp. 22, 110) found certain moths (*Amphipyra*) to be thigmotactic because in tests they crept into crevices and in nature they remain in clefts in the bark of trees. He was able to show that light in such cases was not a factor, for the insects were forced to bring as much of their bodies as possible in contact with solid bodies. The friction and pressure produced by the solid bodies are considered by him to be the cause.

Dewitz (9) says that thigmotaxis is widely distributed among the lower animals and that the mode of living and conduct of many species can be traced back to it. Insects fasten their bodies tightly to promi-

nent objects or squeeze themselves between layers of folded dry goods. On these facts is based the employment of bands around fruit trees to catch codling-moth larvae and the caterpillars of the Tortricidæ of the vine; likewise the use of stones and boards in gardens for collecting beneath them earwigs and slugs, which can then be destroyed wholesale. Female grape-moths (*Clysia ambiguella*), when laying eggs, are guided by the highly sensitive extremity of the abdomen, and this sensitive part aids the females of many insects to lay eggs in fissures and folds of plants, soil, and elsewhere. Dewitz also believes that thigmotaxis is the chief means by which caterpillars and certain other insects are able to live gregarious lives.

McCracken (47), while testing female silkworm moths, determined that eggs might be obtained by touching the sense hairs on the ovipositor with a pencil or fibers of cotton. She says that each contact brings forth an egg, and under natural conditions the stimulus is brought about by means of the ovipositor coming in contact with the surface upon which the insect rests.

2. THIGMOTACTIC EXPERIMENTS ON CODLING-MOTH LARVAE

All instars of the codling moth seem to have a well-developed sense of touch, but the thigmotactic sense is most pronounced in the fully developed larvae at cocooning time. When ready to spin, these larvae prefer a tight and dark place in which to crawl, but if a dark one is not at hand they do not hesitate to spin in a well-lighted place. Years ago economic entomologists took advantage of this habit by placing " codling-moth sticks " in the rearing jars. The larvae readily spin in these sticks, which later may be transferred to other containers.

Another practical application of the thigmopositive and photonegative reactions of these larvae has been utilized for many years. When bands are placed around the trunks of apple trees to serve as a supplementary control method we are merely taking advantage of nature's laws. It therefore seems that so far as tropic responses are concerned the vulnerable period in the life history of codling-moth larvae is brought about by a change in tropisms.

B. TROPIC RECEPTORS

In discussions of tropisms, sensory receptors are usually implied as being the organs which receive the tropic stimuli, but in plants and the lowest invertebrates specific sense organs apparently do not exist. However, in the higher invertebrates and vertebrates specific sense organs do exist, but with regard to certain sense organs in insects we are still guessing at their functions and consequently cannot accurately connect them with any known tropism.

The following discussions pertain to what is generally described under sense organs and the senses, but no attempt is made to give all phases of this subject, and most of the information pertains to Lepidoptera.

I. PHOTORECEPTORS

The photoreceptors are the compound eyes and ocelli and there is no difficulty in connecting the compound eyes of adult moths and butterflies and the ocelli of their larvae with the phototactic responses obtained experimentally. The usual number of ocelli on an adult insect is three, but the sexes of the codling moth have only two each. Judging from sections through the eyes of both adult and larva of this moth, the photoreceptors seem to be normally developed, but since so much work already has been done on the morphology of insect eyes no special study was made on this subject. The reader is referred to the reviews by Schröder (80), Snodgrass (81), and Hering (32).

So far as is known to the writer the only new idea on this subject is advanced by Lammert (40), who believes that lepidopterous larvae have two kinds of photoreceptors—the ocelli and others (probably pigment specks) in the body integument. Therefore, he believes that these larvae have a skin sensitive to light, which might be compared to that in the earthworm and other animals having photopigment widely distributed in the body wall.

The results obtained by Dürken (13) bear indirectly on the subject of body pigment used to direct the movements of larvae. He experimented five years to determine the effects of colored lights on the developing stages of the cabbage butterfly. Glass panes of vivaria were painted white and the effect of reflected light from green food-stuffs on the caterpillars was observed. Darkness produced some reduction of black pigment, while orange or red light produced much reduction of black and white pigments. Blue light caused a slight shifting in the direction of weaker pigmentation. Reaction to light occurred immediately before pupation. There was no effect previous to that time on the pigmentation of pupae. Pigmentation of imagoes was entirely unaffected by darkness or light, being absolutely independent of that of the pupae.

In regard to whether sight or smell plays the greater rôle among flower-visiting insects, Clements and Long (5) present the best recent reviews of the literature. They conclude that phototaxis is more important than chemotaxis. Odors attract from a distance while sight attracts from nearby. Form and size of objects play a lesser part in attraction.

II. CHEMORECEPTORS

Chemoreceptors include both olfactory and gustatory organs. Judging from the anatomy and function of these organs in man and the higher animals, we are not absolutely sure that insects have true chemoreceptors, although their organs certainly belong to the same category.

1. SO-CALLED OLFACTORY ORGANS

(a) *Antennal Organs.*—Several investigators have studied the morphology of the antennal organs, but since Schenk's (79) paper is one of the latest and perhaps best, it will suffice for our purpose here. Schenk carefully studied the various types of antennal hairs in both sexes of the following moths: One geometrid (*Fidonia piniaria*), two bombycids (*Orgyia antiqua* and *Psyche unicolor*), and one zygaenid (*Ino pruni*). He found five types of sense hairs as follows (see fig. 3 of codling moth): (1) Pit pegs (Sensilla coeloconica), (2) end pegs (S. styloconica), (3) sense bristles (S. chaetica), (4) sense hairs (S. trichodea), and (5) pegs (S. basiconica). Relative to the last named only five were found and these on a female of *Fidonia*. These five types of sense hairs were found on the pectinate or feathered antennae of males and on the filiform or non-feathered ones of the females, and not only on the shafts of both types of antennae but also on all the barbs of the male antennae. The total number of sense hairs found by Schenk in various species is included in table 2, which also gives the tabulated results of the present writer's observations on other species.

TABLE 1.—*Number of so-called olfactory organs on codling-moth antennae*

	Number on male antennae							Number on female antennae						
Individual No.	Left antenna		Right antenna		Total		Individual No.	Left antenna		Right antenna		Total	
	Styles*	Pit pegs	Styles	Pit pegs	Styles	Pit pegs		Styles	Pit pegs	Styles	Pit pegs	Styles	Pit pegs
1	36	308	41	319	77	627	1	46	331	35	345	81	676
2	38	268	36	277	74	545	2	40	330	40	360	80	690
3	36	366	33	373	69	739	3	36	386	35	368	71	754
4	37	296	34	294	71	590	4	35	354	35	347	70	701
5	36	284	31	244	67	528	5	47	257	43	260	90	517
Average for male antennae..........					72	606	Average for female antennae.........					78	668

* A few styles on each antennae do not bear end pegs.

TABLE 2.—*Comparative number of sense organs on antennae of adult Lepidoptera*

Family	Number and name of species	Kind and number of sense organs					
		Pit pegs (S. coeloconica)	End pegs (S. styloconica)	Styles	Sense bristles (S. chaetica)	Sense hairs (S. trichodea)	Johnston organs
Sphingidae....	1. Phlegethontius quinquemaculata..	0	0	few	few	very many	....
	2. Ceratomia catalpae	0	0	"	0	"	....
	3. Unidentified species..............	0	0	"	0	"	present
Arctiidae.......	4. Apantesis sp....................	0	0	"	few	"	....
	5. Hyphantria cunea ♀.............	few	few	"	many	many	....
	6. " ♂.............	many	"	"	"	"	....
Noctuidae......	7. Prodenia ornithogalli............	very many	"	"	"	very many	....
	8. Agrotis unicolor .♀.............	few	0	"	"	"	....
	9. Cirphis unipuncta...............	very many	few	"	"	"	....
Liparidae	10. Hemerocampa leucostigma ♀	0	"	"	few	few	....
Lasiocampidae .	11. Malacosoma americana..........	very many	"	"	many	very many	....
Bombycidae ..	12. Bombyx mori ♂................	"	"	"	80	"	....
	13. " ♀................	"	"	"	42	"	....
	14. Orgyia antiqua ♂...............	600	50	....	present	few	....
	15. " ♀...............	75	30	....	0	very many	....
	16. Psyche unicolor ♂.............	very many	0	....	few	"	....
	17. " ♀.............	0	0	....	very many	0	....
Saturniidae ...	18. Samia cecropia ♀	0	0	few	0	very many	present
Geometridae ..	19. Alsophila pometaria ♂	0	few	"	few	many	....
	20. " ♀	0	"	"	very many	very many	....
	21. Fidonia piniaria ♂	350	22	....	117	"	....
	22. " ♀	100	16	....	105	"	....
Psychidae......	23. Thyridopteryx ephemeraeformis ♀	0	0	0	very many	few	....
Aegeriidae.....	24. Sanninnoidea exitiosa ♂	0	0	few	"	"	....
Pyralidae......	25. Achroia grisella ♀.............	0	few	"	"	"	....
Olethreutidae .	26. Carpocapsa pomonella ♂	many	"	"	few	very many	present
	27. " ♀.......	"	"	"	many	"	"
Yponomeutidae	28. Atteva aurea.................	few	"	"	"	"	....
Zygaenidae ...	29. Ino pruni ♂.................	very many	0	....	120	"	....
	30. " ♀.................	"	0	....	120	"	....
Nymphalidae..	31. Argynnis cybele	many	0	0	0	few	present
	32. Vanessa antiopa	very many	0	0	0	many	....
Pieridae........	33. Pontia rapae.................	few	0	0	0	"	"
Papilionidae ..	34. Papilio troilus...............	very many	0	0	0	"	"

The antennal organs of five male and five female codling moths were carefully examined by the present writer. Little or no sexual differences were observed in the antennae or their organs. The antennae of both male and female are filiform and bear the same kinds and practically the same number of organs (tables 1 and 2). The number of segments in the antennae of males ranges from 55 to 61 with 58 as an average; those in the antennae of females from 59 to 63 with 62 as an average. Each antenna bears one Johnston organ
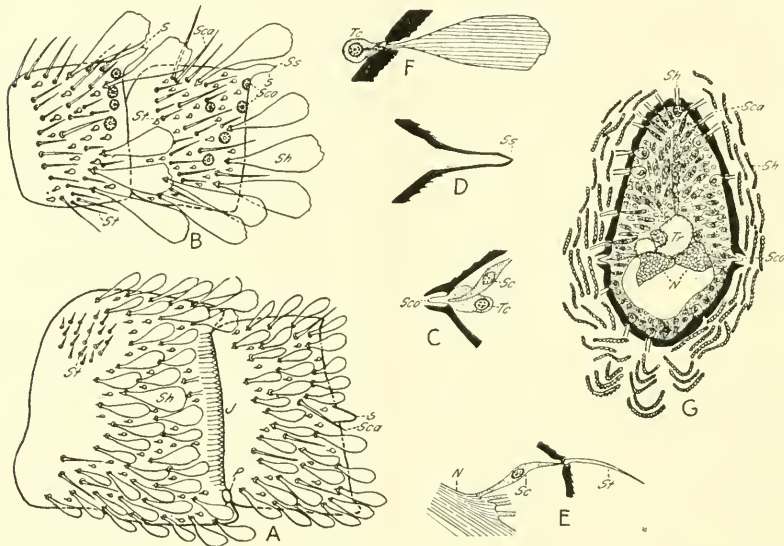

Fig. 3.—Antennal organs of female codling moth, No. 3. A and B, External views, × 125. C to G, Sections; C to F, × 500; G, × 320. A, Second and third antennal segments; B, two segments from middle of antenna; C, pit peg; D, style and end peg; E, sense hair and its innervation; F, non-innervated scalelike hair; and G, cross section through distal end of segment near middle of antenna.

Abbreviations: *J*, Johnston organ; *N*, nerve; *P*, olfactory pore; *S*, style; *Sc*, sense cell; *Sca*, sense bristles (Sensilla chaetica); *Sco*, pit peg (S. coeloconica); *Sh*, non-innervated scalelike hair; *Ss*, end pegs (S. styloconica); *St*, sense hairs (S. trichodea); *Tc*, trichogenous cell; and *Tr*, trachea.

(fig. 3, A, *J*), 2 or 3 olfactory pores (*P*), numerous pit pegs (fig. 3, B, *Sco*), end pegs (*Ss*) on styles (*S*), sense bristles (*Sca*), sense hairs (*St*), and scalelike hairs (*Sh*). Each of these, except the last named, is supposed to be a sense organ, and Freiling (23) has even pictured a slender scalelike hair of another moth as connected with a sense cell. Of these seven structures only the olfactory pores, pit pegs, and end pegs are supposed to be olfactory in function.

Pit pegs may be found on all segments, except the first, second, and the last one or two, of codling-moth antennae. If odors can pass

quickly through chitinous structures, pit pegs (fig. 3, C, *Sco*) would be excellent olfactory organs. Styles, usually terminating in end pegs, may be found on all segments except the first and second. A style (fig. 3, B, *S*) is nothing more than a prolongation of the distal outer edge of the segment and it is supposed to be innervated, but in codling-moth antennae it (fig. 3, D) has no nerve and consequently cannot be a sense organ. The writer has failed to find a drawing by any author showing a nerve connected with this structure.

The antennae of 21 other species (table 2) examined by the writer varied much in respect to barbs, from typical filiform antennae to fully feathered ones. The sense organs, as a rule, were widely distributed on both the shaft and barbs. In *Argynnis cybele* the pit pegs lie only on the club part of the antenna. Some of them are large and irregular in shape, and perhaps a pit bears more than one peg. In 11 of the specimens pit pegs were totally absent and in 12 no end pegs were observed on the comparatively few styles, and even styles were absent in one moth (No. 23) and in all the butterflies (Nos. 31 to 34) examined.

From the preceding it is evident that pore plates (S. placodea), common to three orders of insects (aphids, beetles, and bees and wasps), are totally absent in Lepidoptera, while the pegs (S. basiconica) are practically wanting. These two types are the ones generally considered as olfactory receptors in most insects. It is said that the end pegs and pit pegs of Lepidoptera replace the pegs and pore plates of other orders, but there is no proof whatever for this assumption, and furthermore it is doubtful whether the end pegs are ever innervated.

Granting that the pit pegs and end pegs are the only olfactory organs of Lepidoptera and drawing conclusions from the observations of Schenk and the present writer, eight individuals (table 2, nos. 1 to 4, 17, 18, 23, 24) of the 34 specimens examined cannot smell at all, while four other individuals (nos. 10, 19, 20, 25) have comparatively few end pegs as olfactory receptors.

(b) *Olfactory pores.*—At the suggestion of his reviewers the writer (48) in 1914 called the sense organs herein discussed " olfactory pores." Guenther (27) in 1901 seems to have been the first to describe the internal structure of these organs in Lepidoptera. He called those in the wings " Sinneskuppeln " and found their structure to be similar to that described by the present writer, although he did not see the pore aperture passing to the exterior. Vogel (88) made a more extended study of them in the wings of many Lepidoptera. He con-

sidered them as chordotonal organs. The present writer (50, 51) made a thorough study of the disposition and structure of them in many Lepidoptera and their larvae. Prüffer (77) has most recently described these pores on the wings of certain moths in connection with the antennal organs.

The olfactory pores on five male and five female codling moths were counted. Female no. 3 was examined most carefully and consequently the greatest number of pores was found on it. In figures 4 and 5 they are represented by black dots. The groups are numbered from 1 to 12. The isolated pores which are constant in position are designated by *a* to *e*, the others not being thus marked. Groups 1 to 6 and pores *a* and *b* lie on the wings (fig. 4); groups 7 to 11 and
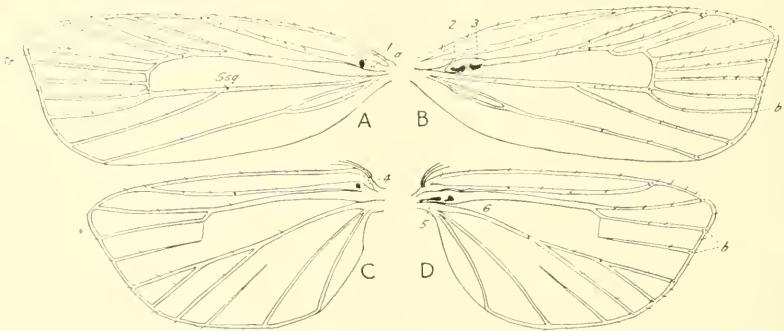

Fig. 4.—Semidiagrammatic drawings of wings of female codling moth, No. 3, showing location of olfactory pores (*1* to *6*, *a* and *b*, and other dots), sense scales (*Ssq*), and sense hairs (*St*), ×5. A, Dorsal side, and B, ventral side of front wing; and C, dorsal side, and D, ventral side of hind wing. Vogel (88) shows " Sinneskuppeln " or olfactory pores similarly located on wings of *Scoria lineata*.

pores *c* and *d* on the legs (fig. 5, A); group 12 on the base of the labial palpus (fig. 5, E); and pores *e* (fig. 5, D) on the maxilla (one-half of proboscis). The number of pores in the groups follows: No. 1, 91; No. 2, 70; No. 3, 52; No. 4, 12; No. 5, 129; No. 6, 52; No. 7, 4; No. 8, 4; No. 9, 5; No. 10, 4; No. 11, 7; and No. 12, 8. The total number counted on female No. 3 follows: Legs, 191; front wings, 462; hind wings, 417; proboscis, 28; labial palpi, 16; and second segments of antennae, 4; making 1,118 in all. The total number of pores on males range from 933 to 1,049, with 986 as an average; and on females from 960 to 1,118, with 1,029 as an average.

Figures 6 to 8 represent the internal structure and innervation of the pores and sense hairs, and also the internal anatomy of the wings and legs where the pores are found on them.
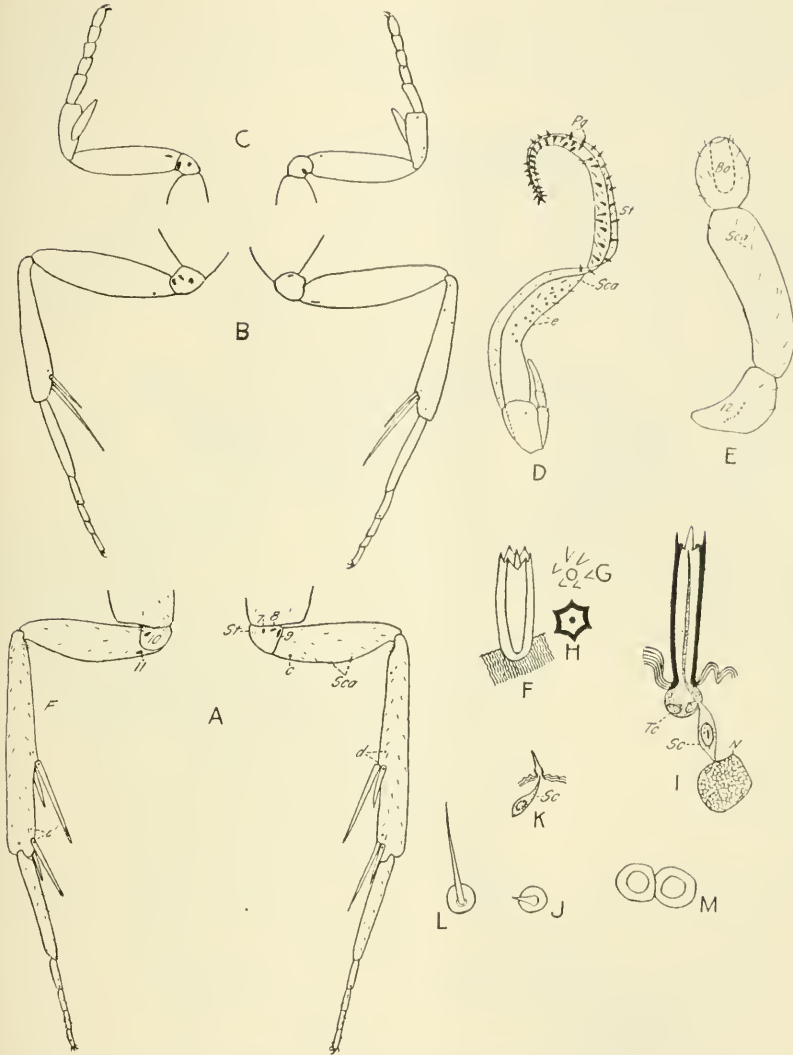
FIG. 5.—Legs, maxilla, and labial palpus of female codling moth, No. 3, show-ing location and structure of sense organs on these appendages. A, Inner and outer surfaces of hind leg; B, same of middle leg; and C, same of front leg, showing location of olfactory pores (*7* to *11*, *c* and *d*, and other dots), sense bristles (*Sca*), and sense hairs (*St*); × 5. D, Maxilla or one-half of proboscis, and E, labial palpus, showing location of olfactory pores (*e* and *12*), pegs (*Pg*), sense bristles (*Sca*), sense hairs (*St*), and labial-palpus organ (*Bo*); × 32. F to M, Structure and comparative sizes of sense organs on proboscis; × 500. F, External view of peg; G, looking down on its tip end; H, cross section of peg; and I, longitudinal section of peg, showing trichogenous cell (*Tc*), sense cell (*Sc*), and nerve (*N*). J and K, External and internal structure of smallest sense hair. L, External view of sense bristle. M, External view of two olfactory pores.

Lepidopterous larvae can smell, but they do not have the so-called olfactory organs such as pegs, pore plates, pit pegs, or end pegs like or even similar to those of adult insects. Therefore, it is only reason-
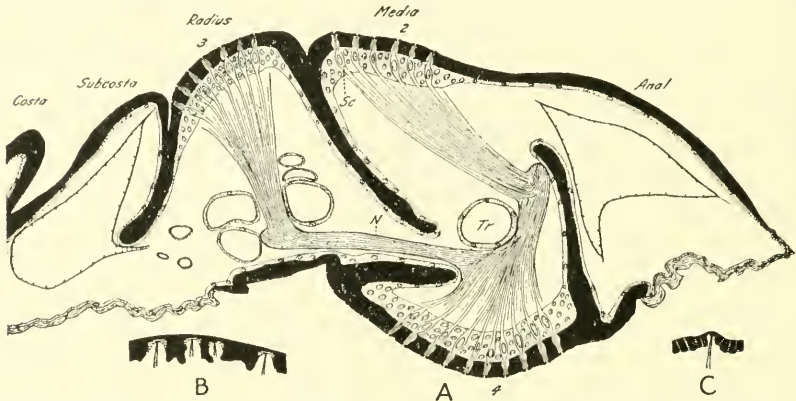

Fig. 6.—Cross sections of wings and proboscis of Lepidoptera, showing internal anatomy of wings and olfactory pores. A, Semidiagrammatic drawing from an oblique section through front wing of cabbage butterfly, showing groups *2*, *3*, and *1*, of pores, sense cells (*Sc*), nerve (*N*), and trachea (*Tr*); × 100. B, Pores from wing of codling moth; × 500. C, A pore from proboscis of codling moth; × 500.
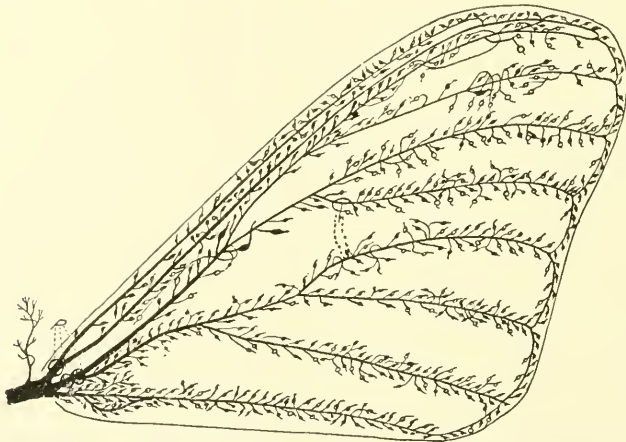

Fig. 7.—Schematic drawing of wing of a male *Saturnia pyri* L., showing innervation of olfactory pores (*P*) and other sense organs, including scattered pores and various types of sense hairs. The black dots represent those on the dorsal surface, and the circles, those on the ventral side. (Copied from Prüffer (77).)

able to suppose that the pores, called olfactory by the writer, act as smelling organs.

The olfactory pores of five specimens of each larval instar were counted. Little or no difference in position and number of the pores

was observed in the six instars. They are found widely distributed (figs. 9 and 10) as isolated pores or " punctures " on the following parts: Head capsule, 24; maxillae, 16; mandibles, 4; labrum, 2; labium, 6; antennae, 2; legs, 30; first thoracic segment, 4; and anal prolegs, 4; making 92 in all. Some of those on the head capsule were incorrectly named in 1919 by the writer (51), but in figure 9 they are correctly named according to Heinrich's (31) first paper and later ones on this subject.

In regard to experimental results concerning olfactory receptors, two papers will be briefly reviewed. The first and most important
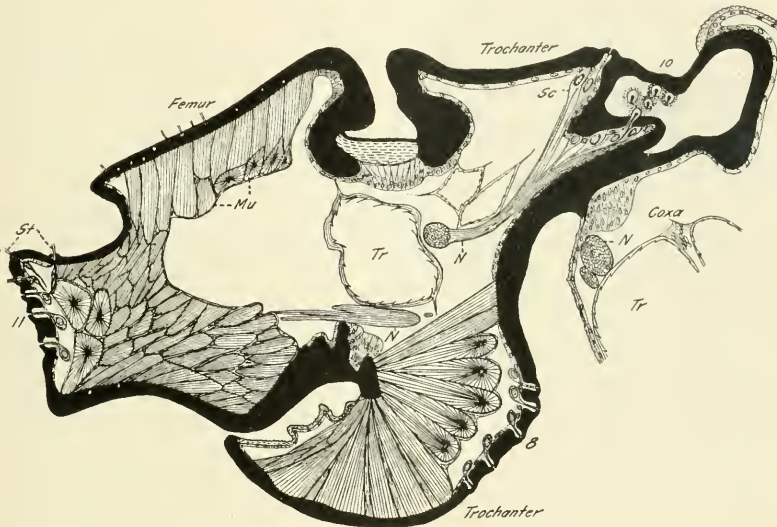

Fig. 8.—Semidiagrammatic drawing of an oblique section through femur, trochanter, and coxa of a silkworm moth, showing muscles (*Mu*), trachea (*Tr*), nerves (*N*), sense cells (*Sc*), sense hairs (*St*), and groups *8*, *10*, and *11* of olfactory pores, No. *10* being shown partially from a superficial view; × 100.

experimental work to decide the function of the olfactory pores was done by the writer (48) on honeybees. Of the six sources of odors used three were essential oils. The writer's critics have apparently overlooked the fact that the results obtained by using the other three odors are reported in such a manner that they can easily be considered alone. Since the odors from the oils might have been irritant, let us consider the other results, which, when expressed in percentages, clearly show how closely the percentage of pores supposed to function corresponds to the percentage of response obtained. On the average, a worker honeybee has about 2,800 olfactory pores. On the bases of the four wings lie 54 per cent of them; the legs possess 23 per cent;
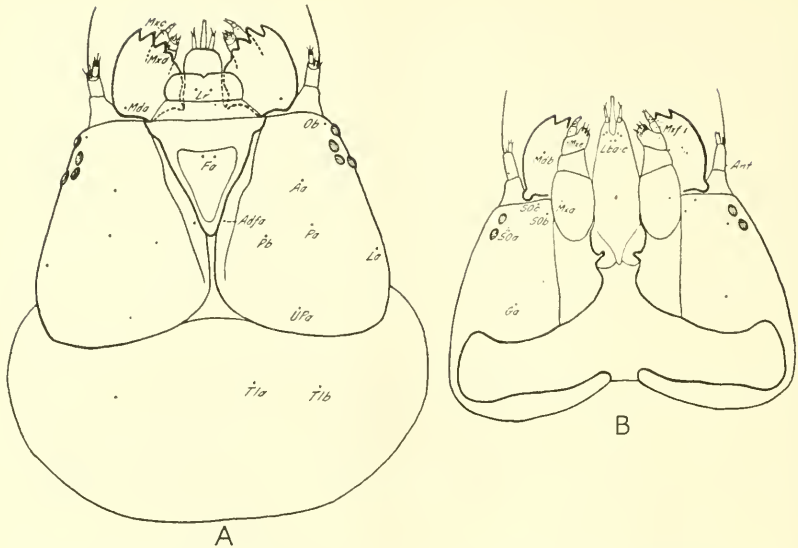
Fig. 9.—Disposition of olfactory pores or punctures on head and first thoracic segment of a fully grown codling-moth larva, × 20; A, dorsal view; and B, ventral view.

Abbreviations: Frontal pore (*Fa*); adfrontal pore (*Adfa*); ocellar pore (*Ob*); anterior pore (*Aa*); posterior pores a (*Pa*) and b (*Pb*); lateral pore (*La*); ultraposterior pore (*UPa*); subocellar pores a (*SOa*), b (*SOb*), and c (*SOc*); genal pore (*Ga*); mandibular pores a (*Mda*) and b (*Mdb*); maxillary pores a (*Mxa*), c (*Mxc*), d (*Mxd*), e (*Mxe*), and f to i (*Mxf-i*); labial pores a to c (*Lba-c*); labral pore (*Lr*); antennal pore (*Ant*); and thoracic pores a (*Tla*) and b (*Tlb*).
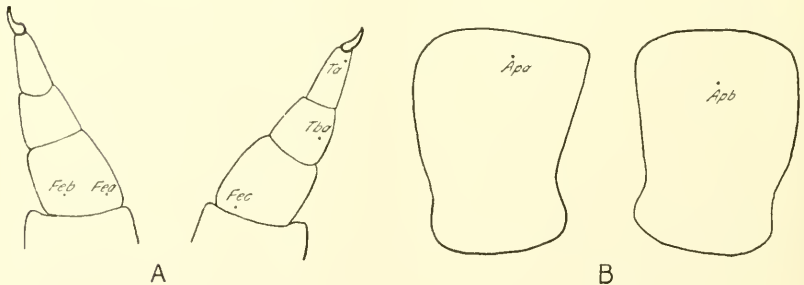

Fig. 10.—Disposition of olfactory pores or punctures on legs of fully grown codling-moth larva, × 30. A, Anterior and posterior surfaces of prothoracic leg, and B, dorsal and ventral surfaces of anal proleg.

Abbreviations: Femoral pores a (*Fca*), b (*Fcb*), and c (*Fcc*); tibial pore (*Tba*); tarsal pore (*Ta*); and anal-proleg pores a (*Apa*) and b (*Apb*).

while the others lie on the sting, head, and head appendages. The indi-
viduals were allowed 60 seconds in which to respond. All of the pores
on 31 unmutilated bees responded to the odors from honey, pollen, and
leaves of pennyroyal in four seconds (48, pp. 283, 284) ; that is, in
one-fifteenth of the entire maximum time allowed for the response.
Twenty bees with their legs covered with a mixture of beeswax and
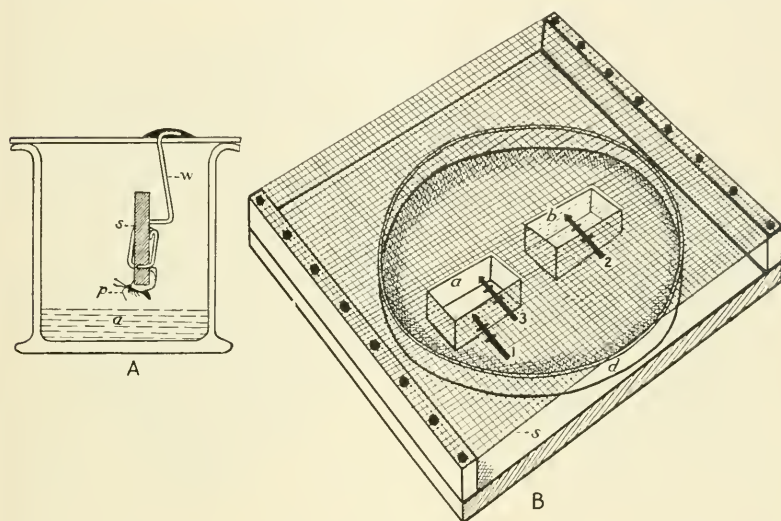vaseline, leaving supposedly 77 per cent of the pores elsewhere to

Fig. 11.—Diagrams of Minnich's apparatus used in testing insects to olfactory
and gustatory stimuli. A, Section of an odor chamber made of a rectangular
museum jar, showing a butterfly, held by a wire (w) and a spring clothes pin
(s), responding with extended proboscis (p) to apple juice (a). (After Min-
nich.) B, Perspective view of apparatus used to show that butterflies "taste"
with their tarsi; a and b, two small rectangular tin pans, a containing a cheese-
cloth pack wet with apple juice and b containing a similar cloth wet with dis-
tilled water; and d, a Petri dish nearly full of apple juice in which stand the
tin pans just beneath two openings in a wire screen (s). The arrows, 1, 2, and 3,
represent the positions in which the butterflies were tested, the position of the
walking legs being indicated by the cross-bars. (Redrawn from Minnich's two
figures.)

function, responded 2. 5 times more slowly (p. 336) or gave a response
of 83.3 per cent. Twenty-eight bees with their wings pulled off,
leaving 46 per cent of the pores elsewhere to function, responded eight
times more slowly (p. 335) or gave a response of 46.7 per cent. And
finally, 20 bees with their legs covered with the beeswax-vaseline
mixture and their wings pulled off, leaving supposedly only 23 per
cent of the pores located elsewhere to function, responded 11 times
more slowly (p. 337) or gave a response of 26.7 per cent.

Cabbage butterflies (*Pontia* (*Pieris*) *rapæ* L.) were confined by Minnich (63) in an odor chamber (fig. 11, A). Since they are fond of apple juice its odor was used to stimulate the smelling organs, and the responses to it were then measured by the extent to which the proboscis was uncoiled for the purpose of partaking of the apple juice, although the insects could not reach it. The antennae were mutilated in three ways: (1) Covered with vaseline; (2) covered with a mixture of paraffin and vaseline; and (3) cut off at the base with fine scissors. When the organs on only one antenna were prevented from functioning, the olfactory response was reduced only 6 per cent; when those on both antennae were eliminated or prevented from functioning, the response was reduced 58 per cent. Thus according to these results nearly half of the olfactory receptors must be located elsewhere than on the antennae. In his own words Minnich (p. 354) says:

After the antennae are eliminated the animals were still 42 per cent responsive. Considering the variety of methods employed and the similarity of results obtained, this figure is much too large to be attributed to a failure to eliminate the antennal organs completely. It must, therefore, mean that there are olfactory organs on other parts of the body as well as on the antennae. . . . I cannot, therefore, concur with McIndoo in the view that the antennae of adult insects in general lack olfactory organs. Certainly, such is not the case with Pieris. Nor can I agree with the opposing viewpoint, that the olfactory organs of adult insects in general are confined to the antennae. In this respect the results on Pieris differ from those obtained by v. Frisch in his ingenious experiments on bees. The results of the present experiments show that a viewpoint intermediate between these two is correct for Pieris, and that while the antennae constitute a very important, probably the most important, olfactory region of the body, they do not constitute the sole olfactory region.

Regardless of the results obtained by testing insects with mutilated antennae, it has never seemed reasonable to the writer to suppose that odorous air can pass quickly through the hard and dry chitin covering the antennal organs. If it can, why not grant the same privilege to all sense organs covered with thin chitin, including all kinds of sense hairs and even the olfactory pores whose sense fibers, according to other authors, are separated from the outside air by a thin layer of chitin? In the higher animals the olfactory organs (fig. 12) are separated from the outside air by only a thin watery layer of mucus, and the latest results show that the free ends of the olfactory cilia actually come in contact with the air. Eidmann (18) erroneously supposed that the chitinous intima of insect intestines is similar to the coverings of the so-called olfactory and taste organs of insects. He proved chemically that aqueous solutions can pass slowly

through the intima when the latter is wet on both sides. From this result he concluded that the olfactory organs of insects need no openings through which the nerve endings can come in contact with the odorous air outside. The present writer cannot see any connection between his findings and the chemical sense receptors of insects.
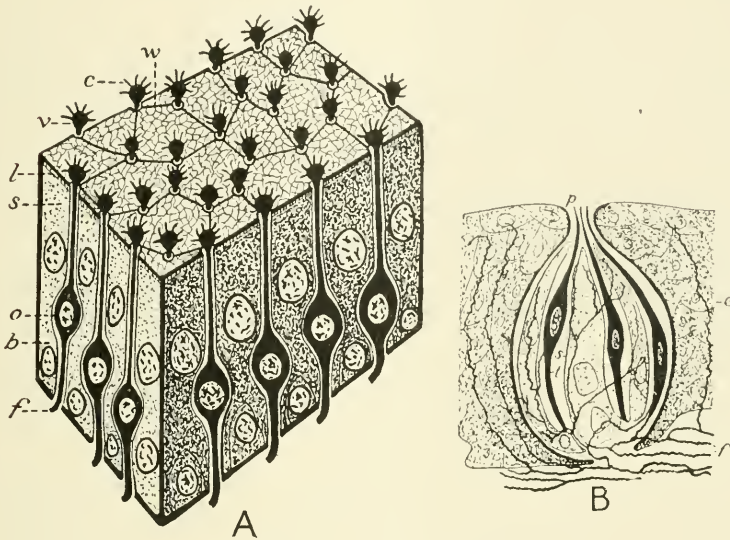

Fig. 12.—Olfactory and gustatory organs of higher animals. A, Diagram of a block from olfactory mucous membrane of a kitten, showing in section and perspective the following: Basal cells (*b*), olfactory cilia (*c*), nerve fibers (*f*), limiting membrane (*l*), olfactory cells (*o*), supporting cells (*s*), olfactory vesicles (*v*), and walls (*w*) of the five- and six-sided supporting cells from a surface view. The olfactory vesicles and cilia, which are embedded in and supported by an outer semifluid (not shown in drawing), are the true receptors of smell. (Redrawn from van der Stricht's (84) photomicrographs and figure 36, the latter in Herrick's book (33).) B, A single taste-bud from human tongue, showing nerve fibers (*f*) indirectly innervating the surrounding epithelium (*e*), supporting cells (*s*), and taste cells (*t*), whose outer ends project into and sometimes beyond the pore (*p*). (From Herrick (33), after Markel-Henle.)

2. SO-CALLED TASTE ORGANS

The so-called taste organs of Lepidoptera, according to Deegener's review (see Schröder (80) p. 149), consist of two round groups of sense hairs on the under side of the pharynx. The proboscides of Rhopalocera, Noctuidae, Geometridae, and Bombycidae bear at their tips more or less numerous peg-shaped structures of varied lengths and shapes in different species. In Sphingidae and Zygaenidae these pegs are distributed over the entire proboscides. These peculiar

structures have been considered both tactile and gustatory in function. Lepidopterous larvae bear on their antennae and mouth parts variously shaped sense hairs, some of which have been called taste organs, some touch organs, and others smelling organs.

Each maxilla on the codling moth bears about 50 pegs or about 100 for the entire proboscis. Female No. 3 had 93 of them (fig. 5, D, Pg). They are always found on the distal half of the maxilla and are usually six-sided (fig. 5, F to H) but a few are five-sided. Each one (fig. 5, I) arises from the proboscis as a fluted column and terminates in five or six sharp pinnacles, which surround the innervated hair. If aqueous liquids, or odors, in order to stimulate the nerves inside the hairs, can pass quickly through the chitinous walls, we can then safely call them taste organs, or smelling organs; if such a condition is not true, they are certainly nothing more than touch receptors. The writer has repeatedly objected to the chemical-sense assumption, but believes that smell and taste in insects are inseparable and that the olfactory pores are their only receptors. Figure 12 shows the similarity of olfactory and gustatory organs in the higher animals and that the stimuli do not pass through any membrane in order to reach the nerves.

Let us now consider the chemoreceptors found by Minnich on the tarsi of butterflies and flies. The two species of butterflies used by Minnich (60) may often be seen to alight on injured tree trunks or on decaying fruit in orchards, apparently for the purpose of feeding on the exuding sap of the tree or on the juice of the fallen fruit. In the presence of food it was further observed that the proboscis would uncoil and then coil up again in a definite manner. Minnich called this reaction of the proboscis a proboscis response, and later made use of it solely in measuring or weighing the responses of butterflies to various liquids. In order to determine the responses of the tarsal chemoreceptors, and at the same time to control the olfactory responses, many experiments with butterflies in confinement were conducted by using an ingenious and specially constructed apparatus. Briefly stated, the apparatus consisted of a shallow dish (fig. 11, B, d) covered with wire screen (s), in the center of which are two small rectangular openings, which lie just above two small rectangular tin pans (a and b) inside the dish, each containing several layers of cheesecloth. The cheesecloth in one pan (a) was wet with apple juice and that in the other pan (b) with distilled water; and the shallow dish was also full of apple juice. A butterfly to be tested was held by the wings with a spring clothes-pin in position 1; that is,

with the four feet of the middle and hind legs touching the wire screen and with the antennae extending directly over the cheesecloth wet with apple juice. Since the front legs are rudimentary and not used for walking, they were not considered in these tests. If the insect responded at all in this position, the response was a truly olfactory one. The butterfly was next held in position *2*; that is, with the head and antennae just above the cheesecloth wet with distilled water and with the feet of the middle legs resting on this wet cloth. If the insect responded at all in this position, the response was either an olfactory one or one brought about by contact with the feet on the cloth, or the response was a combination of both olfactory and contact stimuli. The butterfly was finally held in position *3*; that is, exactly like position *2* except over the cheesecloth wet with apple juice. In this position the insect always responded, and the responses were of the same kind but differed in degree from those in position *2*. As an average for all the responses obtained in the three positions, position *1* gave 29 per cent; position *2*, 17 per cent; and position *3*, 100 per cent; clearly showing that these butterflies can distinguish apple juice from distilled water merely by bringing their feet in contact with these liquids.

In other series of tests Minnich used solutions of common sugar, table salt, hydrochloric acid, quinine, and distilled water. In order to compare closely the results obtained, the first four substances were used on the basis of their molecular weights. Butterflies were able, by means of their feet alone, to distinguish the sugar solution from those of the hydrochloric acid and quinine, or from distilled water; and the salt solution from either sugar solution or distilled water.

Now the question naturally arises: Are there special sense organs in the tarsi of butterflies, which act as contact chemoreceptors? Minnich gives us definite information about their function, but leaves us in the dark concerning their exact location and structure. Experimentally he located them on the four tarsi of the middle and hind legs. Each tarsus is five-jointed, the first joint being about as long as the other four combined. Minnich believes that these organs lie in the distal end of the first joint, and particularly in the other four joints. He further believes that they are not temperature organs, touch organs, or organs to register the penetrating powers of liquids, but are chemical sense organs, perhaps somewhat similar to taste organs in man.

Excepting tactile hairs, there are no other known sense organs in the tarsi of butterflies, although no one apparently has looked for other sense organs at this place. In 1917 the present writer (50) reported finding olfactory pores on the legs of butterflies, but found

none on the tarsi. Recently he has more carefully examined the tarsi
of six species of butterflies. No chemoreceptors were seen on the
dark and hairy tarsi of three species, but on most of the light colored
ones of *Pontia rapæ, Papilio polyxenes,* and *P. troilus* a row of
supposedly olfactory pores were observed on each tarsus. They are
very plain on the tarsi of the cabbage butterfly (*Pontia*). A few
pores were also seen on the tarsi of the codling moth (fig. 5). If
these pores are the only chemoreceptors on the tarsi, it is not con-
ceivable how they can detect differences between liquids except by
the odors which might be emitted. If the tarsi of butterflies, which
are covered with a thick and hard chitin, contain contact chemo-
receptors, the mouth parts of insects in general should be provided
with such receptors.

In other series of tests Minnich (61) repeated his former ones
and obtained similar results. According to his scheme of measurement,
the total response of all the butterflies tested was 100 per cent to the
sugar solution used, 84.7 per cent to the quinine solution, and 51.6 per
cent to the salt solution.

In his third report on this subject Minnich (62) says that the tarsal
sensitivity of the butterflies tested to sugar solution may be as much
as 256 times that of the human tongue. It is scarcely conceivable,
although his carefully planned and admirably controlled experiments
firmly convinced him that the feet of butterflies contain sense organs,
which, when properly stimulated, are 256 times as sensitive as are
the taste organs in our mouths.

A fourth paper on this subject by Minnich (65) deals with three
species of flies. It was similarly determined that these flies can dis-
tinguish water from paraffin oil, or from sugar solution, by use of the
chemoreceptors in the tarsi. Chemical sense organs were also located
in parts of the proboscis. These organs are more sensitive than those
in the tarsi to sugar solution. Minnich believes that all of these
receptors serve as taste organs. Thus, according to these results, taste
organs, at last, seem to have been located on the mouth parts of insects.

In regard to the so-called taste organs of insects, the writer has
repeatedly stated that no one has demonstrated that they actually
receive taste stimuli. Minnich (66) says that the proboscis of a
certain blowfly is clothed with hairs, some of which are long and
curved, and that these have been proven to be taste organs by the
following test: A fly, abundantly supplied with water but otherwise
starved, does not extend its proboscis when these hairs are touched
with a tiny brush wet with distilled water; but when they are touched

with another brush wet with sugar solution the proboscis is quickly extended. These hairs are so sensitive that a single one, when touched, may produce the response. According to the accepted definition of taste, these hairs are true taste organs provided the sugar solution must actually touch them; if only a close proximity is required, then the sense of smell is involved. When asked this question, Minnich was not sure that he had totally eliminated smell. If these hairs are true taste organs, the present writer cannot understand how an aqueous solution can pass instantaneously through their walls in order to stimulate the nerves inside.

III. AUDIRECEPTORS

The common belief that insects can hear is based on three facts: (1) Many of the experimental results obtained indicate that they can perceive sound stimuli, although perhaps they do not hear as we do; (2) many have special sound-producing organs; and (3) many have so-called auditory organs.

The first report on the auditory sense of Lepidoptera was probably made in 1876. Since that date much has been published, but critics are still inclined to doubt whether any insect can really hear. Turner (86) and Turner and Schwarz (87) in 1914 produced good experimental evidence to show that Catocala and giant silkworm moths really hear. They used an adjustable organ pipe, an adjustable pitch pipe, and a Galton whistle. Their field experiments demonstrated that most of the moths tested can hear high-pitched notes, but usually low-pitched ones did not produce responses. They believe that responses of moths to sounds are expressions of emotion and that a response depends upon whether the sound has a life significance to the insect tested.

For many years it has been known that both adult and larval Lepidoptera are able to produce sounds and some of the sound-producing organs have been described. For example, the death's-head moths (*Acherontia*) make shrill chirping sounds, probably by forcing air through certain parts of the anatomy. Their larvae produce " crackling " notes. A hissing noise is made by several species of *Vanessa* and more pronounced sounds are produced by other Lepidoptera. Stridulating organs on the wings have been described by several, including Hampson (28) and Jordan (35). In certain Agaristidae and Geometridae the sound is made by pressing the tarsi against the ribbed areas on the wings. This subject is reviewed by Schröder (80, pp. 61-74) and Hering (32, pp. 190-193).
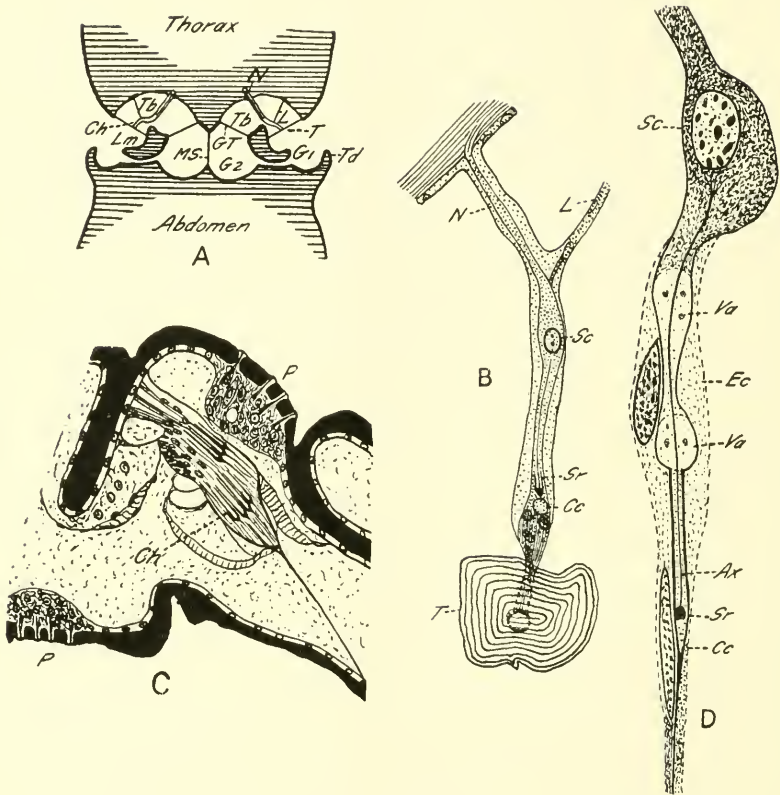
Fig. 13.—So-called auditory organs of Lepidoptera. A, Diagram from longitudinal section through portions of thorax and abdomen of a noctuid moth, showing following parts of tympanic organ: G_1, Tympanic pit at whose base is found the drum head (T) and G_2, tympanic cavity with drum head (GT). The two tympanic cavities are very deep, dorsolateral invaginations of the integument which touch one another at the median line where they form a common division wall (MS). In Catocala they do not touch one another. Tb, Tympanic chamber; N, tympanic nerve; Ch, chordotonal bundle; L, ligament of same; Td, tympanic cover; and Lm, chitinous lamella, separating the true drum head (T) from the other drum head (GT) and serving for the insertion of the chordotonal bundle (after Egger (17)). B, Chordotonal bundle of a notodontid (*Phalera bucephala* L.), showing drum head (T), ligament (L) of chordotonal bundle, tympanic nerve (N), sense cell (Sc), sense rod or " Stift " (Sr), and cap cell (Cc), (after Egger (15)). C, Portion of drawing from longitudinal section through base of front wing of *Lycaena icarus*, showing chordotonal organ (Ch) and "Sinneskuppeln" (P) or olfactory pores. D, Single chordotonal element from front wing of *Chimabacche fag*, showing sense cell (Sc), vacuole (Va), enveloping cell (Ec), axial fiber (Ax), sense rod (Sr), and cap cell (Cc). C and D after Vogel (89).

1. TYMPANIC ORGANS

According to Eltringham's (19) review, tympanic organs in Lepidoptera were first recorded in 1889 in Uraniidae. Since that date several other writers have described these sense organs in Lepidoptera, which are similar in structure and probably in function to those in Orthoptera. As Eggers (15) has presented the most comprehensive paper on this subject, his results are here briefly summarized. In all he examined 150 species of moths and 5 species of butterflies, representing over 40 families. No tympanic organs were found in 39 species of moths and in the five species of butterflies. They were found, however, in various stages of development in the thorax of 95 species and in the abdomen of 16 species of the moths. Thus 71.6 per cent of all had tympanic organs. Judging from this study butterflies and many moths, including Sphingidae, Saturniidae, and Bombycidae, apparently have no tympanic organs, and none was found in the codling moth by the present writer. The location and structure of the organs found by Eggers are represented by figure 13, A and B.

Eggers (17) next determined that the tympanic organs in noctuid moths are auditory in function. Noctuids, when in an excited condition, reacted to different sounds by flying or by raising the wings. They were tested under glass funnels to loud, sharp sounds such as those made by hand clapping, and to soft ones, as the twisting of a glass stopper in a bottle. When the drum heads (fig. 13, A, T) of both of the tympanic organs were destroyed the moths no longer reacted to sounds. When the drum head in one organ was destroyed the moths reacted to sounds in seven-tenths of the cases by flying. Moths with intact tympanic organs but with wings removed reacted to sounds in one-half the cases by running; in the other cases, by quick movements of the leg or antennae. Moths with intact tympanic organs but with antennae removed, reacted to sounds by flying. He concluded that these organs are sound receptors, analogous to the ears of mammals.

2. CHORDOTONAL ORGANS

The name chordotonal means a chord, or string, which is sensitive to tones. Graber (26) in 1882 presented the first comprehensive paper on the chordotonal organs, and much of our present information on this subject is based solely on his report. He apparently found these organs in a wide range of adult and larval insects, but he evidently included other sense organs too. Excluding the olfactory pores on insect wings, he did not find chordotonal organs in adult Lepidoptera.

but found them in the larvae of the codling moth and of *Tortrix scrophulariana*.

According to the review by Turner and Schwarz (87), chordotonal organs are not found in Myriapoda and Arachnida. They are found, however, in some insects which do not need a sense of hearing. They are well developed in caterpillars, even in those of Tortricidae, which spend their entire larval period inside of fruit. Eggers (16) remarks that chordotonal organs have been found in the first antennal segment (scape) of Apterygota, Orthoptera, and Hemiptera; in the second antennal segment (pedicel) of Neuroptera; and in the third antennal segment (first segment of funiculus) of Orthoptera. Some of these are called the Johnston organs, which are discussed later.

In the bases of lepidopterous wings Vogel (89) distinguished two types of sense receptors—chordotonal organs (fig. 13, C, *Ch*) and " Sinneskuppeln " (P) or olfactory pores. The former (fig. 13, D) seem to be true chordotonal organs, but the present writer did not see them in codling-moth wings or in those of other Lepidoptera.

Nothing definite is known about the function of the chordotonal organs, but they are usually considered as sound receptors. Since most of the movements of insects result in rhythms, as pointed out by Eggers, Snodgrass (81) suggests that these organs be regarded as rhythmometers.

3. JOHNSTON ORGANS

Tympanic organs, chordotonal organs, and Johnston organs are all chordotonal organs, because each sense element is chordlike in shape and has a sense rod, scolopala, or " Stift " according to the Germans. A tympanic organ is quite different from the other two types owing to the presence of a drum head or tympanum. A chordontonal organ and a Johnston organ usually differ little; if found in the pedicel, it is generally considered the latter; if found elsewhere, it is called the former; but in many insects both occur in the pedicel. A good review on this subject is by Snodgrass (81). The paper by Eggers (16) is the most comprehensive on this subject. He studied the Johnston organs in the pedicels of most of the insect orders and concluded that they are true " Stift " organs and are common to all insects, including Apterygota. In regard to the antennae of larvae he found them in hemimetabolous forms, but absent in holometabolous ones. Therefore, caterpillars do not have the Johnston organs.

In both sexes of the codling moth the present writer found the Johnston organs (fig. 14) to be highly developed, and the sense rod

or " Stift " (Sr) is only slightly different from that pictured in the Lepidoptera examined by Eggers. The writer also saw external marks of these organs in many other Lepidoptera.

Eggers informs us that their structure is not correlated with that of the tympanic organs. Formerly they were assumed to be auditory in function, but more recently they have been called muscular receptors
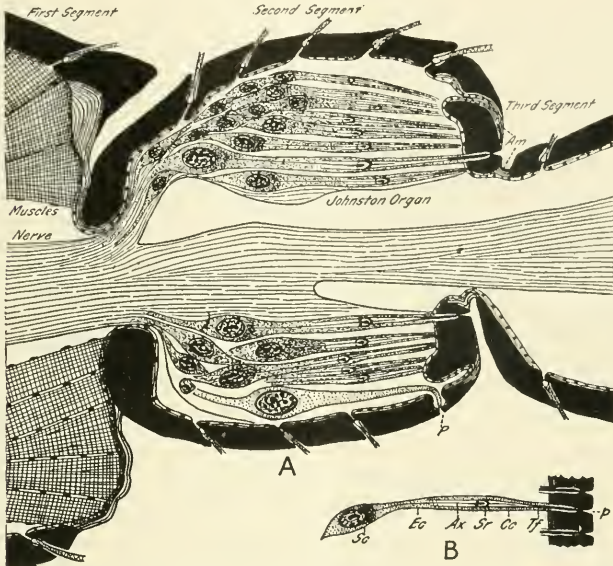

FIG. 14.—Johnston organs of codling moth, × 500. A, Semidiagrammatic drawing, showing one olfactory pore (P) and Johnston organ whose distal end is attached to articular membrane (Am). This membrane consists of three concentric bands of chitin; two thin and flexible ones (represented by lines) and a thick, rigid, and much wider one (solid black) between them. Therefore, it slightly resembles a drum head and apparently may be vibrated by jars or by movements of the flagellum. B, Detailed structure of a single chordotonal element drawn from two sections. All parts, except the nuclei of the enveloping cell (Ec) and cap cell (Cc), were distinctly seen. Other authors have seen these nuclei in other Lepidoptera. The terminal fiber (Tf) of each element is fastened at the bottom of a pit (p) which usually lies in the rigid and thick band of the articular membrane. The other abbreviations are the same as those in figure 13, D.

or statical-dynamic organs to register the movements of the antennae. Eggers believes that they probably perceive the movements of the articular membrane to which they were attached. These movements are caused by the antennae being used as tactile organs, or by the wind vibrating these appendages. In the males of Culicidae and Chironomidae, however, they may be special auditory organs. The present writer (52) in 1922 studied the Johnston organs in the honey-bee in

which the articular membrane, to which the sense fibers are attached, resembles the head of a drum. It was then suggested that these organs might receive stimuli from gusts of wind, weak air currents, or from jars, but the most reasonable function considered was that they registered the movements of the flagellum.

4. AUDITORY HAIRS

Years ago there was a controversy as to whether spiders possessed auditory hairs. When a dead spider was put under a microscope and certain musical tones were produced, some of the hairs on the spider were seen to vibrate. This observation alone is no more proof for an auditory sense in spiders than to say that one stringed musical instrument can hear another if a certain cord of the first vibrates when a cord of the second is struck. Recently Minnich (64) has revived the subject of auditory hairs and shows definitely that certain hairs are the sound receptors in larvae of the mourning-cloak butterfly. When a test such as was given with a dead spider was repeated, no hairs on a freshly killed larva were seen to respond to the same tones to which larvae normally react.

Minnich's review shows that certain caterpillars in all instars react to a variety of sounds, including those made by slamming a door, clapping the hands, the human voice, a violin, and a shrill whistle, but the earlier observers did not locate the sound receptors. Minnich used sounds produced by the human voice, piano, organ, violin, dish pan, Galton whistle, tone modulator, and tuning forks. The larvae responded to all of these, except the whistle and modulator, usually by throwing the anterior third of the body dorsally or dorsolaterally. The extent of the response to sounds varied with the intensity of the tone. For full-grown larvae the upper limit of response was probably not far from C''' (1,024 complete vibrations per second). Responses were obtained from 32 to 1,024 vibrations per second. Responses to sounds increased greatly with age, being least in the first and greatest in the last two instars. The responsiveness was correlated with the number of body hairs, which were fewest on the first instar and most abundant on the last instar. Responses to ordinary mechanical stimulation decreased with age, being greatest in the first and least in the last instar. Headless larvae and fragments of bodies responded to sounds, but the auditory hairs were found to lie chiefly on the anterior two-thirds of the insect. These hairs are probably some of the ordinary tactile ones (Sensilla trichodea) studied by Hilton (34), who claimed that most of the body hairs of caterpillars are innervated. Minnich believes that the

body hairs act as sound receptors for three reasons: (1) Singeing the hairs greatly reduced or abolished the responses; (2) hairs bearing water droplets or flour did not respond; and (3) during the molting periods when the hairs were disconnected with their nerves there was little or no response.

Abbott (2) observed that normal *Datana* larvae gave definite responses to air currents and sudden jars, but to only two notes—C" (512 vibrations) and F sharp (728 vibrations)—by elevating the anterior and posterior parts of the body. These notes were made by using a closed pipe with a movable plunger, a piano, and a mandolin. He assured us that he believed the normal larvae actually responded to the foregoing musical instruments for four reasons: (1) They were protected from air currents when tested; (2) they were several feet from the instruments; (3) vibrations from the substratum were eliminated; and (4) no responses were observed when the body hairs were covered with water or shellac, or when the body surface was anaesthetized with a 2 per cent solution of procain. Since these caterpillars responded to only two notes, which are not experienced in nature, Abbott believed that these responses were not adaptive, but perhaps secondary, resulting from an " adaptation of certain organs to more significant stimuli."

IV. THIGMORECEPTORS

1. TACTILE ORGANS

It seems that no one has made a thorough study of the tactile organs of Lepidoptera, but those in certain beetles have been carefully studied. The writer (53) 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. Besides these three types Lepidoptera have a fourth, the sense scales (S. squamiformia); however, it seems that only the small, narrow scales are innervated, while the large, broad ones (fig. 3, B, *Sh*) have no nerve connection. If the end pegs (S. styloconica) are really innervated, we should add a fifth type of tactile organs.

Sense scales on the wings of Lepidoptera have been described by Guenther (27), Freiling (23), Vogel (88), and Prüffer (77). Vogel states that innervated scales are found on the wings of all Lepidoptera, occurring on both sides, mostly on the veins and particularly on the marginal ones, but they may be found also on the basal parts of the

wings. Quenther believes that the sense scales are wind tactile organs, used in orientation. With the aid of them Freiling believes that night-flying Lepidoptera in their rapid movements are able to avoid obstacles.

In regard to tactile hairs on the codling moth, all parts of the integument were not searched for them and in most cases where found they were identified from external appearances. Most of the tactile hairs on the wings seem to be ordinary sense hairs (fig. 4, A, *St*), but a few sense scales (*Ssq*) were seen. On the legs, maxillae, and labial palpi sense hairs (fig. 5, A and D, *St*) and sense bristles (*Sca*) are more or less numerous. On the antennae are found numerous sense hairs (fig. 3, *St*), sense bristles (*Sca*), and end pegs (*Ss*). The large non-innervated scales (fig. 3, G, *Sh*) overlap one another like shingles on a roof and on some segments they cover nearly all the sense organs. The peculiarly shaped pegs found on the maxillae (fig. 5, D, *Pg* and I) are also to be classified as tactile organs. Some of the tactile hairs on the antennae and mouth parts of codling-moth larvae are shown in figures 9 and 10.

V. GEORECEPTORS

I. BALANCING ORGANS

When an animal responds to gravity a special static or balancing organ is not necessarily involved, but such organs are known in four Phyla—Cœlenterata, Mollusca, Arthropoda, and Vertebrata. Semi-circular canals occur in the vertebrates, while otocysts or statocysts are found in certain medusae, molluscs, and crustaceans. A statocyst may be an open or closed cavity, lined with sense hairs. In the center of the cavity may be one or more concretions of carbonate or phosphate of lime, called otoliths or statoliths. In the shrimp a statocyst is found in a segment of the claw. It is an open sac in which the shrimp places grains of sand. As the animal moves about in all directions, the grains of sand fall against the sense hairs thus enabling the shrimp to keep its equilibrium. A statocyst, therefore, is nothing more than a special touch organ, and the same may be said about the semicircular canals in which the liquid in them takes the place of the statoliths. A good review on this subject is by Dahlgren and Kepner (8, pp. 207-215).

Insects so far as we know do not have organs similar in function to the semicircular canals and statocysts; nevertheless, they certainly have great balancing powers. The only case in which such organs have been surmised is in the Diptera. The so-called balancers or halteres were formerly considered organs of equilibrium, but flies can fly just as well without them.

Vom Rath (78) first described a flask-shaped structure in the distal segment of the labial palpus of the cabbage butterfly. The structure is lined with innervated hairs which he considered olfactory in function. He imagined this structure to be a special olfactory organ for detecting the presence of food. This structure, whose shape varies considerably, seems to be common to all Lepidoptera. It was seen in practically all of the specimens examined by the present writer. It is present in the labial palpi (fig. 5, E, *Bo*) of both sexes of the codling moth, in which it is sac-shaped, opening to the exterior by a wide mouth (fig. 15, A). The innervated hairs (fig. 15, B, *Hr*), instead of being narrow and hollow as figured by vom Rath, are wide, heavy, and club-
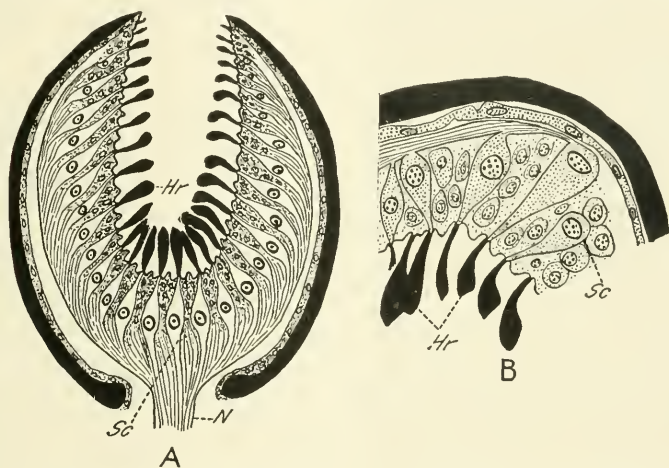

Fig. 15.—Sense organ in labial palpus of codling moth. It is probably a static or balancing receptor. A, Diagram of a longitudinal section through terminal segment, showing organ made up of sense hairs (*Hr*), sense cells (*Sc*), and a large nerve (*N*); B, drawing from an oblique section, showing same parts, × 750.

shaped. They certainly cannot be olfactory in function. Since their slender bases arise from very delicate chitin, their clubbed ends probably swing in various directions as the insect moves about. This organ reminds the writer of the statocysts, especially those of the shrimp and crayfish, and it probably has a similar function. If it does not contain statoliths, the hairs may operate sufficiently without the use of them.

VI. OTHER RECEPTORS

Among the general sensations of Lepidoptera might be mentioned those of temperature, humidity, direction, hunger, fear, and pain, but they are probably not connected with special sense receptors.

4

Much experimental work on various temperatures, particularly as control measures, has been done on Lepidoptera, but little or none of it can be discussed from the tropic point of view. The sense of temperature is probably well developed, although in insects, as in ourselves, there are probably no special thermoreceptors. The subhypodermal nerve plexus, if present in adult Lepidoptera as found in caterpillars by Hilton (34), could easily perform this function. Humidity, which is closely related to temperature, also has much to do with the behavior of Lepidoptera. Hering (32, p. 201) remarked that butterflies have a barometric sense, because sultriness and low barometric pressure have a characteristic effect on both the adults and larvae. He imagined that some of the antennal organs are the receptors. Guenther (27) hazarded the opinion that the " Sinneskuppeln " (olfactory pores) were barometric receptors.

Prüffer (77) states that his results and those of Patijaud demonstrate that female moths cannot lure the males from long distances, in spite of evidence shown years ago by Forel, Fabre, and others. He says that the females of *Saturnia pyri* L., as an example, can attract the males from a distance of not over 50 meters. Noel (68) concluded that neither sight nor smell is sufficient to explain the attraction from long distances. As a hypothesis, he suggested that certain insects emit special waves or rays, resembling X-rays, or the Hertzian waves, or even the N-rays of Dr. Blondlot. He firmly believed that these rays, which have not yet been isolated or verified, really exist and that they are used in distant communication. It has also been suggested that the bushy antennae of certain moths support this theory.

C. Scent-Producing Organs

The study of scent-producing organs follows as a corollary to that of tropisms and tropic receptors. Since chemotaxis 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 in numerous species belonging to most of the insect orders.

Several years ago the writer (49) reviewed the literature on this subject. A brief summary of that review concerning Lepidoptera follows : Scent scales on the wings constitute the almost universal type of scent-producing organs in male butterflies. Clark (4) has recently reviewed this subject and added much new information. A pair of invaginated sacs located at the ventro-posterior end of the abdomen has been found in certain male butterflies. These sacs are

partially lined with scent hairs at the bases of which lie unicellular glands. In a certain female butterfly the same organ is present, but there is also a circle of scalelike scent hairs around the anus. In another female butterfly there is a single invaginated sac, similarly located. In the females of the maracujá butterflies, a pair of styled knobs at the posterior end of the abdomen serves as a scent-producing organ.

The most common type of scent organ in male moths is a tuft of scent hairs on the tibiae of the third pair of legs. Occasionally there are also tufts of hair on the tibiae of the first and second pairs of legs. Another common type in certain male moths is a pair of tufts of scalelike scent hairs at the base of the abdomen. In the males of other moths a pair of invaginated sacs, lined with scent hairs, lies in the ventro-posterior end of the abdomen. In the females of certain moths a paired tuft of scent hairs lies near the anus. The scent-producing organ of the female silkworm moth (*Bombyx mori*) is the most highly developed of any found in a female lepidopteron. This organ is a pair of invaginated and greatly folded sacs in the posterior end of the abdomen. The female attracts the male by evaginating and turning these sacs inside out, thus fully exposing the inside which is moist with an aromatic substance. In all cases where scent hairs are present, each hair is connected with a unicellular gland.

The only scent-producing organ found by the writer in codling moths is a pair of invaginated sacs (fig. 16, A) in the ventro-posterior end of the abdomens of males. The mouth of the sac seems to be a long slit along the ventral median line. Muscles (*Mu*), which nearly surround the sac, apparently change the slit into a wide opening, forcing the 90 scent hairs (*H*) to the exterior between two abdominal segments. Each hair (fig. 16, B) is long and its base is connected with a single gland cell (*Gc*) at the anterior end of the sac. In cross section (fig. 16, C) the hairs are round or oblong, are transparent, and have a spongy texture. The outer wall is rough and a pore (*p*) can occasionally be seen in it. When greatly magnified the gland cells (fig. 16, D) are large and typical for scent-producing organs. Judging from this structure alone male codling moths attract the females by means of emitting odors from an aromatic substance which passes through pores in the scent hairs to the exterior.

No one seems to have described a scent-producing organ like the one in the codling moth, but Freiling (23) has described a similar one in a male butterfly (*Danais septentrionalis*). In this case the mouths of the paired sacs lie on either side of the anus. Most of the

scent hairs are attached to the anterior portion of the sac. When the sac is evaginated and the tuft of hair is expanded, this organ resembles a cylindrical fan whose contents are turned inside out to form the circular part of the fan. The scent hairs are filled with a matrix substance and the secretion passes through tiny pores in the walls of the hairs to the exterior.

Jordan (36) discovered in a number of Notodontidae a flap, which he called a cteniophore. It is movable and partly covers a cavity in
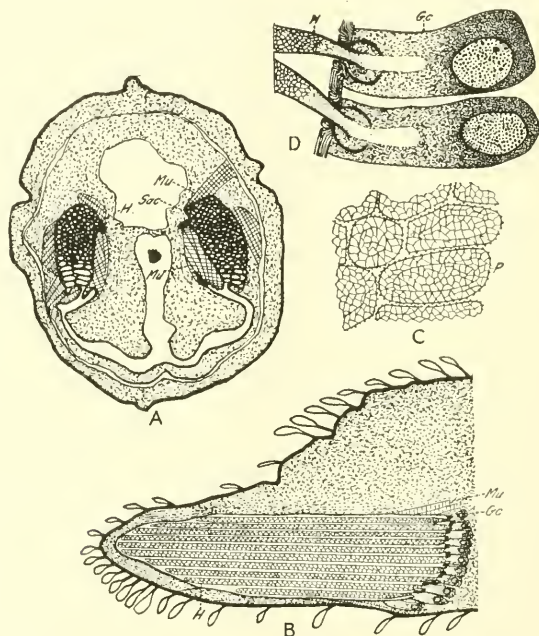

FIG. 16.—Scent-producing organ of a male codling moth. A, Cross section through tip end of abdomen, showing location of a pair of invaginated sacs, which are evaginated by muscles (*Mu*) thereby exposing the hairs (*H*) to the exterior, × 53; B, longitudinal section through tip end of abdomen, showing muscles (*Mu*) attached to invaginated sac filled with scent hairs (*H*) to which are attached unicellular scent glands (*Gc*), × 53; C, cross section of scent hairs, showing their spongy texture and pores (*p*) in outer wall, × 500; D, longitudinal section through bases of two scent hairs (*H*) and their gland cells (*Gc*), × 500.

the pleurum of the fourth abdominal segment. It is a special male apparatus developed in connection with scent organs. He believed that the hind tibia and hind wing were rubbed across the cteniophore to receive an odorous substance, probably from glands in the cavity. A remarkable combination of tympanic organ and cteniophore was earlier discovered by Jordan and more recently pictured by Hering (32, p. 195). In codling moths, a projection, probably a cteniophore, lies on either side of the abdomen of the males, but no cavity is present.

Summary and Discussion

In order to throw light on the biology of the codling moth, a thorough investigation of the tropisms of this insect was begun in the spring of 1927. Definite results were obtained only by using the larvae. In all 154 larvae, belonging to the two broods at Silver Spring, Md., were tested individually in the laboratory under various conditions. In bright light, although not direct sunshine, larvae of the first instar were weakly photopositive. Certain tests indicated that objects are perceived and located by the senses of smell and sight, and by mere chance. Chance alone seemed to be only 30 per cent efficient; sight and chance combined, 40 per cent efficient; whereas smell, sight, and chance combined were 65 per cent effective. Therefore, since larvae of the first instar have photopositive eyes, they remain in the open on apple-tree foliage and search freely for food, apparently not being aided by their senses until within a few millimeters of the food. The larvae were found to be easily repelled by odorous substances, but attracted with difficulty.

Larvae of the second, third, and fourth instars were weakly photopositive to weak light, but indifferent to strong light. Larvae of the fifth instar sometimes acted indifferently to light but generally were weakly photonegative. Larvae of the sixth instar were either weakly or strongly photonegative, the degree depending on their age; and those with blackened ocelli did not respond to light. At cocooning time the larvae were strongly photonegative, geopositive, and thigmopositive, whereas during their earlier instars they either behaved indifferently to light, gravity, and touch, or were photopositive, geonegative, and thigmonegative. Consequently, when the larvae are ready to spin cocoons they avoid bright light as much as possible, usually move toward the ground and hunt for dark and tight places in which to pupate. When bands are placed around the trunks of apple trees to serve as a supplementary control method, we are merely taking advantage of nature's laws. It therefore seems that so far as tropic responses are concerned the vulnerable period in the life history of codling-moth larvae is brought about by a change in tropisms.

It is well known that certain varieties of apples are more susceptible to codling moth injury than are other varieties; why, no one knows, but several factors, including thickness, toughness, and waxiness of apple peel, and the odorousness and acidity of apples, might be considered. Owing to one or more of these factors the larvae probably gain entrance to the more susceptible varieties with less difficulty; or the female moths perhaps distinguish differences between apple trees,

and if so, they probably lay more eggs on the preferred varieties. No attempt was made in the present investigation to determine which was true, but it is certain that the larvae can distinguish apples by smell and touch, and the moths are certainly guided by tropic stimuli to the proper places for depositing eggs. A study of this kind raises more questions than it answers, yet there is no other way to make progress. Not being able to throw light on this question, a thorough study of the morphology of the sense organs of the codling moth and its larvae was made, hoping that a little light might finally be had.

Since the moths are nocturnal fliers, their eyes cannot be their chief sensory receptors for locating the proper host plant. As already stated, the eyes of the larvae change slowly from photopositive ones in the first instar to strongly photonegative eyes in the last instar. This change may be caused by a migration of pigment, as found in certain other larvae, and it seems to be in harmony with the habits of these larvae, which spend most of their time inside of fruit. Before entering apples, photopositive eyes are needed; but after emerging for the purpose of pupating, photonegative eyes are required.

Two kinds of smelling organs—certain hairs on the antennae, and the pores, called olfactory by the writer—are fully described. It seems doubtful whether these hairs, called pit pegs and end pegs, can serve as olfactory organs owing to their hard covering of chitin. Granting that these hairs are the only olfactory receptors of Lepidoptera, eight of the 34 individuals discussed in table 2 cannot smell at all, while four others can smell only slightly. The codling moth, however, has a good supply of them. Larvae do not have these so-called olfactory organs, yet they can smell. The olfactory pores are common to both adult Lepidoptera and their larvae. In the adult they are found on the wings, legs, mouth parts, and second segment of the antennae. In the larvae they occur on the head, mouth parts, antennae, legs, first thoracic segment, and anal prolegs.

There are supposedly two types of taste organs. The first type consists of certain hairs on the mouth parts, but since these are covered with hard chitin the writer does not believe that aqueous liquids can pass quickly through them in order to stimulate the nerves inside. The second type is Minnich's tarsal chemoreceptors, which, when properly stimulated, are 256 times as sensitive as are the taste organs in the human mouth. We know nothing about the structure of these receptors, and the present writer so far has found only two kinds of sense organs—sense hairs and olfactory pores—in the tarsi of insects.

We now have good evidence that both adult Lepidoptera and their larvae can hear, although probably not as we do. Four kinds of so-called auditory organs have been described. They are tympanic organs, chordotonal organs, Johnston organs, and auditory hairs. The first three have been found in adult Lepidoptera, while the second and fourth occur in caterpillars. Of these four the writer found only the Johnston organs in the adult codling moth, but Graber in 1882 saw chordotonal organs in the codling-moth larva. It has been shown experimentally that tympanic organs and auditory hairs are affected by sound waves, but we know nothing definite about the functions of the chordotonal and Johnston organs.

Other special sensory receptors of the codling moth include certain innervated hairs serviceable as tactile organs and a well-developed structure in the labial palpus. The latter might function as a balancing organ. The general senses to temperature, humidity, etc., are not supposedly connected with special sense organs, although these senses seem to be well developed in Lepidoptera. In connection with the olfactory organs the scent-producing organs were studied. The only one found in the codling moth is a pair of invaginated sacs in the abdomen of males; thus it seems that the males attract the females and not the reverse.

In conclusion it has been shown that considerable information is now available on the tropisms and sense organs of Lepidoptera, but there is much yet to be learned, and the problem should be attacked from all angles, using the best equipment obtainable. A recent review by Kennedy (38) helps to clarify certain phases of insect behavior. He remarks that while sensitivity is a function of the nervous system, it is conditioned by other structural features, such as small size and chitinous exoskeleton. Hase (29) has recently described his physiological laboratory and equipment at Berlin-Dahlem, which should be emulated by other scientists doing similar work. Much of his apparatus is used for testing the tropisms of insects.

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