by Philip S. Callahan

INSECTS
and How They Function

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With illustrations and photographs by the author

As we become more aware of the impact of animals and plants on our lives, and of our lives on theirs, the world of insects looms larger than ever. This book explains how the organs and bodies of insects are built, how their marvelous structures function, and how they sense the world they live in.

The author describes the all-important integument, or "skin" — a much more complex organ than one would imagine; how insects fly, and how they compare with man-made flying machines; their digestion and respiration; their sounds and sense of touch; their unusual eyes; their nervous and reproductive systems.

In discussing communication, Dr. Callahan describes his widely accepted theory that the antennae of certain moths at least, and probably many other species of insects, sense odors by acting as electronic resonators that pick up the electromagnetic waves emitted by odor molecules—in effect, a biological form of man's waveguide antennas.

To bring those interested in natural science closer to insects in a practical way, the author has included a number of interesting experiments that anyone can do with simple equipment.

A Holiday House Book

Philip S. Callahan

INSECTS and How They Function

with illustrations and photographs
by the author

HOLIDAY HOUSE · NEW YORK

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MAGNIFICATION OF ELECTRON-MICROSCOPE PHOTOGRAPHS: The magnifications given in the captions refer to the images as seen in the original 8 × 10-inch photographic prints, and are therefore not as great when seen reproduced in this book.

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for Winnie

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The coiled proboscis, or feeding tube, of the Indian meal moth, as seen by the scanning electron microscope. Note the scales on the body surface, and part of the compound eye at left. Microscopes, and more particularly electron microscopes, show insects to be far more complicated in structure than most people imagine.

Chapter One

The Living Insect

Insects have a far greater effect on human life than is generally realized. The very survival of the human race depends on our six-legged friends. This may sound like a contradiction, for in modern times the greatest emphasis has been placed on control of insect pests. Most insects, however, are beneficial; for instance, there are tens of thousands of insects that prey on harmful species. As we trace the life processes of the insect let us keep in mind that they are far more important to men as allies than they are detrimental to his modern way of life.

Insect physiology—the science of the life processes of insects—is very important to developing new methods of controlling insects that destroy man's crops. The intensive cultivation of single crops in rows is favorable to huge build-ups of destructive populations of insects. The farmer sets the table, so to speak, for insect species that feed on the crop plants. Economic entomology, the science that develops insect controls, is one of the most important of all of our applied sciences; it prevents disease and social ills by assuring a wholesome and abundant food supply. To understand how it is related to the study of insect physiology, we must find out the meaning of a third area of study, called ecology.

Ecology is the science that explores the way plants and animals relate to each other in their particular surroundings. We cannot understand the life processes of an insect unless we also understand how the insect fits into its environment. The "inside" life processes of insects are directly related to the "outside" forces around it. When man attempts to apply complicated control methods to his insect enemies, he must consider both these "inside" and "outside" factors.

It is often stated in popular writings that both man and insects have been struggling to dominate the earth and that insects are giving man a good run for his money. The success of the cockroach is the example most often cited. The family of cockroaches, called *Blattidae,* is considered to have been in existence, essentially unchanged, for 250,000,000 years. Fossils differing little from the cockroach of today have been found in the rocks of the Upper Carboniferous period of geological time. Although it is probably true that man strives to dominate the earth, and we might now expand that to include the moon, certainly insects do not consciously strive toward such a goal. It is fortunate that they don't, for they are so marvelously constructed that they would overwhelm us in a short time.

There are probably over 900,000 species of insects, grouped in 700 families; some entomologists estimate many more. Fewer than 1,000 of these species compete with mankind for food. Unthinking man, in his attempt to control harmful insects, often defeats his purpose by eliminating his insect friends. In order to prevent such insect tragedies the trained entomologist must have a thorough knowledge of both insect physiology and ecology.

Corn earworm larva feeding on a tassel of corn. In early spring these larvae feed on the first tassels as they emerge from the growing tip of the plant. Insect physiologists do not know why these young forms come in so many colors: yellow, green, pink, black.

When we speak of insect control we immediately think of insecticides. This is unfortunate, for some of the most subtle insect-control methods have been based on a keen knowledge of insect physiology and ecology and not on the use of insecticides at all. The men who developed these methods have been in the forefront of the entomological sciences. They succeeded because they understood the physiology of the insect species they worked with. They were also able to define the ecological niche to which the insect was adapted by its physiology. "Niche" is the term used for the place in nature occupied by an organism. The niche of a corn earworm larva is the tip and silk channel of an ear of corn. The corn tip provides a home for it, and the temperature and humidity found in it are suitable to the bodily needs of the developing insect. It provides a microclimate, as the ecologist would term it, for the life processes, and also a source of food for the development and growth of the larva.

INSECTS IN AGRICULTURE AND BIOLOGY

The honeybee is man's most useful insect ally. We usually think of bees as the producers of honey and beeswax. However, the fifty million dollars' worth of honey and beeswax produced in the United States is insignificant alongside the one billion dollars' worth of agricultural crops that they pollinate. If it were not for the honeybee, many crops could not be grown at all. Agricultural scientists estimate that this insect is responsible for 80 per cent of all crops pollinated by insects. Crops that depend on bees for pollination include alfalfa, clovers, apples, apricots, cranberries, citrus, cantaloupe, watermelon, peaches, plums, almond nuts, asparagus, broccoli, cabbage, celery, lima beans, artichokes, cotton, and a host of other crops. An impressive list indeed.

When we think of physiology, we usually think of the life processes of a single organism, but in the case of social insects like bees and ants we must expand our definition to include an entire society of insects. Maurice Maeterlinck, the Belgian writer and literary Nobel Prize winner, in his delightful classic, *The Life of the Bee,* treats the entire beehive as a living organism. For him the bee society is an incredible and complex living organism with each type of bee, queen, drone, and worker, functioning through specialized physiological division of labor as parts of the whole. William Morton Wheeler, the great Harvard ant behaviorist, used a similar analogy to compare an ant colony to a cellular organism. Eugène N. Marais, writing about termites, philosophizes on the strange force that holds the colony together and calls it *The Soul of the White Ant*—an appropriate title for his book.

Modern entomologists know that the colonies are held together by complex chemical messengers that control the activities of the various specialized castes. They call these chemical messengers pheromones from the Greek *pherein* ("to carry") and *horman* ("to excite"). These pheromones could be compared to external hormones for, like hormones, which carry messages between the cells within an organism, pheromones function externally to carry messages between individuals. To understand the physiology of the bee, the ant, or the termite we must study not only the individual but the entire colony as well.

The value of honey as food has long been known to man; drawings in a Paleolithic cave at Arana in Spain depict prehistoric man collecting wild bee honey. Besides insect products, however, insects themselves are a source of food. We know that many species of birds and certain mammalian insectivores, or insect-eaters, could not continue to survive without insect prey. The consumption of insects, called entomophagy, was also one of man's early habits. Most people in modern civilizations do not consider insects as eatable. We are limited by our refinement of food habits, which is based on modern agricultural practices.

The fact remains, however, that a good portion of the human population could not survive in a healthy state without insects as food. Scientists who study primitive tribes are aware that their usual diets are often deficient in animal fats and protein, and yet the people appear healthy. This is because insects are a regular part of their diet. An analysis of grilled termites, for instance, shows them to contain 36.2 per cent fat, 45.6 per cent protein, and 5 per cent ash, and to equal 508 calories per 100 grams of weight. These insects are an excellent protein source for human consumption.

I can vouch personally for the value of boiled wood-boring beetle larvae as food. I lived on them for five days while hiking through the jungles of Samar. I learned about eating insects from the Negritos, Pygmy-like people of Luzon in the Philippines. Eugene Fischer, an anthropologist, studied the Pygmies of the African rain forest and found that insects formed an indispensable part of their diet.

With the world population expanding at such a tremendous rate there is no valid reason why certain insects species should not actually be cultivated for human food. We may discover that certain high-protein species are physiologically suited to mass rearing for this use. We could then have, besides an animal husbandry, a food science called insect husbandry.

Insect predators have been used to control destructive insects. Insects are also useful in the control of weeds. Klamath weed was introduced into the United States from Europe about 1900. It completely overcomes the land, killing all other plants except larger shrubs and trees. It is also poisonous to livestock. A leaf beetle, *Chrysolina gemelata,* was introduced from France and rapidly cleared more than 100,000 acres of weed in California. It also reduced the pest weed in Washington, Oregon, and Idaho.

A knowledge of the biology and physiology of insect species is vital to control of destructive species. Certain insecticides do not break down chemically at a rapid rate and thus they build to high concentrations and pollute the environment. Often insecticides that do break down in the soil cannot be used on certain crops for economic reasons. A farmer could not afford to spray vast acres of wheat for an insect such as the Hessian fly.

This fly was named after Hessian mercenaries by the Americans during the Revolutionary War. It was thought to have been introduced on Long Island, New York, near Lord Howe's encampment, in the bedding straw of his soldiers. After 1779 it spread west with the frontiers. It became the most injurious insect enemy of the winter wheat in the Midwest. The entire fall generation of the midgelike fly emerges as adults within a short period after the late summer rains. Entomologists found that if farmers planted wheat after this period no eggs would be laid on the sprouting wheat. They therefore set planting dates, dependent on latitude, to allow plants enough good weather to mature before winter, but late enough to avoid the emergence of the Hessian fly. In Northern Arkansas, for instance, a farmer would be advised to plant after October 16. In northern Illinois, where winter comes earlier, the date of sowing wheat is a month earlier, around September 20. This is an excellent example of how the insect ecologist with a knowledge of the temperature needs of an insect can turn the environment to good use. No insecticides are necessary. Entomologists have been turning out successful controls like this for generations.

THE USES OF DROSOPHILA

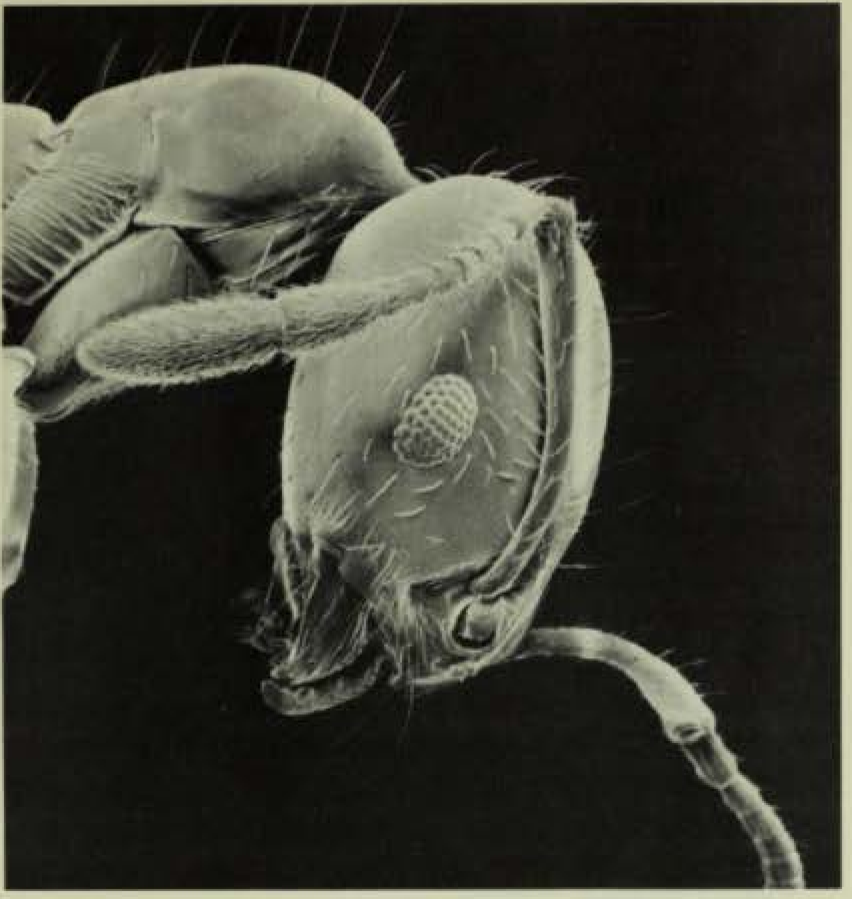
There are two species that lead all others in their use for physiological experimenting. They are the honeybee and the well-known fruit fly, *Drosophila melanogaster.* Genetic studies have stimulated a vast amount of physiological experimentation on the fruit fly. It is the guinea pig of the insect world and its contributions to medicine and biology are unequaled by any other insect species. Tumors have been isolated from the alimentary canal of *Drosophila*. These tumors were found to be genetically controlled, although some environmental factor may also be involved. Such insects are ideally suited for genetic and medical research.

Insect species are utilized for research because they are usually easy to rear and handle, require little laboratory space, and most important of all, pass through many generations in a short period of time. Because they can be easily reared in large numbers they are often used to study biological rhythms. Accurate data require large populations of test organisms for such studies. The literature on insect physiology describes many temperature and radiation experiments directed at solving the secrets of insect rhythms.

THE AESTHETIC VALUE OF INSECTS

Even if the study of insect physiology were not important to the fields of agriculture and biology, it would still attract a great number of interested researchers. We cannot look at the scanning electron microscope photo of the imported fire ant and not wonder how such a strange animal functions. When one steps on an ant he most certainly crushes a marvelous piece of biological engineering.

We look in amazement at the legs and antennae, the compound eye, the mandibles, the thorax, and other parts. Even the least curious might ask how such a creature evolved. The world of insects is a wonderful world and even the youngest among us soon become aware that it is a different world. It is almost as if creatures from another planet existed right in our own backyard, available to study.



Insect parts are often beautiful in form and texture, as this electron-microscope picture shows. The organs in many cases are highly varied from species to species. This fire ant worker, for instance, has far fewer facets in its compound eyes than certain moths and dragonflies, which may have 20,000 to 30,000. Note the structure of its antennae; some moths, by contrast, have antennae shaped like feathers or leaves. The posterior end of this ant is illustrated in Chapter 3.

Many insects are not only useful, but because of their coloration also esthetically pleasing. Volumes could be filled with the lines that poets have written to butterflies.

There is a Japanese haiku (a short 17-syllable verse) that says "What a delightful game it is to set/ Fireflies loose in a bed beneath the net!" The bed net of course is to keep the mosquitos out, but on summer evenings Japanese children collect fireflies and let them loose under the nets. The artistic genius of the Japanese is for perfection in small things. That genius is demonstrated in their love of insects. It is one of the few lands in the world where a child gains enjoyment from a cricket in a cage. Japanese cricket cages are works of art built of fine bars of split bamboo. Every year in August at the Chinzan-so palace grounds in Tokyo there is a cricket singing contest. Children from all over Tokyo bring their caged crickets and the night is filled with cricket music. The recording and analysis of such insect sounds and of insect hearing is an important part of the study of insect physiology.

A Japanese boy in Kamakura catches a cicada in his insect net. Insects are popular pets in Japan.

Just as interesting as the shape, the color, and the sounds of insects are their habits. One of the fathers of early American entomology was John Henry Comstock, professor of entomology at Cornell University. His book *An Introduction to Entomology* is a fascinating excursion through this far-out world. I often use his books to learn about the habits of insects that I observe in the woods and fields. For example, one day while I was hiking along the Appalachian Trail I saw white spots dancing up and down along the pathway; they looked like small silver balloons bobbing a few feet above the littered forest floor. At first I thought they were sparkles of dew caught on cobwebs. I reached for one and it evaporated in my hand. On close examination I found they were male flies, each of which carried a small inflated shining air sac.

These delicate little balloons are produced by the male during the mating flights, which take place early in the morning. The female is attracted to the dancing balloons; it is the visual communication signal of the mating flight. Think of the complex physiological processes within the male to produce this signal! It is one of the marvels of the insect world that is not to be forgotten once it is observed. When I arrived home I found a description of these early-morning creatures in Comstock's book. They are called dance flies.

Perhaps when we have learned more of insect physiology from the following chapters we will better appreciate the marvels of the insect world. Besides the practical benefits of such study to agriculture and biology, perhaps a better acquaintance with the way insects function will give us a deeper appreciation of these animals in our everyday lives.

Chapter Two

The Outside of Insects

The outside of an insect is called the integument, from a Latin word meaning "to cover." The word is also applied to the outer covering of many other animals. Unlike the skin of vertebrates, however, the insect integument is also an outside skeleton; thus the term "exoskeleton." Insects have no framework inside them. Although the exoskeleton serves to support the body, it has many other important functions: for instance, it controls the exchange of water between the insect's body and its environment. In times of stress it serves as a food reserve. In the developing embryo insect, it helps to form the sense organs and portions of the digestive and respiratory systems.

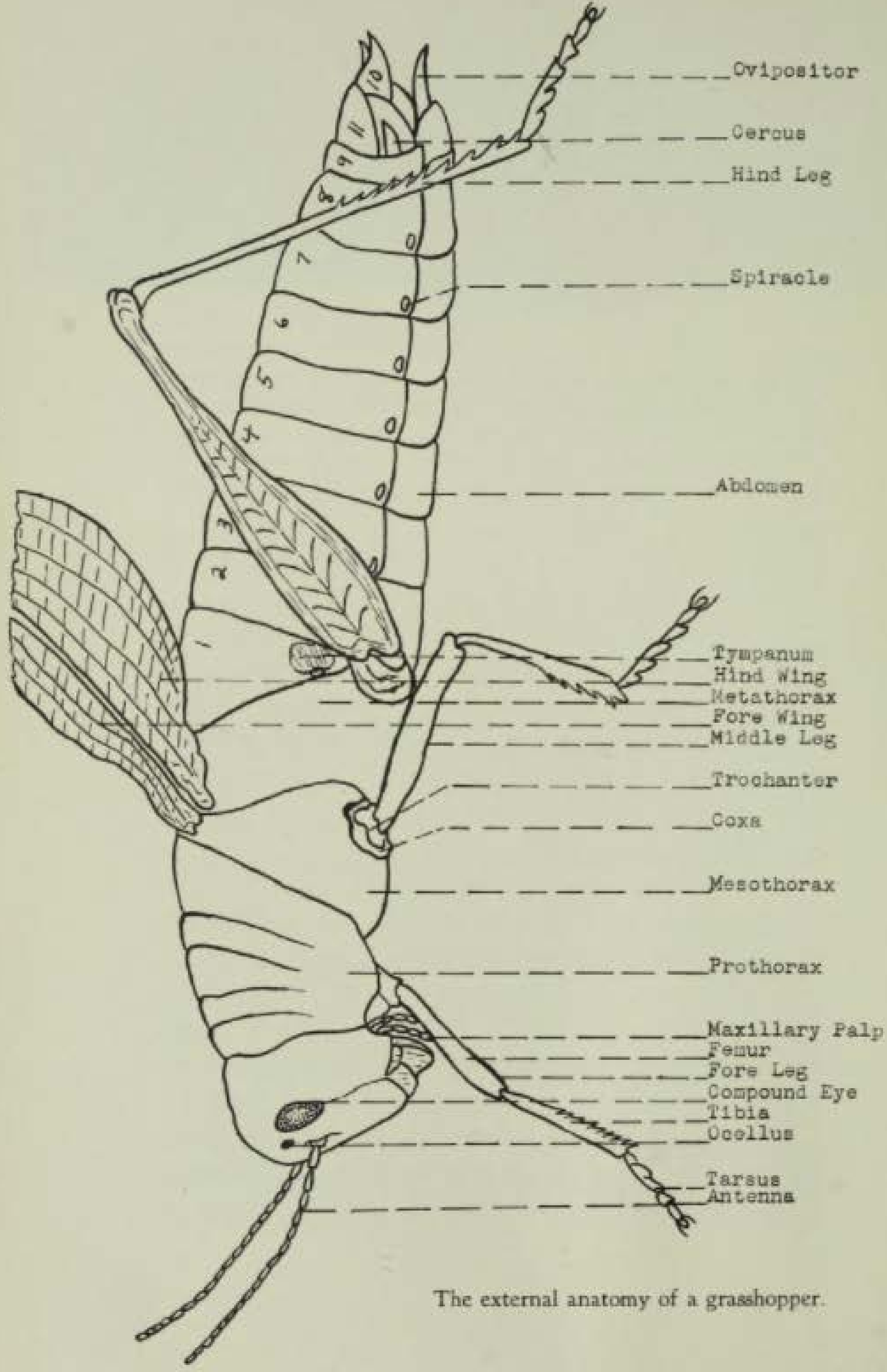
Studying the way the exoskeleton is put together and how it works shows us many important basic processes in biology, so it is important to absorb each of the details that follow. The exoskeleton is made up of layers, and from these biophysicists may learn more about ion exchange, an important chemical reaction involving charged atoms, across layers of membrane. It is composed of large molecules called macromolecules. Studying the position of these molecules, besides increasing our knowledge of molecular biology, may lead to new ideas of solid-state physics as it is applied to living things.

U. S. Department of Agriculture

The earliest larval stage of a corn earworm moth, as seen enlarged 800 times, photographed in three sections by the scanning electron microscope. It has recently emerged from its egg but has not yet molted; its length at this stage is less than one millimeter. The insect will go through six stages, or instars, before it becomes a pupa.

In addition the biologist, in studying the exoskeleton, learns about functional morphology—the relation of the fascinating shapes and structures of insects' and other animals' bodies to their use. The biochemist learns about the makeup of specialized chemicals such as insect hormones and aromatic substances that attract the sexes to each other at mating time.

Since the integument is an outside skeleton, it determines the shape of the insect. It is released, in a fluid state, by the epithelium, the innermost tissue beneath the insect's body wall. Once "set," it forms the hard, rigid plates called sclerites. These are separated from each other by membranes that allow for a certain amount of flexibility between them; otherwise there could be no movement of the body. The wings and legs are constructed of tubes containing flexible joints. The wings are attached to the body through a complicated series of sclerites that pivot at the top of



The external anatomy of a grasshopper.

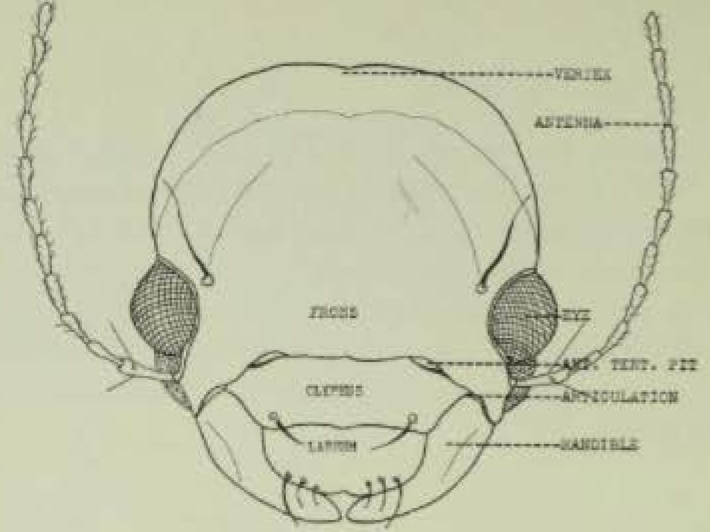
the thorax. The legs are attached by ball-and-socket joints.

Although this describes the outer physical makeup of an insect's integument, it is the layered inner structure of this complicated organ that determines how the insect functions inside. To understand better how the shape of an insect fits it to its surroundings and controls its internal processes, we shall look at the form of a specific example, the moth.

THE FORM OF THE EXOSKELETON

The exoskeleton of the adult moth is divided into three regions: the head, thorax, and abdomen. The head is composed of a series of sclerites that enclose the brain and support the main sensory organs, the compound eyes and the antennae. It is attached to the prothorax—the first region of the thorax—by a pair of sclerites that support the flexible membrane making up the neck. The first pair of legs is joined to the prothorax. The remainder of the thorax is composed of two sections, the meso- and metathorax, each of which supports a pair of legs and a pair of wings.

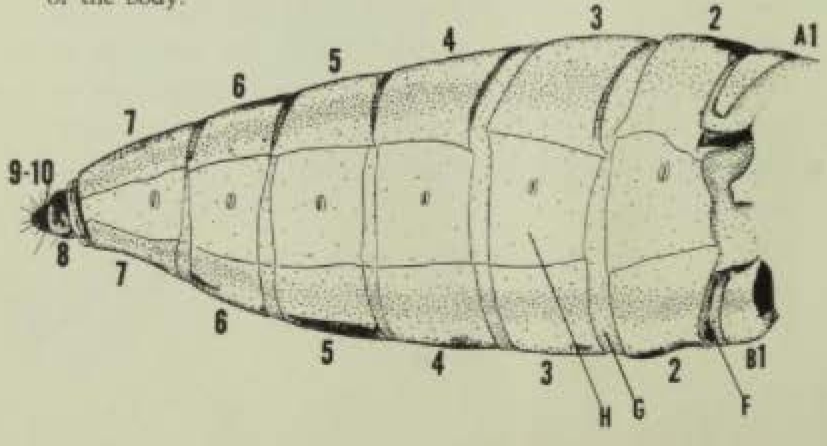
The wing articulation, or flexible joint, of the moth can be seen on page 52, and on page 22 are shown the sclerites making up the insect's abdomen. The many platelike sclerites enclose the powerful muscles for the wings and legs. The muscles are attached on the inside of the thorax to inner projections called furca. The abdomen of the moth joins the thorax just behind the back pair of wings. It is a series of ringlike sclerites separated by membranes and divided top from bottom by a longitudinal membrane.

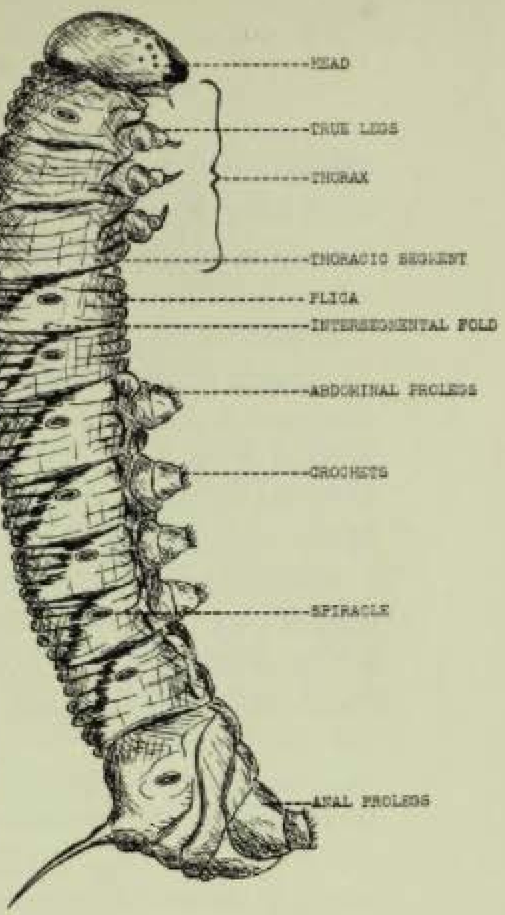


A front view of the head of a ground beetle, showing mouth parts and sense organs. The mandibles are movable jaws which are hinged at the point of articulation near the clypeus and labrum, parts of the upper "lip." The anterior tentorial pits mark depressions where the arms of an internal bracing structure, the tentorium, join the face.

The larval stage of one insect is similar to that of another, with certain modifications. The larvae of moths (and butterflies) are the familiar caterpillars. The moth larva, like the adult, has a three-part thorax. The legs of the thorax are called thoracic legs, and as in the adult there is one pair for each segment. The larvae differ, however, in that each of the middle segments of the abdominal region has fleshy legs called prolegs. There is a small pair of legs on the last segment called anal prolegs.

The abdomen of an adult corn earworm moth, showing the sclerites (*A1* and *B1* to *10*) separated by the membranes (*G*) that lie between them, and the wide longitudinal membrane (*H*). The openings in this membrane are spiracles, which admit air to the interior of the body.





A side view of the tomato hornworm in its larval stage. The true legs of the thorax are shown, as well as the four pairs of abdominal prolegs and the anal prolegs. The plicae are skin folds; crochets are small hooks found on the prolegs.

THE INTEGUMENT

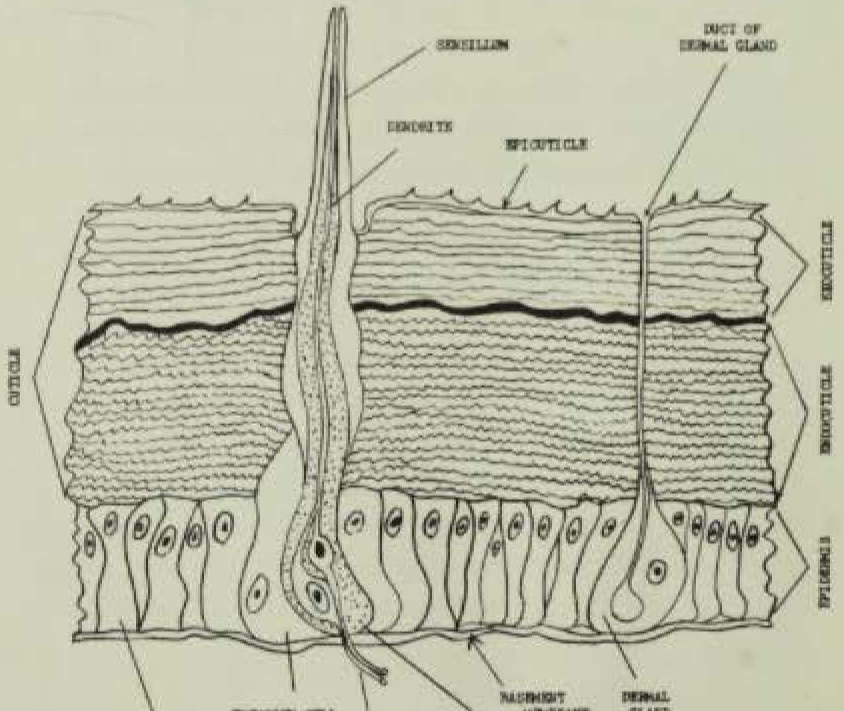
The insect integument is made up of three major layers: the basement membrane, or inner layer; the epidermis, or cellular layer; and the cuticle, or hard outer layer. An insect is such a complicated creature that even the thin cuticle itself is subdivided into three regions: the outermost, called the epicuticle, a hard middle layer called the exocuticle, and a soft inner layer called the endocuticle.

The epicuticle in turn is subdivided into a cement layer called cuticulin and a waxy layer. In most insects the waxy material is of the same general nature as beeswax. The waxy layer is covered with the protective layer of cuticulin.

In most insects a substance called chitin makes up about 20 per cent of the exocuticle. Since the endocuticle is also composed of chitin—about 60 per cent—chitin is the main material of the cuticle. Chitin is often mistakenly thought to be the substance that makes the cuticle hard, but the hardest cuticles often have less chitin than soft cuticles.

Beneath the cuticle the epidermis consists of a single layer of cells. It appears to degenerate in older insects and is fully developed only when new cuticle develops. Interspersed among the epidermal cells are dermal glands, which send very small ducts through the cuticle to the surface.

Cross section of a segment of typical insect exoskeleton, showing the layered structure and a sensory sensillum.



The basement membrane is the innermost layer of the body wall and supports the entire structure.

HOW THE EXOSKELETON GROWS

Some unique physiological processes take place in insect growth. Unlike the bone of mammals, the insect exoskeleton cannot grow larger, so it must be shed and replaced by a larger integument. The insect grows step after step by molting its skin. The process is called ecdysis. Molting is controlled by a special hormone, ecdysone, which will be discussed in a later chapter. The event is preceded by an increase in the size of the epidermal cells; at the same time the cuticle pulls away from the epidermis beneath it.

When one examines the cuticle with an electron microscope, one can see that extremely small openings called pore canals go through it. Most researchers believe that the pore canals contain cytoplasmic extensions of the epidermis around which the cuticle is secreted. Although they are not lined by any extension of the epidermal membrane, they do contain projections resembling filaments. It is thought that the filaments keep the holes open in a newly secreted cuticle until it hardens and becomes permanent. It also serves to lock the endocuticle against the epidermis. Formerly the canals were thought to be spiral, but present research indicates that instead they follow the arrangement of the layers that make up the cuticle. Electron-microscope studies have shown the cuticle to be composed of thin layers called lamellae. The sheetlike lamellae are made up of bundles of curved vertical fibers of extremely small size.

The growth of insects is controlled by two hormones, ecdysone and juvenile hormone; but this is not the whole story. Construction of the cuticle is also influenced by other things, such as nutrition, the flow of fluids through membranes, secretions from the nervous system, and the pressure under which oxygen reaches the cells. Outside conditions such as temperature and humidity are also important.

The process of molting begins when the epidermal cells become enlarged and the filaments withdraw from the pore canals. In most insects a molting fluid appears and dissolves the old cuticle. This fluid is thought to come from the epidermal cells. It is followed by the outer cement layer, which appears as a thin, delicate membrane over the surface of the body. This cement layer flows from the dermal glands and covers the waxy layer just before molting, the waxy layer having been laid down a few hours before the molt. The wax comes from the pore canals and prevents the insect from drying out during the process by "waterproofing" it. At the same time that the outer epicuticle is in the final stage of formation, the exocuticle and endocuticle are deposited.

That the cuticle is a living skeleton is demonstrated by the fact that wounding or abrasion of the outer shell causes wax to flow from the cuticle to repair the injury. Even in old, hardened cuticles the filaments extend up to the surface of the wax layer, allowing the repair of injury by the pore-canal secretions.

SHEDDING THE SKIN

During molting the greater portion of the old cuticle is re-absorbed by the insect. However, the sclerotin and outer cement layer must be cast off.

Immature insects have what is called an "ecdysial line" where the exocuticle is lacking. Along this line the endocuticle extends upwards to just beneath the outer epicuticle. After the endocuticle is digested by the molting fluid a "line of weakness" is formed and the least pressure from beneath splits the skin along the back. You may have seen such split skins of cicadas clinging to trees in the woods.

Many insects have special structures that aid in the escape from their old cuticle. Certain grasshoppers have an inflatable bladder in the neck that helps to split the cuticle. Sometimes the split is caused by the insect's contracting its abdomen and forcing blood under pressure into the thorax. Land insects may also swallow air, and aquatic species water, as an aid in the process.

WATER BALANCE

Water evaporates from an organism at a rate that depends on the amount of its surface area, not on the volume of the animal. As its size decreases, the ratio of the surface area to volume increases; thus small insects lose relatively more water than larger ones in a given time. Such insects face the necessity of keeping the small bit of water in their bodies from evaporating. It is the epicuticle, and especially the waxy layer, which prevents excessive drying out of their bodies. Experiments have shown that during molting there is very little loss of water, even though the insect is in the process of changing its epicuticle. With high temperature the cuticle usually allows more water to pass through. However, the membranes between segments, as well as the spiracles (openings of the breathing tubes), are the areas that lose most water.

Insects differ a great deal in being able to stand drying. P. A. Buxton found that mealworms, insect larvae that live in stored grain, survived over 210 days without food or fluid. It is obvious that if the water content of the body is to remain steady, the amount of water gained must equal the amount lost. Buxton decided that the water balance of mealworms is maintained by their eating the stored products they live in and retaining the water produced by metabolism, the process in cells that converts food to cell chemicals and the chemicals to energy.

Sir V. B. Wigglesworth, the famous English insect physiologist and the founder of modern insect physiology, subjected insects to dry air for successive periods of time. He noted the highest rate of water loss during the first period, followed by a steadily decreasing loss. He attributed the rapid decrease in the loss of water to a lessening of the permeability of the cuticle—the ease with which water molecules flow through it. Thus the cuticle becomes more and more resistant to the passage of the molecules in hot, dry weather and so keeps the insect from drying out.

FORMATION OF THE SENSE ORGANS

The exoskeletons of insects and other arthropods, such as spiders, are covered with a complicated set of sensory organs. These include the compound eyes for vision, sensory hairs (called sensilla) for smell, and spinelike sensilla (called mechanoreceptors) for sensing touch and pressure.

The formation of the sensilla depends on special cells in the epidermis. These are called trichogen and tormogen

Above, the head and prothorax of a cotton boll weevil, photographed at 2300 times' magnification, showing sensory spines on the integument, or outer tissue, and the compound eyes. Below, the spines at still greater magnification are seen clearly projecting from pits, and their surfaces are seen to be fluted.

cells. The first is a large cell containing a duct that passes through the cuticle to the surface. The secretions from this cell build up the sensilla above the duct. The tormogen cell secretes the materials that lay down the socket around the base of the sensillum. These parent cells often degenerate after the sensilla are formed.

Studies by Dr. Glenn Richards have shown that the cuticle of the sensilla is formed somewhat differently from the cuticle in general. After molting, the hardening of the body cuticle usually proceeds from the outside inward. This is apparently not true for the sensilla, which harden equally from the outside in and the inside out. They maintain an equal hardness right through the thickness of their tubular walls. As we shall see in Chapter 10, this is important to the way the spines operate.

In the upper part of the picture are seen scales of the corn earworm moth in cross section. The ridges on the scales look like pegs here. Their small size is comparable to that of some infrared light waves and enables them to interfere with the waves; on some insects visible light is thus broken up into brilliant colors that do not depend on pigments.

The integument, then, is one of the most important organs for fitting the insect to its environment. Besides the optical organs and sensilla, it contains various types of pigments that color the insect. Some insects have specialized scales or structural ridges on the integument that reflect light or break it up into colors by causing interference in the light waves. The beautiful metallic colors of some beetles and butterflies are so-called "structural colors" that are based on the ability of the exoskeleton to break up light.

Chapter Three

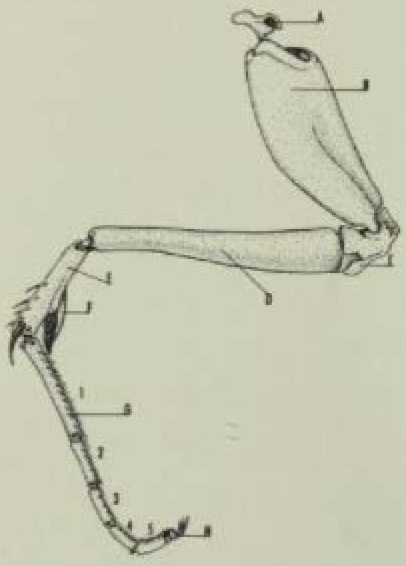
They Crawl and Creep

Insect legs are as varied as the insects themselves. They range all the way from the short, stubby prolegs of caterpillars to the long, powerful jumping legs of the grasshoppers. Everyone is aware that grasshoppers are capable of jumping great distances. The shape of the hind leg, with the heavy femur (first portion of the leg) making an angle over the back with the tibia (second portion), makes the grasshopper able to leap. It is a leg arrangement suitable for pushing the body up and away from the ground. The grasshopper's capabilities as a jumper are, however, more the result of size than of brute strength. The power of muscle tissue varies with the square of its cross section, whereas the volume of the body varies with the cube of the cross section.

As a result, the smaller the body size, the relatively more powerful, in relation to the size, are the muscles; and vice versa. That is why an ant, in relation to its size, can lift such tremendous loads. For the same reason insects could not possibly attain any greater size. If an ant were to grow to the size of those well-known monsters of science fiction it would be unable to move because of the weight of its exoskeleton. As it grew and grew its mass would increase by the cube, while its power to move would increase only by the square. A critical point of largeness would be reached at which the ant would collapse from its own weight. Although insect legs are remarkable appendages we should not endow them with superpower.

THE ADULT LEG

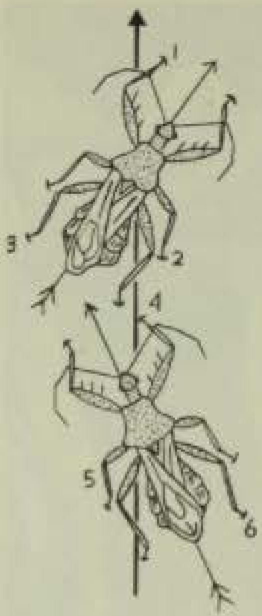
An insect's leg consists of six major segments separated by five movable joints. The part next to the body, the trochanter (*A*), inserts into a socket-like joint called the coxa (*B*). The largest portion of the leg is named, as in other animals, the femur (*C*). The next two parts, the tibia and tarsus (*D, E*), are fused in some insects. In adults the tarsus is usually subdivided into five segments. The last part, the pretarsus (*F*), is the foot.



The prothoracic leg of the corn earworm moth. Leg parts vary greatly in size and shape from species to species, and occasionally do not occur (a grasshopper has no trochantin, for instance). *A*, trochantin; *B*, coxa; *C*, trochanter; *D*, femur; *E*, tibia; *F*, epiphysis; *G*, tarsus; *H*, pretarsus. The epiphysis is a built-in cleaning "tool"; the moth pulls its antennae between the tibia and the comblike epiphysis and so cleans debris and pollen from the sensilla of the antennae, which if dirty could not function efficiently as frequency detectors.

The insect leg is a wonderfully jointed, complex structure, as seen in the legs of this fire ant. The order Hymenoptera, to which ants, bees, and wasps belong, is distinguished by the constricted first abdominal segment—hence the expression "wasp-waisted" for the tightly laced waistlines of our great-grandmothers' day.

Adult insects appear to walk with only three legs touching the ground at any one time, the fore and back leg of one side and the middle leg of the opposite side. The front leg acts to pull the body forward while the middle leg supports the opposite side. The hind leg pushes and turns the body slightly sideways. The result is a somewhat zigzag course as the insect progresses forward. This is only a



An assassin bug walking. Legs 1, 2, and 3 touch the ground and are then followed by legs 4, 5, and 6. The arrows through the insect's body indicate (by exaggerated orientation) the slightly zigzag movement of the bug. The heavy center line is the direction of travel. (Modified from Wigglesworth.)

generalized description of walking; many insects depart from this form. Motion pictures show that in certain cases the three legs do not touch the ground simultaneously, but rather the foreleg, the opposite middle leg, and the hind leg, in that order. Sometimes as many as four or five legs may be on the ground at the same time and the course followed practically straight.

Insect legs, although mainly for locomotion, are often used for activities other than walking. They may be modified for hopping, clinging, grasping, carrying, digging, or swimming.

We usually think of the head as carrying the sense organs, but this is not always the case in insects, where ears may be on the legs, or even in the abdomen. Long-horned grasshoppers—the familiar katydids—have ears called tympana in the tibias of the front legs.

The praying mantis has developed an elongated thorax and modified coxae and femora for grasping its prey. The coxae are elongated so that the heavy femora fold back against it, giving the mantis its prayer-like attitude. The

femur and tibia are armed with heavy spines that grasp the victim. All the species are carnivorous and depend on the holding ability of their forelegs for survival.

Another species with remarkable appendages for holding prey is the predacious diving beetle. The males of certain species of these voracious predators have cuplike suckers on the first three segments of the front tarsi. They are so efficient that they will attack and hold small fish.

Many insects, especially the flies, have a structure called the pulvillus on the tarsus. There are pores or hollow hairs on the pulvillus from which a sticky substance comes that enables the fly to walk upside down.

The hind leg of the worker honeybee is modified for carrying pollen. On the outer surface of the tibia there is a smooth area that is ringed by some highly specialized curved hairs to form a structure called the pollen basket. The honeybee also has hairs arranged in rows on the hind legs and uses these to comb pollen from the body.

The first leg of a predacious diving beetle, photographed in three sections by the scanning electron microscope. The first three segments of the tarsus are widened and form a hinged disk. On the underside of the disk are small cuplike suckers that cling to slippery prey such as small fish. Another view is given in the following picture.

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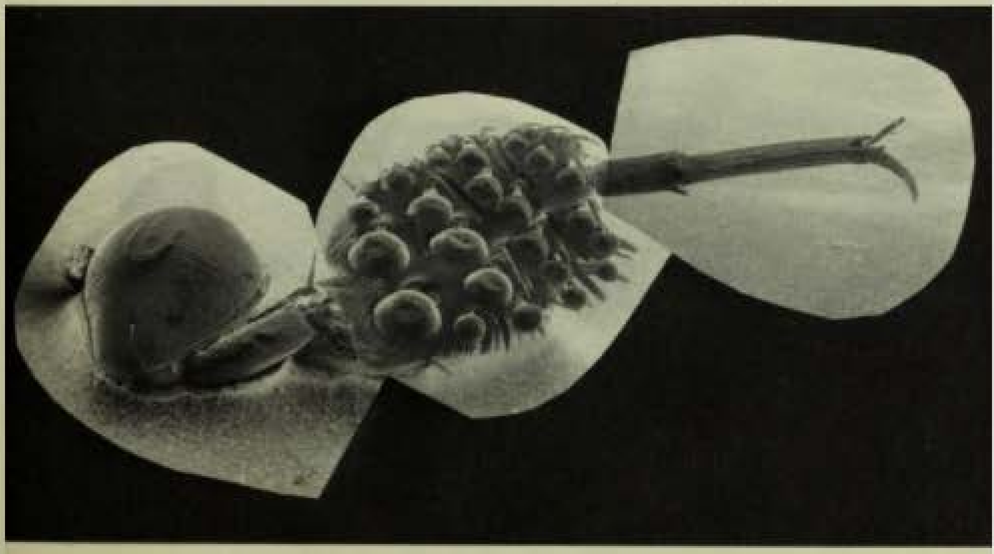

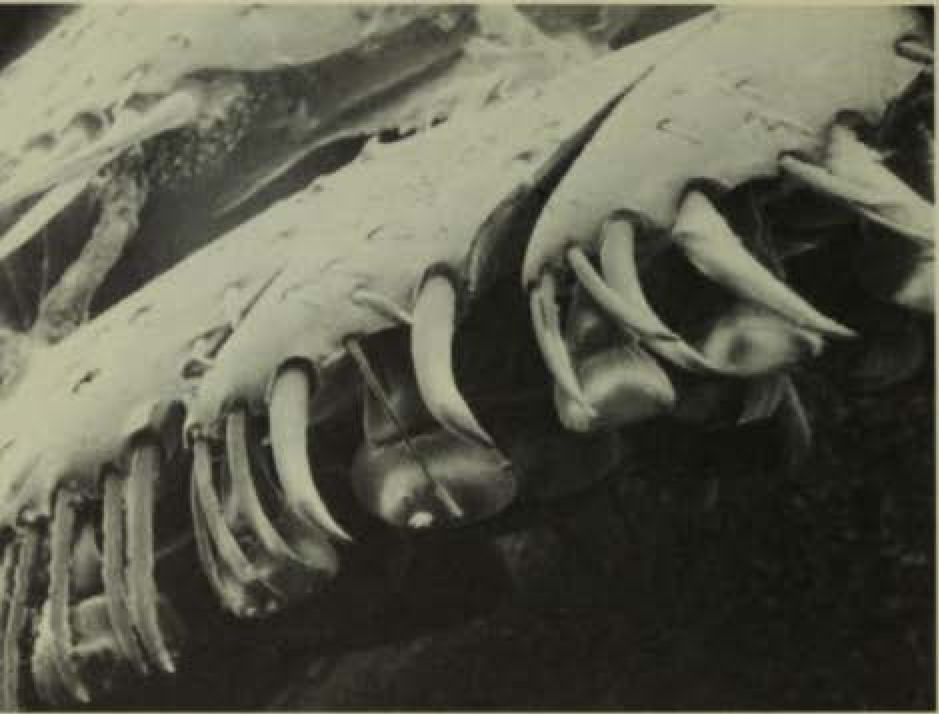

U. S. Department of Agriculture

Side view of the tarsus of the diving beetle shown in the preceding picture. Magnification is 560 times. Note the suckers and claws that are so well adapted for holding, and how the three segments are hinged, allowing them to curve about a rounded form such as the body of a fish. Such highly specialized adaptations took millions of years to develop to their present state of high efficiency.

The second, or mesothoracic, leg of a predacious diving beetle. Magnification is 260 times.

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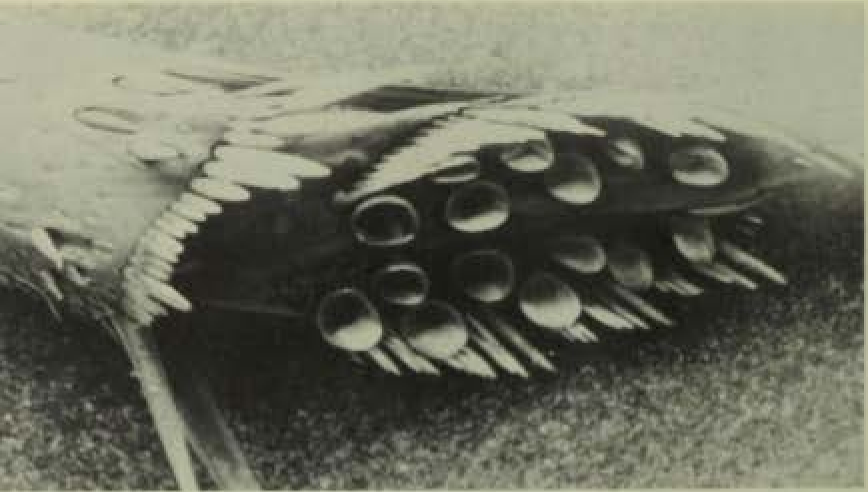
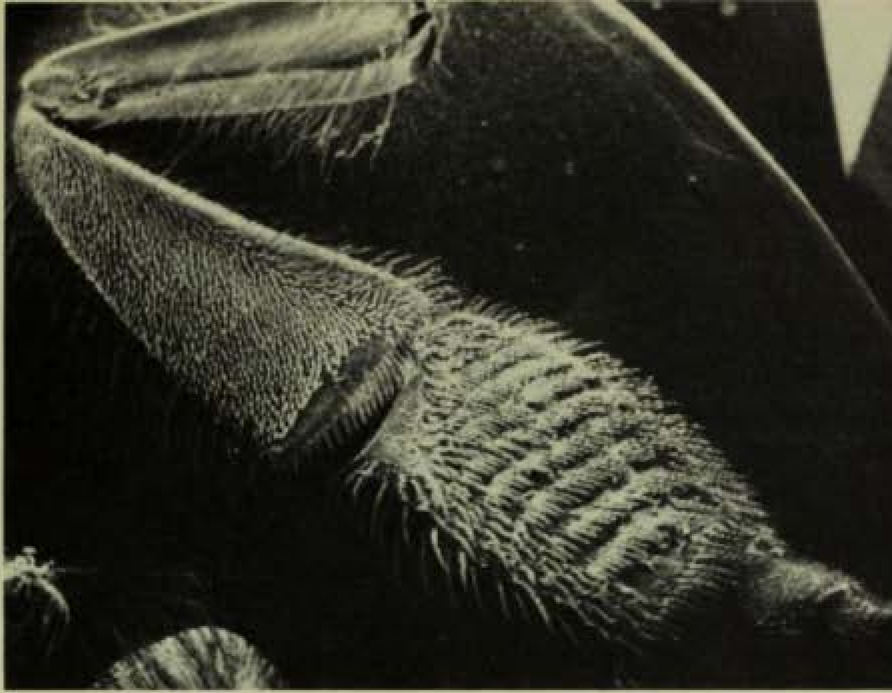




The leg of a worker honeybee, showing the pollen basket (the hairs on the edges of the second leg section from top, the tibia).

The front tarsi of the aquatic bug called the waterboatman are concave and fringed with long bristles. The hind legs are long and flattened like oars and also fringed. The oarlike legs propel the beetle with quick darting motions suggesting the manner in which a rowboat is propelled.

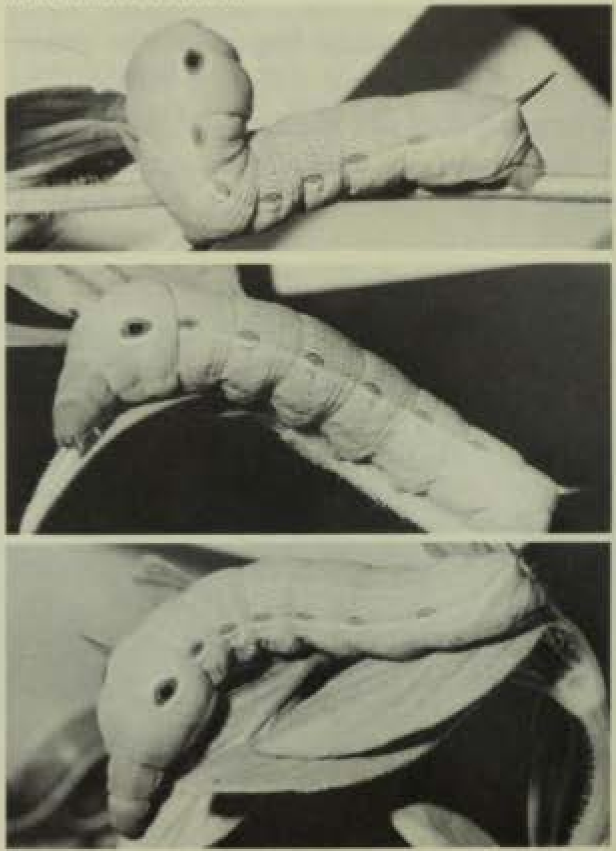
These are but a few examples of the diversity of the adult insect legs; but none of these highly specialized legs are really suited for crawling, and even less for creeping.

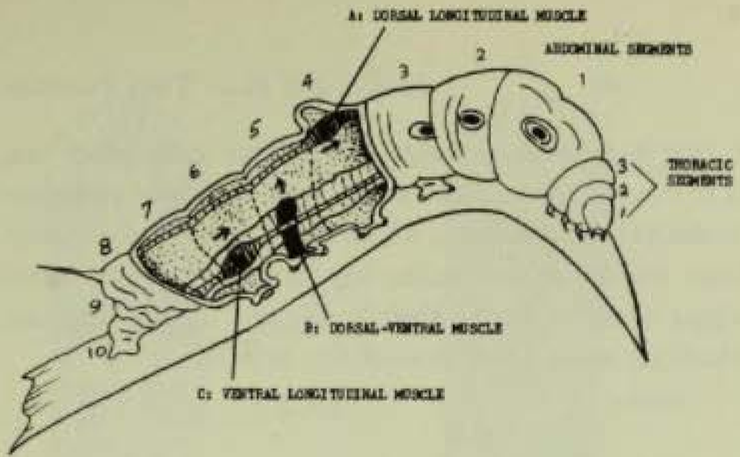
THE LEGS OF LARVAE

It is the locomotion of larval forms that is best described by "crawling." Insects that creep, such as the legless larvae of flies, push themselves forward by a wavelike motion, at the same time twisting the entire body to the side. Spines on the body, pointed in a backward direction, provide friction against the surface.

Adult insects move entirely by the use of their leg muscles, but caterpillars and other crawling insects are aided by the wavelike movements of the entire body. Anyone who has watched a caterpillar inch its way up a tree is certain to be impressed by the undulating crawling motion of its segmented body. The inside walls of caterpillars are lined with small bands of muscle that run across the many folds in the skin. They help to maintain a steady internal pressure, almost like bands of stretched elastic, and are called turgor muscles. If you puncture a caterpillar, it appears to shrivel in size because of the fast contraction of these muscles.

A hornworm larva crawling. At top, the forward segments are raised in a scanning position; the middle picture shows the thoracic and abdominal segment (first segment with a spot) in normal position; bottom, these segments in stretched-out position as the larva moves forward.





Crawling mechanics of a hornworm larva. The dorsal longitudinal muscle (*A*) of segment 4 contracts, folding the top of the segment. This is followed by contraction of the dorsal-ventral muscle (*B*) of segment 5, which lifts the proleg. Then follows the contraction of the ventral longitudinal muscle (*C*) of segment 6, which folds the bottom of that segment, drawing the proleg forward. This sequence is followed segment by segment, giving the larva an undulating movement.

The muscles that move the caterpillar are the dorsal (top) longitudinal muscle, the ventral (bottom) longitudinal muscle, and the dorsoventral (vertical) muscle, which is attached inside the prolegs.

As the insect moves forward, the dorsal longitudinal muscle of one segment (*A* in the picture) contracts at the same time as the vertical muscle immediately behind it (*B*), which lifts the proleg. At this moment the ventral longitudinal muscle (*C*) pulls together the lower portion of the third segment, drawing the leg forward. The rest of the larva's body is kept sufficiently tense by the turgor muscles during the time the active part of the body is in motion.

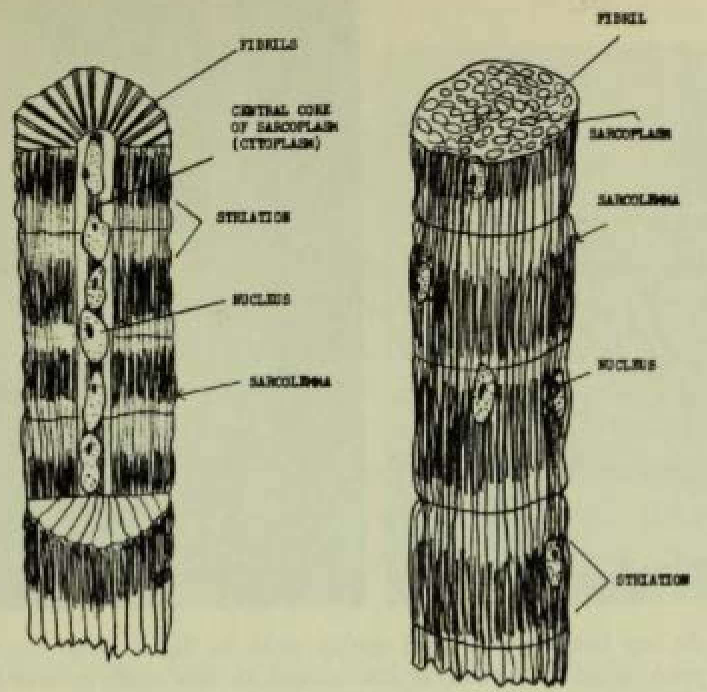
Most aquatic insects swim by moving their legs on opposite sides of their bodies in an arc, and simultaneously, so that the forces on each side balance each other out, as in rowing a boat. An exception is the water scavenger beetles (*Hydrophilidae*), which move the legs alternately. Some insects do not utilize legs at all. Mosquito larvae wiggle along by flexing their bodies and their taillike fins, which are made up of rows of fine bristles.

LEG MUSCLES

Leg movement is controlled by two types of muscles. Extrinsic (outside) muscles arise in the thorax and attach to the coxa of the leg. They function to move the entire leg. Intrinsic (inside) muscles lie wholly within the leg and run from one segment to another. Intrinsic muscles are paired antagonistic muscles—that is, in whichever direction one muscle moves a leg segment, its antagonist moves it in the opposite direction.

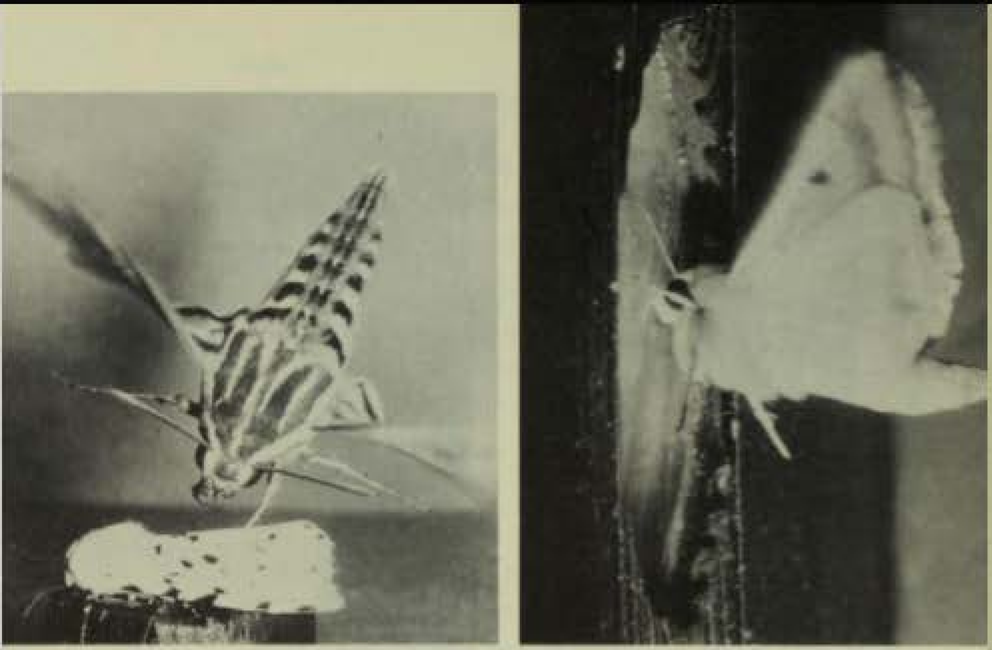
Insect appendages are moved by muscle of different cellular forms. The muscle is made up of large fibers that parallel each other side by side in bundles. Each fiber is actually a long cell, with many nuclei, that runs the length of the muscle. The cytoplasm of a fiber is called sarcoplasm. Within the sarcoplasm of each fiber are much smaller fibers called fibrils. Fibrils extend the entire length of the muscle fiber. The arrangement of the fibrils differs and there are considered to be four types of insect muscle cells.

Under the microscope muscle is seen to have alternating light and dark bands called striations (striated muscle). Two types of striated muscle are found in insect legs. In adult bees, wasps, and flies the small fibrils that are embedded in the larger fiber are arranged in flat bundles that radiate from a central core of sarcoplasm. The sarcoplasm contains a row of nuclei. This type is called "tubular" muscle. The second and most common type of leg muscle is formed of fibrils laid down in irregular arrangement in each fiber. The fiber is sheathed in a tough membrane called the sarcolemma. The nuclei of the sarcoplasm are directly beneath the sarcolemma membrane or are scattered throughout the sarcoplasm.

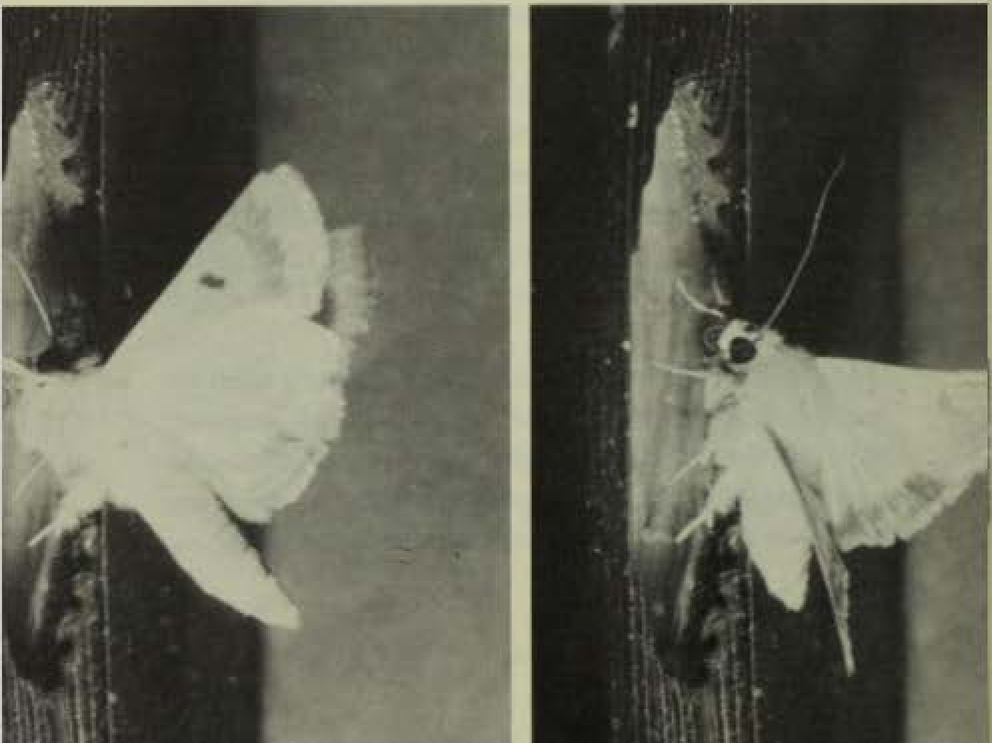


Two types of muscle fibers from insect legs. Left, a single fiber from the leg of a honeybee, showing regular arrangement of fibrils. Right, a single fiber from the leg of a May beetle, with irregular fibrils. (Modified from Wigglesworth.)

Muscles are inserted in the cuticle by different methods —some directly in the inner surface of the cuticle, some by specialized fibrils, called tonofibrils. The tonofibrils might be compared to tendons of insertion in the vertebrates. Muscles are attached to the integument at both ends, cross-



At top left, a white-lined sphinx moth in flight. Note the high pitch (angle of attack of the wings) in this moth in making a sharp turn. The legs are thrown wide and upward, acting as stabilizers in flight. The other three pictures show a corn earworm moth landing on a vertical surface. At top right, the prothoracic legs are raised across the eyes just before landing. At bottom, left to right, the legs touch the surface just below the eye, and then the moth stands at alert position, ready for takeoff if necessary.



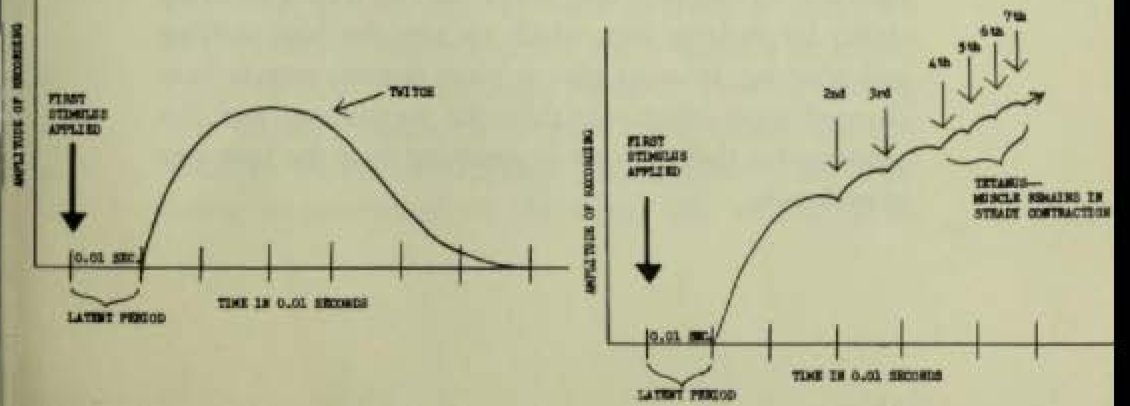
ing various joints so that as they function they move one segment of the appendage in relation to another.

We have discussed legs mainly in relation to walking or swimming, but they are also useful to the insect in flight. High-speed photographs of moths in full flight show that they use their legs as stabilizers. In a sharp turn the legs are thrown out and curve upward, keeping the body essentially level. This is in contrast to birds that keep their legs pulled up tightly in fast maneuvers. In landing, a moth uses its prolegs as buffers, raising them horizontally in front of its face when coming down on a vertical surface.

RESPONSE TO ELECTRICAL STIMULUS

Experiments throw light on the speed of nerve impulses and the responses of muscles. As in vertebrate animals, the striated muscle of insects responds to a small current of electricity with a contraction or twitch, which may last from 0.10 second to five seconds, depending on the species. When a current is applied to such muscle, however, there is a pause of variable length (approximately 0.010 second

Left, recording of the muscle twitch of an insect's leg after electrical stimulus, showing the latent period of 0.01 second. Right, recording of a successively stimulated insect-leg muscle, showing the cumulative effect: tetanus, or steady contraction, after seven externally applied shocks.



to 0.050 second) before the muscle responds by contraction, after which it relaxes.

If a second or third shock is applied during the pause, the contraction, when it comes, is increased as a result of each shock, and the extent of it is greater, as shown by the peak on the recorder. If the rate of electrical stimulation is stepped up, a point is reached where no relaxation is possible and the contraction becomes fixed in a steady state called tetanus.

Chapter Four

How Insects Fly

The evolution of insects differs from that of other flying animals in that their wings have been added to their earthbound legs. Such is not the case with birds and bats, which have lost the ordinary use of their front legs as these evolved for flight. The thorax of the insect has evolved to provide the mechanism for insect flight, but not at the expense of its ability to move the legs also. The praying mantis is an excellent flier, but it has not traded its flying ability for its front legs, which are used for both walking and grasping. It seems that in some respects insects have changed more effectively than the vertebrates, and this accounts for their success in surviving over the vast ages of evolution.

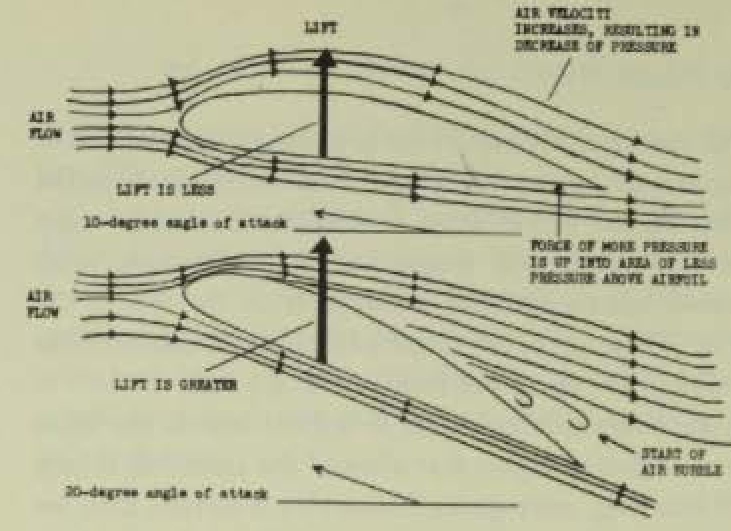
All insects, of course, do not have wings, and many have wings modified into other structures. Fossil insects from the Carboniferous period (two hundred million years ago) have fully developed wings, but they also have small flattened lobes projecting sideways from the top of the thorax. These are called tergal lobes and it is believed that the wings have developed from just such lobes.

Some scientists think that in ancient insects the lobes served as gliding organs that allowed the animal to launch itself into long, steep glides. If this idea is correct, then we may look at these lobes as true airfoils, or fixed wings. In order to understand how insects fly we must first understand the principles behind the working of an airfoil; for the modern insect wing is, after all, a movable form of such a structure.

BECOMING AIRBORNE

An airfoil is that portion of a flying object that produces lift. The wings of an airplane are fixed airfoils, those of birds and insects movable airfoils. The forces that act on the wings of a plane are the same as those that get a kite airborne.

The lifting action of a wing is explained best by Bernoulli's principle. This states that the pressure of any fluid stream, whether liquid or air, is least where the velocity is greatest, and the pressure varies inversely as the square of the velocity. Efficient airfoils are designed with curved upper surfaces and flat under surfaces. Thus air flowing over the upper surface is forced to travel farther and as a result its velocity is increased. This increase causes a decrease in pressure above the wing. The air that flows



Comparison of a 10-degree angle of attack (*top*) and 20-degree angle of attack of a conventional wing (airfoil). As the angle increases, the lift increases, since the air is forced to flow farther and faster above the wing, thus creating a partial vacuum. At too high an angle of the airfoil, air would "burble" back over the wing and force it down into a stall.

beneath the wing has less distance to travel and is slowed up slightly, resulting in an increase in the air pressure on the lower surface of the wing. The greater pressure below forces the wing upward into the region of lesser pressure (partial vacuum) above. The total lift produced is equal to the difference between the two pressures.

WING LOADING

The lift that is produced by each square foot of wing surface is called wing loading and is given in pounds per square foot for airplanes. The wing loading of an airplane may range from six or seven pounds per square foot for small planes to 25 pounds per square foot for larger, speedier planes. At sea level the atmospheric pressure is over a ton per square foot, so that only a very slight difference between pressure on the upper and lower surface of a wing is required to produce lift. The table shows the wing-load ratios for several species of moths. Wing loading for these insects was found by getting their weight in grams and dividing the weight into the total area of the front and hind wings, as measured in millimeters. As we see, the corn earworm moth and fall armyworm moth (members of the noctuid family) have a much higher wing-load ratio than do the larger-bodied sphingid group—the beautifully patterned sphinx moths.

Because the sphinxes have heavy bodies and thin, tapered wings, they more closely resemble the faster swept-winged jets. Since they have a lower wing-load ratio they must maintain a higher speed than noctuids (that is, increase the velocity of air flow across the wings)

Wing-load ratios and lift of several moth species at three different degrees of wing pitch. (Courtesy Entomological Society of America.)

Species	Sex ♂=m. ♀=f.	Weight (g)	Wing load ratio	Lift in grams at indicated angle of wing pitch 3°	6°	12°
corn earworm moth	♂	0.107	8.0	0.118	0.168	0.249
	♂	.226	4.1	.131	.186	.281
	♀	.161	4.7	.108	.150	.232
	♀	.239	4.4	.154	.218	.327
	♀	.279	4.0	.158	.222	.336
Average		.202	5.0	.134	.189	.285
fall armyworm moth	♂	.140	5.6	.113	.159	.241
	♂	.139	5.6	.113	.159	.241
	♀	.156	5.9	.131	.186	.277
Average		.145	5.7	.119	.168	.253
sphinx moth	♀	.628	2.6	.236	.331	.504
white-lined sphinx	♂	.600	3.7	.322	.458	.681
	♂	.322	6.6	.313	.436	.654
	♀	.660	2.9	.276	.386	.581
	♀	.853	2.6	.336	.472	.708
tobacco hornworm sphinx	♀	1.199	4.2	.721	1.017	1.525
	♀	1.604	2.6	.617	.872	1.307
satellite sphinx	♀	1.726	3.0	.767	1.076	1.616
Average		.949	3.5	.448	.631	.947

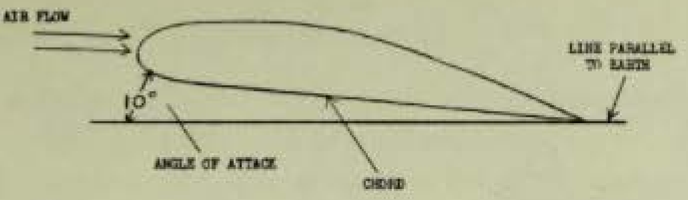
to maintain enough lift to remain airborne. The noctuid moths with their lighter bodies and larger wing surfaces fly at slower speeds and are more maneuverable than the fast-flying sphinxes.

The same comparison can be made for birds. The action of air on the wings of moths is essentially the same as that upon wings of birds if we consider them as airfoils. There is an important relationship among birds that also shows up in insect aerodynamics. High relative wing area in an order of birds signifies a light-weight species with a relatively slow, uneven flight; but low wing area usually indicates heavier birds with swift, direct flight. Thus the light-bodied noctuid moth, averaging 5.4 in wing-load ratio, can be compared with certain perching birds, such as sparrows, for which the wing-load ratio of 22 species averages 4.5. In contrast, the sphingid moths, with a 3.5 ratio, can be compared with the falcons at 2.6. The classical naturalist will readily agree that the swift, direct flight of the falcon and the sphinx moth will have much in common, whereas the corn earworm moth is more like the sparrow, dodging among the cornstalks.

ANGLE OF ATTACK

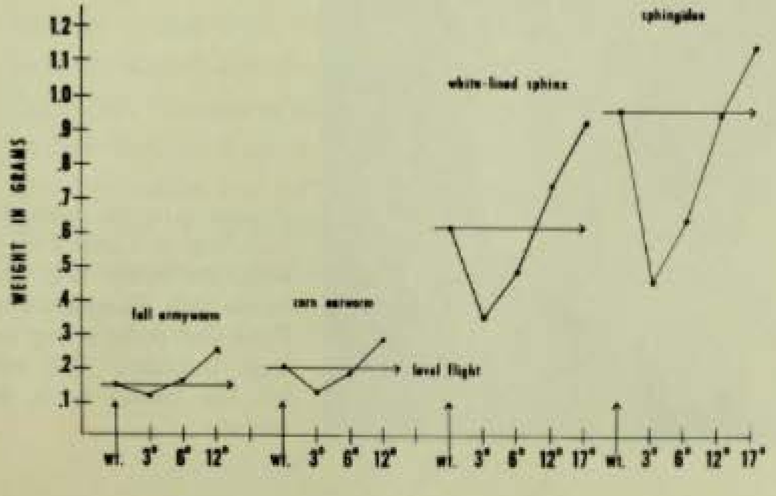
Another aeronautical term that must be considered when studying the airfoil is the "angle of attack." The flat bottom of a wing is called the chord and this term is applied to the distance from the leading edge to the trailing edge of a wing. The angle of attack is the angle between the chord and the horizontal flight path of the flying object.

A basic principle of flight states that the lift increases in almost direct proportion to the increase in the angle of attack up to a certain angle known as the angle of maximum lift (also called the stalling angle). At too great an angle, air, instead of flowing smoothly over an airfoil, starts to burble, so that the stalling angle may be considered the "burble point." Level flights may be attained at the point where lift, depending upon the angle of attack, overcomes the weight of the flying object.



The chord of a conventional wing (airfoil) is the straight-edged bottom of the wing. The angle of attack is the angle between the chord and an imaginary line parallel to the earth.

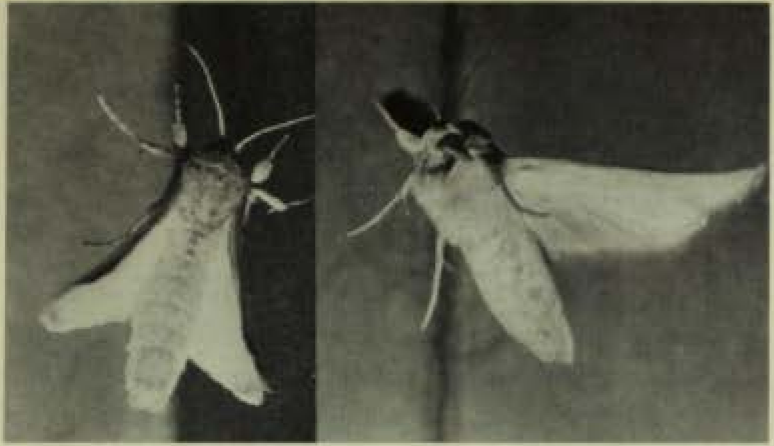
Relationship between the weight of four different species of moths and lift for various angles of attack. The arrows point to the average body weight for each species, and each point is the average calculated lift in grams for each angle of attack at 10 miles per hour. Points below the line of level flight fall below the maximum lift needed to maintain flight. The heavy-bodied sphingid moths would average at least 12 degrees for a flight speed of 10 miles per hour, whereas the light-bodied fall armyworm moth would stay airborne at six degrees.



Among moths, level flight takes place at a much lower angle for the light-bodied moths with high wing-load ratio—for intance the fall armyworm—than for heavy moths with low wing-load ratio. At 10 miles per hour noctuids can remain airborne with a 6-degree angle or less, but the heavier-bodied sphingids with less wing area in proportion to weight require at least a 12-degree angle of attack. Large-bodied sphingids at 10 miles per hour, and a 12-degree pitch within a single instant of flight time, would actually be below the stalling speed. For instance, one large satellite sphinx weighed 1.726 grams and had a wing-load ratio of 3. Such a moth at 12 degrees has a lift of only 1.616 grams.

We must realize that such measurements are valid for and calculated for only one instant during flight and at one speed, so that it is only at this particular instant and angle of attack that the moth could be considered below stalling speed. As the speed of the moth increases, the angle of pitch may decrease, keeping the balance between stalling speed and degree of pitch of the wing. The noctuid moths can maneuver better in tight places than sphingid moths, mainly because of the greater wing-load ratio, but also because they are smaller and beat their wings more rapidly.

A corn earworm moth doing a back loop in a cage four inches wide, ten inches long, and ten inches high. This would equal a Piper Cub doing a loop inside a large cathedral. The moth at left has landed on a vertical surface.



A fall armyworm moth in flight. At left it is climbing in an outside loop. Note how the legs are thrown out for stabilization and the wings are flexed, so that the curved part of the wing is on top, increasing the lift. At right the wings are on a downstroke, curving up at the tips. The hind wing is pulled forward under the forewing, decreasing the total surface area of the wing at high speed.

The insect wing is not just a fixed airfoil but rather is something like a helicopter blade of changeable pitch. It does not flap like a bird's wing but vibrates at high frequencies, and the pitch and angle of attack change continually during these vibrations. Insect wing movement is so complicated and the shape of the wing, because of its flexibility, changes so drastically that wing motion cannot be described by a simple mathematical formula. The high-speed vibration and twisting movements require of an insect almost unbelievable control of its muscles and an extremely efficient method by which the wings are attached to the body.

HOW WINGS ARE ATTACHED

An insect's wings are coupled to its body by a series of complicated plates, but unlike the arrangement for the legs and other appendages, there are no muscles connected inside the wing itself. The wings consist of a thin upper and lower membrane separated by supporting rodlike structures called wing veins. Taxonomists—experts in classifying animals—use the arrangement of these veins to separate families of insects. The veins usually have a specific and unique arrangement in each classification group.

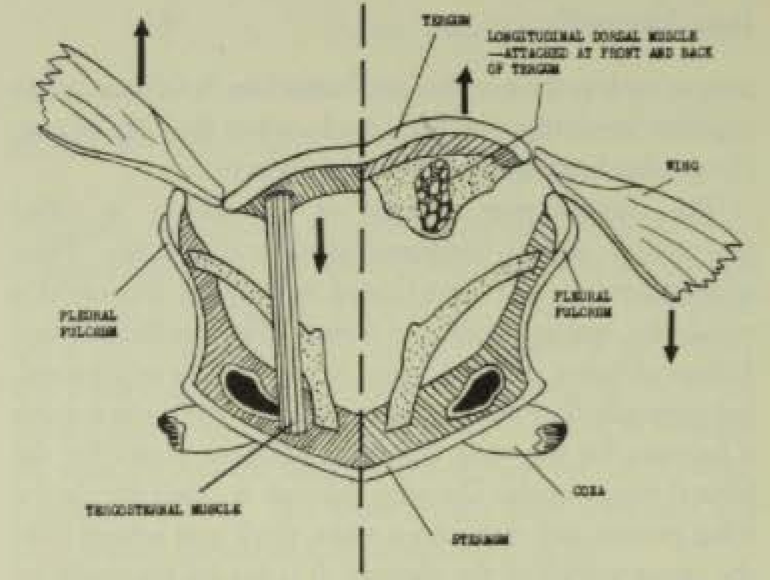
The coupling plates that hinge the wings to the thorax are supported by a thin membrane. The plates are thus quite flexible and are arranged in relation to each other in a way that allows the vibrating wing to pivot freely. All these plates are called the axillary plates, and they are developed only in insects that fold their wings horizontally over their backs, as in the case of moths and flies. Some

The complicated hinge that attaches the front wing (N) of a corn earworm moth to its body is made up of a number of separate sclerites, or hard plates (F to L). A to E are the sclerites of the insect's thorax; M is the tube that supplies air to wing tissues.

insects, such as the mayflies and butterflies, hold their wings together vertically over their backs when they are at rest. Dragonflies keep their wings extended at rest.

The wing-bearing segment of the thorax is called the pleuron and is composed of pleural sclerites. Their arrangement is very complicated and shows considerable variability among families of insects. The mechanical usefulness of many of these forms is not easy to understand, but generally they are arranged in such a way as to furnish a fulcrum for the wing and as attachment plates for the pleural wing muscle. The wing fulcrum is called the pleural wing process and resembles a short, thick arm arising from the upper margin of the pleuron. It is braced internally by a ridge that extends from the wing process to the coxa. The top, or dorsal, part of the wing-bearing portion of the thorax is called the tergum. It lies against the wings and is hinged to them by the first and fourth axillary sclerites.

A dragonfly on barbed wire. Note the wing position, which differs from that of butterflies, moths, beetles, and mayflies when they are at rest.



Insect-wing mechanics. Right side: the wing is depressed as the longitudinal dorsal muscle contracts, warping the tergum and arching it upward, which forces the wing down on the pleural fulcrum. Left side: the wing is elevated as the tergosternal muscle contracts, pulling the tergum downward and forcing the wing up on the pleural fulcrum.

WING MOVEMENT

A completely accurate description of any one insect species' wing movement would be too complex to take up here. In general, the wing stroke consists of an upstroke, a downstroke, a forward and a rearward movement; and, as we know, a partial rotation or change of pitch. Both lift and forward motion are produced by the rapid movements of the wings. Although forward movement is important, most insects can hover (some even fly backward or sideways), and airflow over the wings is not the only thing that causes lift.

The winged insect, although originally a glider, more closely resembles a helicopter than a fixed-winged airplane.

However, the wing movements are of course not rotary, but vibratory. The power for these rapid vibrations comes principally from two sets of muscles in the thorax. They are the longitudinal dorsal muscles which on contraction serve to draw the wings down, and the tergosternal muscles which on contraction lift them. In detail, the longitudinal dorsal muscles contract and arch the wing-bearing terga upward by pulling against each end where the muscle is attached; this in turn deflects the wings downward on the pleural fulcra. The tergosternal muscles are attached to the top lateral edge of the tergum and on the bottom in front of the coxae. When they contract they depress the tergum and lift the wings on the pleural fulcra. The tergosternal and longitudinal dorsal muscles are antagonists and indirectly impart the vibrating motion of the thoracic tergal and pleural plates to the nonmuscular wings.

RESILIN, THE "RUBBER" OF INSECTS

Resilin is a part of the elastic hinges of the insect. It is a rubber-like protein discovered by Dr. Torkel Weis-Fogh; its name comes from the Latin *resilire,* "to jump back." It was originally believed that the recoil of the insect wing was due solely to the elastic movements of the boxlike thorax as the muscles pulled in and out. With the discovery of resilin, however, at least one-third of the energy was shown to be stored in the wing hinge itself. This highly efficient substance was found to come from the epidermal cells. It is springlike in the way it stores and releases mechanical energy. Dr. Weis-Fogh discovered this remarkable insect "rubber" by observing the recoil of the forewings in the isolated thorax of a desert locust. After he removed the wing muscles and dorsal tergal plate, there remained considerable recoil in the wing hinges themselves. A simple chemical color test later confirmed the presence of the substance in many parts of the insect cuticle. Parts of insects that contain resilin can be stained deep blue, and this technique has shown it up in such widely different parts as wing hinges and the margins of abdominal tergites. This remarkable material contributes to the overall elasticity of an insect's exoskeleton.

FLYING HEIGHT

The evolutionary development of highly efficient wings has contributed to the far-reaching spread of insect species into a great many different environments. Many species are known to make long dispersal or migratory flights. It is difficult to attach tags to or visually follow migratory insects as we do birds. Little is known of their dispersal and migratory routes and still less of the heights at which they fly. Certain species have been taken at high altitudes by trap nets mounted on the wings of airplanes. Are these insects blown to such heights or are they actually flying, as in the case of migratory birds? In one experiment I collected corn earworm moths as high as 1,000 feet by attracting them to light traps mounted on a television tower of that height. They were shown to be actually flying higher than the traps, as the lights were mounted inside a cone and visible only from above. They were also observed coming directly to the trap at a height of 1,000 feet at night. When we consider that the earworm moth weighs less than one gram and lives an average of approximately 10 days as an adult flying moth, we can appreciate the remarkable flight powers of such an insect.

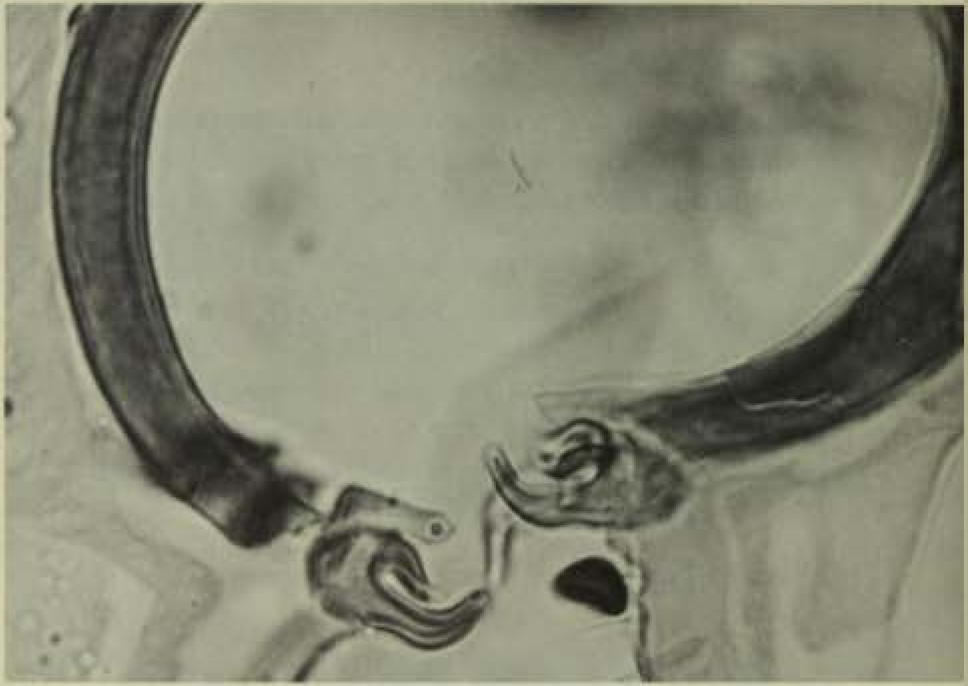
Chapter Five

In Search of Food

The parts of the head that surround the mouth of an insect are used in feeding. They vary as much as the actual methods of taking in food. Though the shapes of these appendages are complicated, all insect mouth parts are thought to have evolved from a few common simplified structures. The feeding organs of a stinkbug, which sucks plant juices, do not physically resemble those of a grasshopper, which chews plant tissue. Since they evolved from similar mouth appendages, however, they have common names.

There are six generalized types of mouth parts:

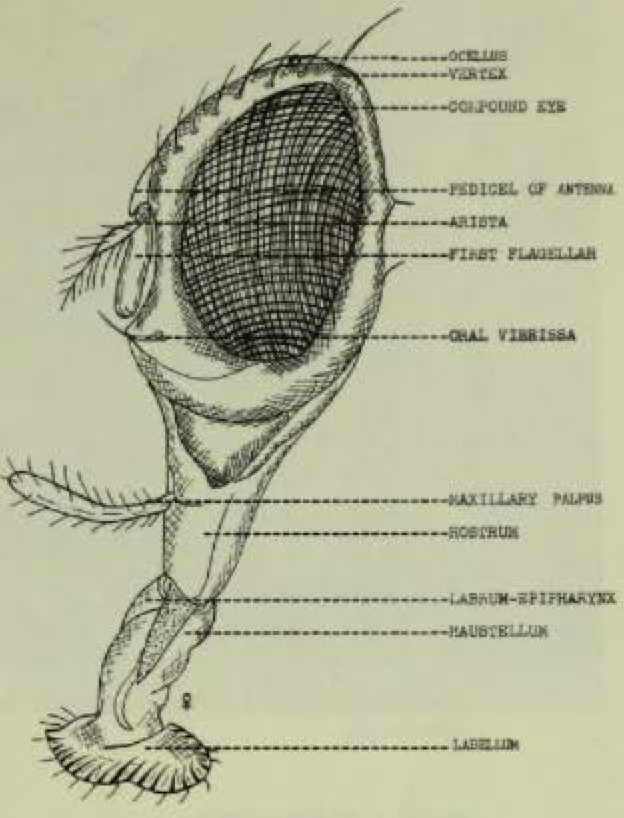
TYPE	FUNCTION	INSECT EXAMPLES
chewing	grinds solid food	beetles and grasshoppers
piercing-sucking	sucks juice or blood	aphids and mosquitoes
siphoning tube	sucks nectar	moths and butterflies
sponging	sponges up liquids	houseflies
cutting-sponging	cuts and sponges	horseflies and blackflies
chewing-lapping	chews and laps up liquid	wasps and bees



Cross section of the two galeas of the corn earworm moth's proboscis. The galeas, or separate halves of the proboscis, are fastened together with the hooklike locking mechanism shown.

THE MOTH

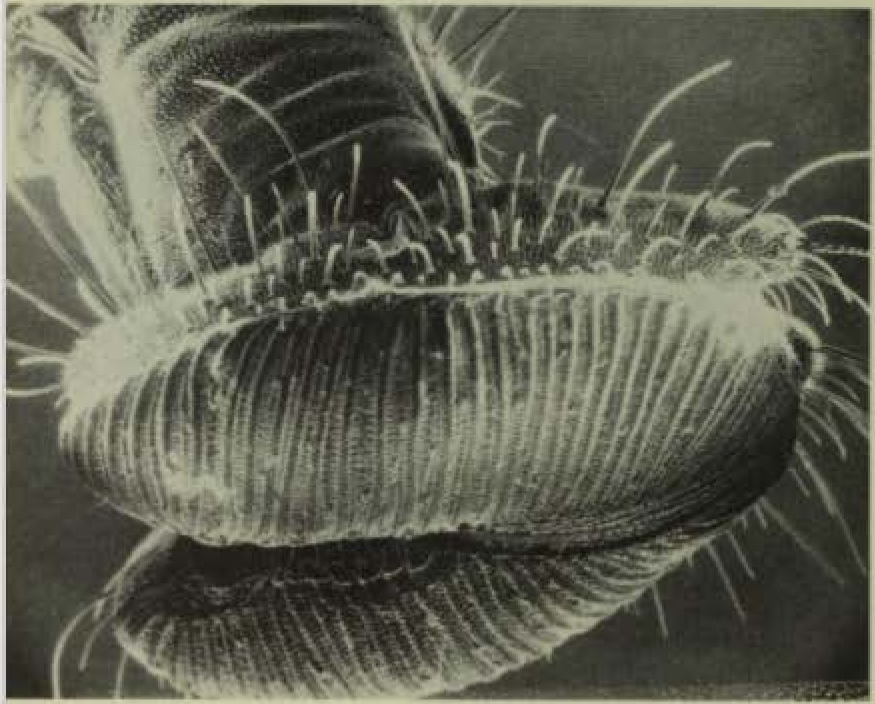
Most of these unique types of mouth parts have developed from the chewing type. Even in those as specialized as the siphoning mouth part of a moth, rudimentary mandibles are found. The long tubelike proboscis of the mouth is actually composed of two interlocking halves, each called a galea. It is a remarkable flexible structure and is kept in a coiled position beneath the moth's head. During feeding the moth uncoils the long proboscis and inserts it into the portions of the flower that contain nectar. A sucking pump located below the brain pulls the nectar into the esophagus.



The head of a housefly from the side, showing the labellum that sponges up fluid foods.

THE HOUSEFLY

The sponging mouth parts of the housefly are extremely complex. As in the moth, the mandibles are not used, but the lower lip (called the labium) is formed into a heavy, hollow food channel and ends in a spongelike structure called the labellum. A salivary duct follows the food channel to the labellum. Liquids or solids that are easily dissolved in saliva are sponged up with the labellum. Bacteria and fragments of disease-infected manure, to which the housefly is attracted, are easily picked up by this type of mouth part. For this reason the housefly is an effective carrier of many dangerous diseases.



The labellum of a housefly as seen by the scanning electron microscope.

THE MOSQUITO

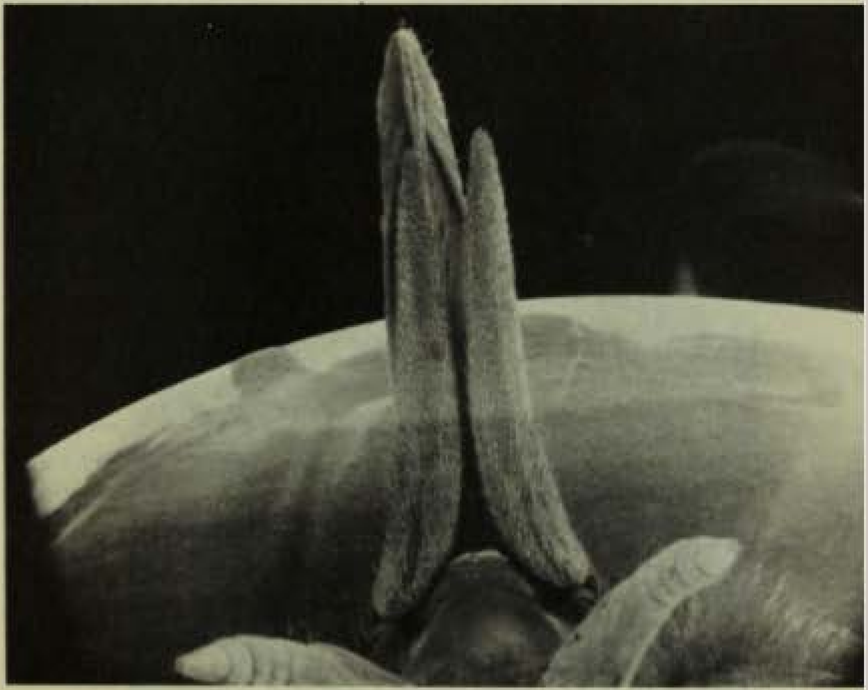
The mouth parts of the mosquito are modified for piercing and sucking. In species such as this the mouth parts, including the specially adapted mandibles, are long and quite slender. They interlock to form a long, hollow needle. The labrum, a platelike sclerite attached above the mouth parts of insects, forms a heavy sheath that holds the needle rigid.

THE HORSEFLY

Horsefly mandibles are formed into structures like sharp knives. These, along with a pair of long, probing stylets,

The tip of the piercing-sucking mouth part of the stable fly. Magnified almost a thousand times, this organ, which pierces the skin, looks quite blunt. Under the same electron microscope a needle also looks blunt.

The cutting mouth parts of the horsefly.

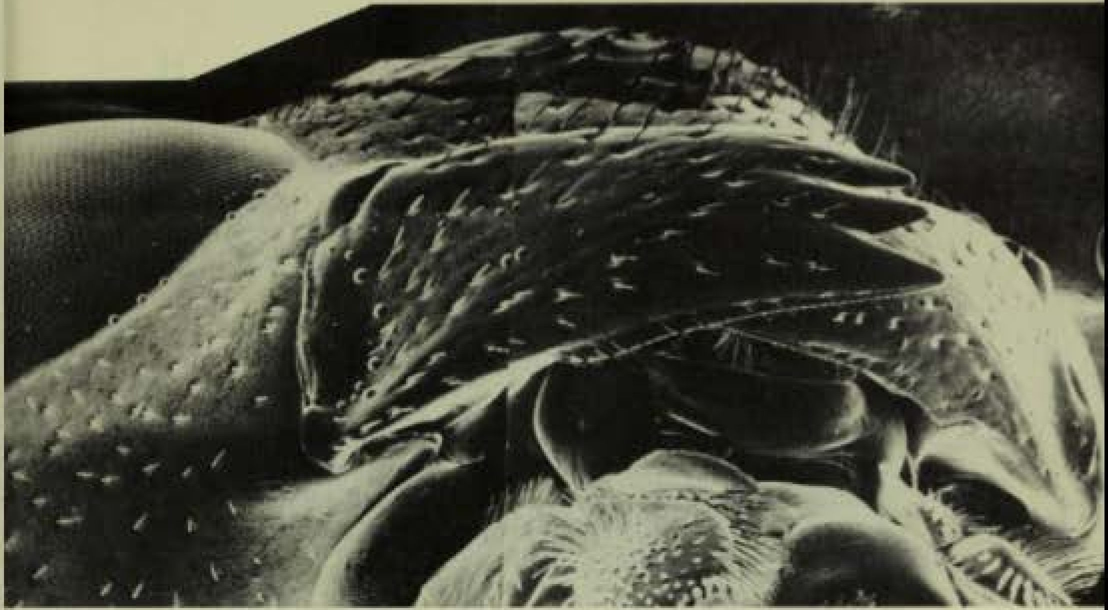


cut and tear the flesh of mammals. A labium, much like that of the housefly, collects the freely flowing blood from the cut. Small buffalo gnats, and blackflies that annoy campers, have similar mouth parts. Their cutting bite can be quite painful. Like mosquitos, only the females suck blood. The southern buffalo gnat is a terrible pest to domestic animals. Swarms have been known to drive cattle into a frenzy, sometimes causing their death.

THE PAPER WASP

The chewing-lapping mouth part is found in both bees and wasps. In this type the mandibles are the chewing type and are suitable for holding prey, molding wax or, in the case of the paper wasp, molding the paper-like materials used in the construction of their nests. These large, grayish structures seen hanging from woodland trees are worked into shape with the mandibles, using the fibers of much-weathered wood. An organ called the glossa forms a short channeled tube for taking up nectar from blossoms.

A close-up of the chewing-lapping mouth parts of *Polistes*, the paper wasp. The large overlapping mandibles with their toothed ends, seen just below the compound eyes, are efficient in molding the paper-like material (made of chewed wood fiber) used in building the nests.



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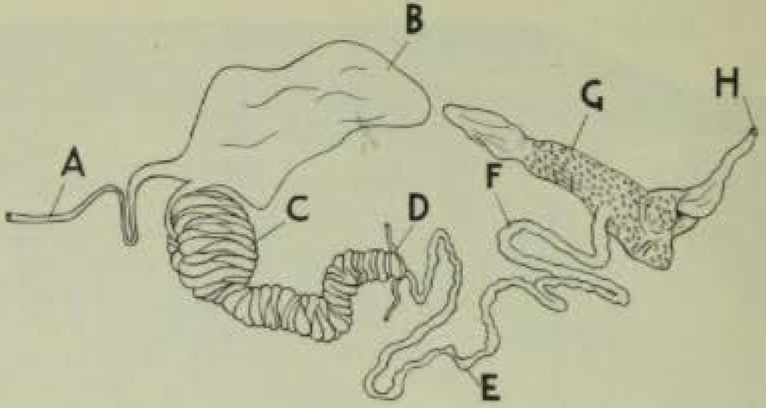
Another view of paper-wasp mandibles, photographed in two sections by the scanning electron microscope.

THE DIGESTIVE ORGANS

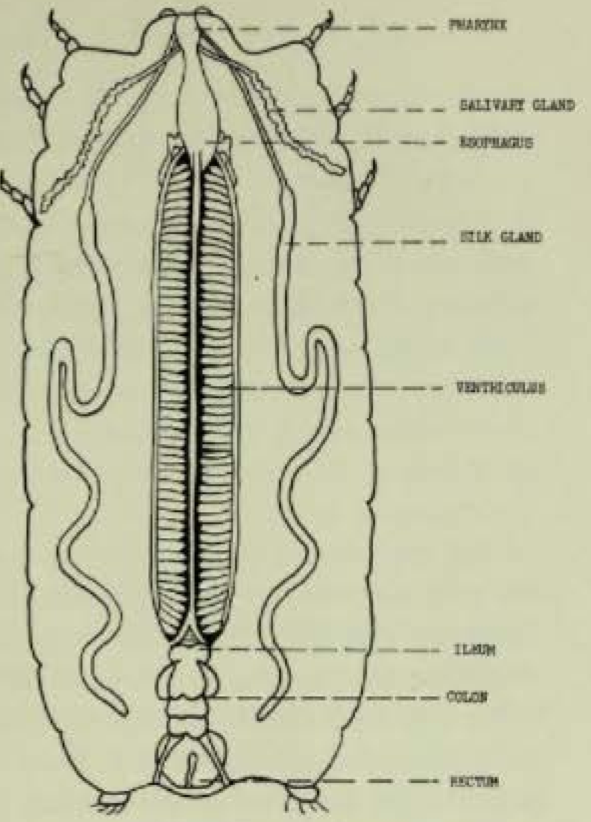
The tubelike digestive system of the insect is divided into three parts, each with its own physiological function. The first part is called the foregut; it takes in and temporarily stores food. This portion consists of the mouth and pharynx, which lead into an elongated, narrow esophagus. Following the esophagus most insects have a crop. In moths it is a large membranous sac that stores nectar. In



Digestive tract of a female corn earworm moth. *A*, esophagus; *B*, crop; *C*, ventriculus, or stomach; *D*, area where the Malpighian tubules join the digestive tract; *E*, ileum, or small intestine; *F*, colon, or large intestine; *G*, rectum, covered with rectal pads; *H*, anus.

the larvae of moths and butterflies, however, it is hard to distinguish an organ that could definitely be called a crop, since there are such changes of form as the insect becomes an adult. This extreme alteration in the digestive tract, and in other organs, takes place during metamorphosis by a process called histogenesis—the formation of adult tissue and organs after the larval organs have degenerated.

The next portion, the midgut, consists of an organ called the ventriculus (the stomach), followed by the ileum, or so-called small intestine, and the colon, or large intestine. There is no distinct separation between the ileum and the colon. The midgut is the area of digestion and is separated from the crop by a valvelike structure called the proventriculus. Six finger-like digestive glands called gastric ceca are attached behind the crop. The final portion, or hindgut, excretes waste products. It consists of the Malpighian tubles, rectum, and anus. In most insects the rectum is covered with small rectal pads which reabsorb water, salts, and amino acids from the urine.



Digestive tract of a hornworm larva.

MALPIGHIAN TUBULES

These excretory tubes were named after the great Italian anatomist Marcello Malpighi, who first described them in the silkworm in 1669. They occur in almost all insects and may vary in number from two to 150. The cockroach has 60 and the moth six. In species which have few in number they are extremely long. They join the intestinal tract at the junction of the ventriculus and ileum. Malpighian tubules collect and excrete uric acid and other harmful waste chemicals, much like the kidneys in human beings.

FOOD INTO ENERGY AND TISSUE

A tremendous variety of organic material is taken by insects as food, and their digestive systems are modified in different ways. Some insects digest materials in fluid form; others, such as termites, must break down and digest cellulose, a carbohydrate that is indigestible by mammals. Plant foliage, wood, nectar, blood, skin, decaying matter, dried grains, and other insects are but a few of the food preferences of insects.

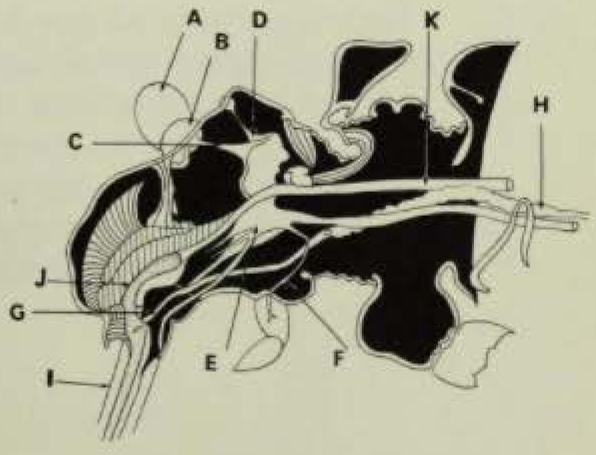
The chemistry of digestion in insects generally follows the enzymatic reactions that are found in all animals. An enzyme is a complex organic chemical that speeds up the transformation of food in the digestive tract. With the aid of enzymes, complicated organic materials are reduced to simpler basic substances. The basic foods are sugars, amino acids, fatty acids, and a whole series of various soluble substances that are easily absorbed by the digestive tract. Proteins are broken down into amino acids, and fats to free fatty acids and glycerol. Foods such as wool, hair, or feathers, which are digested by skin beetles, are chemically reduced in the midgut and prepared for attack by special enzymes.

Carbohydrates such as cellulose are fed upon by termites, and also by the larvae of some beetles and wood-feeding cockroaches. In termites and cockroaches that eat wood, intestinal protozoa are responsible for the breakdown of cellulose. The digestive system of termites is modified and the hindgut contains a huge rectal pouch which is filled with many types of flagellate protozoa. The protozoa digest the particles of wood for the termite. This is an example of cooperation between an insect and intestinal organisms. The termite takes in the food and provides the proper micro climate for the protozoa to survive in. It also removes the metabolic wastes that would otherwise kill the protozoa. If the protozoa are experimentally removed from the rectal pouch, the termites will starve to death. Such dependence of two living organs, one upon the other, is called symbiosis. In this case we have an example of digestive symbiosis.

INSECT SALIVA

Digestion and the movement of food to the midgut is aided by salivation from specialized glands. The salivary glands of the corn earworm moth, which feeds on nectar, resemble a long entangled tube and are buried between the muscles of the thorax. The saliva is ejected from the tip of the proboscis, where it is mixed with the nectar and then drawn up into the pharynx by the sucking pump. These glands give off invertase, an enzyme that breaks down the carbohydrate nectar.

In most insects, saliva is mixed with the food before it is taken in. Chewing insects such as the grasshopper mix salivary enzymes with food in their mouths much as chewing mammals do.



Longitudinal cut through the head and prothorax of a corn earworm moth. *A*, pedicel, or second joint of the antenna; *B*, scape, or base of antenna; *C*, antenna nerve; *D*, optic nerve of ocellus; *E*, prothoracic ganglion; *F*, prothoracic leg nerve; *G*, opening of salivary gland into mouth cavity; *H*, salivary gland; *I*, proboscis; *J*, pharynx and sucking pump (striped muscle above the pharynx); *K*, esophagus.

Blood-sucking insects do not produce digestive enzymes in their salivary glands, but rather an anticoagulin that prevents the blood meal from clotting, and plugging up their mouth parts.

In many insects the food-enzyme mixture is passed on through the esophagus to the crop, where it is stored and partially digested. The epithelial layer of the foregut (the esophagus and crop) is covered with a thin cuticular layer that prevents absorption of the partially digested food stored in the foregut. Complete absorption takes place only in the midgut. Insects have no mucus glands to lubricate and protect their digestive tracts as vertebrates do. The epithelial cells of the midgut are covered by a delicate membrane composed of chitin. This membrane forms a continuous lining that surrounds the food. Unlike the foregut lining, it lets through the digestive enzymes and food products.

GETTING RID OF WASTES

Excretion is the process by which the waste products of metabolism are removed from an insect or any animal. Excess nitrogenous wastes such as uric acid will do real damage if they are allowed to accumulate. Uric acid is the final product of protein breakup. As we know, the organs of excretion are the Malpighian tubules. The tubules are lined with large epithelial cells which project into the cavities of the tubes and practically close off the passage. These cells absorb the uric acid, and certain salts and other metabolic substances, from the blood. The waste products are discharged in a water solution into the digestive tract. Both the solid wastes of digestion and the liquid wastes of excretion are voided through the anus. When water is scarce, the uric acid, instead of being in solution, forms into crystalline spheres. They are present in the Malpighian tubules of insects starved for a long period of time. In some insects the Malpighian tubules have additional functions. In the larvae of certain beetles they are known to produce silk for the construction of the cocoon.

FINDING FOOD

The mouth parts of insects give us clues as to how they digest their food and what types of food they eat. To understand their food habits, however, one must observe their behavior as they go about their daily routine. For instance, if we observe certain ants closely, we are surprised to learn that some species are actually farmers. Ants are social insects. Many species are carnivorous and hunt for a living but it is the plant- and dairy-farming ants that have most unusual feeding habits. They could be compared to humans in that they have built a much higher social civilization than the hunting insects. Hunters are nomads, but farmers provide for the future and form the basis for an advanced social structure.

It is not surprising that in dry, hot areas, where insect food is scarce, there exist tribes of ants that are harvesters. The harvesting ants store seeds in underground granaries. In 1834 W. H. Sykes first described the storing of seeds by ants. Near Poona, India, he watched a species of Indian harvester ants collecting seeds from plants, and bringing other seeds, which had been flooded by rain, out of the

A corn earworm moth feeding on honeydew in a grass seed head. Note the tattered wings of this moth, indicating an old individual that has spent a considerable time flying in search of food.

nest to dry in the sun. The nests of these ants consist of flat storage chambers connected by long galleries. The worker ants collect the seeds; they remove the sheath and cast the chaff and empty capsules outside the nest.

Although the ancients referred in their writings to harvesting ants (Pliny, Aesop, Plutarch, and Virgil all mentioned these fascinating creatures), early eighteenth-century entomologists were skeptical. Unable to find harvester ants in temperate Europe, it remained for workers in India and America to prove the ancients correct. This is a good object lesson for those who believe that science began only after the Renaissance.

The real farmers among the ants are the fungus-growing ants. Some species, called leaf-cutting or parasol ants, are large, powerful insects that inhabit tremendous colonies. They are most often observed cutting half-circular pieces from the edges of leaves. They carry the pieces parasol-

style over their heads and follow one after another in single file along trails leading to their colonies. T. Belt in his interesting book *The Naturalist in Nicaragua*, first discovered their farming habits:

> Notwithstanding that these ants are so common throughout tropical America, and have excited the attention of nearly every traveller, there still remains much doubt as to the use to which the leaves are put. Some naturalists have supposed that they use them directly as food; others, that they roof their underground nests with them. I believe the real use they make of them is a manure, on which grows a minute species of fungus, on which, they feed; they are, in reality, mushrooms growers and eaters.

His extraordinary explanation was proven correct by later entomologists.

There are certain species of ants that tend aphids, or plant lice, as they are also called. These "nurse" aphids exude droplets of honeydew from the anus. Ants caress the aphid's abdomen, stroking it alternately with first one antenna, then the other. The aphid responds by exuding a large droplet of nutrient honeydew. In turn the ant protects the aphid; observers have often seen ants drawing predatory insects away from them. The nurse aphids trade food for protection, and the relationship is termed "mutualism." It has evolved to the degree that certain root-feeding aphids are completely dependent upon the ants. The ants remove earth from roots and provide the aphids with extensive underground chambers where they have easy access to their food. The aphids are confined underground and even placed on the roots by the ants and also moved by them. The aphids extract the sap from the roots and provide the honeydew for the ants. We might call such ants insect dairy farmers.

From these few examples one can understand the complexity of nutritional habits and get some idea of the many unique methods by which insects feed.

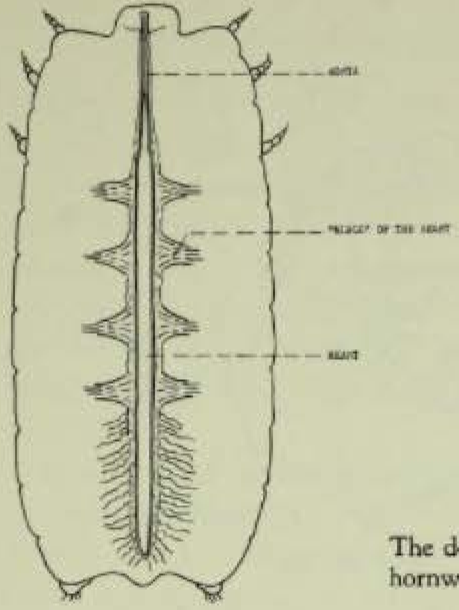
Chapter Six

The Unusual Blood and Oxygen Systems

The insect circulatory system is quite different from that of vertebrates, which is entirely enclosed in tubelike blood vessels. To understand what is called the "open system" of insects we must look at the way in which the body cavity is partitioned. The nerve cord runs along the bottom of the cavity, and the heart is at the top. Both are partitioned off from the central portion of the cavity by sheathlike muscular diaphragms.

THE DORSAL VESSEL

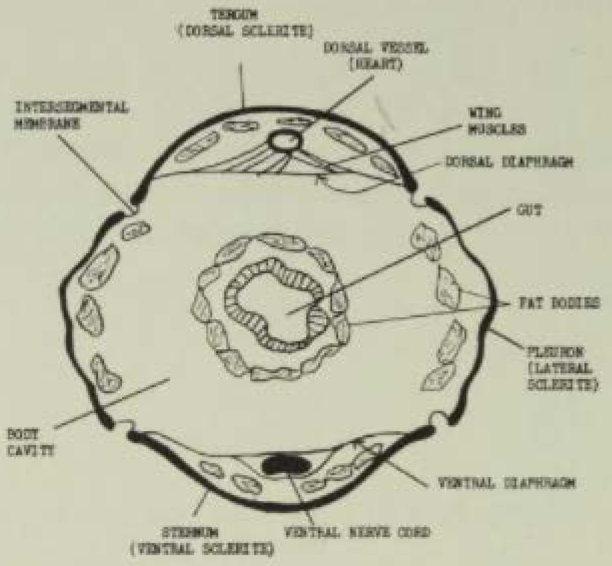
The dorsal blood vessel is made up of a front portion called the aorta and a rear portion, the heart. The entire structure lies beneath the dorsal body wall and is separated from the body cavity by the dorsal diaphragm. The aorta is a tube that carries the blood forward into the head.



The dorsal vessel, or heart, of a hornworm larva.

The heart, which is usually in the abdominal area, consists of a series of expanded chambers with small valvelike openings called ostia in the constricted area between chambers. Bands of muscle known as wing muscles are attached to the underside of the heart. They connect to the body wall on each side and form the dorsal diaphragm. The wall of the dorsal vessel is composed of spiral muscle fibrils which can contract.

Circulation takes place by the pulling in and relaxing of the dorsal vessel. During relaxation blood is drawn in through the ostia. Waves of contraction pump the blood forward into the aorta and out its open end into the head cavity. From this point the blood flows back into the body cavity, bathing the organs of the posterior portion of the body. This is not generally as hit-or-miss as it may seem, for in many insects the diaphragms in the abdomen help to direct the flow, and a partition down the middle of each leg insures that the blood enters it on one side and



Cross cut through the body of an insect, showing the separation of the dorsal vessel, or heart, and the ventral nerve cord from other organs by diaphragms.

comes out the other. In some cases there are additional tubes and pumps in the body.

BLOOD WITHOUT REDNESS

Insects have no red blood cells and thus no hemoglobin; the fluid is clear, greenish, or yellowish. There is no mechanism for absorbing oxygen in chemical combination. The blood, or hemolymph, is composed of a fluid (plasma) and four main types of blood cells. The plasma percolates throughout the tissues of the body carrying the suspended cells. As in vertebrates, digested foods are absorbed and transported to the tissues. Waste products are carried out to the excretory system for disposal. Although oxygen is not chemically combined in the blood, a certain amount

of it in dissolved form is present and is used by the insect's tissues.

There are several types of blood cells, generally called hemocytes. Hemocytes multiply throughout the life of the insect and vary in both appearance and use. Some "swallow" debris and bacteria; they are protective mechanisms and destroy foreign particles. This protective process is called phagocytosis. Others clump together and thus plug any wounds.

In addition to the hemocytes, insect plasma carries various inorganic chemicals such as chlorides. It is also rich in amino acids. Almost every known amino acid has been found in insect blood. In addition to nutrition and the other functions mentioned, the blood may be used for hatching a young insect from the egg and expanding its wings after hatching; for breaking the old skin at molting time; in forming connective tissue; and in changing certain metabolic chemicals.

DISTRIBUTING OXYGEN

Oxygen reaches an insect's cells by means of a complex network of internal tubes called tracheae. These branch into even smaller tubes called tracheoles. Tracheoles extend to the various tissues so that the oxygen is carried directly to the tissue cells. The gas diffuses into the tissue and meanwhile fresh oxygen is pumped in and out of the tracheae by balloon-like air sacs that connect to the tracheal system.

Tracheae are tubes leading from the ectoderm of the exoskeleton. They are lined with a membrane that is part of the outside cuticle. Under the microscope this lining is seen to be made up of a spiral thickening called a taenidium. The rings of the spiral help to keep the tube from collapsing inward.

The external openings of the tracheae are called spiracles. In some insects these are simple holes in the wall of the exoskeleton. In certain insects these openings are lined with hairs; in others they are covered with a sieve plate of small pores. The hairs and sieve prevent dust and water from entering the air tubes. Most land insects have valvelike closing mechanisms at the openings operated by muscles. Experiments have shown that the control of spiracle valves is dependent on the balance between oxygen and carbon dioxide. The length of time the valves stay open depends on the amount of carbon dioxide that has accumulated when they are closed, and this in turn depends on the amount of oxygen taken in. If the carbon dioxide content of the air is high the spiracles remain open. Open spiracles allow a good deal of water to escape and so are normally open for as short a time as is necessary to take in sufficient oxygen. Knowledge of the physiology of spiracle mechanisms is used to advantage in insect control. It is easier to kill insects by fumigation if the room is first flooded with carbon dioxide. The spiracles open and the fumigant poison quickly fills the tracheal system.

Scanning electron photomicrograph of the trachea in the antenna of a corn earworm moth. Note the spiral taenidium that forms the walls of the trachea. Magnification is 8000 times.
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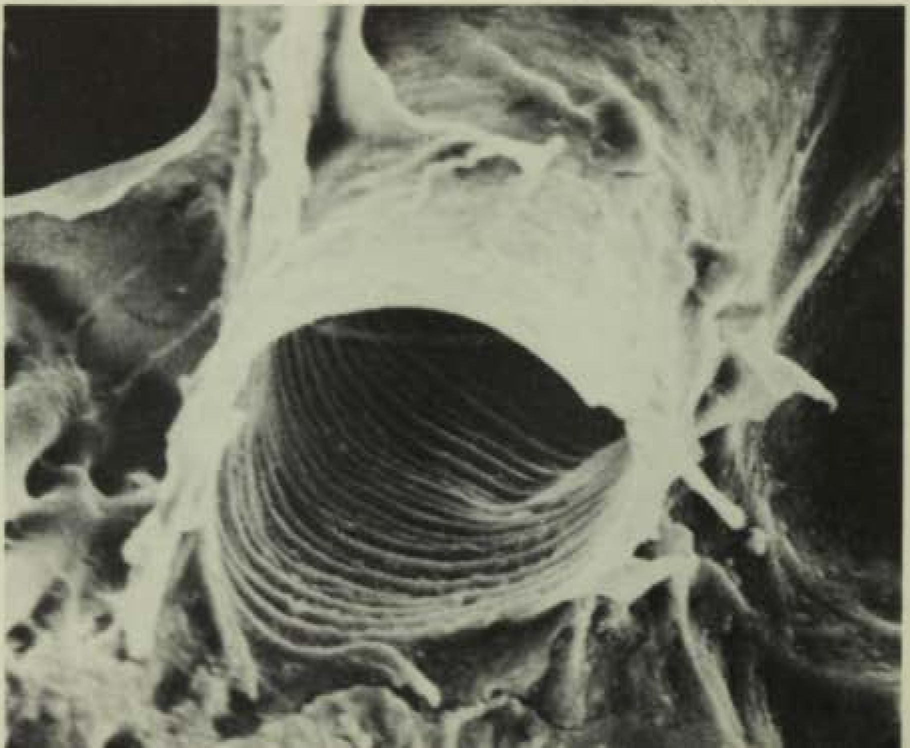

INSECTS OF PONDS AND STREAMS

Most aquatic insects get oxygen from the air. They periodically surface to replenish their supply. While they are beneath the surface, water must be prevented from entering the spiracles. Some insects produce an oily secretion around the spiracles; thus the surface cannot be wetted. Others have hairs that close inwards from the water pressure and block the spiracles.

Aquatic insects, such as the predacious diving beetle, carry a store of air under the water and thus extend their diving time. They trap water between the abdomen and the wing coverings. Their spiracles open up into the bubble. Certain aquatic fly larvae that live in mud which contains little oxygen stick breathing tubes into aquatic plants and get oxygen from the plant. Their spiracles are at the end of long siphon tubes that are pointed and able to pierce the plant.

Many aquatic larvae have organs called tracheal gills. These are flattened leaflike extensions of the body wall. A heavy network of small tracheoles lies just beneath the

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Pupae of twisted-winged insects, Strepsiptera, protruding from between the last abdominal segments of a paper wasp, *Polistes metricus*. Females of some species of the twisted-winged insects are parasitic inside bees and wasps. Note the compound eye and the mouth parts forming under the pupal skin of the parasite at upper left. Magnification is 80 times.

thin cuticular covering. The larvae of damselflies and stone flies have such tracheal gills.

The ways that insects get oxygen are as varied as the ecological niches of the various species. Endoparasites, insects that live inside other organisms, have special respiration problems and are adapted accordingly. For example, the larvae of certain tachinid flies tap their own tracheal systems directly into those of their hosts; others perforate the host's body wall with their spiracles and take in out-

side air. In general, however, endoparasites get a portion of their oxygen by its diffusion from the host's tissues through the cuticle of the parasite.

Chapter Seven

That Drowsy Hum

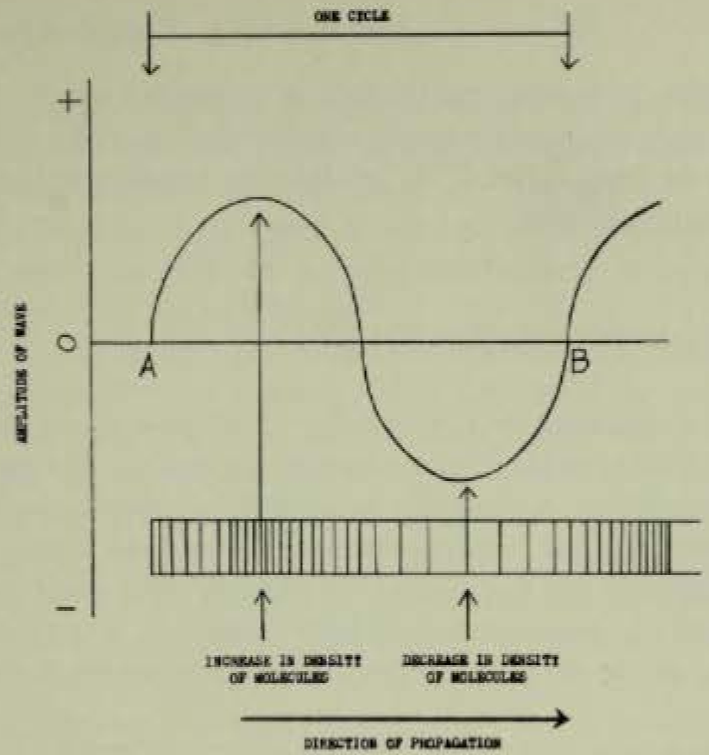
The chirping of a cricket on a fireplace hearth is considered a lucky omen in most rural areas of the world. Man has always listened to insect songs, and the ancients wondered about the mechanism of such insect sounds. Even Aristotle speculated on the source of the hum emitted by certain insects. In Japan, as we know, crickets are kept as pets, and cricket music is much enjoyed.

Though we detect cricket songs with our ears, we should not interpret what an insect transmits and receives, and what we call sound, in terms of our own ear. Human hearing is limited to a very narrow range of air-wave frequencies when compared to insect hearing. To understand how an insect "sings" and "hears," we must first define sound. I use the word "sing" and "hear" in quotation marks, for these are after all human terms and cannot apply to insects except as we interpret sound within the narrow range of our hearing.

WHAT IS SOUND?

"Sound" may be defined as a purely mechanical wave motion in air or other matter, along with the brain sensation it produces. The motion consists of waves that follow one after another. Air is made up of millions of molecules. In regions of compression—areas where the vibrations of the sound-producer have hit against them—these molecules are closely packed; in regions of rarefaction they are sparse and widely separated. We see then that sound waves consist of alternating pressure waves. There can be no sound in a vacuum because there are almost no molecules present.

Any mechanical disturbance sets the surrounding air in motion and produces these alternating pressure waves. The scraping of a pencil across paper as one writes produces a sound audible to the ear. A grasshopper scraping its leg against the sound organ on its abdomen produces sound by the same principle. The number of complete vibrations or alternating waves, called cycles, that occur per second gives us the frequency of the sound. At 5 to 10 cycles per second the human ear hears each separate vibration as a separate sound. Above about 40 cycles per second the vibrations are heard as a continuous low-pitched hum. Increasing the frequency, in cycles per second, increases the pitch of the note. The human ear can hear up to 15,000 or 20,000 cycles per second. Some insects can detect frequencies up to 100,000 cycles per second. This region, above the range of human hearing, is called the ultrasonic (beyond-sound) region. Many species of night-flying moths have extremely high-frequency ultrasonic ears. They use these to detect the ultrasonic cries of bats. We shall see why a little later on.



The cyclic propagation of sound. One cycle is represented from *A* to *B* and occurs in one-fiftieth of a second. Fifty such cycles in succession produce a hum to the human ear, a little lower than the hum that can be created by the 60-cycle alternating current in one's home.

HOW INSECT SOUNDS ARE PRODUCED

Dr. P. T. Haskell of the Anti-Locust Research Center in London is an expert on insect sounds. He has divided the sound-producing mechanisms of insects into three types: 1. Sounds produced by the vibration of wings, as in the hum of a bee. 2. Sounds produced by the impact of parts of the body against some other object; an example is a wood-boring beetle called the death-watch beetle, which strikes its head against the floor of its wooden tunnel. 3. Sounds produced by special sound-producing organs such as the "scraper" and "file" mechanisms found on crickets and grasshoppers.

WING-PRODUCED SOUNDS

The corn earworm moth vibrates its wings at an average of 2500 beats per minute (about 40 per second). The low-pitched hum is detectable by holding the vibrating moth close to the ear. The honeybee wing beat is much higher—about 250 per second—and the sound is easily detectable from a considerable distance by the human ear. In general, the smaller the insect species the higher the wing-beat frequency and flight tone. Very little research has been conducted to determine if these wing-beat frequency sounds, which often have ultrasonic harmonics, are significant to the behavior of the insect. In the case of the mosquitos, however, the tone from the wing-beat frequency is important to their mating behavior.

One segment of an antenna of a female yellow-fever mosquito. The short white sensilla detect odors. The long and heavy barlike sensors pick up sounds.

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The antennae of the yellow-fever mosquito act as a hearing organ. When a tuning fork is vibrated at the same frequency as the sound produced by a flying female, the male flies towards the hum of the tuning fork. It exhibits clasping and mating behavior toward the fork. Certain sensilla, or sensory hairs on the antennae, respond to the frequency of the female wing beat and stimulate a nervous receptor (called the Johnston's organ) at the base of the antennae. When two sources of the same frequency are presented to the male mosquito it moves towards the louder sound. Males can separate the distinctive frequency of the female from background noises a hundred times louder than the female signal. As in the case of our own ear, however, too high an intensity signal repels the male. Most insects, including the mosquitos, have more than one signal which stimulates mating.

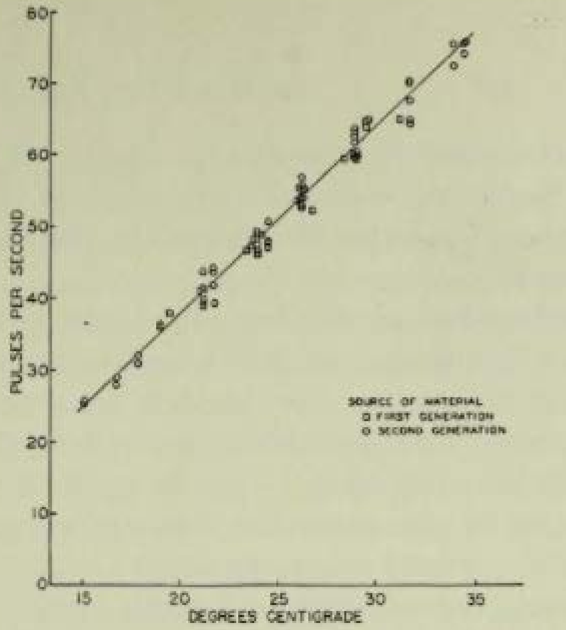
Sexual union in insects, as in all animals, involves a complicated series of signal responses and counterresponses. Even if another species of mosquito were to duplicate the sound frequency of the female yellow-fever mosquito, mating would not take place, because other complex visual or scent signals would not be present to stimulate them to complete the mating. Sexual attraction and mating call for a chain reaction of responses and counterresponses that must follow in sequence to end successfully.

THE DEATH-WATCH BEETLE

Insects that strike surrounding objects with blows from some part of the body produce a ticking noise rather than a steady tone. The peculiar behavior of beetles in the genus *Anobium* have gained for them the rather ominous name of death-watch beetle. They are wood-boring beetles, often found in the wood of furniture of old country houses. They produce the ticking sound by jerking the body forward and striking the floor of their tunnel with the lower part of the front of the head. The eerie ticking sound is considered a mating signal and is heard in the quiet hours of the night during April and May. It came to be called the death-watch beetle by superstitious country people who most often heard it in the quiet of the night while sitting by sickbeds. They believed it foreshadowed death. A legend was made of this harmless courtship sound.

STRIDULATING ORGANS

Stridulation may be defined as any rubbing sound produced by an insect, and a stridulatory mechanism is an organ for producing such sounds. The most common type, although they take many different forms, are simple frictional mechanisms. The usual form is a rigid or toothed surface called the "file" and a knob called a "scraper." The scraper is drawn across the file and produces vibrations of the membrane to which the filelike ridges are attached. Stridulatory organs are found on many species of grasshoppers and crickets. On certain species they are found on the third segment of the antennae, which are rubbed together. On others, stridulatory pegs are located on the femora of the legs. These are rubbed against stridulatory ridges on the side of the abdomen. This type is quite common in both grasshoppers and crickets.



The effect of temperature on the number of pulses per second in the call of the cricket *Oecanthus argentinus*, from research by Dr. T. J. Walker. A pulse is the result of one of the many separate rapid movements the cricket makes with one forewing against the other; it is determined by the intervals and the duration of the separate movements.

Another type of stridulation common in crickets involves a toothed file on the inner side of the elytron (the front wing modified as a heavy wing covering). The edge of the opposite elytron is ridged to form a scraper, and the one elytron overlaps the other. To produce sound the elytra are raised at an angle and opened and closed so that the file and scraper vibrate the whole elytron. The elytron membrane vibrates at the frequency with which the scraper and teeth meet each other. The frequency of the cricket song is within range of the human ear, from 2000 to 10,000 cycles. Dr. T. J. Walker found that there is a direct relationship between the temperature and the pulses per second in the song of crickets of the genus *Oecanthus*. The higher the temperature, the higher the pulse rate.

Cicadas, which are true bugs of the order Homoptera, produce their famous and familiar summertime shrill by vibrating a membrane. Their strident love song from a treetop bower is justly celebrated in literature and poetry. The cicada's sound organ is a circular membrane called a tymbal on the side of the first abdominal segment. The tymbal is supported around the edge by a heavy ring of cuticle and is bowed outwards. A muscle is attached at the center and pulls the drumlike tymbal inward when it contracts. As the muscle relaxes, the tymbal snaps out by its own elasticity and produces the familiar staccato sound many times a second.

COURTSHIP AND ALARM SOUNDS

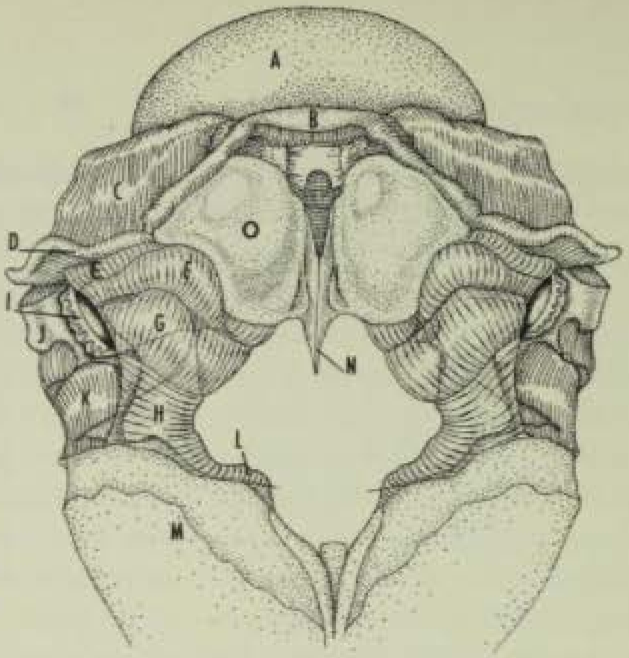
Sounds produced by insects may be concerned with attraction, courtship, or alarm behavior. Many insects produce sounds that act as warnings to potential predators. Some tiger moths when touched produce an audible squeaking sound while at the same time emitting a foul-smelling froth that repels their enemies.

Most of the sound-producing organs that have been described play a role in attraction or courtship. The females of calling grasshoppers respond to the male love song only at certain times. Sexually immature females are not responsive, nor are females that have recently copulated with a calling male. In many species the female grasshopper responds by calling back to the male. They use the mutual calling to locate each other. The distinctive calls of grasshoppers, crickets, and cicadas isolate the various species from each other. Insects do not distinguish pitch, for their hearing organs do not function as frequency discriminators, as does the vertebrate ear. It is the on-off pulse rate (a sort of dot-dash code) that tells a member of a species that it is hearing the same species. Closely related species which resemble each other in shape and size, and even have the same mating behavior, do not cross-mate in nature, although they may in the laboratory. They are prevented from attracting each other by reason of the difference in pulse rate and calling patterns. This is a species isolation by sound.

THE INSECT EAR

As we emphasized before, sound is a mechanical phenomenon; therefore many researchers classify insect hearing organs as mechanoreceptors. Since the insect ear, called a tympanal organ, is a specialized sound organ, we shall include it here.

Tympanal organs are found on the legs of crickets and long-horned grasshoppers, on the metathorax of the night-flying noctuid moths, and on the abdomen of other moths such as the tiger moths and pyralid moths. The tympanal organ of the noctuid moth has been studied in detail. These ears are paired, one on either side, and consist of a thin cuticular membrane, the tympanic membrane, covering the air sac. In the noctuids the tympanic membrane faces a large cavity between the thorax and the abdomen.



The complicated internal and external sclerites of the metathorax of a corn earworm moth. The open space in the center is the area through which the digestive tract (not shown) passes. The tympanic cavities, or pockets (*E, F, G, H,* and their counterparts), and the tympanic membranes (*O* and its counterparts) surround this space. The tympanic pockets make resonance chambers, which preserve some of the strength of incoming sound waves by reflecting them back and forth.

There is also an accessory tympanic membrane which faces a large interior cavity called the countertympanic cavity. These two cavities are considered to be resonating structures for sound. The sense organ called a chordotonal organ, which will be examined in Chapter 8, is attached to the back of the tympanic membrane. This type of sound detector is called a displacement detector because it perceives the displacement of the air caused by the sound vibrations.

Dr. K. D. Roeder has studied the function of the noctuid tympanic organ and found that it detects the ultrasonic cries of bats. Bats of the genus *Myotis* feed on night-flying insects. They produce short pulses of ultrasonic sound

that range from 30 to 100 kilocycles. These pulses are used as a sound-ranging device to tell the bat the location and distance of the moth as it closes in on its prey, acting in effect like our sonar. Since the moth has a maximum sensitivity between 15 and 100 kilocycles it can detect the bat's ultrasonic ranging device. A high-intensity cry (bats closer than 20 feet) causes the moth to take violent evasive action by power-diving to the ground. The reaction time of the moth is so fast that it avoids capture by the bat. This is an example of an insect's sound sensitivity functioning as a protective mechanism to insure the survival of the species. Sound plays an important role in the behavior of insect species.

Chapter Eight

How Insects Touch and Feel Things

Entomologists use the term "mechanoreception" for insects' sense of touch. It is defined as the perception of any mechanical distortion of the body. Dr. Wigglesworth, mentioned earlier, suggests three classes of mechanoreceptors: *contact receptors* that project from the exoskeleton and are called touch (or tactile) spines or hairs; sensory hairs—*proprioceptors*—that respond to strains set up in the cuticle by pressure; and organs sensitive to tension within the body of an insect (*chordotonal organs*).

CONTACT RECEPTORS FOR THE OUTSIDE WORLD

Tactile sensory hairs or spines (sensilla) occur on all parts of the body. The most common type is joined to the body wall by a membranous socket and can move in all directions. Sensitive contact organs are stimulated by movement of the hair or spine in its socket. A nerve ending called a dendrite travels to the socket; usually it has a sheath that ends at the cuticle surface near the base of the hair. Any movement of the hair produces an electric impulse in the nerve.

Tactile receptors respond with an electrical impulse only when they are bent by pressure or straighten out from a relaxation of pressure. They may be called "phasic receptors," because they respond only during the bending or relaxing phase of stimulation.

A sensory hair of a moth set in the socket that allows it free movement. Magnification is 40,000 times.

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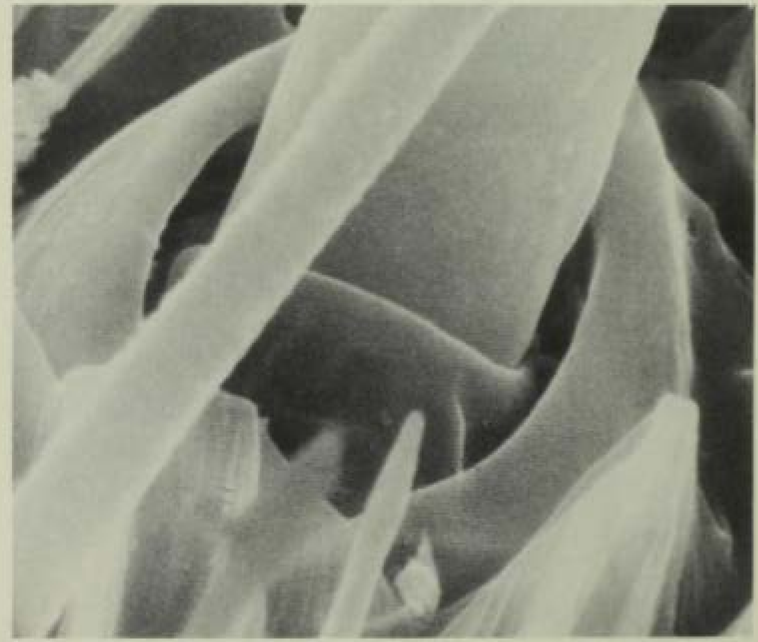
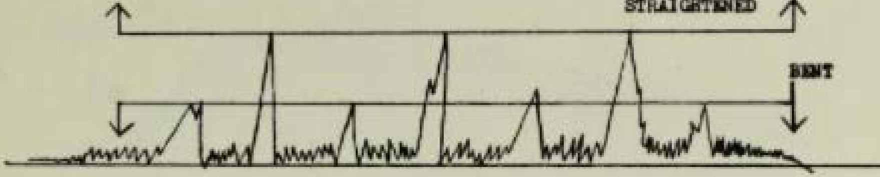
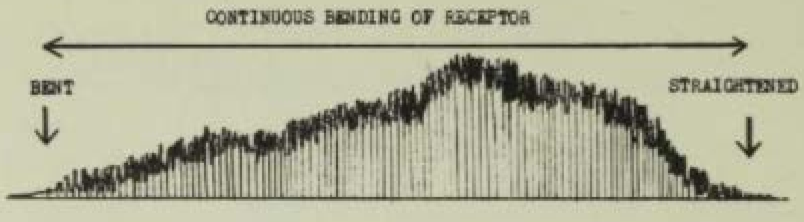




The phasic response of a tactile receptor as recorded on an oscilloscope. The low peaks represent nerve impulses from bending of the hair; the high peaks result from its straightening again.

Most entomologists think that mechanical distortion of the nerve ending (the dendrite and its sheath) leads to the production of an electrical impulse in the nerve. I do not believe this explanation is sufficient and that we must look to solid-state physics for a better one. In 1927 E. P. Adams showed experimentally that certain plant and animal waxes demonstrate piezoelectric effects; beeswax for instance, under certain charged conditions, is a piezoelectric substance. The piezoelectric effect is the unique capacity of a crystalline substance to generate an electric voltage when it is placed under mechanical stress; a crystal microphone is an example. Sound waves from the voice mechanically push against the crystal, which in turn generates an electrical voltage. This represents the transformation of mechanical energy into electrical energy. Since the tactile hairs are thin-walled tubes with a waxy coating, as is the sheath of the dendrite, it seems reasonable to believe that they also possess just such piezoelectric properties. Beeswax is of the same crystalline structure as the waxy coating of the epicuticle and the sensory spines discussed in Chapter 2.



The response of a proprioceptor or position sensor, under continuous pressure. Like all such tonic receptors, it sends an impulse steadily for the full period of bending.

PROPRIOCEPTORS FOR POSITION

The insect body is made up of many cuticular plates and it must also have a sensory system that will provide its body with information about the relationship of one part of its body to another, and also with respect to the forces of gravity. These hairs are called proprioceptors, meaning position-receptors. These are Wigglesworth's second kind of receptors. They occur as groups of hairs or spines, sometimes called hair beds, between the leg joints, body sclerites, and the head, neck, and basal antennae joints. They are in such positions that they are stimulated by contact with the adjoining sclerite. They may be called "tonic receptors," because they send out an electrical impulse as long as they are under continuous pressure. Some hair beds on the face and wings respond to the pressure of wind blowing across the flying insect and help it orient to wind and control yaw (side drift) while flying. Facial hair beds may also stimulate the insect to retract its legs to flying position and to maintain upright flight after takeoff.

CHORDOTONAL ORGANS FOR INTERIOR PUSH AND PULL

Chordotonal organs are internal, with no visible external part such as a hair or spine. They are extremely complex and may occur singly or in large groups of similar structures called scolopidia. Each scolopid unit consists of the nerve cell (neuron) and a scolopale cell that surrounds a tubular rod. The rod tip is covered by a hard cap. In Chapter 7 we mentioned that a sensory chordotonal organ is attached to the back of the tympanic membrane in a moth's ear. The chordotonal organ of a moth consists of two scolopidia. The Johnston's organ, the nerve receptor for sound at the base of a mosquito's antennae, is also a chordotonal organ but is made up of a large group of scolopidia.

Most insect antennae have Johnston's organs, and the number of scolopidia may vary from a very few to hundreds, depending on the species. Johnston's organ does different jobs according to species. In blowflies it serves as a flight-speed indicator and helps to control the speed of flying. In antennae the scolopidia of the Johnston's organ lack the cap found in other types.

Chordotonal organs are also located in the thorax, where they control head movement in those relatively few insects that can move their heads; and at the base of the wing, where they record the pressures that wings put on the thorax. Usually there are four chordotonal organs in each leg, which control the positions of the joints.

Although little is known about how these organs work, their being tubes made of cuticle suggests that they too are piezoelectric.

Chapter Nine

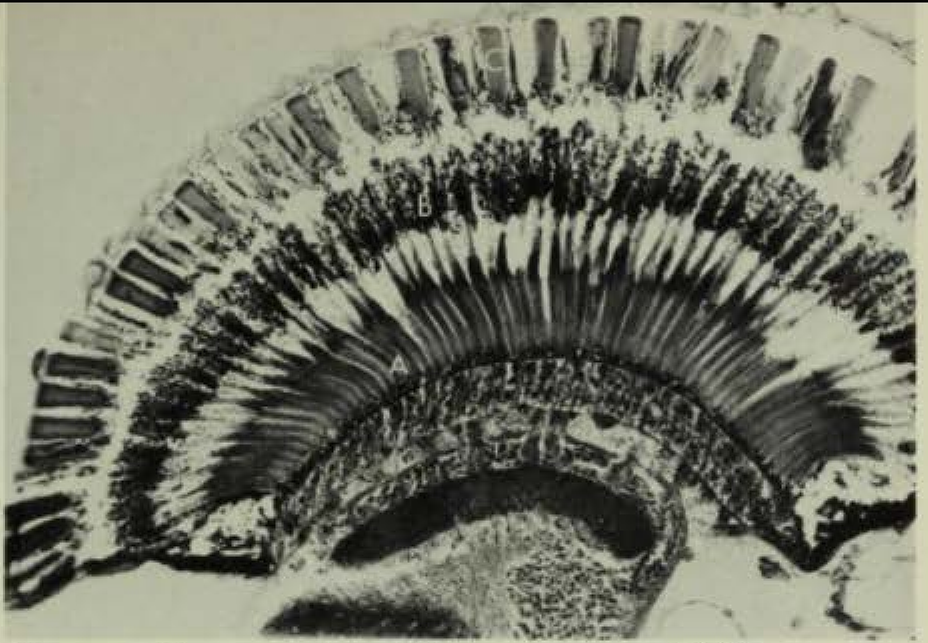
Seeing the World

An insect's eye consists of many light-sensitive organs and lenses. Because of the great number, it is called a compound eye. Most adult insects have a pair of compound eyes, one of which protrudes on each side of the head. Certain insects, such as those that are parasites living inside other animals or those dwelling under the soil, have greatly reduced eyes, or none at all.

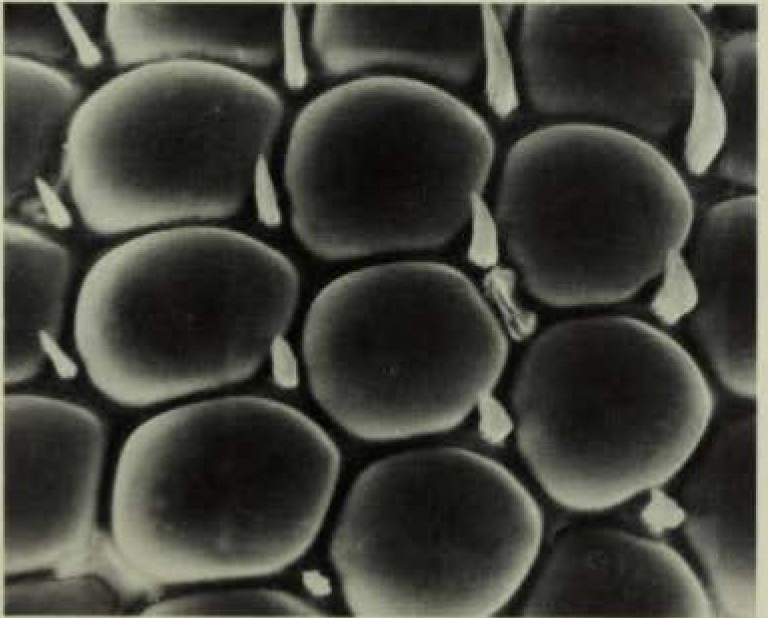
Each external lens of the eye is called a facet. The number of facets may range from six to nine in some worker ants to 20,000 or 30,000 in some moths and dragonflies. All compound eyes have the same general form.

Each separate unit of the compound eye is called an ommatidium and each of these acts as a separate light receptor. Ommatidia are arranged side by side in a compact bundle. The outer part of an ommatidium consists of two light-gathering structures, an external one called a corneal lens, and a long structure beneath it called a crystalline cone. Each cone is surrounded by pigment cells that separate it from neighboring cones.

At the base of each cone are six to eight long, light-sensitive cells called retinular cells. They are arranged in a



The superposition compound eye of the corn earworm moth. This cut through the center of the dome-shaped eye shows the ommatidia parallel to each other. *A*, the area of the retinular cells; *B*, the area of the cytoplasmic filaments (note that the eye is day-adapted, as the dark pigment is in this area); *C*, the crystalline cones with the rounded corneal lenses above.



Facets, or corneal lenses, of the compound eye of the sawtooth grain beetle, as seen magnified 4000 times. Entomologists have no idea at all why many insects have spinelike sensilla between the facets of their eyes. These minute spines are often overlooked.

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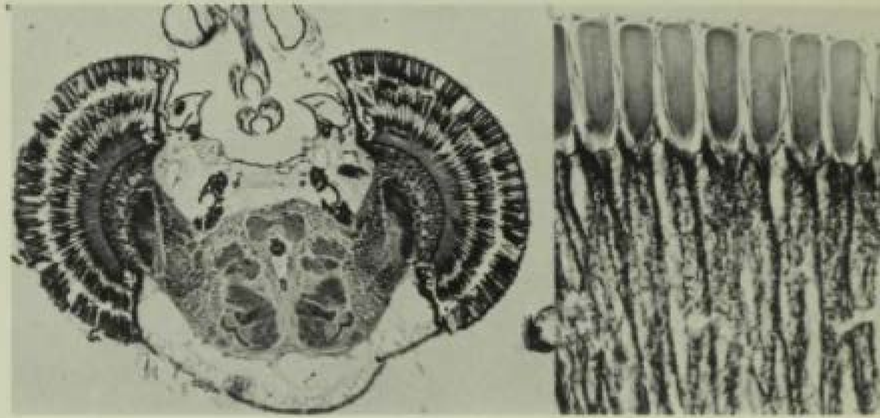


Left, a cut through the optic lobe of the brain and compound eyes of the Indian meal moth. The ommatidia, or light receptors, are packed closely one against another; each ommatidium comprises an entire visual unit, beginning with the facet, or lens, on the outer surface and ending with a light-sensitive retinula and associated basal pigment at the inner end. This eye is day-adapted, as the crystalline cones (just under the facets), though they look dark here, are not covered by the pigment, which is seen just below them, roughly in the midportion of each ommatidium. Right, a close-up of the crystalline cones of the corn earworm moth's eye. The retinular cells at the base—there are six to eight in each ommatidium—are obscured by the black pigment of the pigment cells.

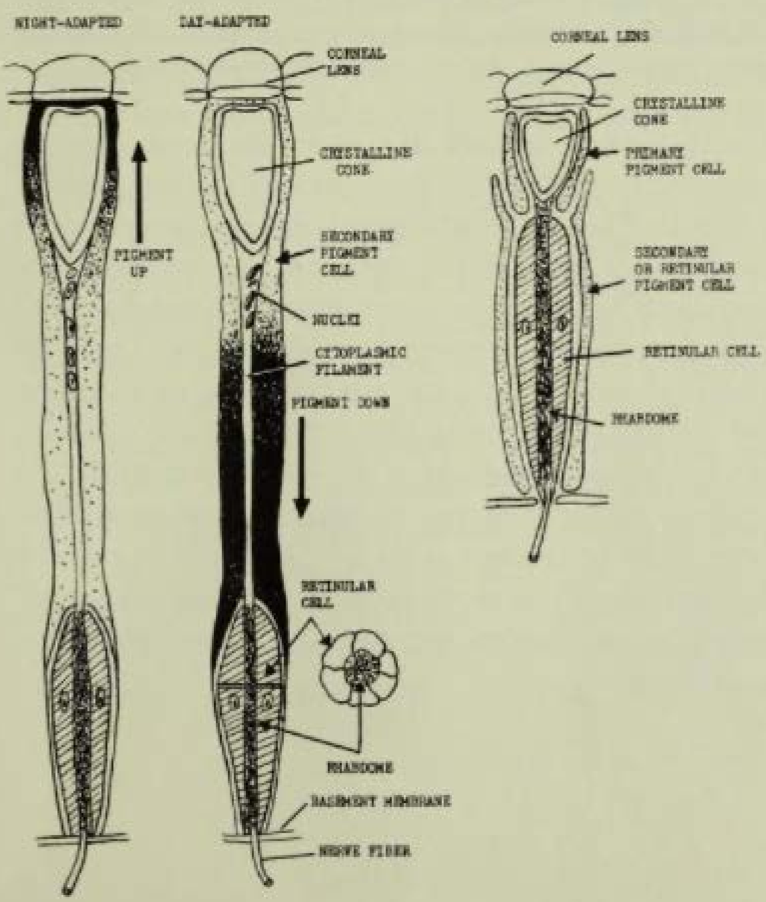
compact circle and their inner margin forms a light-sensitive structure—essentially a rod—called the rhabdome. The rhabdome contains the visual pigment that responds to light. Retinular cells are surrounded by 12 to 18 secondary pigment cells that separate each ommatidium from its neighbor. The retinular cells rest on a foundation called the basement membrane and are connected by nerves to the optic lobe of the brain.

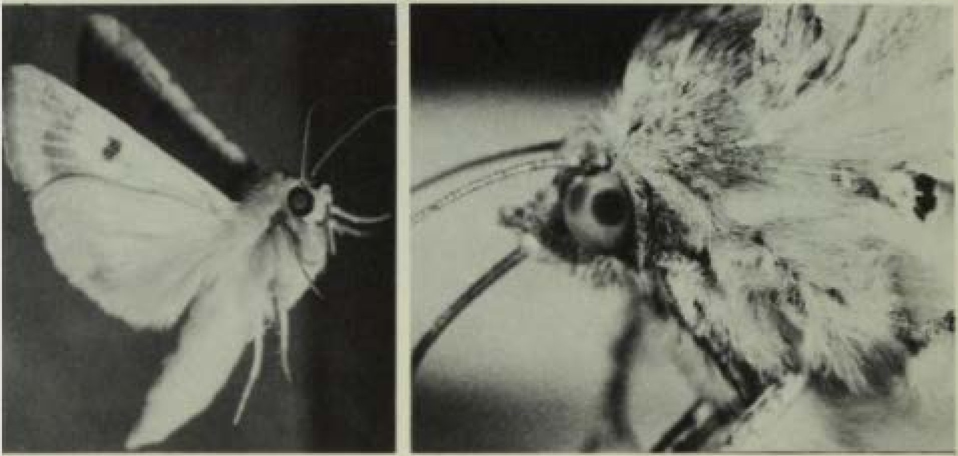
TWO TYPES OF INSECT EYES

Insect physiologists call the two types of compound eyes apposition eyes and superposition eyes. Apposition eyes are found in insects that are active during daylight hours. The reason for the name is that points of light falling on the visual cells are thought to be apposed; that is, to fall side by side into the eye and not overlap each other. In the apposition eye the retinular cells lie directly beneath the crystalline cone, so that light focused through the lens reaches the visual cells directly. Apposition eyes are found in wasps, flies, dragonflies, some beetles, and other day-flying insects such as butterflies.

Insects active at night, but which also sometimes fly in daylight, have eyes in which the visual retinular cells do

Diagrammatic drawing of a superposition eye (*left*), night-adapted and day-adapted, and an apposition eye (*right*).





Left, a corn earworm moth flying in a darkened box. The eye is night-adapted, showing a silvery center and black edge. Right, a corn earworm moth feeding during daylight. The eye is day-adapted, with a black center and green edge. Note the black spot near the right margin; this is the opening to the ultrasonic ear.

not lie directly beneath the crystalline cones but are separated from them by a region of light-carrying filament substance. They are called superposition eyes because under conditions of dim light the light rays are superposed, or overlap each other. Light passes through the nonpigmented wall of one ommatidium into a neighboring one. Thus each visual cell receives light rays not only from its own facet but also from neighboring facets. This condition prevails at night when the pigment of the secondary pigment cells is moved upward to surround the crystalline cone. Most night-active beetles and moths have this type of complex day-night eye. There are of course many type of insect compound eyes intermediate between the apposition and superposition types.

THE MOVEMENT OF PIGMENT

If you look at the eye of a noctuid moth, such as the corn earworm moth, during the daylight it appears a bright green around the edge, with a black center. At night, with a bright light shining into the eye, the green edge becomes black; the center reflects a bright gold or silver glow. The basement membrane of a moth's eye, and of many other night-flying insects, is penetrated by many highly reflecting tracheae making up the tapetum—what we might call a living mirror. This reflects light back into the sensory rhabdome. The center shows a silver glow in the dark because the protective pigments that isolate each ommatidium from its neighbor, and shield the eye from the brilliance of daylight, move up and surround the crystalline cone at night. Light is allowed to cross over between the neighboring rhabdomes and to be reflected from the tapetum.

By moving upward to surround the cones, the pigment leaves the central area of light-carrying filament substance "open," so to speak, to the overlapping of light rays. The pigment thus acts like a camera diaphragm, a variable opening allowing more light or less light to reach the rhabdomes below. When the pigment moves down, it acts as a light-"insulating" substance by preventing the rays of light in adjacent ommatidia from crossing over. In bright daylight the pigment moves downward so that it surrounds the visual retinular cells and protects the rhabdome. Such an eye is called "day-adapted." Eyes in which the pigment has moved upward to surround the cones are "night-adapted" eyes.

THE SIMPLE OCELLI

There is another type of insect eye called a simple eye, or dorsal ocellus. Dorsal ocelli are found on the top of the head of insect larvae that do not undergo complete metamorphosis (see Chapter 12), and on butterflies and moths and many other adult insects. Usually there are three of them, placed so as to form the points of a triangle. Typical ocelli have a dome-shaped lens made of cuticle. The epidermis beneath the lens is transparent. Nerve cells are arranged in groups and form rhabomeres beneath the lens, much like the rhabdomes of the compound eye. In some insects there are pigments between the sensory cells; in others the pigments are lacking. Structures resembling ocelli on larvae of insects with complete metamorphosis are called stemmata. They occur on the side of the head and so are sometimes referred to as lateral ocelli.

Ocelli between the compound eyes of a Hessian fly, magnified 880 times. These simple eyes are usually arranged in a triangle. However, in noctuid moths there are only two, one at the base of each antenna. There is much debate as to the actual function of ocelli.

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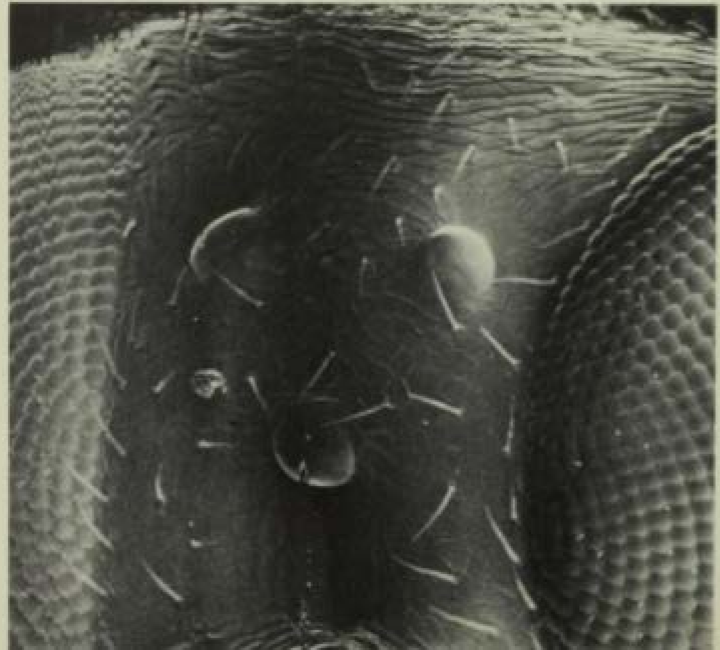


CONFLICTING THEORIES OF VISION

There are two generalized theories as to what and how the compound eye "sees." One, suggested in 1829 by Johannes Müller, is called the mosaic theory; the other was put forth by E. T. Burtt and W. T. Catton in 1960 and is called the diffraction theory of insect vision. Müller thought it likely that each independent ommatidium collects its own light waves and guides them down to the sensory cells independent of all other ommatidia. The sum total of all these single points of light are arranged side by side at the sensory area to make up a single picture, divided by lines as in a mosaic picture, of the object being viewed.

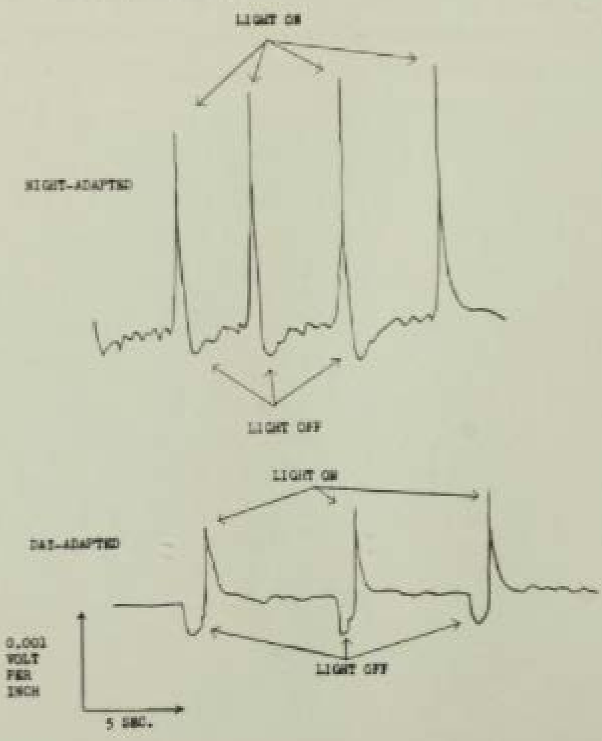
The mosaic theory may be partially correct, but—as with all theories—time and new findings invariably modify the original idea. We now know there is a partial overlapping of the visual field of each ommatidium. This does not mean the total rejection of the mosaic theory, for despite a certain overlapping of light rays, insect vision must remain generally of a mosaic type if we are to consider each ommatidium as a main visual unit. Burtt and Catton, observing an object through a separate piece of corneal lens that they cut from an insect, noticed that the multiple-lens system gives rise to not one but four images, one behind the other. The optical first image lay behind the crystalline cone and the other three were diffraction images and were formed by several corneal facets acting together to form the images. Diffraction is the bending of light rays when light passes through a small opening, such as the facets of the insect eye, or across the edge of an object. According to the later theory the insect eye perceives a diffraction image within itself.

Actually, there is very little data to prove or disprove either theory of insect vision and the answer probably lies with a fusion of the two in which diffraction plays some unknown role.

THE ERG

ERG is an abbreviation for the word "electroretinogram" and was coined to describe the electrical potential that can be recorded from any type of eye. The word "retina" is actually borrowed from the sensory portion of the vertebrate eye. In moths this electrical response is biphasic; that is, it has two peaks. There is a sharp positive peak that occurs as soon as light hits the eye, followed by a slow

Electrical recordings from the compound eye of a corn earworm moth; at top, night-adapted; at bottom, day-adapted. It can be seen that the eye is much more sensitive to each flash of light at night than during the day.

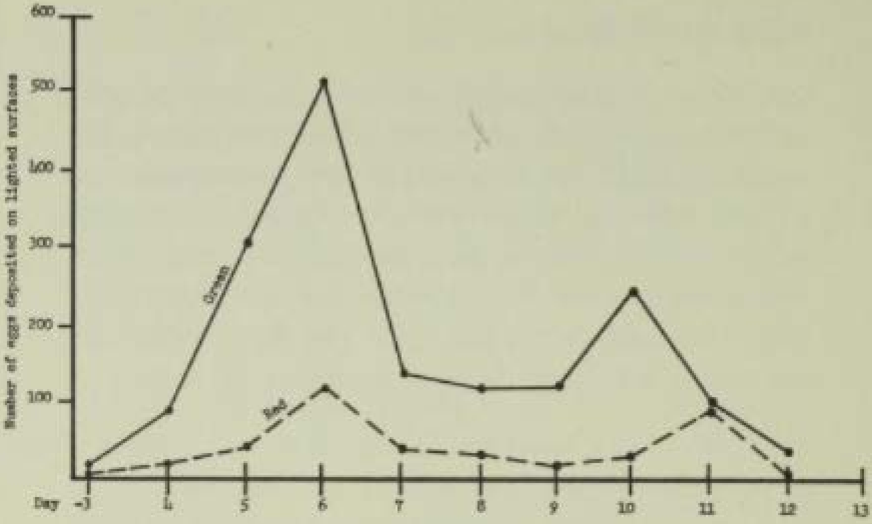


drop-off as long as the light shines and a sharp negative deflection which occurs when the light is switched off. The amplitude (height of the peak) is used by researchers to test the sensitivity of the insect eye to various colors of light. Most insects tested are most sensitive to green wavelengths and may also show a second peak in the near ultraviolet. The height of the ERG peak also changes with light intensity. The brighter the light, the higher the peaks.

DO INSECTS SEE COLOR?

We know from the ERG that the insect eye is sensitive to various portions of the color spectrum to varying degrees, but do they actually see color? Most entomologists believe that they do. The best evidence is found in their behavior. In my own work I have shown that the corn earworm moth, when given a choice of colored surfaces on which to lay eggs, most often chose the surface lighted by the shorter wavelengths (green, blue, and violet). Longer wavelengths were seldom chosen. Such tests showed a response to color but does not prove that the moth actually "sees" color. Karl von Frisch, the famous German bee researcher, trained bees to find different-colored squares of paper among different shades of gray paper. The grays were of the same reflective brightness as the colors used. The famous Russian insect physiologist Mazokhin-Porshnyakov has pointed out, however, that the ability to distinguish white light or grays from other colors is a characteristic of the visual system of human beings and cannot necessarily be equated with what insects actually "see."

We do not at present know the number of insect recep-



The egg-laying reaction of 13 laboratory-reared corn earworm moths to red and green wavelengths of equal intensity, as measured by eggs deposited on surfaces lighted by the two competing wavelengths.

tors (color-sensitive pigments) involved and so cannot be sure that the ERG or behavioral tests actually demonstrate color vision. Mazokhin-Porshnyakov's work is the best evidence for it. He presented bees with different intensities of the colors yellow and orange. He reasoned that if each intensity level of yellow and orange radiation excite a bee's eye differently, then the bee should be able to tell them apart when trained to do so. If the insect were color-blind, certain intensities of orange samples should excite the eye to the same extent as a single yellow sample placed among them. He trained the bees to come for sugar water to a yellow square inserted among the orange squares. When the sugar food was removed the bees still came to the yellow square, showing that they could distinguish yellow from orange. The squares were rotated to make certain that the bees were not learning the yellow square by its position among the rest of the orange squares. He concluded that bees can distinguish color.

PERCEPTION OF POLARIZED LIGHT

Polarized light is light whose waves vibrate in only one plane of direction. Most light vibrates in random directions. Light coming from the sky is polarized not only in different directions but also in different percentages. At an angle of 90 degrees from the sunlight it is about 70 per cent polarized.

Many insects use polarized light for orienting themselves in navigation. In 1940 I. I. Verkhovskaya observed that fruit flies, *Drosophila*, gather in areas of polarized light. She was the first to note this phenomenon but it was Karl von Frisch who showed that bees actually analyze light polarization and steer themselves according to the plane of polarization.

Von Frisch demonstrated that scout bees transmit information about direction by means of a "waggle dance." The direction of the dance indicates the direction the worker bees should steer in relation to the sun to reach a supply of nectar. Once outside the hive the bees steer at the same angle by orienting to the polarized light of the clear sky, which depends on the angle of the sun to the earth. He also showed that bees do not use polarized light in all regions of the spectrum, but only at wavelengths below 5,000 angstroms (green). Many other species of insects, including certain ants, utilize polarized light for pathfinding.

The eye is the organ that is the analyzer of polarized light. It is believed that the instrument of analysis lies in the retinular cells and particularly in the microtubules (small oriented tubes) that make up central rhabdomes of the retinular cells.

Chapter Ten

The Antennae and Insect Communication

Insect antennae are among the most fascinating organs in nature. Many classes of animals have eyes but only insects and a few other arthropods have antennae. Antennae are used to perceive sound or "hear," as we have mentioned, and also to "feel," for some insect antennae have tactile mechanoreceptors on them. In most species, however, their principal use is for olfaction or "smell." I use such terms in quotation marks because they are words which describe human means for detecting external stimuli and cannot be applied with any certainty to insect receptor systems. Entomologists usually use the term "chemoreception" for the detection of chemical substances in either a gaseous state (smell) or a liquid state (taste). "Taste" receptors are called contact chemoreceptors and respond on contact with different liquid chemicals. They usually have a smaller number of sense cells than the antenna chemoreceptors for olfaction, and are generally found on the mouth parts and legs of insects.

Tip of the flagellum, or sensory portion, of the antenna of an ips bark beetle (Scolytidae). The headed tip segment carries the olfactory sensilla that detect the pheromones (sexual scents) and the odors of host plants.

TYPES OF INSECT ANTENNAE

The reason for the great diversity in the shape of the insect antennae is not readily apparent. There is practically nothing in the entomological literature that indicates even a passing curiosity as to the why and wherefore of their many shapes. The forms of the antennae have been used mainly to classify insects; thus a butterfly has capitate (headed) antennae, long and slender with a rounded tip, while a moth has plumose (feathery) or pectinate (comblike) antennae. These two groups of Lepidoptera are easily distinguished by observing the tips of their antennae. Other forms are filiform (threadlike) on long-horned grasshoppers, fusiform (spindle-shaped) on sphinx moths, geniculate (kneelike) on ants and weevils, serrate (sawlike) on many beetles, lamellate (platelike) on May and June beetles, or moniliform (beadlike) on termites. There are

The ball-shaped base segment, or scape, of an antenna of a paper wasp, *Polistes metricus metricus.* The scape fits into the socket on the head of the wasp and is covered with tapered proprioceptors that control the position of the antenna.

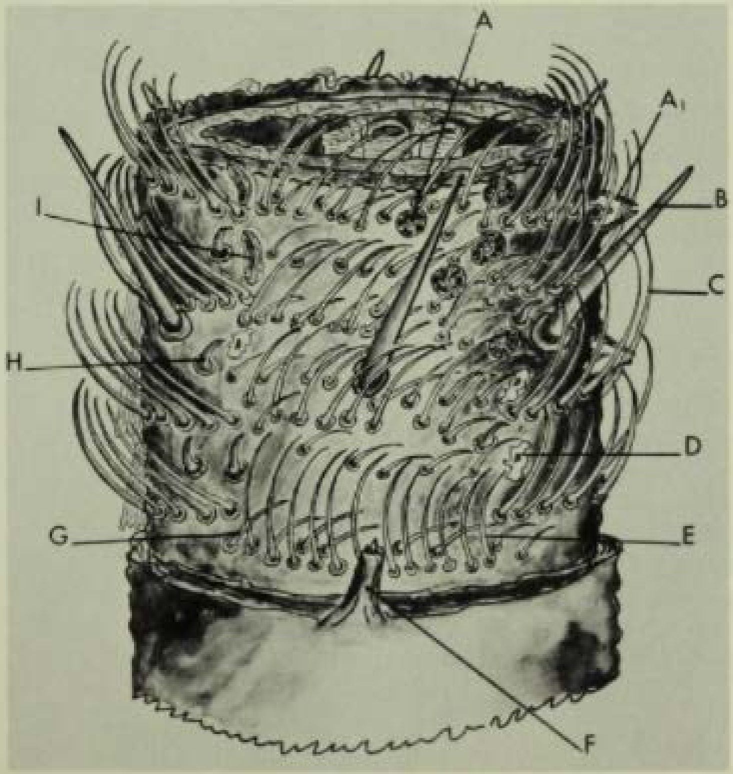
of course many variations of these generalized forms occurring among all classes and families of insects.

Insect antennae consist of three main sections. The first, called the scape, is ball-shaped and fits into a socket on the head. It is covered with proprioceptors, which are position-indicators for the antennae. The second segment, the pedicel, is similar but more elongated. Muscles that move the antennae are attached inside these basal segments. The third and sensory part may have from eight to 90 segments depending on the species and is called the flagellum. The segmented flagellum is the longest portion but there are no muscles in it. Four nerve cords pass up the center of the flagellum and feed the various sensory sensilla.

THE SENSILLA

"Sensilla" is the term used for the microscopic pegs, pits, spines, and platelike structures on the various types of antennae. Before the invention of the scanning electron microscope it was extremely difficult to study these microminiature sensors. They take many different shapes and the terms applied to them are often confusing. Thus a short, thin-walled, peglike sensor is called a basiconic peg; the same type of sensor in a pit is called a coeloconic peg. I have found that there is so much variation from species to species that each sensor must be described individually. On any one species' antennae there may be from three to ten different types of sensilla. There are 90 segments making up one filiform antenna of the corn earworm moth. Each segment is the same and has 10 different types of sensors.

One segment of the flagellum of an antenna from a corn earworm moth. The front of each segment is covered with sensory sensilla, the back with scales. *A*, picket-fence sensor; *A1*, side view of this sensor; *B*, long straight chaetica; *C*, long curved trichodea; *D*, reflective pit; *E*, regular curved trichodea; *F*, taste sensor; *G*, short curved trichodea; *H*, stub trichodea; *I*, shoehorn sensor.



(left)

Sensors on an antenna of a corn earworm moth as seen magnified 2800 times. A group of seven picket-fence sensors is surrounded by rows of curved trichodea. The heavy straight sensor is called a chaetica.

Two picket-fence sensors of the European corn borer moth, magnified 8480 times. The pickets around the central peg are more open at the top than those of the corn earworm moth, and the trichodea are less hooked at the end and more gently curved.

One type that I call a picket-fence detector is found on moth antennae. It consists of 10 to 14 solid tapered pickets that surround a central fluted peg. The pickets slant inward at a much steeper angle on the earworm moth antennae than on the European corn borer antennae. There is even more variation among the different types of spine sensilla, which are called trichodea. Some are short and blunt-tipped, others sharply pointed or pointed and curved. Most of the trichodea have small apertures in their walls. In many cases the apertures occur at the bend in the spine. Besides the various pegs and spines there are plate-like sensors called placodea and types called shoe-horn sensilla, helical, corrugated and conical, and tripod or forked. These various sensors may have from three to 40 dendrites inside their hollow walls.

TWO THEORIES OF INSECT OLFACTION

A theory of the way humans smell things has also been advanced for insects. It is called the "stereochemical" theory. It states that there are several different primary odors and that they are detected by the shape of their molecules. The olfactory receptors are thought to contain various-shaped pits into which the specifically shaped odor molecules fit. It might be termed the "fit" theory of smell (see *Bionics: the Science of "Living" Machines*, by Daniel S. Halacy, Jr.). As Halacy points out, it is interesting that the Roman poet Lucretius over two thousand years ago gave a similar explanation of the sense of smell. Lucretius said that very small pores took in smell molecules (as we call them today) of the correct shape to match the pore.

Many insect physiologists find this theory very attractive, for, as stated before, most insect sensilla do have small pores. The "fit" theory does not appeal to me, however, for it ignores the arrangement, variation of shape, and spacing of the antennal sensilla. My theory, which is based on their geometry, spacing, and electrical properties, says that there is a "fit," but that it is a fitting of frequency to the shape of each type of sensillum. In other words, shape, spacing, and electrical characteristics indicate an electromagnetic mechanism.

Longitudinal cut through a short curved trichodea of the corn earworm moth antenna. Note the small apertures that begin at the curved portion. The center of the tube is filled with about 30 nerve endings (dendrites).

Circular plate-type sensor, placodea, on an antenna of a greenbug, a green aphid very destructive to grains. Magnification, 4640 times.

A shoehorn sensillum on an antenna of the corn earworm moth, magnified 16,000 times.

Helical (spiral), tapered-blunt ended, and plate-type sensilla on an antenna of a paper wasp, *Polistes metricus*, as seen enlarged 8000 times.

Fluted and conical sensilla on an antenna of a paper wasp, *Polistes annularis*. Magnification, 21,200 times.

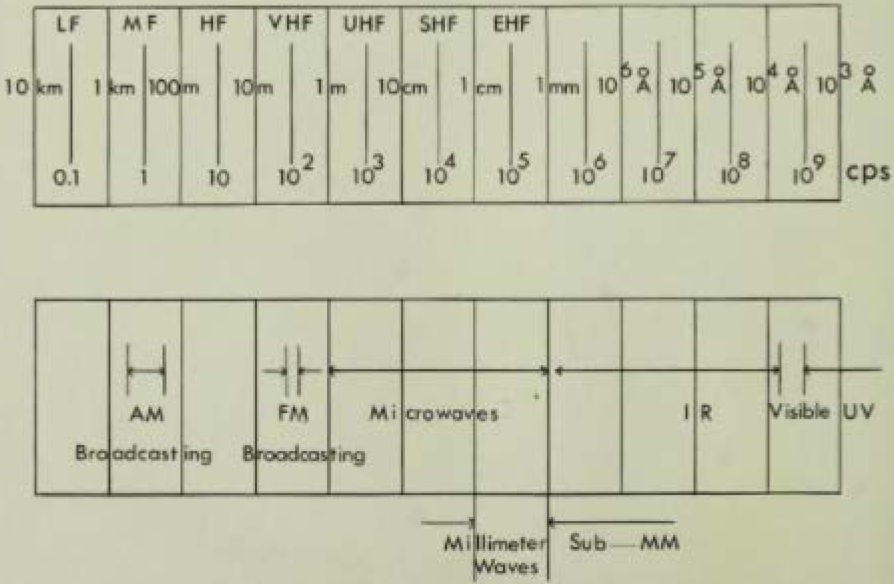
Tripod and forked sensilla on an antenna of a red flour beetle, as seen enlarged 4000 times.

THE DIELECTRIC-ANTENNA THEORY

To understand my dielectric-antenna theory we must first understand the idea of electromagnetic wavelengths and antennae. The wavelength theory states that radiation (electromagnetic emissions) travels in waves and that each wave has a different length that determines its frequency. Wavelengths are measured in centimeters, millimeters, or micrometers (one-thousandth of a millimeter). The known spectrum of frequencies reaches from radio through infrared, visible radiation, and ultraviolet, past X rays and high-energy gamma rays and into the unknown. Radio waves are measured in meters and millimeters; infrared and visible radiation in micrometers. Since each wave is a complete cycle it can also be defined in cycles per second (frequency of so many waves per second).

The reception and amplification (and also the generation) of radio waves is accomplished by what is known as an antennal system. The apparatus consists of an electrically conducting material (wire or metal rod) called an antenna, cut to the same length as the frequency being generated or detected. Thus an antenna for a 10-meter wave would be cut to a 10-meter length, or some to a

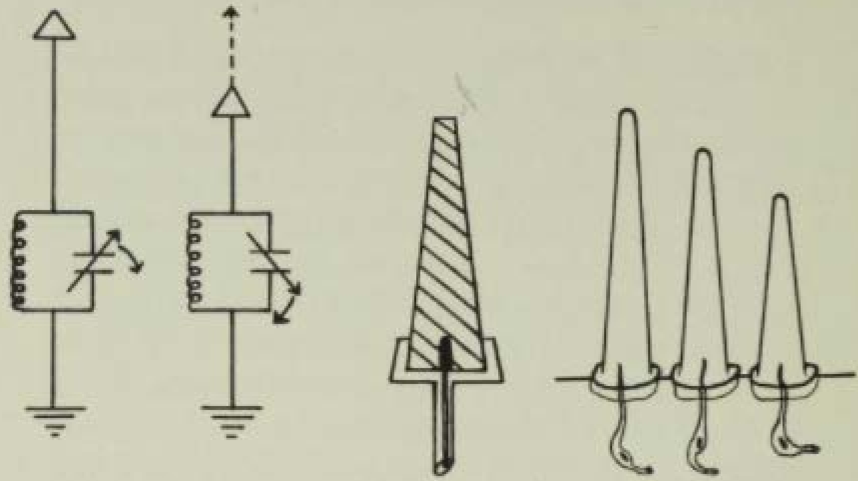
The portion of the electromagnetic spectrum (shown in two versions, the bottom one with common names) from low-frequency radio (top left, 10 kilometers) to far ultraviolet (top right, 10^3 angstroms). Many textbooks give light and ultraviolet in angstroms (A or Å), each equaling one ten-thousandth of a micrometer. Infrared lies between one-millimeter (1 mm) radiation and visible light at slightly below 0.7 micrometers (10^4 angstroms). Radio and microwave regions are divided into low frequencies (LF), medium (MF), high (HF), very high (VHF), ultrahigh (UHF), superhigh (SHF), and extremely high (EHF). The frequency is given on the bottom line of the top spectrum in cycles per second, or hertz.



quarter or half of 10 meters. It would resonate electrically to a wave 10 meters long. Sometimes these metal resonators are designed in arrays, as is your television antenna, in order to obtain gain or amplification of the incoming signal.

A dielectric antenna is formed along the same lines as a metal antenna except that it is constructed of a dielectric material—a substance such as wax, or certain plastics, or plexiglass. These are insulating materials, but they conduct electricity under certain conditions. They resonate to very short frequencies in the light, infrared, and short-millimeter radiation bands. The insect exoskeleton, which is coated with wax, is a dielectric material. When we electrically measured the insect exoskeleton in our laboratory we found that it had the same dielectric constant (measurement of the storage ability of a dielectric substance) as plexiglass.

Another characteristic of a dielectric antenna is that it works best in arrays (more than one rod) of certain special shapes, spacings, and arrangements, and that besides a rod it can also be a hole or pit in a dielectric substance. Dielectric rods or tubes, in order to match incoming frequencies most efficiently, should be tapered. As with metal antennae, there is a relationship between the length and diameter of the rod or tube and the frequency. When the design formulae for the dielectric material, taper of the rods, diameter, and the length of rods is applied to the size and shape of certain insect-spine sensors and pits they indicate frequencies mainly in the infrared region of the spectrum. Furthermore, the sensilla are hardened to the same consistency from the inside out, a characteristic of dielectric rod antennae. Design formulae for dielectric antennae constructed by man show that for efficient resonance to certain



metal aerial dielectric waveguide aerial insect waveguides

Comparison of metal antennae with a dielectric waveguide antenna and with insect waveguides. The resonance of the metal antenna can be shortened or lengthened within 10 meters by a tuning condenser. Dielectric waveguides are cut to specific lengths for resonating at specific frequencies; in this case six centimeters. Insect waveguides might tune in across a statistical curve of an incoming frequency, measured in micrometers, as is indicated by the fact that the spines on the antennae of certain insects such as the corn earworm moth occur in steplike lengths along the body of the antenna or its main branches.

frequencies, without loss of gain, they must have a special form. Distinctive forms include corrugated, tapered, tapered-blunt ended, tapered-curved, conical, helical, picket-fence types, and various arrangements of cavities and pits. I have found every described shape on one insect or another. Dielectric-antenna design, both experimental and theoretical, indicates that for a tapered tube or rod to be highly efficient as a wavelength resonator it should have many small pores or apertures drilled into the sides.

It is quite evident from the pictures that insect sensilla meet every single design criterion for efficient dielectric antennae, and that they occur in mathematically definable arrays on the flagellum of the antenna.

THE EXPERIMENTAL EVIDENCE

If sensilla are microminiature dielectric antennae then they must detect the microminiature radiations of nature. In nature there is continuous exchange of energy between molecules and the environment. All molecules absorb and emit radiation.

The infrared portion of the spectrum is plotted by using a frequency detector called a spectrometer. By such means chemists have shown that organic molecules emit radiation in a way that is much like a transmitting radio antenna. In other words, the emission from molecules, stimulated to radiate by exchange of energy, is quite comparable to what happens in the antenna of a radio or TV station. Dr. Karl H. Drexhage has even plotted the output of molecules in certain organic dyes and finds that they send out radiation in a single direction when all the molecules are lined up in the same plane.

Female insects give off a scent chemical called a pheromone which attracts or stimulates the males to mate with them. Plants also give off odor molecules which attract insects for feeding or egg-laying. Such organic chemicals are extremely complex and their emissions, over most of the infrared spectrum, have not been identified. The mathematics of the dielectric antennae on insects indicates frequencies that resonate between 3 and 400 micrometers (intermediate and far infrared).

Insect pheromones and scents from "host" plants are not the only gaseous chemicals detected by insects. Certain insects and other arthropods, such as ticks and mites, are attracted by carbon dioxide. Living organisms, man and animals, give off this gas. Blackflies and mosquitos, that feed on mammals, are attracted by it. In other words, carbon dioxide, CO_2, is as much a feeding stimulant for host animals as organic molecules are for host plants. Therefore the detection of CO_2, or any gas, even water vapor, is as much olfaction as the detection of pheromones or plant scents.

In 1965 I suggested that blackflies, mosquitos, ticks, and other such arthropods detect CO_2 by sensilla that resonate to infrared frequencies in the 10-micrometer region. Preliminary experiments with a laser that produces 10.6-micrometer radiation caused blackflies to give a feeding response. Dr. William Bruce showed that the spiny rat mite could detect 4.2- to 4.5-micrometer and 10.6-micrometer radiation with tapered dielectric sensilla on their front legs. Ticks and mites do not have antennae but do have sensilla on their front legs which they use in the same way. In our laboratory Dr. Bruce and I set up a 10.6-micrometer laser source and refined our experiments. By using mirrors and filters we were able to reduce the radiation until there was no measurable temperature, less than 0.2 milliwatts (a milliwatt is one-thousandth of a watt). When we exposed the front legs of the mites with half-second flashes of 10.6-micrometer radiation, they responded immediately. They made movements with their front legs toward the radiation. The mites proved to be much more sensitive than the $6,000 bolometer we used to detect the radiation.

In this experiment we separated the frequency from the CO_2 gas, the gas being enclosed in the laser. We obtained the same responses as if the gas were blowing across the leg sensors. Of course in nature the gas would surround the sensor and the emission of a molecule floating

U. S. Department of Agriculture

Loop sensilla on the antenna of a gall-gnat, Cecidomyidae, a type of fly. Loop shapes are found in some insects. Man uses loops to detect radiation in the radio part of the spectrum. Magnification is 4500 times.

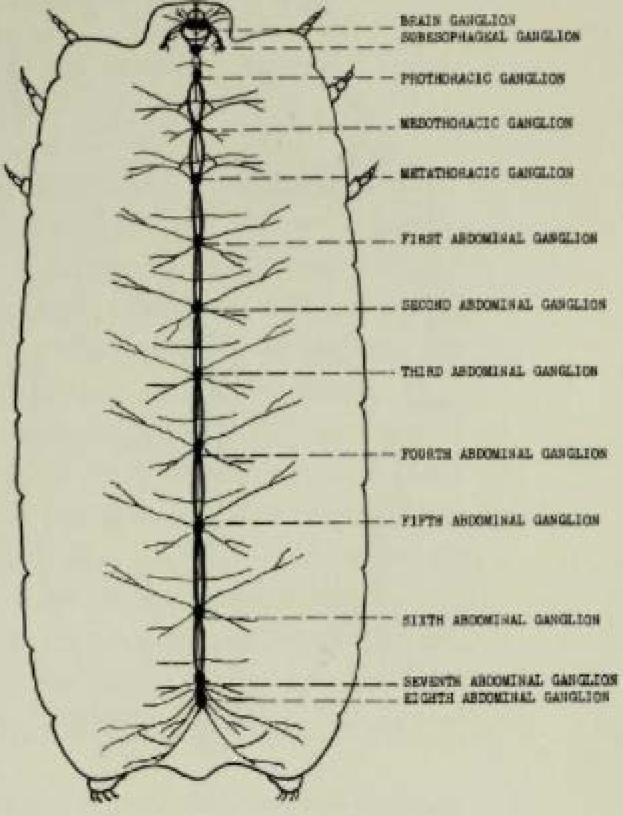
through the air would be very low, much lower than 0.2 milliwatts from the laser. The importance of the laser is that it allowed us to amplify the 10.6 emission and move it a considerable distance away from the sensilla, proving that sensilla do detect a CO_2 frequency in the infrared region. Later, a cyanide laser attracted moths to 337 micrometers, adding further proof.

Our experiment in the infrared does not mean that the stereochemical theory is completely wrong, for the frequency output of a molecule does indeed depend upon its shape. As Dr. E. R. Laithwaite of Imperial University, London, who like myself has postulated the infrared electromagnetic theory of olfaction, so aptly points out, "Any scientific theory remains good until the facts which fail to explain it become too numerous to be disregarded. In the light of such new evidence the theory is either discarded or modified. If the weight of evidence in favor of the theory is large, it is unlikely that it contains no truth, and it is probably only one facet of a much wider theory." Thus does science progress, for most proven theories are modified as science and time change our concepts. No one scientist ever discovered anything by himself—except in the popular press—for each must build on his predecessors.

Chapter Eleven

The Internal Switchboard

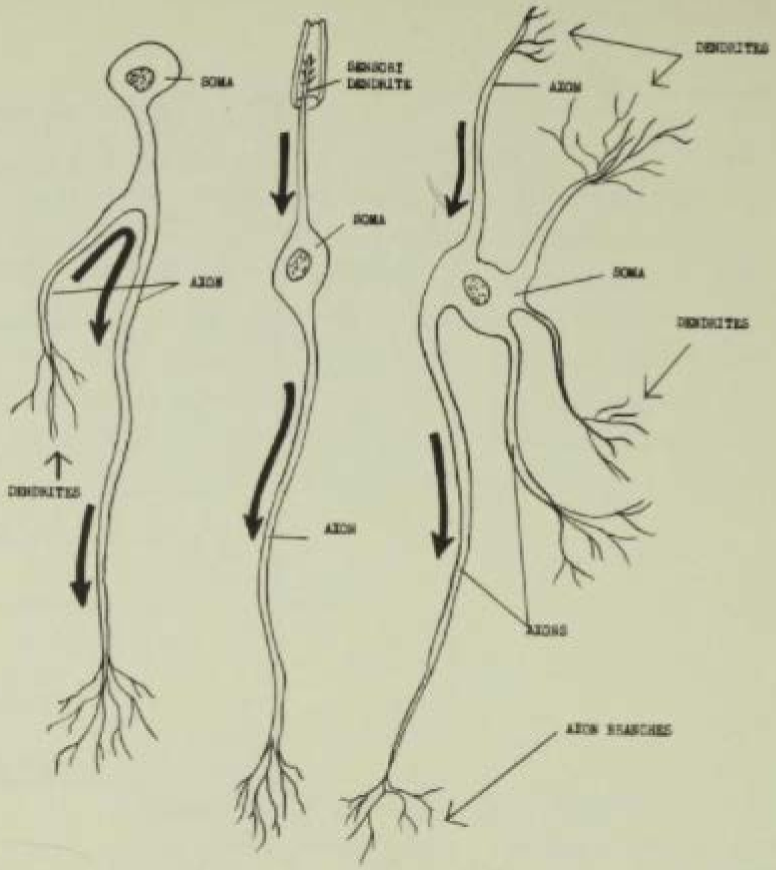
As the title of this chapter suggests, the nervous system is an electrical conducting and switching system. It collects information from the output of the environment, by means of the external sense organs, and feeds it to the internal effectors. The effectors are the organs of response such as muscles or glands. The impulses that flow through the nervous system ensure the coordinated and integrated functioning of the entire insect body. The central nervous system consists of the brain, located above the esophagus in the head, and a series of ventral nerve groupings called ganglia connected by nerve cords. The ventral ganglia send out small branched nerves to the muscles, glands, reproductive tract, digestive system, and surface sense organs.



The central nervous system of a hornworm larva.

THE GANGLIA AND NEURONS

The nerve tissue of insects is made up of three different types of nerve cells called neurons. Collections of neurons are called ganglia, and fused ganglia make up the brain. A neuron consists of a cell body, the soma, and a long cytoplasmic extension called the axon. The axon ends in branches, which make contact with neighboring axons through terminal branches called dendrites. The dendrite is the input end of the neuron. The majority of insect nerve cells are monopolar, that is, there is a single branched axon coming from the soma. Peripheral sense cells are usually bipolar. In these the dendrites extend from the



Three types of neurons, or nerve cells. Left, monopolar; middle, biopolar; right, multipolar. Arrows indicate the direction of the nerve impulses.

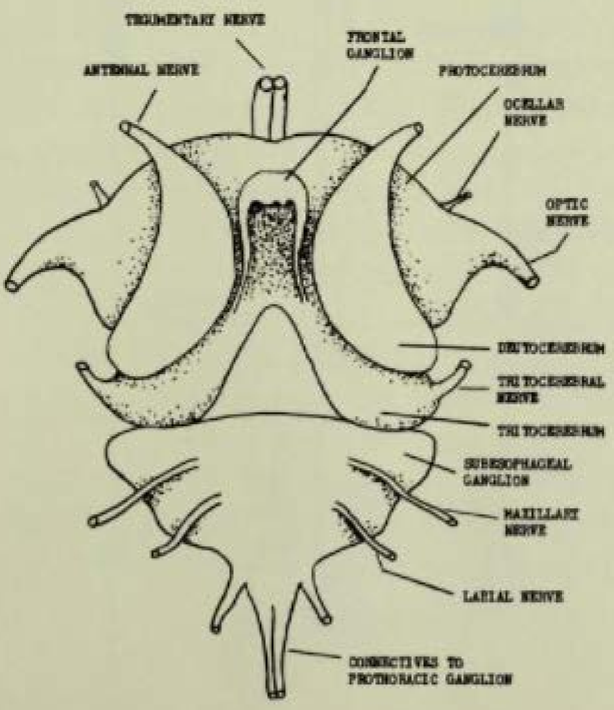
sensor, where they receive stimuli from outside, to the cell body. The axon emerges from the opposite side of the cell body and extends to the point at which its branches join neighboring neurons.

There is a third type of nerve cell, usually associated with a ganglion called the frontal ganglion, that is multipolar. Dendrites and axons come from many directions in these neurons. The region of connection between the branch ends of two or more neurons is called the nerve synapse.

THE BRAIN

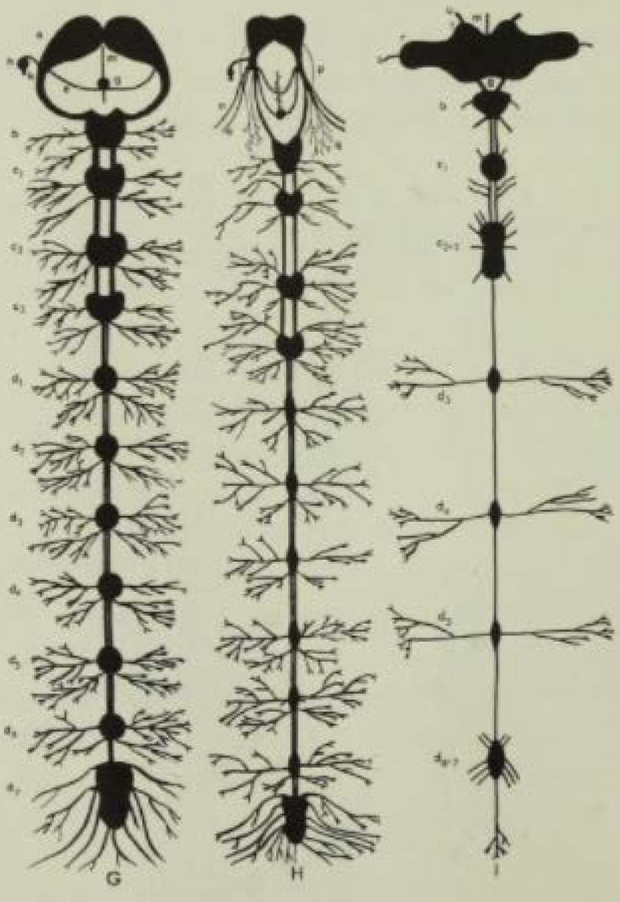
The size of the insect brain varies considerably. It may range from the small brain of the Dytiscid water beetle, 1/4000 the size of the beetle, to the much larger brain of a social insect, the honeybee, which is 1/174 the size of its body. The brain is divided into three regions, the protocerebrum, deutocerebrum, and tritocerebrum. Each of these regions, considered as a whole to be a ganglion by most entomologists, is made up of two lobes, one on each side, which are fused in the center. (Some investigators consider each lobe itself to be a ganglion.) The protocerebrum has connections to the ocelli, or simple eyes, and to the compound eyes. The next region, the deutocerebrum, connects to the nerves of the antennae. The tritocerebrum, the hindmost and lowest portion of the brain, sends two

Front view of the brain of the corn earworm moth.



connecting nerve cords, called the circumesophageal connectives, around the esophagus to a ventral ganglion called the subesophageal ganglion. This is the first ganglion of the ventral cord.

Nevous systems of a corn earworm 15-day-old larva (*G*), the prepupal stage (*H*), and a 10-day-old pupa (*I*). *a*, brain; b, subesophageal ganglion; c_1, prothoracic ganglion; c_2, mesothoracic ganglion; c_3, metathoracic ganglion; c_2 plus c_3, pterothoracic ganglion; d_1 through d_7, abdominal ganglia; *e*, frontal ganglion connective; g, frontal ganglion; *h*, corpus cardiacum; *k*, corpus allatum; *m*, recurrent nerve; *n*, optic nerve; *o*, antennal nerve; *p*, labral nerve; *q*, mandibular nerve; *r*, lobe of protocerebrum; *s*, optic nerve; t, lobe of deutocerebrum; u, antennal nerve. From a paper by Chauthani and Callahan in the *Annals of the Entomological Society of America*.



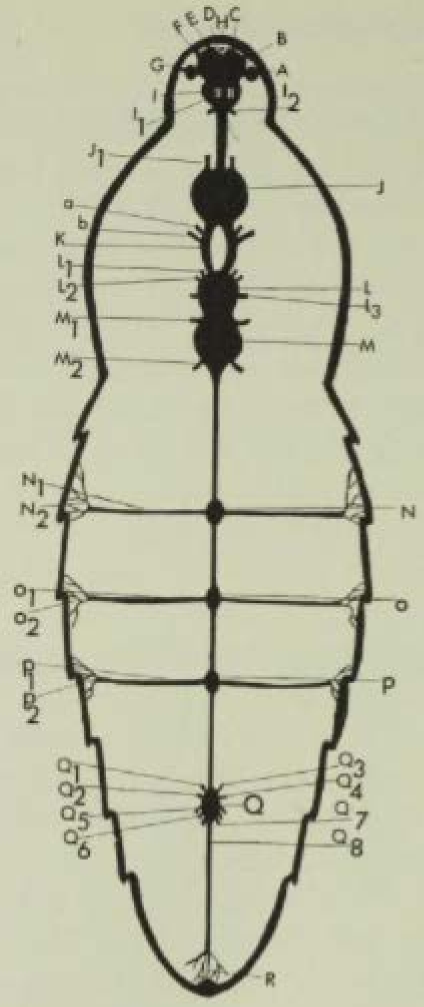
THE VENTRAL NERVE CORD

The subesophageal ganglion is considered to be the fusion of three ganglia that control the organs of the lower portions of the head. It sends nerves to the mouth parts and to the labial palps, or feelers, neck, and salivary glands. There are usually three thoracic ganglia, but in many adult insects, such as the moth, the second and third are fused to form a single ganglion. The nerves of these ganglia innervate (that is, supply with nerves) the legs, wing muscles, and sensilla of the thorax.

The abdominal ganglia may range from as many as seven or eight in moth larvae to as few as one, such as the large fused abdominal ganglion in the adult housefly.

The progression of change in nervous tissue during metamorphosis from larva to moth is tremendous. In the early instars (the forms of insects between molts) the ganglia are close together, but as the larva grows with each molt the connections between ganglia get progressively longer. The moth larva has three separate ganglia in the thorax and seven in the abdomen. The last abdominal ganglia are the seventh and eighth. During pupation the number of ganglia is reduced and adult moths emerge with only two thoracic and four abdominal ganglia. The abdominal ones are much smaller than those of the thorax. They innervate the muscles, reproductive system, and other organs of the abdomen. The fused seventh and eighth abdominal ganglia send nerves to the external reproductive organs.

Connectives, which are bundles of axon fibers and their suporting cells, join the ganglia and are paired. The nerves extending from each ganglion to the peripheral



Nervous system of an adult corn earworm moth. *A*, protocerebrum, or optic lobe; *B*, deutocerebrum, or antennal lobe; *C*, tritocerebrum; *D*, frontal ganglion; *E*, tritocerebral nerve; *F*, antennal nerve; *G*, optic nerve; *H*, frontal ganglion connective; *I*, subesophageal ganglion (I_1, dorsal esophageal nerve, I_2, lateral subesophageal nerve); *J*, prothoracic ganglion (J_1, prothoracic nerve); *K*, thoracic connective (*a*, first median nerve, *b*, second median nerve); *L*, mesothoracic ganglion (L_1, L_2, L_3, mesothoracic nerve); *M*, metathoracic ganglion (M_1, M_2, metathoracic nerve); *N*, first abdominal ganglion (N_1, abdominal ganglion connective, N_2, abdominal nerves); *O*, second abdominal ganglion (O_1, abdominal ganglion connective, O_2, abdominal nerves); *P*, third abdominal ganglion (P_1, abdominal ganglion connective, P_2, abdominal nerves); *Q*, fourth abdominal ganglion (Q_1 through Q_4, lateral intestinal nerves, Q_5 through Q_8, abdominal nerves); *R*, genital nerves. From a paper by Chauthani and Callahan in the *Annals of the Entomological Society of America*.

effectors and sensory cells are composed of both motor and sensory fibers. We have already discussed sensory fibers in the chapter on antennae. The motor fibers control motion and lie entirely within the body (as distinguished from the peripheral nerves of the sense organs). They transmit stimuli to the motor elements of the body, for example, the sucking pump of the esophagus. Aside from a few that control the antennae, motor neurons are generally absent from the brain.

THE MOTOR SYSTEM OF DIGESTION

In front of the brain just above the esophagus is the frontal ganglion. It is connected by a nerve on each side to the tritocerebrum. Nerve fibers from the frontal ganglion go to various parts of the digestive system, especially the gut. The hypocerebral ganglion lies just beneath the brain and connects to the frontal ganglion by a nerve that runs along the esophagus under the brain. Nerves from the hypocerebral ganglion run backward to the ingluvial ganglion that controls the front and middle parts of the gut.

ELECTRICAL IMPULSES IN NERVES

Nerve axons carry an electrical potential, or voltage, called a membrane potential, or resting potential. If we consider the axon as a membranous tube, then the resting potential is the difference in electrical charge between the inside of the tube and the outside. The insect axon has a resting potential of between −50 and −70 millivolts. The theory that explains the mechanism for producing a nerve potential is called the ionic pump theory. Sodium ions (charged sodium atoms) are pumped out of the axon while simultaneously there is an inward flow of potassium ions. The result is a lower concentration of sodium ions inside the axon than outside, which at equilibrium causes the inside of the axon to become negatively charged. The theory is based on the belief that ions in cell water are free to move about.

The classical pump theory is being challenged in the light of what is now known about solid-state physics. Proponents of the solid-state theory of conduction say that there is not enough energy in the cell to work the ion-pump mechanism and that it is thermodynamically impossible. Dr. Freeman Cope and Dr. Gilbert Ling have obtained evidence that cell water may actually be in a somewhat solid molecular state resembling ice and therefore potassium and sodium ions are not free but are attached to the other large cell molecules. Because of this, they say, the ions hop from site to site through an icelike matrix, obeying laws governing the conduction of electrons in solid-state semiconductors. Making the same point that I make about the insect exoskeleton, they say that the cell should be treated as a semiconducting solid.

THE ACTION POTENTIAL

The nerve impulse is called an action potential. It is propagated along the axon of the nerve as a wavelike change in electrical voltage due to the fast depolarization of the axon

surface. The action potential has a constant high peak or amplitude above the negative resting potential. Each wave is also called a nerve spike, because it makes a sharp point on a graphic recording. It is of very short duration, being only one or two milliseconds long.

The stimulation of a nerve produces a series of these spikes. Since they are of the same amplitude (height), information is carried by the spacing and frequency of the spikes. The action potential is an all-or-none nerve impulse. Once it is started it is self-propagating and no further stimulation can start another impulse or add to the one in progress. After the spikes occur there is a time period during which no other action potential can occur. This period is about 10 to 15 milliseconds long.

Action potentials are recorded by inserting microminiature electrodes into a nerve and amplifying the spikes for display on an oscilloscope. The science of recording nerve activity is called electrophysiology.

THE GENERATOR POTENTIAL

Electrical potentials produced in the dendrites of a sensory neuron are called generator potentials. The incoming stimuli, whether chemical, mechanical, or electromagnetic, must be transformed to electrical energy. The generator potential varies according to the strength of the incoming stimuli and unlike the action potential it varies in strength. The generator potential, as the name implies, triggers the all-or-none action potential of the axon.

THE NEUROSECRETORY SYSTEM AND HORMONES

Along with the central nervous system there are two important endocrine-gland systems. One contains neurosecretory cells situated in the central nervous system. The other includes three glandular organs, the corpus cardiacum and the corpus allatum, which are located near the brain, and the prothoracic gland, located in the head or thorax. The neurosecretory cells in the brain, and also in certain thoracic and abdominal ganglia, produce a granular material that may carry hormone molecules. In most respects the neurosecretory cells resemble regular nerve cells. The hormones that are produced act on effector organs or on other endocrine organs which are stimulated in turn to produce hormones—a sort of bodily chain reaction. Neurosecretory cells in the brain relay secreted chemicals to the corpus cardiacum and corpus allatum, where they are stored and released. In addition to storing hormones from the neurosecretory system, the corpus cardiacum produces hormones which regulate certain physiological processes such as the heartbeat.

The function of the many different neurosecretory cells is not well known or understood. In general, however, they control egg development, the loss of water, and growth and development, stimulate the making of proteins, and enter into the control of nerve impulses that shape the behavior of the insect.

The corpus allatum spreads out on each side of the esophagus and is connected by a nerve to the corpus cardiacum. In the corn earworm moth the corpus allatum is smaller than the corpus cardiacum and is attached to it.

The corpus allatum produces a chemical, called the juvenile hormone, that regulates metamorphosis. The prothoracic gland produces the molting hormone, ecdysone, mentioned earlier.

DIAPAUSE, THE STOPPAGE THAT PROTECTS

Diapause is a form of delay in the growth and reproductive development of an insect. It is an adaptation which makes the insect able to survive dangerous conditions in the environment, such as the extreme cold of northern winters. Since hormones control growth and reproduction, interference with the production of hormones leads to a prolonged stoppage of growth and development. In some insect species diapause is obligatory; that is, it occurs in every generation regardless of environmental conditions. In other species diapause is facultative, or triggered by environmental signals, such as the amount of light, due to change in the day from summer to winter (photoperiodism), and temperature.

The environmental signal which triggers diapause occurs before the arrival of adverse weather conditions, thus putting the dormant stage in synchronization with the period of unfavorable environmental stress. Depending on species, diapause may occur during any single stage of the insect life cycle—egg, larva, pupa, or adult. The triggering signals are commonly processed and integrated by the insect during an earlier stage of its development. Corn earworm larvae exposed to 10 hours of light per day (the amount of fall light) enter diapause later as pupae, whereas larvae exposed to 14 hours of light (the amount of summer light) do not diapause. The length of the photoperiod (amount of light per 24 hours) determines whether or not diapause is initiated.

Temperature is also involved, however. Under identical light periods larvae held at 21 degrees centigrade enter diapause, whereas at 27 degrees diapause does not start. Many researchers consider the difference between obligatory and facultative diapause as merely one of degree. The relationships between environmental factors such as light, temperature, air pressure, and humidity are very complex. Insects with obligatory diapause respond to such a wide range of these environmental conditions that it is difficult to separate and study cause and effect in the laboratory.

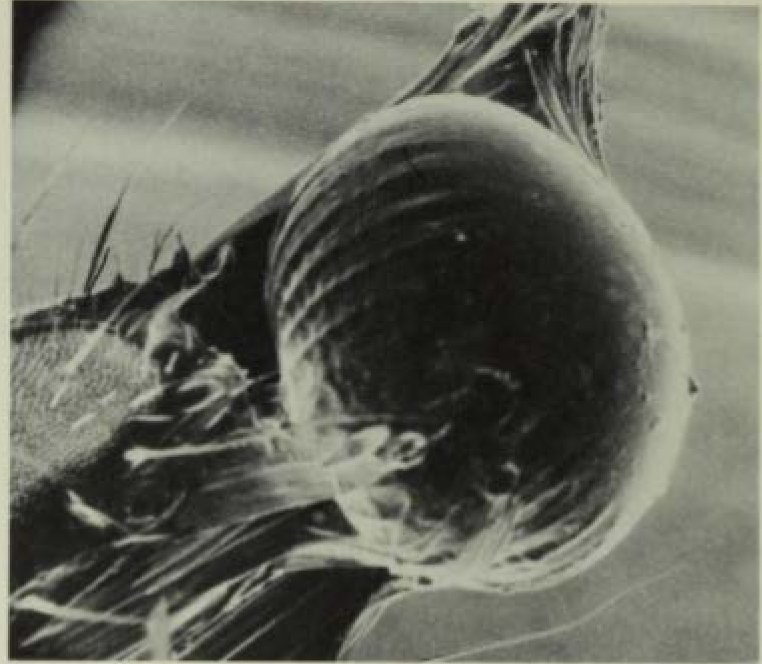
Diapause is closely linked with the nervous system and with the neurosecretory activity of the brain. It has been shown in the moth *Hyalophora* that diapause in the pupal stage follows the failure of neurosecretory cells to release a necessary chemical to the prothoracic gland, which in turn fails to produce the molting hormone. Much is yet to be learned about control of growth and diapause by these chemical messengers from the nerve cells.

Chapter Twelve

Insects by the Millions

There are millions of insects simply because they have a very high rate of reproduction. There are exceptions, of course, but generally a high rate of egg production for a species means a high death rate from predators, parasites, and disease. A multitude of young are produced but not all reach maturity. There are some species that live in special protective environments and consequently produce relatively few young at a time.

The life cycle of most insects begins with the egg and proceeds through a variable number of molts, depending on the species, to the adult form. As in all things biological, there are exceptions to this generality and some insects produce live young that are nurtured inside the body cavity like the young of mammals. Such insects are called viviparous and include aphids, the Strepsiptera, commonly called "twisted-winged" insects, and certain flies such as the tsetse fly. Since most insects develop from eggs, we will follow growth and reproduction through the egg, larval, pupal, and adult stages.

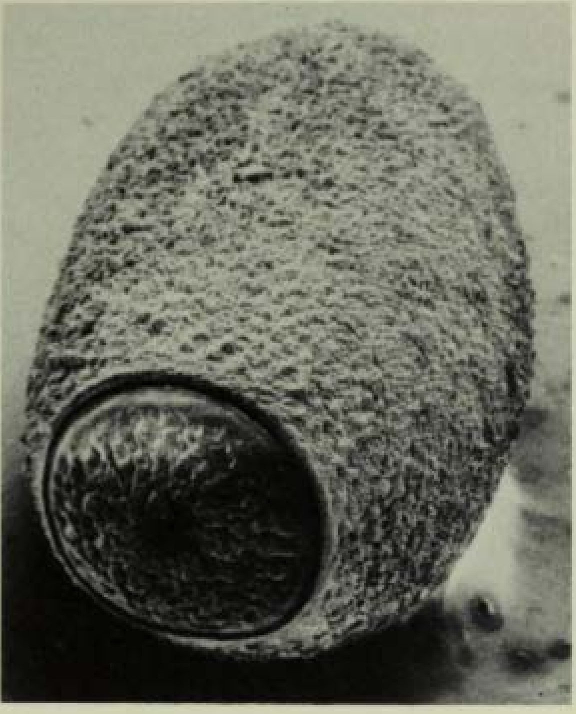


U. S. Department of Agriculture

An egg emerging from the ovipositor, or egg-laying organ, at the tip of the abdomen of a cabbage looper moth. Magnification, 400 times.

THE EGG

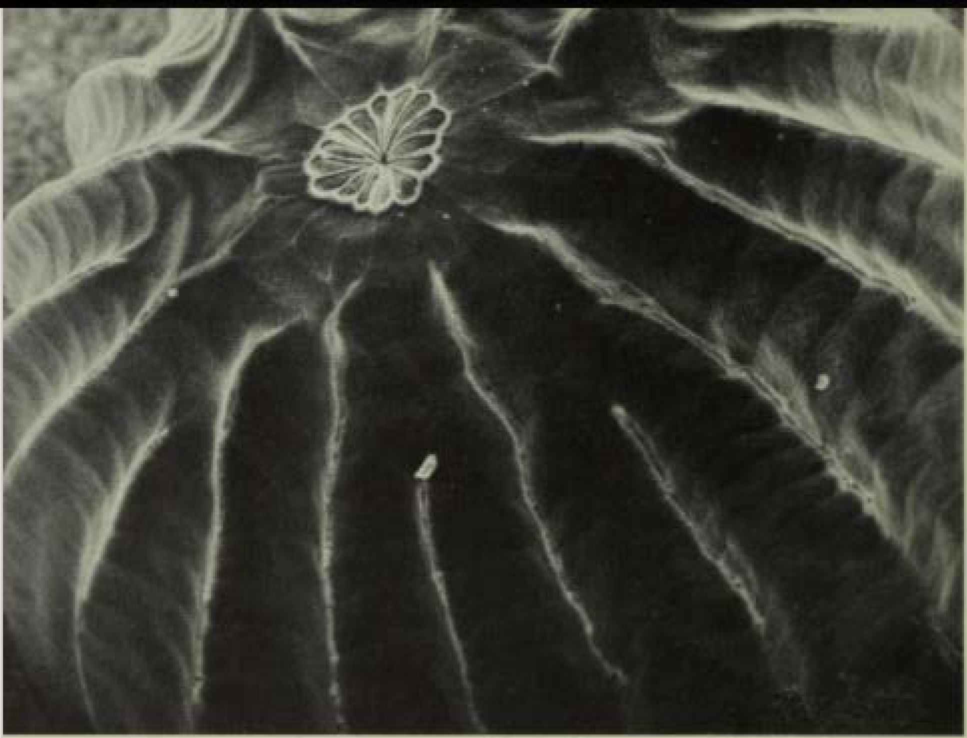
The shape of insect eggs is as variable as the number of species. Eggs are usually round, but may be pumpkin-shaped, sausage-shaped, barrel- or dish-shaped, conical or elongated. They may be attached directly to a host plant or carried at the tip of a long stalk made of a gluey secretion from the insect's body, as in a lacewing. The eggs of moths and butterflies are often deposited with a mass of glued-on scales covering them. The surface of the egg may be covered with ridges, grooves, spines, pits, or knobs, or be otherwise ornately "sculptured."



U. S. Department of Agriculture
An egg of *Aplopus mayeri*, a species of walkingstick. Note the pebbled surface and the circular cap surrounding the micropyle, or sperm-entrance hole, in the center. Magnified 84 times.

The shell of an insect egg is called the chorion. The architecture of the chorion is complex. Because of its small size the eggshell must be able to exchange oxygen and carbon dioxide without loss of excessive water. The chorion is made up of a mesh of layers which are penetrated by small air-exchange pores called aeropyles. With the aid of the scanning electron microscope H. E. Hinton of Bristol University showed that the aeropyles extend through the chorion and connect the air-filled mesh to the outside environment. They allow the egg to "breathe" in the moist environment where eggs are usually deposited.

The time required for the egg to hatch depends on the temperature. The higher the temperature, the shorter the time of larval development within. Corn earworm eggs laid on moist corn silk, in a cornfield at an average day temperature of 90 degrees, hatch in four or five days. As



U. S. Department of Agriculture

An egg of the corn earworm moth. Note the beautiful ridged chorion, or shell, and the chrysanthemum-like pattern around the micropyle. This pattern changes from species to species of noctuid moths.

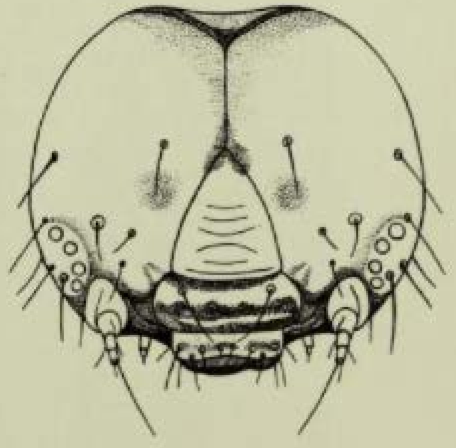
the hatching time approaches, the head capsule of the larva can be seen as a dark spot through the chorion. The larva chews out of the chorion, then turns and feeds on a portion of the empty shell.

THE PROCESS OF GROWING

Growth in insects, as we have described it in Chapter 2, is by molting, or ecdysis. The time between each molt is the stadium. "Instar" is the term for the form of an insect during any one stadium. H. G. Dyar demonstrated many years ago that insects, with certain exceptions, grow in geometrical progression. The head capsule of caterpillars increases in width at each molt by a constant ratio, of approximately one to four. This ratio is consistent for each species. By counting and measuring the width of each shed head capsule, entomologists can determine the instar of a molted larva. Because of its consistency this technique has become known as Dyar's Law.

In some species of insects the number of instars varies. Corn earworm larvae may have from five to seven instars, making it very difficult to relate Dyar's Law to this species. Different species of insects undergo a different number of molts. Lepidoptera larvae average from five to seven; the Thysanura (bristletails) undergo but one. The progress of molting may take from a few hours to several days.

Growth in insects involves a phenomenon called a metamorphosis. "Metamorphosis" means "change." It is a type of growth and development that enables the insect to specialize in a specific way of life during each stage of its life cycle. This division of labor between different stages allows for an efficient concentration of effort from stage to stage. The larva is the growing and feeding stage. The



The head of a corn earworm larva. The lines making an inverted Y in the middle are sutures, division lines which weaken and break during molting, allowing the head capsule to split open.

pupa is the resting and reorganizing stage, during which the insect "rebuilds" its organs for adult life. The adult stage is the mobile reproductive stage in which the organs have been reorganized for mate-searching and reproduction.

METAMORPHOSIS AND JUVENILE HORMONE

In the case of insects, metamorphosis means a very conspicuous change. An insect that goes through transformation from egg to larva, pupa, and adult is called a holometabolous insect, and is said to have complete metamorphosis. An insect with incomplete metamorphosis is called a hemimetabolous insect. The latter do not pass through the larval and pupal stages. Their young leave the egg in a relatively advanced stage of development and are called nymphs; generally they resemble the adults rather closely.

The juvenile hormone controls change in insects, and the molting hormone is under the control of the juvenile hormone which is produced in the corpus allatum. The juvenile hormone was so named because of experimental evidence that it brings about the suppression of adult characteristics by promoting larval characteristics. Metamorphosis to the adult stage takes place in the absence of the juvenile hormone. The corpus allatum changes in size, becoming smaller with successive instars, so that after each molt there is less concentration of the hormone. This allows for more differentiation of adult tissue as growth progresses. The final change to the pupal and adult form occurs when the concentration of the hormone drops below a critical level and adult tissue develops.

REORGANIZATION WITHIN

We have already seen the changes in the digestive and nervous systems of moths during metamorphosis from larval to adult forms. These alterations, which are triggered by the using up of the juvenile hormone, are brought about by histogenesis, which is the formation of new organs after the old ones have been broken down. During the pupal period the breaking down (called histolysis) of old tissues is completed.

The degree of change in holometabolous insects varies according to the order it belongs to. In beetles, where there is some similarity of shape between larval and adult forms, less reconstruction takes place than among moths and butterflies, the larvae of which are quite different from the adults.

The rudiments of the appendages—legs and antennae, for instance—are present in the embryo. During the larval stage the epidermal tissue expands in thickened, folded regions that have gradually become separated from the larval cuticle. During the pupal stage this thick, folded epithelium slowly unfolds and forms into an adult leg.

When the organs are completely different or new, as in the case of wings, the process is quite complicated. New organs develop from epidermal thickenings called imaginal (adult) buds or disks. Most of the adult features of Diptera, the flies, and Lepidoptera, the moths and butterflies, develop from imaginal disks. The disks are groups of cells that remain as embryonic tissue until they develop into adult organs. Instead of laying down larval cuticle, they fold inward, forming an epidermis-lined cavity beneath the cuticle. The appendage—a wing, for instance—forms from the epithelium lining the cavity and is folded within the cavity until the pupa develops, when it unfolds and turns outward as a wing pad, from which the wing grows to full size so far as amount of tissue is concerned, though remaining in a flattened, cramped state. After the adult emerges from the pupa case and cocoon, if any, the wings expand from blood, water, or air pumped into them.

In the case of the digestive tract, which must reorganize itself to accommodate a new diet, the reformed structures grow from imaginal rings of tissue at the ends of the foregut and hindgut. The adult midgut develops from regenerative cells located at the base of the midgut epithelium.

There is little reconstruction of the tracheal and circulatory systems, but the muscles are almost completely destroyed by histolysis and are rebuilt as new muscles. Changes in the nervous system consist mainly of the fusion of various ganglia and the shortening of connections between them.

The fat body, which in freshly dissected insects resembles clusters of whitish grapes tied together, is almost completely replaced. The fat body is the storage tissue for food, fats, and other energy-generating substances.

THE MOLTING HORMONE

Secretions from neurosecretory cells of the brain pass, by way of the corpus cardiacum, to the blood of the insect. The prothoracic gland is stimulated by this secretion in the blood to produce ecdysone, the molting hormone. Experiments on the larvae of insects have shown that the neurosecretory chemical must be present for several days to stimulate the prothoracic gland. If the brain is removed during this essential period of time the insect will fail to molt. Removal after the period will not prevent molting.

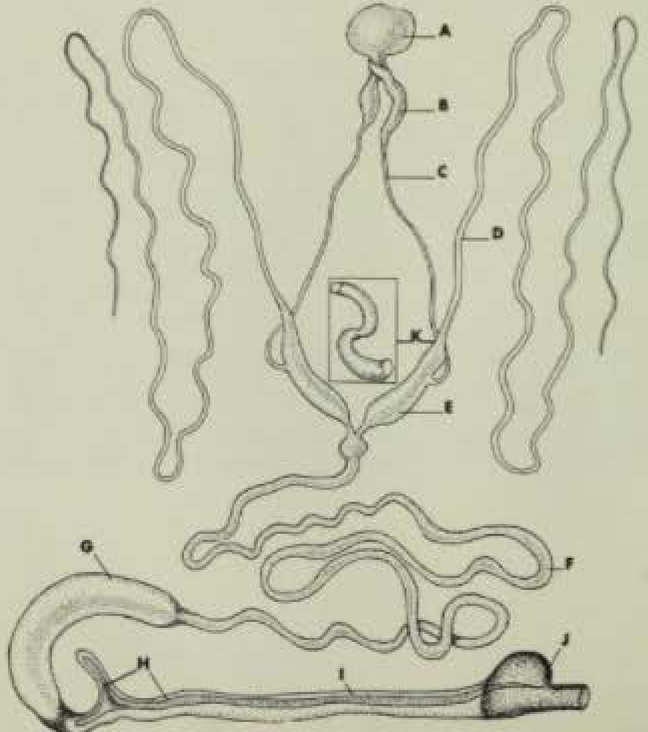
REPRODUCTION

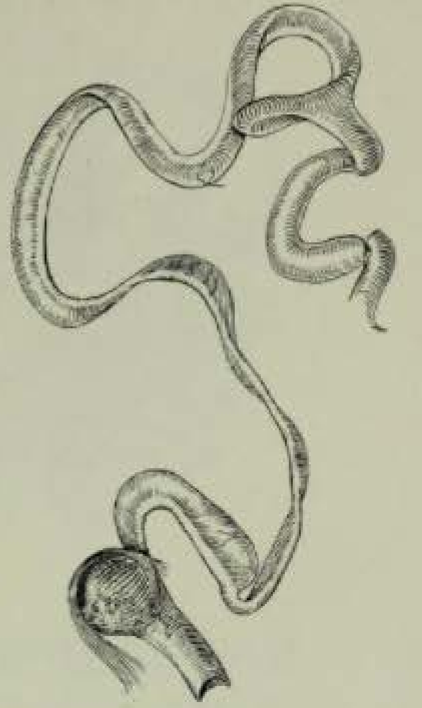
There are two forms of reproduction in insects, sexual and asexual. Asexual reproduction, called parthenogenesis, is reproduction by direct growth from the egg cells without fertilization by male sperm. It occurs in gall wasps, aphids, some weevils, and certain other insects. Most insects, with complete metamorphosis, reproduce sexually. The egg, contained in the ovary, is fertilized by sperm from a male during sexual union (copulation) and insemination. The sexual organs complete development during the final growth stage of the insect, the pupal stage in the case of those with complete metamorphosis. Most insects emerge from this stage reproductively mature.

The passing of sperm into the female (insemination) is a process quite apart from fertilization, which is the process whereby the male sperm actually enters the egg. Sperm passed to the female are first stored in an organ of her reproductive tract called the spermatheca. The sperm may not be utilized for fertilization for hours or even months after insemination, depending on the species.

There are two methods of sperm transfer. They may be passed directly to the spermatheca or else be encased in a protein capsule called a spermatophore. The latter method is common among butterflies, moths, grasshoppers, some wasps and beetles, and a few flies. Although it is considered a primitive method of sperm transfer, this is an extremely complex and interesting process of mating, especially when considered in terms of evolution. It is the usual method among so many common sexual insects. We shall use a moth as our example.

The male reproductive system of the variegated cutworm moth. The parts through *F*, the ductus simplex, or simple duct, are explained in the text. *G* is the heavy, muscular area of the ductus simplex; *H* and *I* are the muscular part of the ductus simplex where the spermatophore is molded; *J* is the aedeagus. The insert *K* shows the constriction in the tube where the accessory glands join the double duct, or ductus duplex. The sperm are immersed in fluid from the accessory glands as they enter the ductus duplex.

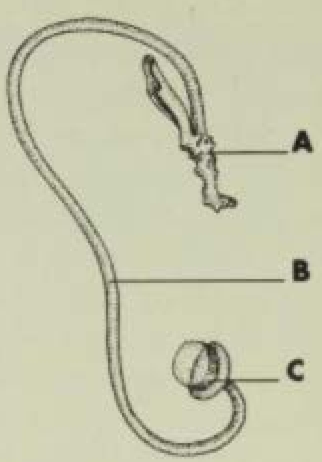




Details of the muscular ductus simplex, lined with cuticle, of a male armyworm moth—the same areas as *H, I,* and *J* of the preceding picture. (This portion differs among species.) The duct is attached to the rounded portion of the aedeagus, bottom. Heavy muscles along one edge of the duct help feed the forming spermatophore out the tip of the aedeagus.

THE MALE REPRODUCTIVE DUCTS

The reproductive ducts of the male variegated cutworm moth are shown in the picture. They consist of paired testes, where sperm are produced, enclosed in a single sac (*A*), and an area of sperm storage called the seminal vesicles (*B*). Sperm are stored in bundles in the vesicles. They move down a duct, the vas deferens (*C*), to a swollen duplex (double) duct (*E*) where sperm bundles break up. Two long accessory glands (*D*) empty into the duplex duct. The sperm and fluid from the accessory glands mix in the duplex duct and move down into a long coiled single duct, (*F*). In this the sperm fluid and sperm mix with a soft protein substance which is molded into a spermatophore in the muscular duct shown in the following picture. The male reproductive ducts of all Lepidoptera are, in most essentials, similar to this example.

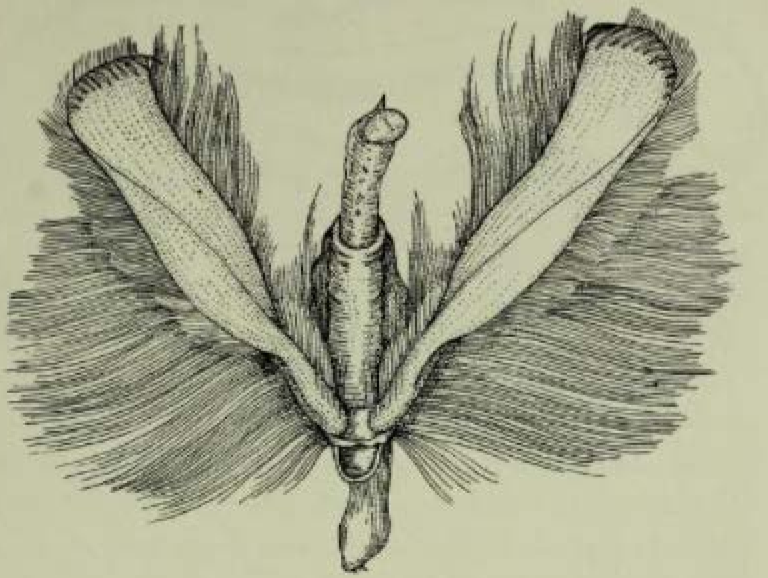


Spermatophore of the male armyworm moth. A, aperture end of the spermatophore; B, collum, a necklike part; C, bulb end containing the sperm. At the aperture end the shoehorn-shaped extension locks the tip of the spermatophore to the seminal duct in the female bursa copulatrix.

HOW THE SPERMATOPHORE FORMS

The spermatophore is molded in the extremely muscular last portion of the male ducts. The inside of the duct is lined with a tube made of cuticle and for this reason called the cuticular simplex. The muscles on one side of the duct help to move the spermatophore substance down the cuticular tube. The spermatophore gradually hardens in this portion and is fed out the tip of the male copulatory organ by the heavy muscle. At this stage the spermatophore resembles a long piece of spaghetti emerging from the tip.

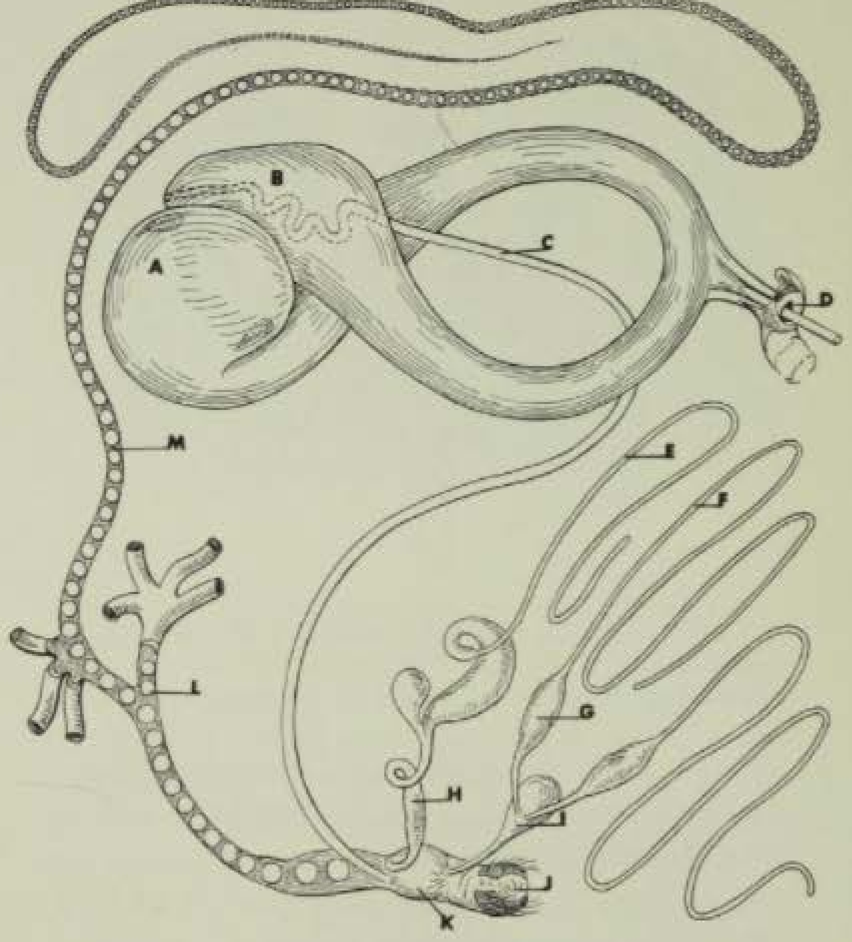
The male copulatory organ of insects is called an aedeagus and is inserted during copulation into an organ of the female called the bursa copulatrix, which receives the spermatophore. Among the nocturnal moths of the family Noctuidae the aedeagus and the bursa copulatrix have a distinctive form. The aedeagus fits into the bursa copulatrix like a key into a lock. During copulation, which proceeds for more than an hour, the gradually hardening spermatophore is fed, with the help of a membranous extension of the aedeagus, called the endophallus, into the bursa copulatrix.



The aedeagus of the male corn earworm moth, with the two hooked claspers at the sides. The claspers hold the female's abdomen during mating.

THE FEMALE REPRODUCTIVE SYSTEM

The female reproductive organs of the variegated cutworm moth consists of the bursa copulatrix, where the spermatophore is deposited, and eight long ovarioles, where the eggs are formed. There are two additional organs, the spermatheca, where sperm are stored, and the accessory gland. These two organs are connected by short ducts to the oviduct, through which the eggs move to the external ovipositor, or egg-laying organ.

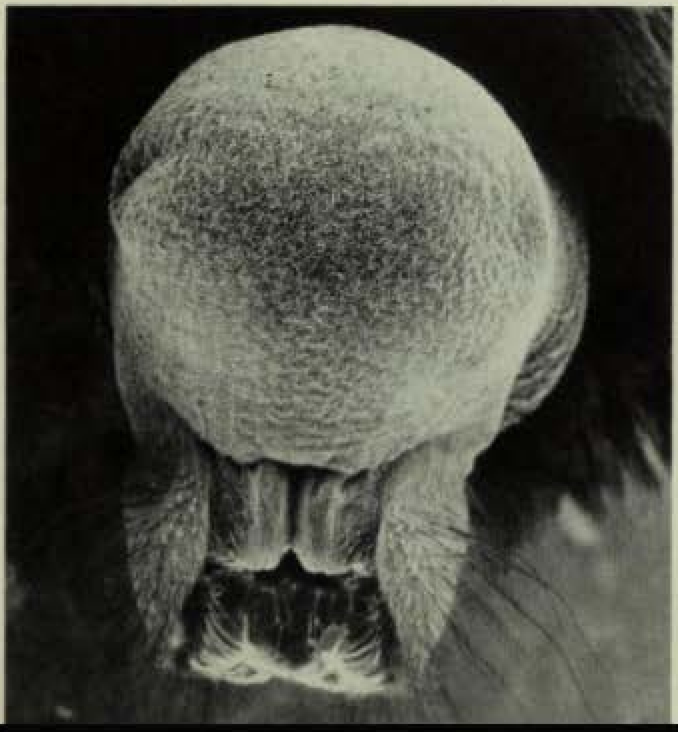


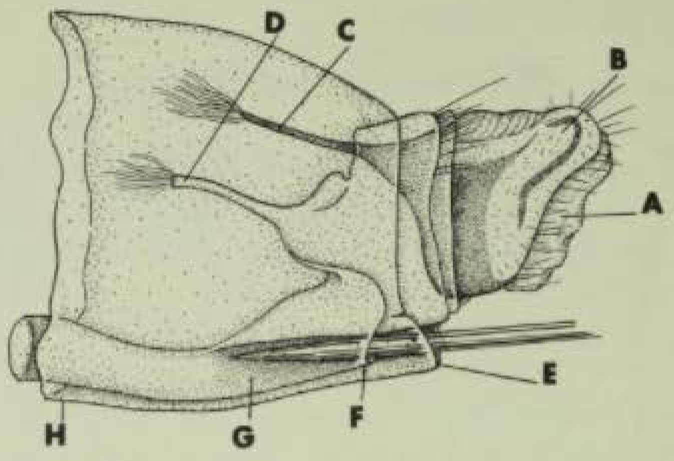
The female reproductive system of the variegated cutworm moth. In copulation the male moth deposits the spermatophore in the bursa copulatrix, with the bulb end of the spermatophore placed at A and its aperture end placed at B, where the sperm leave the spermatophore and travel down the seminal duct (C) to the spermatheca (*H*), where they are stored. *E* is the long accessory gland of the spermatheca. Eggs leaving one of the eight ovarioles (*M*) pass down the oviduct (*L*) to the chamber (*K*), where sperm stored in the spermatheca enter the micropyle of the egg and fertilize it. The fertilized egg is deposited on the host plant by the ovipositor, *J*. *D* is the stretchable vulva (with a pin inserted for clarity) where the male inserts his aedeagus. *I*, *G*, and *F* are parts of the accessory gland. Some researchers believe the accessory gland furnishes a glue that sticks the eggs to the host plant.

INSEMINATION AND FERTILIZATION

The male moth is stimulated to mate by a chemical scent from the female. The scent, called a pheromone, is given off by a gland located, in most noctuid moths, between the eighth and ninth abdominal segments just above the ovipositor. The female noctuid moth vibrates her wings rapidly, at the same time protruding her ovipositor and exposing the gland. In the case of the corn earworm moth, the male lands beside the calling female and arches the tip of his abdomen toward her. The pheromone stimulates the male to protrude a paired organ called claspers from the tip of his abdomen. He holds the tip of the female's abdomen with the claspers and turns backwards so that the tips of the two abdomens are pulled together.

The ovipositor of the fall armyworm moth. At the bottom are the vulva, or genital opening, and the ovipositor; at top is the pheromone gland, which produces a sex-stimulating volatile chemical. This gland is ordinarily retracted between the sclerites, but when in use, as seen here, it pushes out and releases the pheromone.

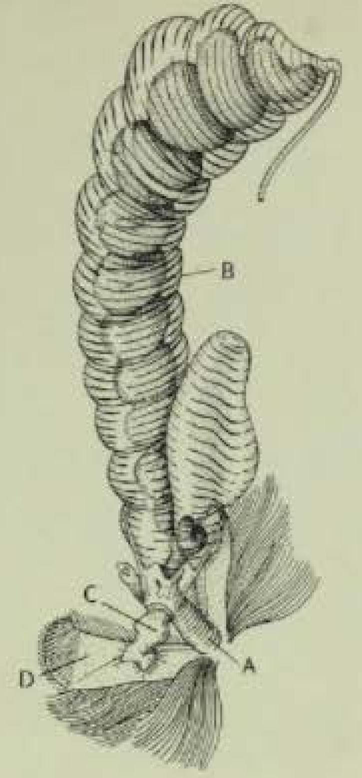




Ovipositor of the armyworm moth, as seen from the side. *A*, ovipositor; *B*, sclerites that support the ovipositor, which is retractable; *C* and *D*, arms of sclerites to which muscles are attached for extending the ovipositor; *E*, vulva (with a pin inserted), the female genital opening; *F* and *G*, plate and duct leading to the bursa copulatrix where the spermatophore is deposited; *H*, abdominal wall.

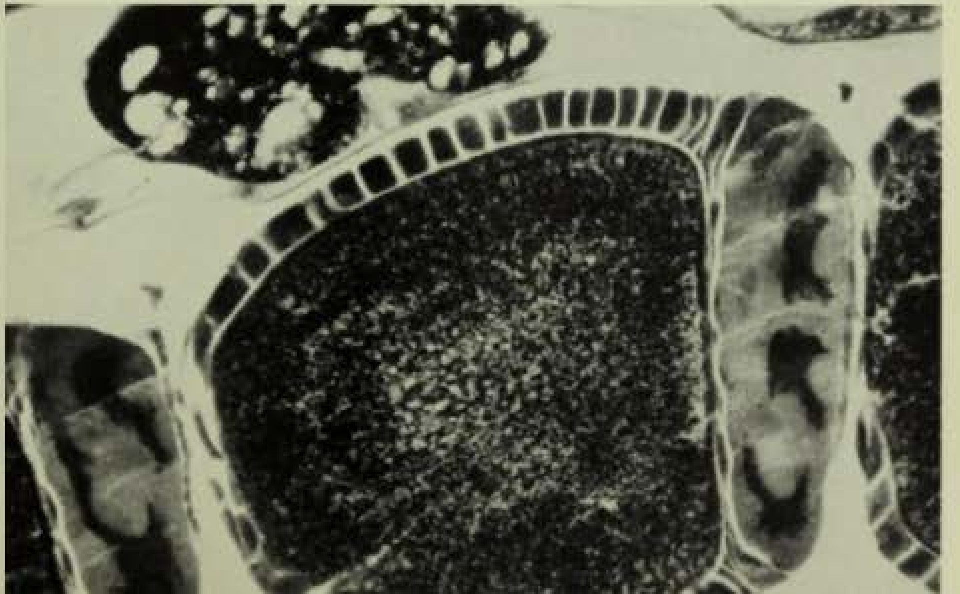
While holding the female tightly he inserts his aedeagus into her external opening, the vulva, of the bursa copulatrix. He extends the endophallus inside the bursa copulatrix and gradually feeds the partially hardened spermatophore out the tip so that it is deposited. He then retracts his organ. The spermatophore immediately expands at the one end into a large bulblike structure. The opposite end remains a long tube with a hook and aperture at its tip. The tip end of the spermatophore lies locked against a long duct, the seminal duct, which leads to the oviduct.

The sperm move from the bulb of the spermatophore, down the long neck and out the aperture into the seminal duct. They migrate down the seminal duct to the oviduct, where mature eggs are stored. However, they do not



The male aedeagus (*A*) inserted into the female bursa copulatrix (*B*) during mating. A membranous organ called the endophallus unfolds from the inside of the aedeagus and feeds the spermatophore into the bursa (as seen through the transparent wall of the bursa). *C* and *D* are the ovipositor and the male claspers pushed aside to show the complex union of the male and female.

Longitudinal cut through a forming egg in the ovary of a corn earworm moth. The chorion has not yet formed and the inner egg plasma is surrounded by follicular cells of squarish shape. The gray cap on the right of the egg is a group of five nurse cells, which obtain food from the blood and pass it into the egg plasma. As the egg grows, the nurse cells are slowly absorbed and in later stages the follicular cells nourish the egg.



A boll weevil puncturing a cotton boll with the mandibles at the tip of its elongated snout. She will turn around and deposit an egg in the hole.

fertilize the eggs at this time. Instead they cross the oviduct and enter the highly complex, two-lobed spermatheca. There they remain, mixed with a secretion from the long spermathecal gland, until they are used. Egg-laying seldom takes place on the night of mating.

The eggs are fertilized as they move through the oviduct and out the ovipositor to be laid on host plants. Mature eggs move down the single oviduct from the eight ovarioles and, as they pass the duct leading to the spermatheca, the sperm enter the eggs. At the top of the egg is a small pore called the micropyle, which can be seen in the first picture of this chapter. The sperm enter the chorion and

fertilize the egg through this microscopic opening. A noctuid moth may lay as many as 2,000 eggs in an adult life span of from 10 to 14 days. A corn earworm moth can lay as many as 200 per night on the silks or tassels of growing corn. The peak of egg-laying for the corn earworm moth is from the third to the tenth day after it leaves the pupa case.

ENTOMOLOGY—A COMPLEX FIELD

I have presented a fairly generalized outline of insect organs and senses in this book. Throughout I have used night-flying moths as my main subject of discussion. However, there are so many species of insects that it is difficult in a book like this to present an overall view without a certain amount of generalizing. It is certainly impossible, in such a complicated field as entomology, to study the life history of any insect and not find exceptions and also extreme variations between different species. If I have succeeded in giving my readers even an elementary knowledge of the way insects function, and if I have stimulated them to marvel at the wonderful world of these creatures, this is sufficient. Although I am an entomologist, and work as such in the United States Department of Agriculture, I still like to remind myself of the wise words of Oliver Wendell Holmes in *The Poet at the Breakfast-Table*:

> "I suppose you are an entomologist."
>
> "Not quite so ambitious as that, sir. I should like to put my eyes on the individual entitled to that name. No man can be truly called an entomologist, sir; the subject is too vast for any single human intelligence to grasp."

Experiments with Insects

Insects are easy to rear and handle, and require little laboratory space. For most amateur naturalists, who do much of their work in the limited confines of a bedroom or back yard, insects are ideal experimental animals.

Before these times of giant research grants, students and scholars at universities and colleges often did their entomological research with limited facilities and handmade equipment. In most cases a binocular microscope was sufficient for a rather thorough piece of research on structure or behavior. I completed my own dissertation in a little screened wooden insectery in a field which is now a parking lot at Kansas State University. On my first job as a professional entomologist, my laboratory was a broom closet under the steps of the bleachers at L.S.U.'s coliseum. Today my laboratory in Gainesville is equipped with a hundred thousand dollars' worth of complex instruments, including a computer and a scanning electron microscope. Although I thoroughly enjoy my research, I am not at all sure that I am having more fun than I did in my broom closet at L.S.U. Besides, the entomologist,

amateur or professional, has the woods and fields of the countryside as his great outdoor laboratory.

I suggest to the young experimenter who feels that insects have but slight "personality" and that snakes or white-footed mice are far to be preferred as subjects of study a reading of the delightful book *To Know a Fly,* by V. G. Dethier. The common housefly emerges from that book as an almost human antagonist to the researcher who attempts to unlock the secrets of its life history. If one could interview an insect, in the way that people are interviewed on television, one would be astonished at the things that an insect "personality" might reveal. Indeed, there seems to be no form of survival or manipulation of life processes that some species of insect does not use. They exist, quite sufficiently, from the deepest and darkest caves to the tops of high forest canopies, and from the frozen Arctic tundra to the blistering heat of the Arabian deserts.

Since we obviously cannot interview an insect, we attempt to unlock its life secrets by another method of asking it questions. It is an investigative procedure called the scientific method, by which, through direct observation and experimentation we put together the "life history" of a species. We shall concentrate on experiments using moths. The experimental procedures, however, apply to any species you may wish to study. These projects will require little in the way of equipment. In most cases what is needed is available in almost every household. The one exception is a good magnifying glass or inexpensive microscope; a binocular microscope will be especially convenient.

WHERE TO GET INSECTS

Since insects are the most numerous of animals, we are seldom without them. In many cases, however, the ones we are most apt to see, in and around our dwellings, are not necessarily the ones we may wish to study. In my own case I am particularly interested in night-flying moths, and thus an ordinary light bulb attracts my subject. A special bulb called a blacklight bulb, which emits near ultraviolet light, is far superior to an ordinary light bulb for attracting not only moths, but thousands of other species of insects as well. The blacklight bulb is wired in a fixture like an ordinary fluorescent bulb. In my book *Insect Behavior* there are directions for wiring and building a blacklight trap, and for trapping ground-dwelling and other species. A good way to pick up flying insects at night, without damaging them, is to hang a blacklight fixture in front of a white sheet between two trees and pick the insects off the sheet as they land. A blacklight fixture is an inexpensive and indispensable piece of equipment for the insect collector, professional or amateur. Since a bulb sold under the word "blacklight" may in some cases radiate also the harmful portion of the ultraviolet spectrum, avoid close and frequent exposure to it.

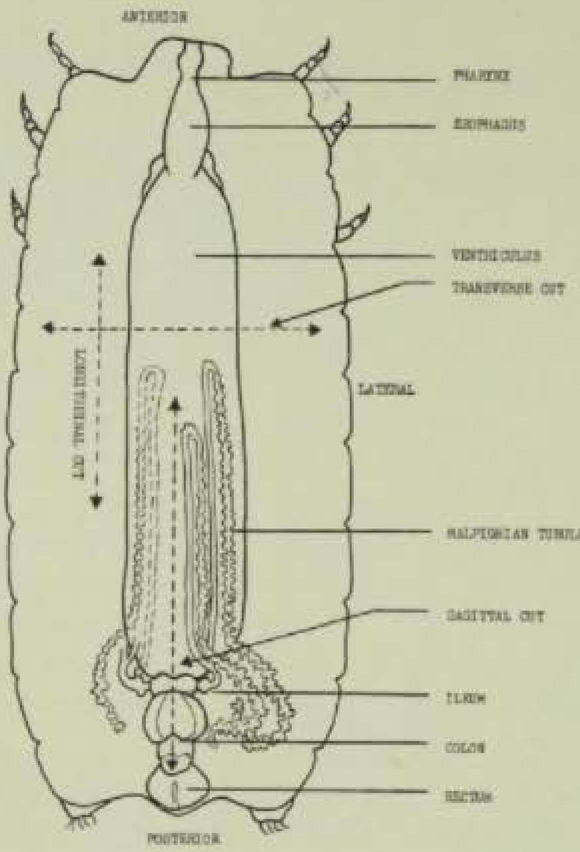
Borror and White's *A Field Guide to the Insects of America North of Mexico* and William Hillcourt's *Field Book of Nature Activities* both have excellent chapters on how to find and collect insects (see "Suggested Reading").

SEEING THE INSIDE OF INSECTS

Insects of the larger sizes are easy to take apart for a look inside. The exoskeleton is hard and tends to hold internal organs in place. Insect blood plasma is not a messy substance and the overly squeamish will not be disturbed by the process of dissecting an insect.

A good subject to begin with is a caterpillar, the larger the better. The larvae of sphinx moths are best. They are easily recognizable and are called hornworms because of the long spike at the posterior end of the larva. They are easy to find and one species, the tomato hornworm (a similar species in the South is called the tobacco hornworm), is common on tomatoes in the late spring. Any moth larva will make a good subject and if you are rearing a species of noctuid moth (see next project), the last instars of the larvae of that family are quite suitable.

Since this is a morphological project it might be a good idea to define some of the basic terms that describe positions, as shown in the illustration. *Anterior* and *posterior*, terms used earlier in this book, refer to the front and rear respectively; *lateral* refers to the side. *Dorsal* means "on or along the back," and *ventral* "on or along the bottom." A *transverse* cut is one from side to side, and a *longitudinal* cut is made down the length of the insect or other animal. *Sagittal* refers to a longitudinal cut down the midline of the larva from dorsal to ventral so the subject is cut completely into right and left halves and the organs of either side of the body are seen. *Distal* means "away from," and *proximal* "close to"—for example, an insect's tarsi are distal to the thorax but the femur is proximal to the thorax



Dorsal view of a dissected hornworm larva, showing Malpighian tubules and other excretory parts, and illustrating types of cuts made in dissections.

in relation to the tarsi.

Insects are dissected under water. Obtain a plastic or tin dish of about four by six inches and approximately one inch deep. Fill the bottom with about half an inch of a melted mixture of half paraffin and half beeswax; if necessary, paraffin alone is a second choice. A little lampblack powder added to darken the color somewhat will aid in

seeing insect organs that are white or pale yellowish. Fill the dish with water to the edge. Kill the larva by dropping it in boiling water (or use a killing bottle if you have one). Slit it open along the mid-dorsal line, with manicure scissors (preferably straight), from just behind the head to the most posterior abdominal segment. Pull the body walls to either side and pin them to the wax bottom with straight pins.

The internal organs will float in the water. They will at first be obscured by masses of the fat body (whitish sausage-shaped or grape-shaped clusters) held together by silvery tracheae. Decide what physiological system you wish to observe and draw. (The picture here shows the Malpighian tubules; the nervous system is pictured in Chapter 11; the dorsal blood vessel in Chapter 6; the digestive tract and salivary glands in Chapter 5.) Then carefully pick away the fat body and tracheae with tweezers and a fine dissecting needle. Dissecting needles can be made by mounting a long pin or sewing needle on a match stick. Pick away at the fat body until the organ you want to see is floating free in the water, and rinse with fresh water until it is completely visible. While pulling away the fat body note how the tracheal system ties all the organs together and note also the attachment of tracheae to the insides of the spiracles. You may wish to draw each system and turn out a complete morphological work for your science class. Remember, there is variation in internal structure among all species of insects, and far more insect species haven't been examined than have.

You may also wish to examine in the winter some of the species that you trap in the spring and summer. One way is to freeze the specimen or fix it in a 10 per cent solution of formalin for a few days until it hardens. Make a sagittal cut with a razor blade so that the organs can be seen and drawn in position on either side. This is a good method for getting the correct position of organs and also for studying muscle attachments.

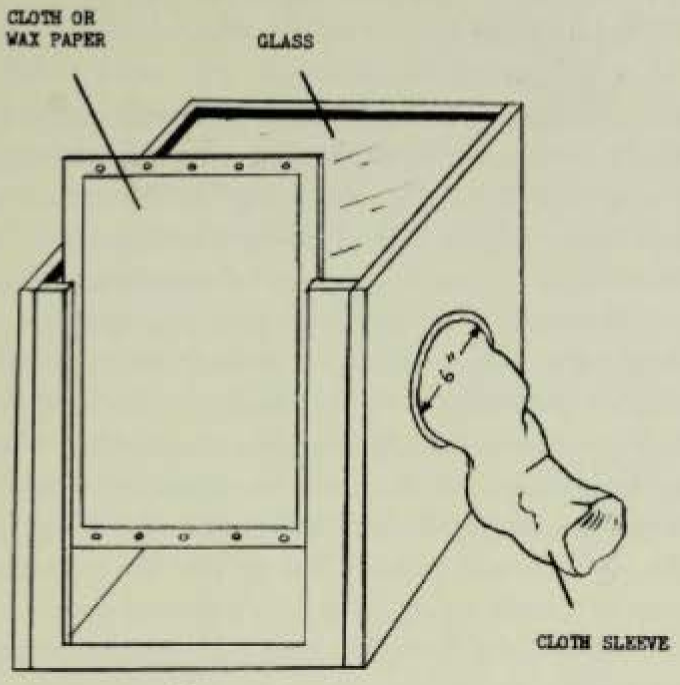
REARING MOTHS

Insects are great fun to observe and follow through their life cycles. There is one place in the world where one can spend an entire day observing a variety of insects in their own habitat. It is an insect zoo. Where else but in Japan would one find an insect zoo? Tokyo has such a place, where the public can watch insects under natural conditions as they pass through their life processes of metamorphosis, feeding, reproduction, and death. You can start your own insect zoo in a corner of your bedroom, garage, or basement.

Some beetles and certain insects, such as cicadas, may take years to go through their life cycle, but others, especially among the Lepidoptera, require only a few weeks. Sphingid and noctuid moths may pass through two or three generations in one spring or summer season.

THE MOTH CAGE

Many species of moths will mate and lay eggs in a cage two feet square by two feet high. This is an ideal size for the large saturnid and sphingid moths. Noctuid moths will mate in a smaller cage of one-foot dimensions. The type that I use for the corn earworm measures one foot by one foot by one and one-half feet high. Three sides are made of plywood; the top has a glass pane set in it for observation. In one side is a six-inch hole with a cloth sleeve tacked to its edge. This is the doorway for one's arm in and out of the cage; a rubber band keeps it closed. Another side of the cage has a sliding door to hold a piece of wax paper or stretched white cloth for an egg-laying surface. This is the side to face toward a window or dimly lighted portion of the room at night.



A cage for ovipositing moths, which may be about one or two feet square and about the same height.

GETTING EGGS

You may wish to get a well-known species to start with, perhaps a corn earworm or cabbage looper from your light trap or garden. Use W. J. Holland's *The Moth Book* to identify your species. July, August, and September are the best months to trap noctuid and sphingid moths. Place two to five pairs of one species in your cage and observe them at night with a flashlight covered with red cellophane. Moths that have already mated in the wild will begin oviposition as soon as the sun goes down.* They will crawl around on the dimly lit doorway facing the evening light, curving their abdomens and depositing eggs on the cloth or wax paper. Observe how the ovipositor emerges to deposit an egg. The corn earworm prefers the hairy surface of the cloth (like corn silk) but the cabbage looper prefers wax paper (like a smooth cabbage leaf). Divide the sliding doorway into quarters and cover each quarter with a different-textured surface: coarse cloth, smooth cloth, cellophane, wax paper, etc. Then see which surface collects the most eggs. This test is called an oviposition surface test.

Place the host plant of the species in the cage. If it is a little-known species of moth, check Holland's book to see if the host plant is known. If it is not, make a guess and try some plants at random. Record the number of eggs on the plant and at the various doorway surfaces. Where are the most eggs deposited? Surprisingly, more may be deposited on the cloth against the dim light than on the host plant. Shine very dim, different-colored lights on each quarter of a sliding doorway of one material and draw a graph showing the colored segment of the lighted cloth receiving the most eggs. Use your camera light meter to see if the intensities of light are about the same. This is a color preference test.

If the moths taken at the blacklight are virgins, you may be able to watch their first mating, but you must observe them often enough after 10 P.M. When the moths die, dissect the females and open up the bursa copulatrix. How many spermatophores do you find? This will tell you if the female has mated and how many times.

THE PHEROMONES

If you watch closely enough late at night you may be lucky and see the female "calling" a mate. Noctuids vibrate their wings at a very high rate, holding them partially raised over their backs. They sit in one place while vibrating and slowly move the tip of the ovipositor in and out of the tip of the abdomen. They are exuding a "sex stimulant" pheromone, and the males will soon become agitated and very active in the cage. Observe and describe how a male finally clasps the female abdomen.

You can carry the pheromone to a male yourself; but this experiment must be done at night under very dim light. Gently squeeze her abdomen toward its tip until she pushes out her ovipositor. Rub the tip of a toothpick on

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* See *Insect Behavior* for an inexpensive electronic method to alert you to oviposition activity.

the top of her ovipositor and along the last intersegmental membrane that separates the ovipositor from the abdomen (see the ovipositor picture in Chapter 12). This operation may take some patience in the dim light, but ordinarily you have no choice; daylight "programs" the moth so that it does not respond. Females call with the pheromone, and males respond, only after a certain minimum length of "dark time." If you wish to observe them during the day, some species (not all) can adapt to reversed day and night cycles by being kept in bright light all night and dark all day.

Bring the toothpick near the antennae of a resting male. They will vibrate up and down if you have picked up the pheromone from the ovipositor. The male will soon become active and start trying to mate with the end of the toothpick. He will fly about arching the tip of his abdomen, and his extended claspers will stretch out in a grasping motion toward the toothpick, or even toward another male flying nearby. A pheromone such as this is called a "releaser," since it releases a certain pattern of behavior. It does not attract from a very great distance—a few feet at most—but it stimulates and releases sexual behavior in the males of the species. See how many males you can stimulate with the toothpick. How long does the stimulation last, as judged by their holding their claspers out? Cut off a male's antennae with fine scissors. Does he still respond?

I have obtained the same clasper response from the males of certain species of moths—the pretty *Hieroglyphica* moth of the South, for instance, by radiating the male with narrow-band infrared radiation in the four-micrometer region. There is an atmospheric "window" in that region and water will not block such radiation by absorbing it. This frequency is also given off strongly by burning candles which, as we know, attract moths to their death. Remember that chemicals are small oscillators giving off infrared frequencies, and that the insect antennae "decode" these chemical frequencies because they are really multiple-array dielectric antennae tuned in phase to the oscillations of the molecule. An antenna is most certainly an electrical instrument; otherwise it would not vibrate in an alternating electrical field or respond to infrared and to light, as I have well proven in my laboratory.

LARVA-FEEDING EXPERIMENTS

Host plants placed in your cage can be kept green several days in vials of water. Take the cloth oviposition surfaces, or leaves from the plants with eggs on them, and place them in a glass jar or pint ice-cream carton until they hatch (three to five days at room temperature). Many species of moth larvae are cannibalistic, the corn earworm especially so; thus it is best to rear them separately. Collect a number of wide-mouth glass jars (baby-food jars are good) or small half-pint ice-cream cartons. With a small watercolor brush transfer the tiny millimeter-long larva to a leaf of the host plant. Place one in each container. Keep a little moisture (sand or a piece of wet sponge) on the bottom and cover each container loosely with a cardboard top so the container can exchange air and moisture with the outside. You may need to cover the cardboard with a screen to keep the large instar larva from chewing his way out.

Each time a larva molts, search for the tiny dark head capsule and measure it. It will be bigger with each molt. Unless you have a good microscope, or you can use one in your school biology lab, you may be able to measure for only the last few instars. In any case, measure these. How do the capsules increase in size? Remember Dyar's law in Chapter 12.

I sometimes transfer last instar larvae to an egg-crate type of rearing container. If you are handy you can make one of wood or galvanized tin. The bottom has a screen on it so that the frass, or droppings, will fall through it. It is excellent for larvae that eat the fruiting parts of plants. Earworm larvae can be raised on chunks of corn in each compartment. Remember that before the food gets dried out and hard the larvae should be transferred to fresh food in the containers.

Try different host-plant foods and see which the larvae feed on best. If they survive on various food plants, measure them and compare their size with larvae on the preferred food plant.

PUPATION AND EMERGENCE

Lepidoptera, before they pupate, get very pale, shriveled, and sickly-looking. They also get restless and may chew their way out of a cardboard container and escape. After they pupate, take them out and place them in the bottom of your moth cage on a soft cloth or in sawdust on the floor. In about 12 to 15 days some will begin to emerge from the pupa. Watch them work their way out of the pupal case. Sixty per cent of the time moths will emerge between 7:00 P.M. and midnight. This is the best time for observation. They will crawl up the cloth oviposition surface or rough wooden surface and cling there while the expanding wings are drying. Take notes on the length of time that it takes for the wing pads to expand to full form. How long does the moth hold them over its back, folded together, drying them?

ADULT FEEDING EXPERIMENTS

All you need for this experiment is a small paint brush and some women's hair clips. Clamp the moth's wings over its back between the tips of a hair clip. Set up 10 moths in a row by hanging the clips from small nails along a strip of wood. Suspend the wooden strip above a wooden

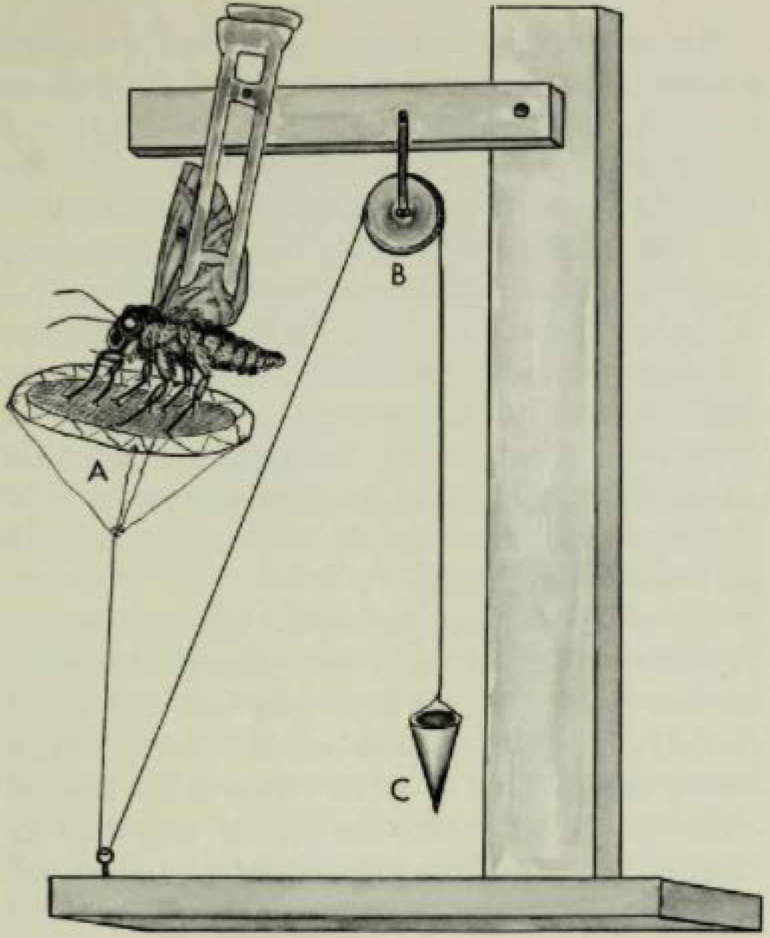
Corn earworm moth held by a hair clip and feeding from the tip of a paint brush soaked in sugar water. Note the opening of the ultrasonic ear in its side.

base by attaching a support at either end, keeping the strip just high enough so that the moths' legs will rest on the bottom strip. Most species of moths have a taste sensor on each segment of the antennae and the coiled proboscis. Some species may also have taste sensors on the bottoms of their prolegs.

From a high school chemistry book or science teacher, learn how to dilute solutions. Mix different concentrations of sugar water and dip a separate brush in each one to feed the moth. When the sugar food comes close to the antennae, the moth will uncoil its proboscis and suck up the food. Test for taste sensors by putting the wet brush tip near the antennae, front feet, and proboscis. Which organ, or organs, cause the moth to uncoil its proboscis? As the moth gets older it requires more and more food. Feed them on different concentrations of plain water, sugar water, and honey water, and compare the length of moth life on the various types and concentrations of foods. How much does each one drink? I have fed corn earworm moths in this manner and have found that they can be kept alive much longer than normal in this inactive position.

TESTING STRENGTH AND CLINGING ABILITY

You can build a simple rigging for testing the clinging ability of moths or other insects. Construct a wooden support with a base and a horizontal arm coming off the top. Obtain a small plastic or metal pulley about the size of a quarter and suspend it on an axle below the arm. With a length of stiff wire make a circular frame and attach the edges of a small piece of cotton cloth to it with thread. From four points on the frame run thread lines down to a point below the middle of the cloth surface and continue with a long single piece of thread. Run the single thread through an eye in the base and up over the pulley. At the end of the thread attach a small paper cup or cone to hold weights; this will hang free below the pulley.



Apparatus used in testing the clinging ability of a moth. *A*, test surface; *B*, pulley; *C*, paper cone for holding BB shot as weights.

Nail a hair clip to the arm a couple of inches from the pulley and clamp the moth's wing in it. Place the cloth surface under the insect's feet. The moth will cling to the surface and support the paper cone, at the other end of the thread, in the air. To test clinging ability, add BB shot to the cone until the weight of the cone increases enough to pull the surface away from the moth's feet. Count the number of BBs, or weigh them if you have a sensitive scale, and see how many it takes to pull the surface from the moth. You can calibrate your BB weights with a high school chemistry lab balance. Weigh them singly and in groups of 2, 3, 4, 5, etc., to set up weight standards. You will be surprised at how much an insect can support with just the bottom of its tarsi.

Test moths of different species and ages with weights. Try different leaf surfaces by taping host-plant leaves to the wire frame. Can the moth cling best to a villous (hairy) surface, to the top or bottom of a leaf, or to a smooth surface? Some leaves are villous on one side and smooth on the other. How are the leaf veins used for clinging? The earworm moth clings best to villous surfaces and chooses them for oviposition.

MECHANORECEPTORS AND HEARING

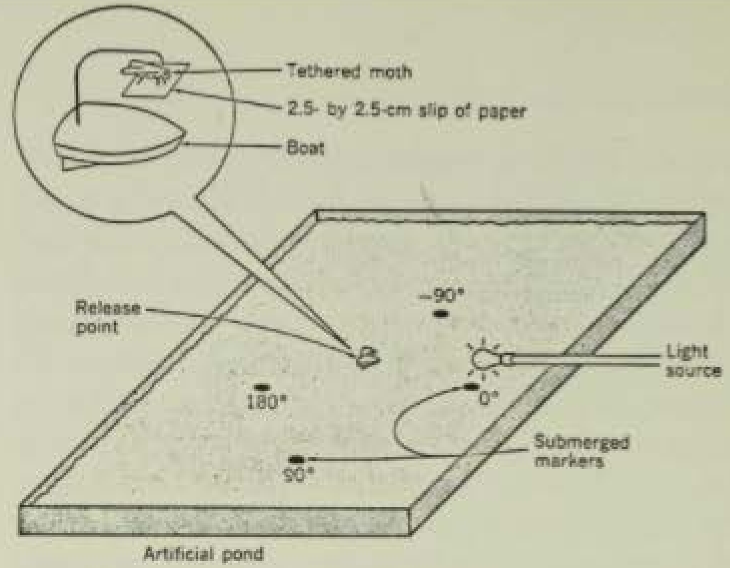
Note that when the surface is finally pulled away the moth often starts vibrating. Mechanoreceptors tell it that its legs are not touching a surface and that it is airborne. It makes no difference that the body is suspended in place by the tightly held wings. If the moth stops "flying," blow

gently and it will start again as the mechanoreceptors respond to the air flowing across the body. See if you can locate the sensors by cutting off the legs, edges of wings, etc.; see if the moth still responds by "flying" in place. Note the lengths of time moths fly while being held in place, comparing time spans of fed and unfed moths.

While the moth is suspended, or held for feeding experiments, make a sharp hiss through your teeth, or better yet, shake a group of keys on a key chain so that they rattle sharply. Note that some moths will be startled and pull the abdomen up. Click the keys over and over again until the sensitive moths no longer respond. The ultrasonic ear is well exposed to the high-frequency sounds, as can be seen in the photograph of a suspended moth. Your own ear is unable to hear the ultrasonic sounds, only the lower ones, from the clinking. The moth ear soon becomes conditioned and stops responding. This type of conditioning is similar to what happens in your ear. A car backfiring startles you once or twice, but you soon become conditioned to ignore it after a certain period of time. You might be startled again a half hour later, however. How long do you have to wait before the moth will give the startle response again?

FIELD OF VISION

With this very simple apparatus, designed by H. S. Hsiao, you can examine a moth's response to a point source of light. It consists of a tin tray about two feet square and a flashlight or small bulb as a light source. With a protractor mark off a series of angles on the bottom of the pan,



Apparatus developed by H. S. Hsiao using tiny keeled "boats," used to measure the attraction of the corn earworm moth to light.

with the zero degrees mark under the light. Make a small wooden boat or pointed platform about four times the size of your moth. Attach a keel on the bottom so that the boat won't spin in the water. The moth is suspended from a flat wire over the center of the boat. Attach the wire to the center of the top of the moth's thorax, between the wings. Rubber cement or some other good cement will sometimes hold, but a mixture of melted beeswax and rosin is better. Heat the tip of the wire and stick it into the mixture. Press the flat tip of the wire against the moth, allowing the mixture to harden. If you allow the moth to hold a small slip of paper while suspended (as in the clinging experiment) it will not fly. When the slip of paper is removed the moth will fly and propel the boat across the water.

Start it at different angles in front of the light. Plot the percentages of time a moth heads directly for the light from different angular positions. Paint out one eye with black enamel. In Mr. Hsiao's experiment he found that the moth response dropped off when the insects were started at a larger and larger angle from the side with the eye painted out. Cut off your moth's antennae and see if the percentage of times the moth flies directly to the light increases or decreases. Both Mr. Hsiao's and my own research have shown a connection between the eye and the antennae, but its significance to sensory perception is unknown at present.

After you have dissected a few insects and learned more about their organs, and have followed a species through its life cycle, you will certainly have a new appreciation of the wonderful diversity of insect life. These few simple experiments, or ones similar that you devise, will give you a much better understanding of the many fascinating ways that insects function.

Glossary

aeropyle A small air exchange pore that penetrates the shell of an insect egg.

airfoil Any flat surface, such as a wing, designed to produce lift.

amino acid A nitrogen-containing component of proteins that is the basic food reduced from the protein by the action of digestive enzymes.

amplitude The maximum height of departure of an alternating wave from the average value.

angle of attack The angle between the chord of the airfoil and the direction in which the airfoil is moving through the air.

aorta In insects, the anterior, nonchambered, narrow portion of the heart opening into the head.

axillary A sclerite of an insect wing which joins the wing to the thorax.

axon The principal nerve fiber of a neuron (nerve cell).

burble point Stalling angle of a wing; point at which air eddies over the wing and cause a dropoff of the lift.

bursa copulatrix The copulatory pouch of the female of moths and butterflies that receives the male spermatophore.

carbohydrates Compounds, such as starches and sugars, which contain carbon, hydrogen, and oxygen and are the most available source of energy for living cells.

chemoreception Perception of chemical stimuli, especially in liquid form—i.e., taste.

chitin A secretion of the epidermis found in the exoskeleton of insects.

chord The line extending from the leading edge to the trailing edge of a wing.

chordotonal organ An organ responsive to vibrations, especially sound.

chorion The outer shell of an insect egg.

corneal lens An individual outer lens structure of the compound eye.

corpus allatum A glandular organ near the brain that, like the corpus cardiacum, stores and relays hormones from the neurosecretory cells. It produces the juvenile hormone.

corpus cardiacum A glandular organ near the brain that stores and transfers hormones produced by the neurosecretory cells, and also produces hormones of its own.

crystalline cone The transparent subcorneal lens of the compound eye.

cytoplasm The protoplasm of a cell exclusive of the nucleus.

dendrite A fine branch extending from a nerve cell.

deutocerebrum The middle section of the insect brain, consisting of the paired antennae and olfactory lobes.

diapause A condition of suspended activity and reduced metabolic rate in insects.

dielectric antenna An antenna made of an insulating material such as plexiglass.

dielectric material An insulating substance capable of recovering as electrical energy all or part of the energy required to establish an electric field.

ecdysis The process of casting off the insect skin in molting.

ecdysone The hormone that causes molting.

endocuticle The inner, softer, colorless layer of the exoskeleton, consisting of chitin and protein.

enzyme A complex organic chemical produced by cells and causing change in other organic substances by catalytic action.

epicuticle The nonchitinous, external, filmlike layer of the exoskeleton.

epithelium The layer of cells that covers a surface or lines a cavity.

esophagus The part of the digestive system between the mouth and the crop.

exteroceptor An external receptor; usually refers to tactile hairs or spines on the exoskeleton.

fibril The finer fibrous structure of a muscle or nerve.

galea One of the outer two lobes that are joined together to form the coiled proboscis of moths and butterflies.

ganglion A nerve center composed of a mass of cells and fibers, and forming a center of the central nervous system.

glossa The paired inner lobes of the labium; sometimes also applied to the coiled proboscis of moths and butterflies.

hemimetabolous An adjective referring to an insect with incomplete metamorphosis.

hemocyte A blood cell of an insect.

hemolymph The lymphlike nutritive fluid (blood) of insects.

histogenesis The development of new tissues and organs in a pupa in preparation for adult life.

histolysis The degeneration of old tissues and organs in preparation for histogenesis.

holometabolous An adjective referring to an insect with complete metamorphosis—with egg, larval, pupal, and adult stages.

hormone An active catalyst, or chemical accelerating agent, of the ductless glands of an animal, which causes and regulates changes in its cells.

imaginal disk Thickenings of epidermal tissue in a pupa, from which new organs develop.

imago An insect in its final, adult state.

instar The form (stage) of an insect between molts of the larval stage; e.g., the first instar is the stage between the egg and the first molt.

invertase A digestive enzyme which converts sucrose (ordinary sugar) into glucose and fructose (invert sugars).

ion An atom that carries a positive or negative electric charge as a result of having lost or gained one or more electrons.

Johnston's organ An auditory organ located in the second segment (pedicel) of an insect's antenna.

juvenile hormone A chemical that controls the development of an insect by keeping tissues in a larval stage until the insect is ready to change into an adult.

labellum (pl., *labella*) The sponging portion at the tip of the housefly mouth part.

labium (pl., *labia*) The lower lip of an insect; a structure which forms the floor of the mouth.

larva (pl., *larvae*) An insect in the young stage, such as the grub or caterpillar stage.

lift That component of the total air force which is perpendicular to the relative horizontal air flow; the force which opposes gravity.

macromolecule A large molecule.

mechanoreceptor An insect receptor that responds to mechanical energy; e.g., sound, pressure, or touch.

metamorphosis The series of changes in form and organ arrangement that an insect passes through in its growth from egg to adult (e.g., egg, larva, pupa, adult).

microclimate The climate of a very small, restricted environment; e.g., the microclimate of a larva of the sugarcane borer is the climate inside the stalk of sugarcane.

micropyle The minute opening in the insect egg through which the sperm pass to fertilize the egg.

microtubules Small tubules, oriented in different directions, that make up the central rhabdomes of the retinula.

neuron A nerve cell.

neurosecretion A secretion given off by a neuron.

ocellus (pl., *ocelli*) The simple eye in adult insects, consisting of a single lens.

olfaction The perception of gaseous chemicals.

ommatidium (pl., *ommatidia*) An individual visual element of the compound eye.

ostium (pl., *ostia*) A slitlike opening in the insect heart.

oxygen tension The partial pressure of oxygen with which a liquid (within a cell) would be in equilibrium; the amount of oxygen dissolved in a given volume of liquid in equilibrium.

parthenogenesis Reproduction by direct growth from egg cells without fertilization by the male.

peritrophic membrane The thin cuticular membrane forming the inner lining of the ventriculus.

phagocyte A blood cell which destroys or absorbs harmful organisms and also absorbs the organs of the larval stage in the development to the adult stage.

phagocytosis The destruction of microorganisms or tissue by phagocytes.

pharynx The back part of the mouth, beginning of the esophagus.

pheromone A chemical released by a female insect that stimulates sexual response in the male. Many other pheromones are used for various types of insect communication.

pleuron (pl., *pleura*) A lateral (side) sclerite between the dorsal (upper) and sternal (lower) portion of the thorax.

polarized light Light in which the waves vibrate in a single plane.

proboscis A sucking organ of many insects.

prolegs The fleshy unjointed abdominal legs of caterpillars and sawfly larvae.

proprioceptor An internal sense organ that responds to changes taking place within the insect; e.g., movement of one sclerite in relation to another.

proventriculus The posterior (back) portion of the crop.

rectal pads Padlike columnar epithelium of the rectum that reabsorbs water, salts, and amino acids in the rectum.

resilin The chemical substance that gives resilience to the sclerites of the body that vibrate or snap.

retinula A group of two or more visual cells that contain on their inner margins the portion that makes up the longitudinal optic rod called the rhabdome.

rhabdome The optic rod lying in the axis of the retinula immediately below the crystalline cone of the eye. The light-sensitive unit of the eye.

rhabdomere A division of a rhabdome.

sarcolemma The elastic covering of the striated muscular fiber.

sarcoplasm The cytoplasm of striated muscle.

sclerite Any piece of the insect body wall enclosed by sutures, or boundary lines.

scolopale A hollow peglike structure enclosed in a scolopidium (scolophore); a sense rod enveloping the distal end of the sense cell in certain sense organs.

scolopidium (pl., *scolopidia*; same as *scolophore*) A spindle-shaped bundle of sensilla, usually attached to the integument and sensitive to pressure.

scolopoid sheath A cuticular sheath that surrounds the dendrites of certain mechanoreceptors.

semiconductor One of a class of solids whose feeble electrical conductivity is neither metallic nor electrolytic.

sensillum (pl., *sensilla*) An insect sense organ other than the eye or ocellus; usually spinelike.

solid-state physics The branch of physics that deals with electron movement in solids.

soma (pl., *somata*) The main body of a nerve cell.

spermatheca The sperm-storage organ of female insects.

spermatophore A sperm-containing capsule that is inserted into the female's bursa copulatrix during mating.

spiracle The breathing pore through which air enters the tracheae.

stadium (pl., *stadia*). The interval between the molts of larvae.

stereochemical An adjective referring to the shape and spatial arrangement of atoms and atom groups in molecules; e.g., the stereochemical theory of olfaction is based on the molecular form of the chemical.

stomatogastric Pertains to the nervous system that innervates the gastric (digestive) system.

taenidium (pl., *taenidia*) The chitinized thread that forms the tracheae of insects.

tapetum A reflecting surface within a compound eye, formed of densely massed tracheae.

trachea (pl., *tracheae*) A spirally ringed internal elastic air tube in insects, part of the insect respiratory system.

tritocerebrum The posterior division of the insect brain.

tymbal The drumlike circular membrane on the side of the first abdominal segment of a cicada. It produces the characteristic summer hum of the cicada.

tympanal An adjective pertaining to the membrane stretched across the air space in the ultrasonic auditory ear of the moths.

ultrasonic An adjective referring to wave phenomena of the same physical nature as sound but above the range of human hearing.

Upper Carboniferous A geological period during which the coal forests endured, approximately 300 million years ago.

vas deferens One of the paired tubes which carry sperm from the testes to the ejaculatory ducts of the male.

ventriculus The true stomach of an insect; midgut.

viviparous Bearing living young; e.g., as in plant lice (aphids).

wing loading The lift produced by each square foot of wing surface; given in pounds per square foot for airplanes.

Suggested Reading

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The author with Shillelagh, his trained Cooper's hawk. Birds as well as insects have a strong appeal for Dr. Callahan.

DR. PHILIP CALLAHAN was born in Fort Benning, Georgia, and grew up there. In World War II he served as a navigation and electronics specialist. After studying at Fordham University, he majored in zoology at the University of Arkansas. Later he studied entomology at Kansas State University, from which he received his Ph.D. degree in 1956. Dr. Callahan has been active in biological investigation for many years and has received three awards for his research. He is the author of 70 papers in scientific journals, magazine articles, and the book *Insect Behavior*.

He is at present teaching entomology at the University of Florida, Gainesville, and does research as an entomologist of the Insect Attractants, Behavior, and Basic Biology Research Laboratory, United States Department of Agriculture, in the same city. Dr. Callahan and his wife and four children live in Gainesville. His hobbies include falconry, photography, painting, and travel.

JACKET PHOTOGRAPH:
The earliest larval stage of a corn earworm moth, enlarged 800 times by a scanning electron microscope. (*Courtesy U. S. Department of Agriculture*)

Jacket design by Millicent Fairhurst