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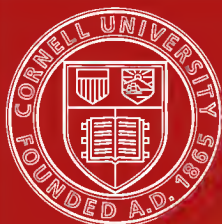
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TECHNICAL SERIES, No. 18.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY.

L. O. HOWARD, Entomologist and Chief of Bureau.

Gift of J. H. Comstock

THE ANATOMY OF THE HONEY BEE.

*Castell and Snodgrass — Papers on
Anatomy of Honey Bee.*

BY

R. E. SNODGRASS,

Agent and Expert.

ISSUED MAY 28, 1910.



WASHINGTON:
GOVERNMENT PRINTING OFFICE.
1910.

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Casteel (2nd & 3rd parts. in this vol.)

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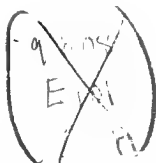
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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY,
Washington, D. C., October 19, 1909.

SIR: I have the honor to transmit herewith a manuscript entitled "The Anatomy of the Honey Bee," by Mr. R. E. Snodgrass, agent and expert, of this Bureau. It embodies the results of detailed studies made by Mr. Snodgrass and should prove of value as bringing to the bee keeper reliable information concerning an insect of such great economic importance, and also as furnishing a sound basis in devising new and improved practical manipulations. I recommend its publication as Technical Series, No. 18, of the Bureau of Entomology.

Respectfully,

L. O. HOWARD,
Entomologist and Chief of Bureau.

Hon. JAMES WILSON,
Secretary of Agriculture.

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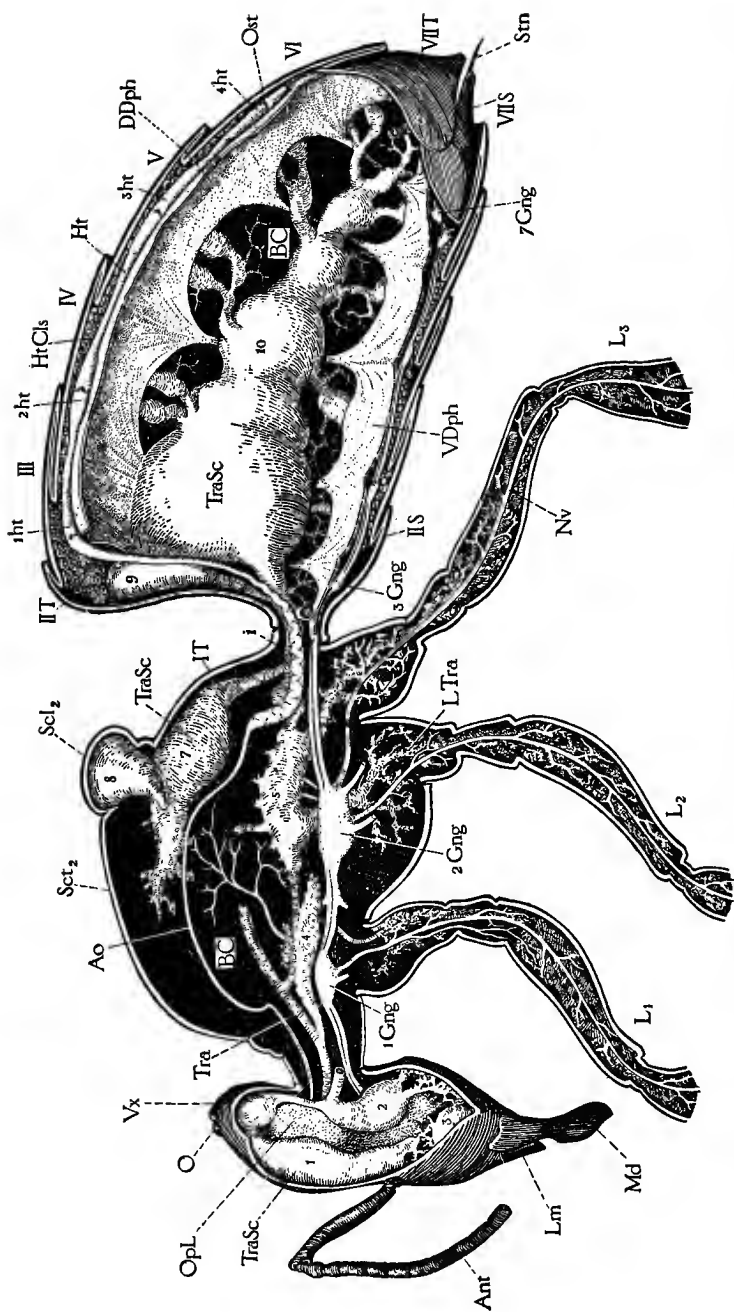


FIG. 1.—Longitudinal, median, vertical section of entire body of worker, showing nervous system (*OpL-7Gng*), tracheal system (*TraSc*, *1-10*), dorsal and ventral diaphragms of abdomen (*DDph* and *VDph*), and dorsal vessel consisting of heart (*Ht*) and aorta (*Ao*).

THE ANATOMY OF THE HONEY BEE.

I. INTRODUCTION.

The anatomy of the honey bee has been for years a subject of much interest to those engaged in bee keeping both for pleasure and for profit. This interest is due not only to a laudable curiosity to know more of the bee, but to the necessity of such information in order to understand fully what takes place in the colony. All practical manipulations of bees must depend on an understanding of the behavior and physiology of bees under normal and abnormal circumstances, and those bee keepers who have advanced bee keeping most by devising better manipulations are those, in general, who know most of bee activity. In turn, a knowledge of bee activity must rest largely on a knowledge of the structure of the adult bee.

Studies on the anatomy of the bee have not been lacking, for many good workers have taken up this subject for investigation. The popular demand for such information, however, has induced untrained men to write on the subject, and most accounts of bee anatomy contain numerous errors. This is probably to a greater extent true of the anatomy of the bee than of that of any other insect. Frequently the illustrations used by men not trained in anatomical work are more artistic than those usually found in papers on insect anatomy, and they consequently bear the superficial marks of careful work, but too often it is found that the details are inaccurate. It has therefore seemed the right time for a new presentation of this subject based on careful work.

The drawings given in the present paper are original, with the exception of figures 12, 54, and 55, and have been prepared with a thorough realization of the need of more accurate illustrations of the organs of the bee, especially of the internal organs. Mistakes will possibly be found, but the reader may be assured that all the parts drawn were seen. Most of the dissections, moreover, were verified by Dr. E. F. Phillips and Dr. J. A. Nelson, of this Bureau, before the drawings were made from them. An explanation of the abbreviations and lettering is given on pages 139-147.

It is hoped that the work will furnish the interested bee keeper with better information on the anatomy of the bee than has heretofore been offered to him, that it may provide a foundation for more detailed work in anatomy and histology, and, finally, that it will be

of service to future students of the embryology and physiology of the bee. With this last object in view the writer has tried to sum up under each heading the little that is at present known of insect physiology in order to bring out more clearly what needs to be done in this subject.

II. GENERAL EXTERNAL STRUCTURE OF INSECTS.

When we think of an animal, whether a bee, fish, or dog, we unconsciously assume that it possesses organs which perform the same vital functions that we are acquainted with in ourselves. We know, for example, that an insect eats and that it dies when starved; we realize therefore that it eats to maintain life, and we assume that this involves the possession of organs of digestion. We know that most insects see, smell, and perform coordinated actions, and we recognize, therefore, that they must have a nervous system. Their movements indicate to us that they possess muscles. These assumptions, moreover, are entirely correct, for it seems that nature has only one way of producing and maintaining living beings. No matter how dissimilar two animals may be in shape or even in fundamental constitution, their life processes, nevertheless, are essentially identical. Corresponding organs may not be the same in appearance or action but they accomplish the same ends. The jaws may work up and down or they may work sidewise, but in either case they tear, crush, or chew the food before it is swallowed. The stomach may be of very different shape in two animals, but in each it changes the raw food into a soluble and an assimilable condition. The blood may be red or colorless, contained in tubes or not, but it always serves to distribute the prepared food which diffuses into it from the alimentary canal. The situation of the central nervous system and the arrangement of its parts may be absolutely unlike in two organisms, but it regulates the functions of the organs and coordinates the actions of the muscles just the same.

Hence, in studying the honey bee we shall find, as we naturally expect to find, that it possesses mouth organs for taking up raw food, an alimentary canal to digest it, salivary glands to furnish a digestive liquid, a contractile heart to keep the blood in circulation, a respiratory system to furnish fresh oxygen and carry off waste gases, excretory organs for eliminating waste substances from the blood, a nervous system to regulate and control all the other parts, and, finally, organs to produce the reproductive elements from which new individuals are formed to take the places of those that die.

The study of anatomy or the structure of the organs themselves is inseparably connected with a study of physiology or the life functions of the animal. While physiology is a most interesting and important subject, and, indeed, in one sense might be said to be

the object of all anatomical research, yet the mere study of the structure of the organs alone, their wonderful mechanical adaptations, and their modifications in different animals forms a most fascinating field in itself, and besides this it gives us an insight into the blood relationships and degrees of kinship existing between the multitudes of animal forms found in nature. In the study of comparative anatomy we are constantly surprised to find that structures in different animals which at first sight appear to be entirely different are really the same organs which have been simply changed in a superficial way to serve some new purpose. For example, the front wing of a bee and the hard shell-like wing cover of a beetle are fundamentally the same thing, both being front wings—that of the beetle being hardened to serve as a protection to the hind wing. Again, the ovipositor of a katydid and the sting of a bee are identical in their fundamental structure, differing in details simply because they are used for different purposes. Hence, in the study of anatomy we must always be alert to discover what any special part corresponds with in related species. In order to do this, however, it is often necessary to know the development of an organ in the embryo or in the young after birth or after hatching, for many complex parts in the adult have very simple beginnings in an immature stage.

Thus it becomes evident that the structural study of even one organism soon involves us in the subjects of anatomy, physiology, and embryology, and, if we add to this a study of its senses, its behavior, and its place in nature, the field enlarges without limit. The student of the honey bee realizes that a lifetime might be spent in exploiting this one small insect.

The differences between animals are much greater on the outside than on the inside. In the descriptions of the organs of the honey bee anyone will know what is meant by the "alimentary canal," the "nervous system," or the "respiratory system," but the external parts are so different from those of animals with which we are more familiarly acquainted that no general reader could be expected to know what is meant by the names applied. Moreover, the bee and its allies are so modified externally in many ways that, at first sight, their parts look very different even from those of other insects. Hence, we shall give a preliminary account of the external structure of insects in general, for it is hoped that the reader will then more easily understand the special structure of the honey bee, and that the application of the terms used will appear more reasonable to him.

Since all animals originate in an egg, the change into the adult involves two different processes: One is *growth*, which implies merely an increase in size, the addition of material to material; the other is *development*, which means change in shape and the produc-

tion of a form with complex organs from the simple protoplasmic mass of the egg. The part of development that takes place in the eggshell is known as *embryonic development*; that which takes place subsequent to hatching is known as *postembryonic development*. In insects there are often two stages in the postembryonic development, an active one called the *larval stage* and an inactive one called the *pupal stage*. During the first of these the young insect is termed a *larva*; during the second, a *pupa*. When there is no resting stage the immature creature is often called a *nymph*. The final and fully developed form is an *adult*, or *imago*.

Since this paper is to deal only with the anatomy of the adult, the attractive fields of embryonic and postembryonic development must be passed over, except for a few statements on fundamental embryonic structure, a knowledge of which is necessary to a proper understanding of the adult anatomy.

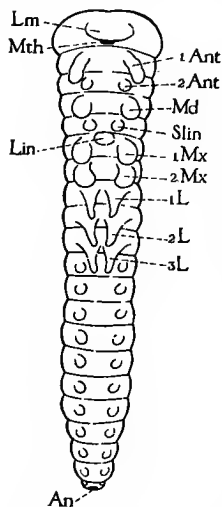


FIG. 2.—Diagram of a generalized insect embryo, showing the segmentation of the head, thoracic, and abdominal regions, and the segmental appendages.

When the embryo, in its course of development, first takes on a form suggestive of the definitive insect, it consists of a series of segments called *metameres*, or *somites*, and shows no differentiation into head, thoracic, and abdominal regions. Typically, each segment but the first is provided with a pair of latero-ventral *appendages*, having the form of small rounded protuberances. These appendages are of different sizes and take on different shapes in different parts of the body, for some of them are destined to form the antennæ, some the mouth parts, others the legs and perhaps the cerci, while the rest of them remain very small and finally disappear. What we know of the embryology of insects is based on the observations of a number of men who have worked mostly on the development of different species. Their observations are not all

alike, but this is probably due in large part to the fact that the embryos of different insects are not all alike. Embryos have a very provoking habit of skipping over or omitting little and yet important things in their development, but fortunately they do not all omit the same things. Therefore, by putting together all the reliable information we possess, we can make up an ideal embryo which would be typical of all insects. Such a generalized embryo is represented diagrammatically by figure 2.

The first six or seven metameres very early begin to unite with one another and continue to fuse until their borders are lost. These consolidated embryonic segments form the head of the adult insect.

Observers differ concerning the fate of the seventh segment, but it is most probable that a part of it fuses with the sixth segment, thus taking part in the formation of the head, and that a part of it forms the neck or some of the neck plates of the adult.

The appendages of these first seven segments form the antennæ and mouth parts, except one or two pairs that disappear early in embryonic life. It is not certain that the first segment ever possesses appendages, but from it arise the large compound eyes and apparently also the upper lip, or labrum (*Lm*). The appendages of the second segment form the feelers, or antennæ (*1Ant*) of the adult, those of the third (*2Ant*) disappear in insects, but they correspond with the second antennæ of shrimps and lobsters. The appendages of the fourth segment form the mandibles (*Md*). Those of the fifth segment (*Slin*), when present, fuse with a median tonguelike lobe (*Lin*) of the following segment, and the three constitute the hypopharynx, or lingua of the adult. The next pair (*1Mx*) form the maxillæ, while the last (*2Mx*), or those of the seventh segment, coalesce with each other and constitute the adult labium, or lower lip.

The bodies of the head metameres fuse so completely that it is impossible to say positively what parts of the adult head are formed from each. The last, as already stated, possibly takes part in the formation of both the head and the neck. Some embryologists attribute the plates which usually occur in this region to the last embryonic head segment, while others believe they come from the next segment following. Sometimes these plates are so well developed that they appear to constitute a separate segment in the adult, and this has been called the *microthorax*. If this name, however, is given to the embryonic segment from which these plates are said to be derived, it must be remembered that it is not "thoracic" at all and belongs partly to the head. The name *cervicum* has been applied to the neck region with greater appropriateness since it does not imply any doubtful affiliation with adjoining regions. What we really need, however, is not so much a name as more information concerning the development of the rear part of the head and the neck plates in different insects.

The next three segments remain distinct throughout life in nearly all insects, but, since they bear the legs and the wings, they become highly specialized and together constitute the *thorax*. The individual segments are designated the *prothorax*, the *mesothorax*, and the *metathorax*. The legs are formed from the embryonic appendages (fig. 2, *1L*, *2L*, *3L*) of these segments, but the wings are secondary outgrowths from the mesothorax and metathorax and are, hence, not appendages in the strict embryological sense.

The remaining segments, nearly always 10 in number, constitute the *abdomen*. The appendages of these segments, except possibly

those of the tenth, disappear early in embryonic life in all insects, except some of the very lowest species, in which they are said to form certain small appendages of the abdominal segments in the adults.

An adult insect is often described as being "divided" into a head, a thorax, and an abdomen, but this is not true in most cases. While all insects consist of these parts, the divisions of the body are usually not coincident with them. The prothorax in the adult is separated from the head by the neck and is very commonly separated from the mesothorax by a flexible membranous area. On the other hand, the mesothorax and metathorax are almost always much more solidly attached to each other, while, in most insects, the metathorax is solidly and widely joined to the first abdominal segment, though in the flies these latter two segments are usually separated by a constriction. In such insects as ants, wasps, and bees a slender, necklike peduncle occurs between the first and second segments of the abdomen, the first being fused into the metathorax so that it appears to be a part of the thorax. This is the most distinctive character of the order Hymenoptera, to which these insects belong.

The body wall of insects is hard on account of the thick layer of chitin which exists on the outer side of the true skin. Chitin is a substance similar to horn, being brittle, though tough and elastic. It gives form and rigidity to the body and affords a solid attachment for the muscles within, since insects have no internal framework of bones such as vertebrate animals have. The skin between the segments is soft and unchitinized and thus forms a flexible *intersegmental membrane* which is often very ample and, in the abdomen, allows each segment to telescope into the one in front of it.

The chitin of each segment is not continuous, but is divided into plates called *sclerites*. The most important of these are a *tergum* above and a *sternum* below, but, in the case of the thorax, these two plates are separated on each side by another called the *pleurum*, which lies between the base of the wing and the base of the leg. Pleural plates are sometimes present also on the abdominal segments. These principal segmental plates are usually separated by membranous lines or spaces, which permit of more or less motion between them. Such lines are called *sutures* in entomology, though strictly this term should be applied only to the lines of fusion between adjoining parts.

The terga, pleura, and sterna of each segment are furthermore subdivided into smaller sclerites, which may be termed *tergites*, *pleurites*, and *sternites*, respectively. The sutures between them are sometimes membranous also, but most frequently have the form of impressed lines or narrow grooves. In such cases they are generally nothing more than the external marks of ridges developed on the inside of the body wall to strengthen the parts or to give attachment to muscles. Since these sutures are conspicuous marks on the outside

of an insect, they are usually regarded as morphologically important things in themselves, representing a tendency of the tergum, pleurum, or sternum to separate into smaller plates for some reason. The truth about them would appear to be just the opposite in most cases—they are the unavoidable external marks of an internal thickening and strengthening of the plates. In a few cases they may be the confluent edges of separate centers of chitinization. Hence, most of the sutural lines in insects appear to signify a bracing or solidifying of the body wall rather than a division of it.

Since the body wall of insects is continuous over all the surface it contains no articulations of the sort that occur between the bones in the skeleton of a vertebrate. Although insects and their allies belong to the class of animals known as the Articulata, yet an articulate articulation is simply a flexibility—two chitinous parts of the exoskeleton are movable upon each other simply by the intervention of a nonchitinated, flexible, membranous part. While there are often special ball-and-socket joints developed, these are always produced on the outside of the membranous hinge and simply control or limit the movement of the articulation.

The head of an adult insect is a thin-walled capsule containing the brain, the ventral head ganglion of the nervous system, the pharynx and anterior part of the œsophagus, the tracheal tubes, and the muscles that move the antennæ and the mouth parts. Its shape varies a great deal in different insects, being oval, globular, elongate, or triangular. In some it is flattened dorso-ventrally so that the face is directed upward and the mouth forward, but in most, including the bee, it is flattened antero-posteriorly so that the face looks forward and the mouth is directed ventrally. In a few it is turned so that the face is ventral. The walls of the head are usually divided by sutures into a number of sclerites, which in general are located and named as follows: The movable transverse flap forming the upper lip is the *labrum*. Above it is a sclerite called the *clypeus*, which is a part of the solid wall of the head and carries the anterior articulations of the mandibles. The clypeus is sometimes divided transversely into an *anteclypeus* ("clypeus anterior," "epistoma") and into a *post-clypeus* ("clypeus posterior"). Above the clypeus is the *front*, a plate usually occupying the upper half of the face between the compound eyes and carrying the antennæ. The top of the head is called the *vertex*, but does not constitute a separate sclerite. The sides of the head below the compound eyes are often separated by sutures from the anterior and posterior surfaces and are known as the *genæ*. The back of the head is formed by the *occiput*, which surrounds the large opening or *foramen magnum* that leads from the cavity of the head into that of the neck. The parts posterior to the genæ, carrying the posterior mandibular articulations,

are sometimes separated from both the occiput and the genæ and are known as the *postgenæ*. In a few insects, especially beetles, one or two median plates occur in the ventral wall of the head posterior to the base of the labium. These are the *gular* sclerites. Finally, small plates are sometimes found about the bases of the antennæ and between the bases of the mandibles and the genæ. The latter have been termed the *trochantins of the mandibles*. The term *epicranium* is often used to include all the immovable parts of the head, but is frequently applied only to the dorsal parts. Most of these sclerites preserve a pretty definite arrangement in the different orders, and they are probably homologous throughout the entire insect series, though they are in some cases very much distorted by special modifications and are often in part or wholly obliterated by the disappearance of the sutures. Embryologists are coming to the conclusion that the sclerites of the head have no relation to the primitive segments. The latter very early consolidate into a head with a continuous wall, while the sutures defining the sclerites are formed later. Some of the older entomologists were led, from a study of the sclerites, to suppose that the head consisted of a number of segments, but it has been shown that these anatomical segments do not correspond with the embryonic ones.

The appendages growing from the front of the face are the **antennæ** (fig. 9A, *Ant*) or "feelers" and consist of a series of joints or segments.

At the lower edge of the face is the front lip or *labrum* (fig. 9A, *Lm*), behind which are the median *epipharynx*, the paired *mandibles* (*Md*) and *maxillæ*, the median *hypopharynx*, and the *labium* or under lip. All these organs together constitute what are known as the *mouth parts* or *trophæ*. They vary greatly in shape and appearance in different insects according to the nature of the food, but their typical form is usually taken to be that shown by the lower insects which feed on solid food and have biting mouth parts. Figure 3, representing the jaws and lips of the common black cricket, is given as an example of generalized insect mouth parts.

The **labrum** (fig. 9A, *Lm*) is usually a simple transverse flap in front of the mouth, being developed, as already shown, from a similarly situated lobe on the first segment of the embryo (fig. 2, *Lm*).

The **epipharynx** (fig. 19, *Ephy*) is a sort of dorsal tongue, and is situated on the membrane leading into the mouth from behind the labrum.

The **mandibles** (figs. 3A; 9A, *Md*) are typically formed for biting, being heavy organs situated immediately behind the labrum and working sidewise on a hinge articulation with the head. Their cutting edges are usually notched and toothed, though smooth in the worker bee.

The **maxillæ** (fig. 3 B and B) are complicated appendages in their typical form. Each consists of a principal piece called the *stipes* (*St*), which is hinged to the head by means of a smaller basal piece, the *cardo* (*Cd*). Terminally the stipes bears an outer lobe, the *galea* (*Ga*), and an inner lobe, the *lacinia* (*Lc*). On the outer side, at the base of the galea, it carries a jointed appendage called the *maxillary palpus* (*Plp*).

The **hypopharynx** (fig. 3 C and D, *Hphy*) is a median, ventral, tonguelike organ, called also the *lingua*, situated either on the upper surface of the labium or on the membrane between this organ and the mouth. It is developed principally from a median lobe of the head of the embryo behind the mouth (fig. 2, *Lin*), but some entomologists claim that it is compounded of this lobe and two smaller lateral ones developed from the appendages of the fifth embryonic head segment (fig. 2, *Slin*), the *superlinguæ*.

The labium (fig. 3 C and D) constitutes the under lip of the adult, but it is formed from the two appendages of

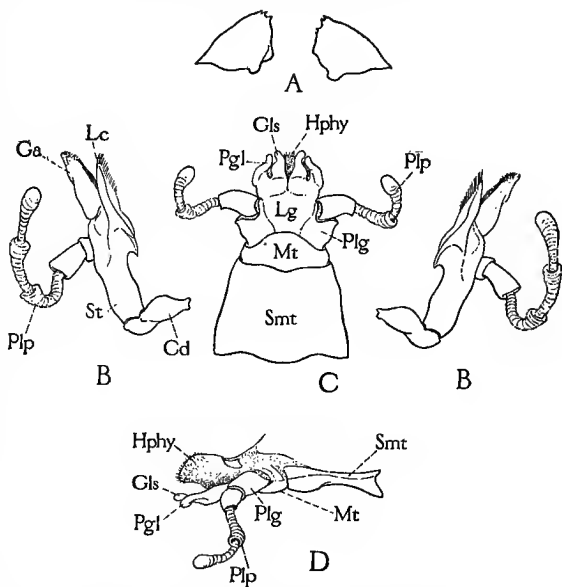


FIG. 3.—Example of generalized insect mouth parts, from common black cricket (*Gryllus pennsylvanicus*): A, mandibles; B, B, maxillæ, ventral view; C, labium or second maxillæ, ventral view; D, labium, lateral view.

the seventh segment in the embryo, which fuse with each other. For this reason it is often called the *second maxilla*. It consists of a basal *submentum* (*Smt*) bearing the *mentum* (*Mt*), which in turn carries three parts, a median *ligula* (*Lg*) and two lateral *palpigers* (*Plg*). The latter support the *labial palpi* (*Plp*), while the ligula bears four terminal lobes, of which the median ones are called the *glossæ* (*Gls*) and the lateral ones the *paraglossæ* (*Pgl*). If we should cut the labium into two parts along its midline we should see that even in the adult stage each half is very similar to one maxilla. The only discrepancy to be noticed in the example given (fig. 3) is that, there

is no maxillary palpiger, but many insects possess a corresponding part in the maxilla, frequently distinguished as the *palpifer*.

The **neck** or **cervicum** is usually a short membranous cylinder which allows the head great freedom of motion upon the thorax. In nearly all insects its lateral walls contain several small plates, the *cervical sclerites*, while, in many of the lower species, dorsal, ventral, and lateral sclerites are present and highly developed. As already stated, the origin of these plates is doubtful. Some entomologists would derive them from the prothorax, others think they come from the last head segment, while still others think that they represent a separate segment. Only pure anatomists, however, entertain this last view and call this supposed segment the "microthorax," for embryologists have not yet reported a metamere between the labial segment and the prothoracic segment. Most embryologists who have studied the subject admit that some of the cervical sclerites may be formed from the last embryonic head somite which carries the labium and probably forms a part of the back of the head. Therefore, if it is desirable to retain the word *microthorax* as a name for a true segment, it can be applied only to this labial metamere.^a

The **thorax**, as has already been stated, is a distinct anatomical region of the body rather than a "division" of the body, since it carries both the legs and the wings and contains the large muscles for each. Since the prothorax does not possess wings, it is not so highly developed otherwise as the two wing-bearing segments, and is, indeed, generally reduced in some ways, some of its parts being frequently rudimentary. Therefore we shall base the following description of a typical segment on the structure of the wing-bearing segments.

A typical thoracic segment, then, presents four surfaces, as does also the entire body. These are a *dorsum* above, a *venter* below, and a *latus*^b on each side. From these names we have the terms "dorsal,"

^a In a former paper on the thorax of insects (Proc. U. S. Nat. Mus., XXXVI, 1909, pp. 511-595) the writer probably drew a too definite conclusion on the subject of the "microthorax." The origin of the neck sclerites has probably never yet been actually observed. Comstock and Kochi (Amer. Nat., XXXVI, 1902, pp. 13-45), in summarizing the segmentation of the head, accredited the gular and cervical sclerites to the labial segment, but did not recognize the latter as taking part in the formation of the true head capsule. Riley, however, in his study of the development of the head of a cockroach (Amer. Nat., XXXVIII, 1904, pp. 777-810), states that in *Blatta* the labial segment does form a part of the back of the head and that the posterior arms of the tentorium are derived from it. Börner (Zool. Anz., XXVI, 1903, pp. 290-315) and Crampton (Proc. Acad. Nat. Sci. Phila., 1909, pp. 3-54) believe that the cervical sclerites are derived principally from the prothoracic segment. The notion that they constitute a separate segment, the "microthorax," equivalent to the maxilliped segment of the centipedes, has been elaborated principally by Verhoeff in his numerous writings on the Chilopoda and Dermaptera.

^b The writer introduces this word here because he knows of no other term applied to the side of the segment in this sense.

"ventral," and "lateral." The chitinous parts of the dorsum constitute the *tergum*; of the venter, the *sternum*; and of the latus, the *pleurum*.

The *tergum* of the wing-bearing segments usually consists of two plates—a front one or true *notum* (fig. 4, *N*) carrying the wings, and a posterior one, which the writer has termed the *postnotum* or *pseudonotum* (*PN*), having no connection with the wings. The first is often more or less distinctly marked into three transverse parts called the *prescutum* (*Psc*), *scutum* (*Sct*), and *scutellum* (*Scl*). In such cases the exposed part of the postnotum is called the *postscutellum* (*PscI*). From either the anterior or the posterior margin of the *tergum*, or from both, a thin transverse plate projects downward into the interior of the thorax for the attachment of muscles. These plates are the *phragmas* (*Aph* and *Pph*). The notum supports the wing on each side by two small lobes, the *anterior* and *posterior notal wing processes* (*ANP* and *PNP*). Behind the latter is the attachment of the *axillary cord* (*AxC*) or basal ligament of the wing. A large V-shaped ridge on the under surface of the notum having its apex forward is the "entodorsum." (A better name would be *entotergum*.)

The *pleurum* consists principally of two plates, the *episternum* (fig. 4, *Eps*) and the *epimerum* (*Epm*)' lying before and behind a vertical groove, the *pleural suture* (*PS*), which extends from the *pleural coxal process* (*CxP*) below to the *pleural wing process* (*WP*) above. The pleural suture marks the position of a heavy internal ridge, the *pleural ridge* or *entopleurum*. The epimerum is connected with the postnotum (*PN*) behind the base of the wing. These parts occur in almost all insects. In some of the lower ones another plate is present in front of the episternum which may be called the *preepisternum* (*Peps*).^a Lying along the upper edge of

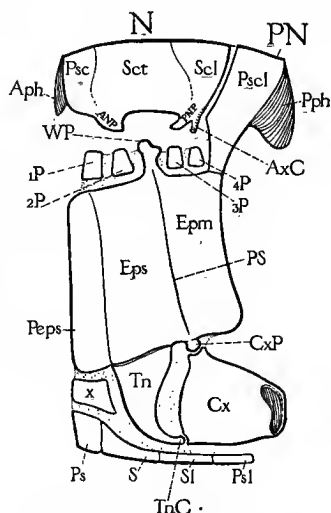


FIG. 4.—Diagram of generalized thoracic segment, left side.

^a Objection may be made to the use of the term "preepisternum" on the ground that it combines a Latin prefix with a word compounded of Greek elements. The same may be urged against "prephragma," "postphragma," "preparaptera," and "postparaptera," words introduced by the present writer in a former paper on the thorax (Proc. U. S. Nat. Mus., XXXVI, 1909, pp. 511-595). However, we are barred from making up equivalent terms with the Greek prefixes *pro* and *meta* because these are used to designate the first and the third

the pleurum and associated with the under surface of the wing base are several small plates known as the *paraptera* (*P*).^a Two lie above the episternum in front of the pleural wing process and are the *episternal paraptera* or *preparaptera* (*1P* and *2P*), while one or occasionally two are similarly situated behind the wing processes and are the *epimeral paraptera* or *postparaptera* (*3P* and *4P*). The preparaptera afford insertion for the muscle concerned in the extension and pronation of the wing.

The *coxa* (*Cx*), or basal segment of the leg, is hinged to the segment by a dorsal articulation with the pleural coxal process (*CxP*), and by a ventral articulation (*TnC*) with a plate called the *trochan-tin* (*Tn*) lying in front of it and connected above with the lower end of the episternum (*Eps*). Hence, while the leg is of course continuous all around its base, by means of membrane, with the body-wall, its movement is limited to a hinge motion by these two special articulations of the chitin.

The **sternum** or ventral plate of the segment is not so complicated as are the tergum and pleurum. It is often divided transversely into three parts, however, and some authors say typically into four. These parts have been named the *presternum* (*Ps*), *sternum proper* (*S*),

segments of the thorax or their respective parts. Entomologists have already established the system of referring a part to the front or back of any individual segment by the Latin prefixes *pre* (or *præ*) and *post* as used in "prescutum," "presternum," "postscutellum," and "poststernellum." Furthermore, *pre* and *post* are so indiscriminately used in English combined with Latin, Greek, and even Anglo-Saxon words that they may be regarded as general property. Hence, in order not to sacrifice an anatomical system, which certainly needs to be fostered in every way, the writer has preferred to sacrifice strict grammatical rules by applying *pre* and *post*, regardless of the origin of the noun in the case, to designate anterior and posterior parts of the same segment. We already use such hybrid terms as "presternum," "mesotergum," and "metatergum."

The name "preepisternum" has been applied by Hopkins (Bul. 17, Pt. I, technical series, Bur. Ent., U. S. Dept. Agr., 1909) to a part of the mesepisternum of *Dendroctonus*—a plate apparently not homologous with the preepisternal element of the thorax in primitive insects.

"The name "parapterum" is taken from Audouin's term *paraptère* (Ann. des Sci. Nat., I, 1824, pp. 97-135, 416-432), and its application, as used by the present writer, is based on Audouin's definition given in his Chapter III, "*Considerationes generales sur le Thorax*," where he says (p. 122): "Finally there exists a piece but little developed and seldom observed, connected with both the episternum and the wing. It is always supported by the episternum and is sometimes prolonged ventrally along its anterior margin, or again, becoming free, passes in front of the wing and may even come to lie above the base of the latter. At first we designated this sclerite by the name of *Hypoptère* but on account of its change of position relative to the wing base we now prefer the name of PARAPTÈRE." The first part of his description leaves no doubt that Audouin referred to the little pleural plate beneath the front of the wing which is usually very inconspicuous except in carefully dissected

sternellum (*Sl*), and *poststernellum* (*Psl*). In some of the lower insects a plate (*x*) occurs at each side of the presternum or of the sternum which seems to fall in line with the preepisternum of the pleurum. This has been variously called a *part of the presternum*, the *coxosternum*, an *accessory sternal plate*, and the *sternal laterale*. The inner surface of the sternum carries a large two-pronged process called the *furca* or *entosternum*.

This plan of structure for the mesothorax and the metathorax prevails throughout all insects. The honey bee probably presents the greatest departure from it, but even

here the modification consists principally of a suppression of the sutures of the pleurum resulting from a condensation of the parts.

The leg (fig. 5) of an adult insect consists of a number of joints or segments. It is attached to the body, as just described, by a thick

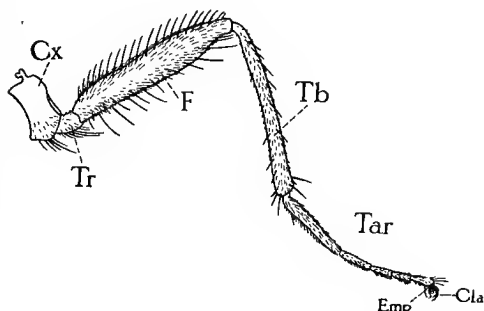


FIG. 5.—Typical insect leg.

specimens. In such preparations, however, one finds that there are in most cases two sclerites here instead of one, and, furthermore, that one or occasionally two others are similarly situated beneath the rear part of the wing base behind the pleural wing process. The present writer has, therefore, made the term "paraptera" cover this whole row of little plates, distinguishing those before and those behind the pleural wing process by the designations given above.

In the latter part of Audouin's definition it would seem that he may have confused the rudimentary tegula as it exists in some insects with the parapterum, but even this is not probable since he says it is always connected with the episternum, which is never true of the tegula. In his description of the thorax of beetles, *Dytiscus*, *Carabus*, *Buprestis*, and *Curculio*, it is evident that he regards the anterior upper part of the episternum as the parapterum fused with the latter plate. In fact, in each case he definitely states that such is the case and, in describing *Dytiscus circumflexus*, he says (p. 420): "The episternum, the parapterum, and the epimerum all fuse dorsally and constitute a support for the wings and tergum." While Audouin is undoubtedly mistaken in this homology, especially in the mesothorax, he at least shows that his "paraptère" is a part of the plenium. Hence modern writers such as Packard and Folsom who make the term "paraptera" synonymous with "tegulae" are certainly wrong. The tegula is a dorsal scale or its rudiment at the humeral angle of the wing, while the parapterum is a co-existent sclerite below this part of the wing base. The present writer agrees with Comstock and Kellogg, who, in their *Elements of Insect Anatomy* (first edition), define the little sclerite in front of the base of the wing in the locust, articulated to the dorsal extremity of the episternum, as the "parapteron," though in this insect there are here really two of these parapteral plates instead of one.

basal joint called the *coxa* (*Cx*). Beyond this is a smaller joint called the *trochanter* (*Tr*), this is followed by a long and strong segment, the *femur* (*F*), which extends outward from the body, while bending downward from its distal end is the long and slender *tibia* (*Tb*), followed finally by the foot, or *tarsus* (*Tar*). The tarsus itself consists typically of five small segments of which the last bears a pair of *claws* (*Cla*). The under surfaces of the tarsal joints are often provided with small cushions or pads called *pulvilli*. Those between the claws are generally specially prominent and are called the *empodia* (*Emp*). The leg varies greatly in shape in different insects but usually preserves all of these parts. The segments of the tarsus, however, are frequently reduced in number.

The **adult wing** is a thin expanse of *membrane* supported by hollow branching rods called *veins*. It originates as a hollow outgrowth of the body-wall, but soon becomes flattened out dorso-ventrally and the

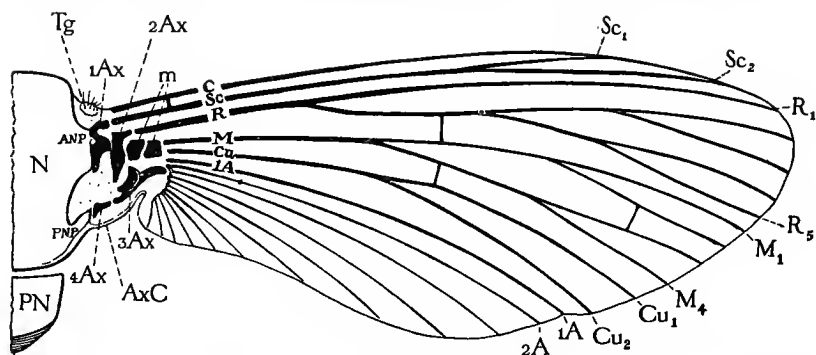


FIG. 6.—Diagram of generalized insect wing and its articulation to first plate (N) of the tergum.

contained tracheæ or air tubes mark out the courses of the veins. These veins form various patterns in different insects, but they can all be derived by modification from one fundamental plan. This plan is shown diagrammatically by figure 6. The first vein, which usually forms the anterior margin of the adult wing, is the *costa* (*C*). The next vein is the *subcosta* (*Sc*), which in typical cases divides into two branches (*Sc*₁ and *Sc*₂). The third and usually the principal vein is the *radius* (*R*). It divides dichotomously into five branches (*R*₁ to *R*₅), the anterior branch of the first fork remaining single. The next vein is the *media* (*M*), which forms four branches (*M*₁ to *M*₄). The fifth is the *cubitus* (*Cu*), which again is two-branched. The remaining veins are called the *anals* and are designated individually as the *first anal* (*1A*), *second anal* (*2A*), etc.

Several *cross-veins* of common recurrence should be noted. The first is situated near the base of the wing between the costal and subcostal veins and is known as the *humeral cross-vein*. A second

occurs between the radius and the media near the center of the wing and is called the *radio-medial cross-vein*. Another one, the *medio-cubital*, is similarly located between the media and the cubitus, while a fourth, called the median, occurs between the second and third branches of the media. The areas of the wing surface inclosed by the veins, the cross-veins, and the margins of the wing are known as the *cells*.

A great many different names are applied by different entomologists to the veins of the wings, both of the same and of different insects. The nomenclature here given is the one first consistently applied by Comstock and Needham and now used by a large number of entomologists working in different orders of insects.

The wing is articulated at its base (except in mayflies and dragonflies) to the anterior and posterior wing processes of the notum (fig. 6, *ANP* and *PNP*) and to the wing process of the pleurum (fig. 4, *WP*) by several small articular sclerites called *axillaries*. Two of these, the *first* (*1Ax*) and the *fourth* (*4Ax*), form a hinge with the anterior and the posterior notal wing processes, respectively, while the *second* (*2Ax*) articulates below with the wing process of the pleurum, constituting thus a sort of pivotal element. The *third axillary* (*3Ax*) intermediates between the bases of the anal veins and the fourth axillary—except when the latter is absent (as it is in nearly all insects except Orthoptera and Hymenoptera), in which case it articulates directly with the posterior notal process. The thin membrane of the wing base may be called the *axillary membrane* (*1xM*). On its anterior edge is a hairy pad, the *tegula* (*Tg*), which is sometimes a large scale overlapping the humeral angle of the wing. The posterior margin of the axillary membrane is thickened and may be called the *axillary cord* (*AxC*) or *basal ligament* of the wing.

The base of the costa is not directly associated with any of the axillaries, but is specially connected by tough membrane below with the episternal paraptera. The subcosta abuts against the end of the curved neck of the first axillary. The radius is either attached to or touches upon the anterior end of the second. The media and cubitus are usually associated with each other at their bases and also more or less closely with one or two *median plates* (*m*) in the wing base. These plates, however, are not of constant shape and occurrence as are the articulating axillaries. The anals are generally attached to the outer end of the third axillary, which acts as a lever in the folding of the wing.

A few insects have a generalized wing almost identical with the diagram (fig. 6), but most of them depart from it in varying degrees. Few go so far, however, as the honey bee, whose venation is very different, but yet the fundamental basal structure is the same even

here, as will be shown in the special description of the wing of the bee.

The **abdomen** consists almost always of 10 segments. There are never any more than this number well developed in adult insects, and if there are fewer the reduction is due to a modification of the terminal segments to accommodate the external organs of reproduction. The posterior opening of the alimentary canal is at the end of the tenth segment, which carries also two small appendages at the sides of the anus. These are called the *cerci* (fig. 8, *Cer*). In some insects they are short, styletlike processes, in others they are long and many jointed, while in many they are absent. The cerci are supposed to be developed from the embryonic appendages of the tenth segment, although, on the other segments, these appendages disappear before the embryo hatches, except in some members of the lowest wingless order of insects, which have a pair of cercuslike appendages on each segment of the abdomen.

Each abdominal segment presents a tergum above and a sternum below; the former usually also reaches far down on the sides and overlaps the edges of the sternum. In some insects one or more small pleural plates intervene between the tergum and the sternum, but the abdominal pleura are never developed in any way suggestive of a thoracic pleurum. Very frequently there is present an upper pleural plate, or *epipleurite*, adjoining the edge of the tergum and a lower, or *hypopleurite*, adjoining the edge of the sternum. The line separating these two sclerites, however, is horizontal and can not correspond with the vertical suture of a thoracic pleurum between the episternum and the epimerum extending from the base of the leg to the base of the wing.

The most complicated structures on the abdomen are the external organs of reproduction. In the male these serve as *clasping organs* and take on a great variety of forms in different species. The organs in the female form an *ovipositor* and are of much more definite and constant structure.

The *ovipositor* (fig. 8), in its most perfect development, consists of three pairs of long, closely appressed bladelike processes called *gonapophyses* (1*G*, 2*G*, 3*G*). These six pieces fit neatly together and form an organ by means of which the female makes a hole in the ground or in the bark of a tree, or punctures some other insect, and then places her eggs in the cavity thus produced. An interesting fact in this connection is that the sting of a wasp or bee is simply a modified ovipositor. This can be proved by a comparison of the organs themselves or by a study of their development. Each is formed from six little peglike processes that grow out from the sterna of the eighth and ninth abdominal segments of the larva or young soon after hatch-

ing (fig. 7, *1G*, *2G*, and *3G*). At first there is only one pair of these processes on each of the two segments, but those on the ninth soon split each into two, thus producing two pairs on this segment. The opening of the oviduct (*OvO*) is on the eighth segment between the bases of the first gonapophyses.

The ovipositor of the longhorned grasshopper, shown by figure 8, may be taken as a typical example of this organ. The median pair of gonapophyses on the ninth segment (*2G*) remain slender and fuse at their bases into a small bulblike swelling open below (*ShB*). The pair from the eighth segment (*1G*) form two long blade-like pieces, which fit by sliding articulations upon the lower edges of the corresponding second gonapophyses (*2G*). The first can therefore be worked back and forth while they are braced and held in position by the second pair. The third gonapophyses (*3G*), or the outer pair of the ninth segment (the left one in figure 8 is shown as if cut off near its base), form two long flat blades which are closely appressed against the outer surfaces of the others. In the detailed study of the bee it will be shown how closely the structure of the sting corresponds in every way with that of this ovipositor.

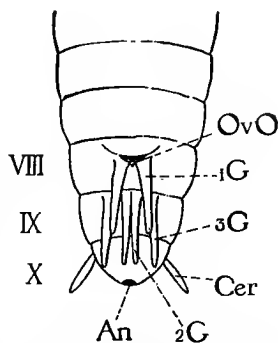


FIG. 7.—Diagram of terminal abdominal segments of a female insect and early stage in development of gonapophyses (*1G*, *2G*, and *3G*), from which is formed the ovipositor of most insects and the sting of wasps and bees.

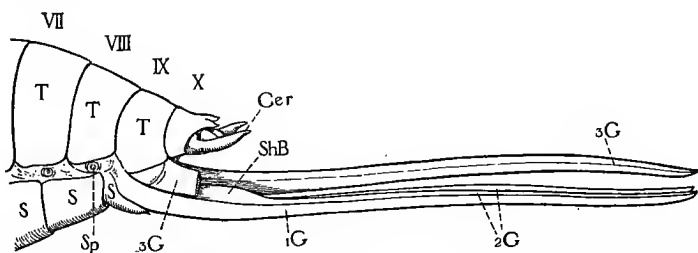


FIG. 8.—Example of a swordlike ovipositor, from a longhorned grasshopper (*Conocephalus* sp.), illustrating the fundamental similarity of structure with the sting of the bee, fig. 3G.

Some entomologists have supposed that the original two pairs of gonapophyses represent the embryonic appendages of the eighth and ninth segments, and they would thus establish a homology between the ovipositor or sting and the legs and mouth parts. It has been shown, however, that the true appendages of the abdominal segments disappear in embryonic life while the gonapophyses appear much later, during early nymphal or larval life. Furthermore, each pair

of gonapophyses arises in a median depression on the ventral side of the segment while the true appendages are latero-ventral. Hence, the evidence is very much against this theory and the gonapophyses appear to be special secondary processes of the body wall.

All insects do not have ovipositors of the sort described above. Flies, beetles, moths, and butterflies do not. Such insects simply drop their eggs from the orifice of the oviduct or deposit them in masses upon the external surfaces of various objects. In some of the flies, however, the terminal segments are long and tubular and entirely telescoped into one another. They are hence capable of being protruded in the form of a long tapering tube having the opening of the oviduct near the tip. This enables the insect to deposit its eggs in deep crevices, but the structure is not a true ovipositor—it is simply the abdomen itself stretched out.

Insects breathe through a series of small holes situated along each side of the body. These breathing apertures are called *spiracles* and they lead into a system of internal air tubes called *tracheæ*. There are nearly always 10 spiracles present on each side of the body. Two are located on the thorax, the first between the prothorax and the mesothorax, the second between the mesothorax and the metathorax, while the other eight are situated on the first eight abdominal segments. Some embryologists believe that the spiracles of the prothorax move forward in early embryonic life and unite with each other in front of the hypopharynx to form the salivary opening, their tracheæ constituting the salivary ducts.

After this review of the general external structure of insects we may proceed to a more detailed account of the parts and organs of the honey bee.

III. THE HEAD OF THE BEE AND ITS APPENDAGES.

The head of an insect, as already explained, is a composite organ formed of six or seven primitive segments, each of which, except the first, typically bears a pair of appendages (fig. 2). The antennæ are developed from the embryonic appendages of the second segment, the mandibles from the fourth, the maxillæ from the sixth, and the second maxillæ, or labium, from the seventh. The appendages of the third segment disappear in early embryonic life while those of the fifth segment, when the latter is present, fuse with a median tonguelike lobe of the next segment to form the hypopharynx of the adult.

1. THE STRUCTURE OF THE HEAD.

The general appearance and outline of the head of a worker bee are shown from before and behind by figure 9, A and B. In facial view the head is triangular, with the apex below. The side angles

are rounded and capped by the large compound eyes (*E*). In the opposite direction the head is very much flattened, the greatest diameter being crosswise through the middle of the eyes. The face is convex, while the posterior surface is somewhat hollowed out and fits snugly upon the anterior end of the thorax.

The large lateral eyes (fig. 9 A, *E*) are called the **compound eyes**, because each is composed of a large number of separate eye elements forming the little hexagonal *facets* visible on the surface. All of these facets together constitute the *cornea*, or the transparent outer surface of the eye, which in the bee is densely clothed with long hairs. The dark color of the eye is located in the deeper parts, but these will be described in the section dealing with the nervous system. On the

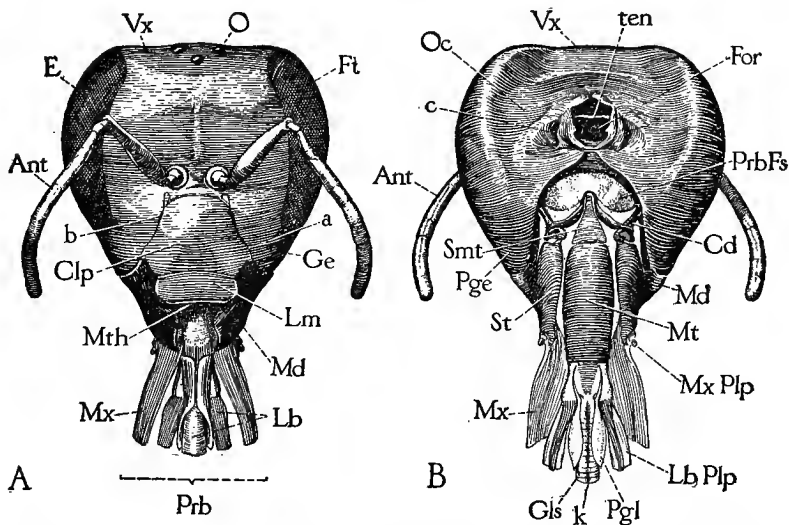


FIG. 9.—A, front view of head of worker bee with mouth parts (*Prb*) cut off a short distance from their bases; B, corresponding view of posterior surface of head.

top of the head between the compound eyes are the three simple eyes, or *ocelli* (*O*), arranged in a triangle with the median ocellus in front.

Between the lower halves of the large eyes and near the center of the face arise the *antennæ* (*Ant*), each of which is inserted into a small, circular, membranous socket of the head wall, and consists of a long, basal, 1-segmented stalk carrying a terminal 11-jointed arm movably articulated to the stalk and generally hanging downward from it. (In the drone the terminal arm consists of 12 joints.)

The **mouth parts** are attached at the lower part of the head, and consist of the *mandibles* (*Md*) laterally and the *maxillæ* (*Mx*) and *labium* (*Lb*) mesially. The latter two include the set of elongate bladelike organs surrounding the protrusible "tongue," which together constitute what is commonly known as the *proboscis* (*Prb*).

When not in use the parts of the proboscis are bent back beneath the head. By referring to figure 9B, giving a posterior view of the head, it will be seen that the basal parts of both the maxillæ (*St*) and the labium (*Mt*) are suspended in a large hollow on the back of the cranium. This may be called the cavity or *fossa* of the proboscis (*PrbFs*). Between the mandibles on the front of the head (fig. 9A) is a transverse movable flap, the *labrum* (*Lm*), attached to the lower edge of the front wall of the head and constituting the upper lip. The *mouth* (*Mth*) lies behind the labrum and the mandibles close beneath it.

Below the antennal sockets is a transverse, slightly arched suture (*a*) which turns downward on each side and extends to the inner angles of the bases of the mandibles. The area bounded by this suture is the *clypeus* (*Clp*) and the suture itself may be called the *clypeal suture*.

On the posterior surface of the head (fig. 9B) is seen the pentagonal *foramen magnum* (*For*) by means of which the cavity of the head communicates with that of the thorax and through which pass the nerves, œsophagus, blood vessel, and tracheal tubes. A small rod (*ten*) inside the head arches transversely over the foramen magnum, cutting it into a dorsal and a ventral half. At each side of the foramen is a large pit (*c*) which marks the base of an internal chitinous beam of the head known as the mesocephalic pillar. The opposite end of this pillar unites with the front wall of the head on the clypeal suture below the antennæ, where it produces another smaller pit (*b*).

Below the foramen magnum and separated from it by a wide transverse bridge of the cranial wall is seen the large fossa of the proboscis (fig. 9B, *PrbFs*) having the shape of an inverted U. The side walls of this cavity are chitinous and from their upper edges are suspended the maxillæ, while the base of the labium is contained in the membranous floor of the fossa. The base of the labium projects from the head beneath or behind the mouth opening and its dorsal surface forms the floor of a preoral cavity surrounded by the bases of the mouth parts and labrum.

It will be seen from the above description that the head wall of the bee contains no suture except that bounding the clypeus and the one which separates the labrum from the latter. Many of the higher insects have the head wall completely continuous, showing no division at all into sclerites, but, in such forms as a grasshopper or cockroach, and, in fact, most of the lower insects, the head as well as the other parts of the body is made up of a number of plates. Hence this may be regarded as the primitive condition, and it is presumed that the head of the bee has been produced from one whose wall was divided by sutures into a number of distinct parts. Therefore the different

regions of the bee's head may be named according to the sclerites with which they correspond in other insects. Thus, the part of the face above the clypeus and between the compound eyes may be called the *front* (fig. 9A, *Ft*), the parts below the compound eyes the *genæ* (*Ge*), and the top of the head the *vertex* (*Vx*). The area on the back of the head around the foramen magnum may likewise be termed the *occipital region* (fig. 9B, *Oc*) and the parts behind the genæ and the lower halves of the compound eyes the *postgenæ* (*Pge*).

The worker, queen, and drone differ conspicuously in the shape and size of the head, as will be seen by comparing A, B, and C of figure 10. In these drawings the front has been removed in order to show various internal parts, which will be described later. While the head of the worker (A) is triangular in facial view, that of the queen (B) is more rounded and wider in proportion to its length. The head of the drone (C) is much larger than that of the female and is nearly circular in outline. In shape the head of the queen is intermediate between that of the worker and that of the drone, but in size it is somewhat smaller than the head of the worker. The eyes (*E*) of the worker and queen are about equal, but those of the drone are enormously enlarged and are broadly contiguous on the vertex and the upper part of the front. On this account the ocelli (*O*) of the drone are crowded down on the front nearer the bases of the antennæ and the front itself is very much narrowed above. The antennæ of the drone consist of 13 segments, while those of the females have but 12 segments. The mandibles are largest proportionately in the queen and are very small in the drone. Those of the worker have a smooth terminal edge, while this edge is notched in the queen and the drone. The parts of the proboscis are much longer in the worker

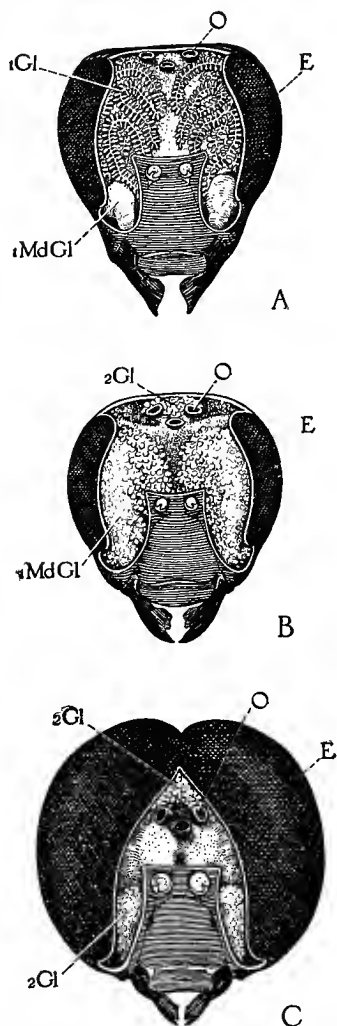


FIG. 10.—A, anterior view of head of worker, with front, antennæ, and proboscis removed; B, corresponding view of head of queen; C, same of drone.

and capable of much more action than in the queen and drone, which are almost entirely dependent upon the workers for their food.

The internal structure of the cranium may be studied best in a longitudinal section of the head (fig. 11). In order to prepare a section for this purpose imbed the head in paraffin and then carefully slice off one side with a sharp knife or razor just outside of the bases of the mandible and antenna. Holding the remainder in the block of paraffin or fastening the whole in a dish of water or alcohol, carefully dissect away the soft parts from the head cavity so as to expose

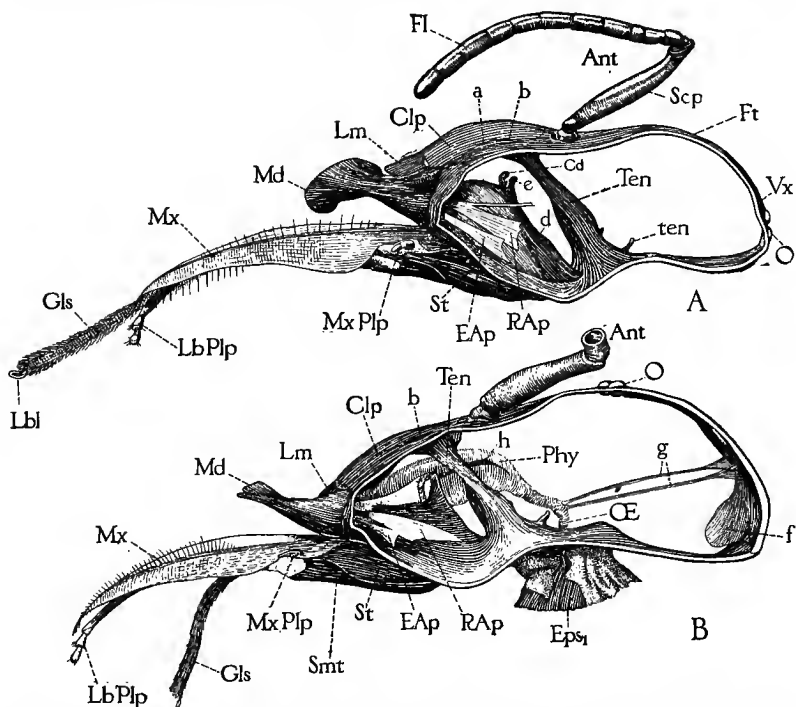


FIG. 11.—A, longitudinal section through head of worker between the median plane and outer edges of mandibles (*Md*) and antennæ (*Ant*) of left side, all internal soft parts removed; B, corresponding section through head of drone, except that the pharynx (*Phy*) and œsophagus (*CE*) are not removed.

the internal chitinous parts shown in figure 11 A and B. These figures, however, represent a slice of the head taken from between the median plane and the outer edges of the antennal and mandibular bases of the left side. Thus only the parts on one side of the mid-line are shown. Figure A is from a worker and Figure B from a drone. In the latter the pharynx and œsophagus are retained and the neck is not removed. Figure 20 shows the head cut open from above and the mouth parts removed. A specimen so cut and boiled a short time in caustic soda or potash to remove the soft parts will be found a valuable adjunct to this study.

The principal parts of the internal skeleton of the head, or *entocranium*, consist of two large, oblique, strongly chitinous bars forming a brace between the anterior and the posterior walls of the head (fig. 11 A and B, *Ten*, showing the parts on the left side only, and fig. 19, *Ten*). These bars have been named by Macloskie (1881) the *mesocephalic pillars*. As already pointed out the base of each is marked externally by a conspicuous pit (fig. 9 B, *c*) laterad of the foramen magnum, and its facial end by a smaller pit (fig. 9 A, *b*) in the clypeal suture near the upper end of each side of the latter. The bases of these pillars are connected by the slender bar (fig. 11 A, *ten*), already noticed, arching over the foramen magnum (fig. 9 B, *ten*). This bar and the two pillars represent what is called in other insects the *tentorium*. In the embryo the tentorium is formed from tubular ingrowths of the head wall which unite internally and assume different shapes in different insects. Since the air tubes of the body also first appear as tubular ingrowths of the body wall, some entomologists have supposed that the hollow tentorial ingrowths of the head represent the spiracular tubes of the head which are, otherwise, lacking. However, there is not sufficient evidence to support such a view as this, and there is no reason why the tentorium should not have been originally designed simply to give greater rigidity to the walls of the head where the latter support the appendages.

The usual form of the tentorium in the lower insects is that of an X, with a large central body, situated like a brace across the lower part of the head, having two of the arms directed anteriorly and laterally and two directed posteriorly and laterally, and while the former are said to be ingrowths from the mandibular segment, there is some difference of opinion concerning the segment to which the latter belong. Riley states that they are formed in the labial segment of the cockroach and Carriere and Burger describe the same thing for the mason bee. Other authors have ascribed them to the maxillary segment, but they may, in later stages, lie in this segment and thus appear to belong to it, while they originated in the one following, having moved forward on account of the condensation of the back part of the head. The tentorium of the honey bee, consisting as it does of the two great mesocephalic pillars (fig. 11 A and B, *Ten*) and the small arched bar (*ten*) is so highly modified that it is hard to see just how its parts are to be homologized with the parts of an X-shaped tentorium. Probably the two pillars represent the separated halves of the X, while the slender arch is an additional structure. In any case we have not enough evidence to warrant us in regarding the tentorial invaginations as modified tracheæ, or their external pits as rudimentary spiracles. Similar processes extend inward from the walls of the thorax to strengthen it or to give attachment of muscles. Such processes in general form the

entoskeleton and are individually called *apodemes*. Those of the head constitute the *entocranium*, those of the thorax the *entothorax*.

The side walls of the fossa of the proboscis form two high, thin, vertical plates, as seen from the interior of the head (fig. 11), in front of the mesocephalic pillars. The posterior edge (*d*) of each of these plates is so much thicker than the rest of it in the worker that it appears at first sight to be a separate rod. Its upper end projects above the body of the plate as a free arm (*e*) to which is articulated the basal piece of the maxilla (*Cd*). It thus constitutes the *maxillary suspensorium*. (Macloskie includes under this term both the arm of the cranial wall and the cardo of the maxilla.)

The head of the drone (fig. 11 B) presents, besides the parts described, a thin plate (*f*) depending from the vertex of the cranium along the line between the compound eyes.

Besides these apodemes of the cranial wall itself there are others which project into the head cavity from the bases of the appendages to afford points of insertion for their muscles. These are specially developed in connection with the mandibles and will be described in the discussion of these organs. Still other internal chitinizations are developed in the walls of the pharynx, but these likewise will be described later.

2. THE ANTENNÆ AND THEIR SENSE ORGANS.

The antennæ of the bee are the two slender, jointed appendages movably attached to the center of the face, where each is inserted into a circular membranous area or socket just above the upper part of the clypeal suture. Their general shape and position are shown by figures 9 A, 11 A, and 19, *Ant*. Each is seen to consist of two parts, forming a prominent elbow with each other, and usually so held that the first or proximal part extends outward and upward from its frontal attachment and carries the other in a pendent position from its distal end. The first part thus forms a basal stalk, called the *scape* (figs. 9 A; 19, *Scp*), consisting of a single joint inserted into the antennal socket of the front by a prominent basal condyle bent toward the face. This articular knob is attached to the rim of the socket by a circle of membrane, but it is also pivoted on a slender peglike process projecting upward from the lower edge of the socket. Hence, while the flexible membrane allows each antenna to revolve freely in any direction, the latter is at the same time held firmly in position by the pivot. The antennæ are moved by special sets of muscles inserted upon their bases within the head. The second or distal division of the antenna is cylindrical and longer than the first, forming a flexible *flagellum* (fig. 9 A; 19, *Fl*) hanging downward from the distal end of the scape. It is composed of 11

small joints in the worker and queen and of 12 in the drone. The male antenna thus consists of 13 joints in all, while that of the female has but 12. The first joint of the flagellum is freely articulated to the scape, but the others do not have much play upon one another, though they give flexibility to the flagellum as a whole.

Each antenna is a hollow tube containing the large antennal nerve, minute extensions of the tracheal system, and the small muscles which move the segments upon one another.

Popularly the antennæ of insects are known as the "feelers," because they are constantly moved about in all directions with a nervous kind of motion as if the creature were feeling its way along by means of them. In fact "feelers" is a better name for these appendages than the scientific term, for there can be no doubt that the sense of touch is very highly developed in them and that by means of them insects acquire a great deal of information concerning their surroundings and their companions. Moreover, a large mass of evidence derived from experiments shows unquestionably that the organs of smell also are located upon the antennæ in a great many if not all insects, while some investigators believe that in some species they carry in addition the organs of hearing.

The study of the senses of insects is a most elusive subject, and becomes more so the more we ponder on the results of experiments. In the first place, it is manifestly impossible for us to acquire any real knowledge of an insect's sensations, for what is to us an odor, a taste, a color, or a sound may be something quite different to such a differently organized creature. We can, however, by experiments determine that some things which give us the sensation of an odor are perceived also by insects when placed near them. Also it can be shown that some of them distinguish substances of different taste in their food, and likewise that they perceive movement and distinguish the colors and in a vague way the outlines of objects. Furthermore, it is known that some of their perceptions are more delicate than ours, and that some insects at least see color where we see none. They may even possess senses of which we have no conception.

Hence, while it can be positively stated that insects perceive differences of touch, taste, smell, sound, and light, and act accordingly, we can not say what the sensations they acquire are like. In fact we do not know that they have conscious sensations at all. What looks like an action due to intelligent perception may be purely a reflex one, unaccompanied by any sensation. This of course involves the question as to whether such creatures or insects are possessed of consciousness or not—a question which can not be answered one way or the other.

Understanding, then, that our knowledge of insect senses amounts only to this, that what gives us the sensation of light, sound, taste,

touch, or smell makes also some sort of an impression on the insect and varies in degree and kind much as it does in us, we may go on to a study of the senses located on the antennæ.

Here, again, however, we are confronted by a difficulty, for while, at first thought, it seems very easy to hold some strong-smelling substance near the antennæ of a beetle, ant, or bee and observe the evident displeasure with which the creature turns away, yet we may be entirely wrong if we conclude that the insect "smells" the substance that repels it. Strong-smelling, volatile liquids may simply produce pain in some of the delicate nerve endings of the antennæ. Some other kind of a being, experimenting on our senses, might close up our nose and mouth and prove that we smell by means of our eyes on observing the blinking we should perform when strong formalin or ammonia was held close to the face. Furthermore, irritant gases and volatile liquids affect the mucous membranes of our noses and throats in a way quite independent from the odor that we perceive, and there is no reason why the same may not be true of insects. As pointed out by Forel, experiments on the sense of smell should be made with odorous substances that the insect meets with in a state of nature, which would be principally the materials it feeds on. Insects are indifferent to almost every mildly odorous substance not used as food, which, however, does not prove that they do not smell them.

Again, in many cases, it would be difficult to decide whether the results of an experiment should be accredited to smell or sight. For example, every bee keeper knows that hungry bees are attracted to honey a long distance from their hives, and it would seem almost self-evident that they are guided by a sense of smell. Yet one might contend that they find the honey by sight, as, indeed, is claimed by a number of entomologists who have made experiments on the olfactory powers of bees. This question has been decided in some other insects by painting the eyes with some opaque substance or by removing the antennæ, but the evidence is not conclusive on either side in the case of bees.

Experiments made by a large number of competent investigators, including Lubbock, Schiemenz, and Forel, have proved conclusively that the organs of the sense of smell in insects are located principally on the antennæ. The most interesting of these experiments are perhaps those which Forel (1903) made on carrion-feeding beetles. He found the dead and putrid bodies of a hedgehog and a rat infested by a swarm of these beetles belonging to several genera. He collected more than 40 specimens from the carcasses and removed their antennæ. Then he placed them all at one place in the grass and moved the dead bodies to a distance of 28 paces from the beetles where he concealed them in a tangle of weeds. Examination the next day

revealed the fact that not one of the mutilated beetles had found the carcasses. Repeated experiments gave the same results—no beetle without its antennæ was ever found on the dead animals, although at each examination new individuals of the several species were present. It might be supposed that the mutilation itself distracted the beetles to such an extent that they did not care to eat. In order to test this point Forel next cut off all the feet on one side of the body from a dozen intact beetles and changed the location of the dead bodies again. The next day five of this lot were found on the carcasses.

The same results have been obtained from experiments on other insects. Ants distinguish between their comrades and enemies by means of their antennal sense organs. Males of the silkworm moth and many other moths and butterflies perceive the presence of the females and are guided to them by an evident sense of smell located on the antennæ, for they fail completely to find them when these appendages are removed, although one immediately recognizes a female when placed in contact with her.

Similar experiments have been made on the bee, testing the ability of the workers to find honey hidden from their sight. The results, according to Forel, seem, curiously enough, to indicate that bees can perceive odors but a very short distance from their heads. Forel found that hungry bees in a cage would pass and repass hundreds of times within a few millimeters of some honey concealed from their sight by a lattice without discovering it. They ate it greedily, however, when the lattice was removed, though it had been perfectly accessible to them all the time. Forel believes that "bees guide themselves almost exclusively by vision," and Lubbock holds the same opinion. At the same time it would probably be a very difficult matter to convince many practical bee keepers that bees do not "smell" from long distances. It is a well-known fact that at times when nectar is scarce bees are attracted in large numbers to the houses of an apiary where honey is stored, though, when the natural flow is sufficient, they pay no attention to it. Tests of the olfactory sense should undoubtedly be made under natural conditions. Bees inclosed in a box with some honey concealed from their sight might not be able to locate it in such close quarters though they might be smelling it all the time. An odor in a room may so fill the air that it does not seem to come from any particular direction and we ourselves would have to exert our intelligence to discover its source.

While, then, it does not seem probable that bees have such limited olfactory powers as some investigators claim their experiments indicate, it may be accepted as proved that the organs of smell are located principally on the antennæ. It has already been stated that the sense of touch also is very highly developed on these organs, although in a less sensitive degree it is distributed over most of the other parts of

the body. It is again specially developed on the palpuslike appendages of the sting. (See figs. 36 and 37, *StnPlp.*) Sections of a bee's

antenna show that there are on its surface a great number of minute structures of several different kinds, though all apparently are to be regarded as modified hairs, which are undoubtedly the sense organs. Now the difficulty arises of deciding which of these to assign to the sense of touch and which to the sense of smell. Different authors have made such different interpretations of the sense organs of insects that the student attempting to get information on the subject from books must soon be discouraged by their conflicting statements. But it must be realized that only intelligent guessing is possible where several senses are located on the same part. In the case of the bee some authors have ascribed even a third sense, that of hearing, to the antennæ, but there is little evidence that bees possess the power of hearing. The senses of taste and touch are possessed by the mouth parts, and some entomologists think that they contain organs of smell also. Thus, the organs of sight are apparently the only ones that can not be confused with some other sense.

The best account of the antennal sense organs of the

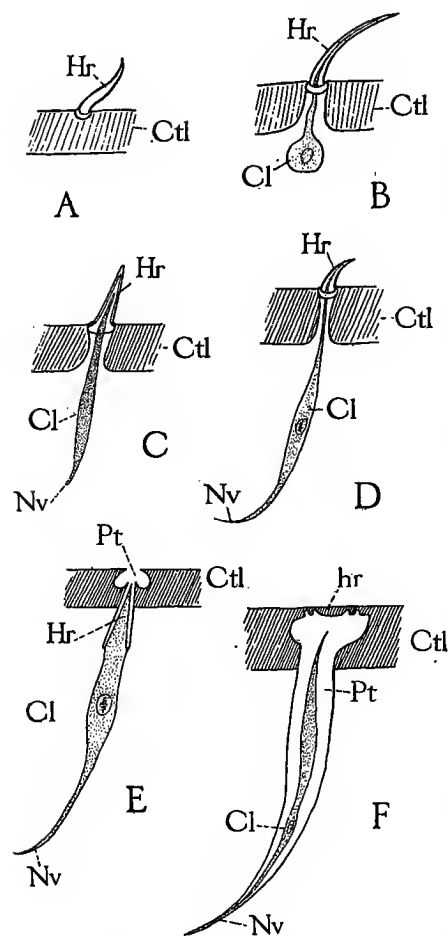


FIG. 12.—Antennal hairs and sense organs (after Schiemenz). A, example of antennal hairs (*Hr*) imbedded in cuticle (*Ctl*) but having no nerve connection; B, hollow hair containing prolongation of special cell (*Cl*); C, D, straight and curved tactile hairs connected with basal cells (*Cl*) and nerve fibers (*Nv*); E, conical hair (*Hr*) sunken in a pit (*Pt*) of the cuticle, probably an olfactory organ; F, closed sac shut in by thin disc (*hr*) on surface of antenna and containing a delicately poised cell (*Cl*) with nerve connection (*Nv*).

bee is that of Schiemenz (1883), whose drawings are here reproduced (fig. 12) and whose text is the basis of the following descriptions. The organs consist, as before stated, of modified hairs and their basal

insertions which are connected with the ends of nerve fibers. Some of them stand exposed on the surface of the cuticle while others are sunken into, or entirely concealed within, pits of the integument. In addition to these, there are two other kinds of special hairs on the antennæ which have no nerve connections, while, finally, the ordinary hairs, such as are found on all parts of the body, occur also on them, especially on the scape.

The special hairs not provided with nerve endings are of two sorts. One is a solid curved or hooked hair (fig. 12 A, *Hr*) which is simply articulated into a socket of the cuticle (*Ct*), while the other (B) is hollow and is situated over a channel through the cuticle, and contains a prolongation of a specially enlarged epithelial cell (*Cl*) lying beneath it. These hairs can not be regarded as sensory, since they have no communication with the central nervous system, and it is not clear just what purpose they do serve.

The simplest sensory organ is a short, hollow, conical hair (C, *Hr*) arising directly from the surface of the cuticle, over a wide opening through the latter, and containing the end of a sensory cell (*Cl*) connected with a nerve fiber (*Nv*), which goes into the main trunk of the axial antennal nerve. A modified form of this organ consists of a curved hair (D, *Hr*) set into a small depression over the cuticular channel. Such hairs are probably tactile in function; that is to say, by means of them the bee can perceive that its antennæ are in contact with some surface. The general integument is too thick and dense to allow of any sort of delicate touch sensation being communicated through it, but if one of these movable hairs brushes against an object the nerve within it must be at once stimulated. Tactile or touch hairs are distributed especially over the outer surface of the antennæ and at its apex, but occur also scattered over the other parts of the body and on the mouth parts.

Microscopic sections of the antennæ reveal still other organs which are not so apparent on the surface as the hairs just described. One of these is shown at E of figure 12. It consists of a small pit (*Pt*) in the integument, widened basally, and having a small papilla on its floor, in whose summit is the opening of a still deeper cavity which also expands toward its deeper end. This inner cavity is almost filled up by a conical plug (*Hr*) which arises from its floor and ends just below the aperture into the outer pit. The plug contains a thick nerve ending which arises from a ganglion cell connected with the antennal nerve by a nerve fiber. Ten or more of these sense organs occur on the terminal and the first three segments of the flagellum. It is evident that each is simply a sensory hair which has been doubly sunken into a cavity of the integument.

As before stated, it has been conclusively proved by several investigators that bees perceive odors, and it is said that if the antennæ are covered with shellac, bees can distinguish between distasteful substances only by means of the proboscis. Schiemenz and most other writers on the subject therefore conclude that the sunken cones are the organs of smell, since, being below the surface, they could not be organs of touch. Some other authors, however, among whom are Cheshire, regard these inclosed cones as hearing organs. They suppose that the sound waves of the air enter the pit, as into an ear cavity, and these set up a vibration in the cone which stimulates the attached nerve ending. However, the appearance of one of these cones would suggest that it is too stable a structure to be affected by sound waves, so the olfactory theory seems much more probable.

Finally, Schiemenz describes the most specialized of all the antennal sense organs as a closed cavity (*Pt*) in the cuticle (*Ctl*) extending into the hollow of the antenna as a long, curved, tapering sac. This is shown at F of figure 12. A nerve (*Nv*) enters the lower extremity of the pouch, expands slightly into a nucleated ganglion cell (*Cl*), and then extends toward the top as a delicate spindle drawn out into a fine tapering point. The surface covering of the pit is a thin layer of chitin presenting several concentric light and dark rings surrounding a central disc (*hr*). Sections show that this appearance of rings is due to circular thickenings of the membrane, and Schiemenz points out that the central disc is probably a modified hair, while the whole structure is to be regarded simply as a modification of a tactile organ such as that shown at D with the nerve-ending and its ganglion inclosed in a sac. These organs are most abundant on the antennæ of the drones, where they are situated, especially on the under surface, so close together that but little space is left between them for the tactile hairs, while in the workers and queens they are farther apart and are interspaced with many tactile hairs. Hence, whatever sense they accommodate must be much more highly developed in the males than in the females. Schiemenz described these organs, as well as the sunken cones, as organs of smell. He ascribed only the senses of touch and smell to the antennæ, and both Cheshire and Cowan concur in his view of the closed pits. Arnhart (1906), however, argues that an organ of smell must be open to the air in order to permit the ingress of odor particles. Such an organ is constituted by the sunken cones, but the closed pits have nothing to recommend them for an olfactory function. Arnhart then further points out that the buried sacs, inclosing a delicately poised nerve-ending and covered by an external tympanum, have all the mechanical elements of an organ of hearing. He finally argues that bees must hear, since they produce special sounds such as the piping of the queens, and that, since no possible

organs of hearing have been discovered on any other part of the body, some of the antennal sense organs must be auditory in function. His conclusion from these premises is, of course, inevitable that the closed sacs on the antennæ are the hearing organs of the bee. What invalidates the argument, however, is the fact that no one has yet produced any actual evidence that bees perceive sound.

The following, then, may be stated as a general summary of the evidence concerning the antennal senses and their sense organs in the bee: (1) The antennæ are highly sensitive to touch and are the seat of the sense of smell. (2) They are covered by several kinds of minute structures which are modified hairs containing special nerve-endings. (3) By inference, it would seem certain that these are the sense organs, but we can only form an opinion, based upon their structure, as to which are tactile and which olfactory. (4) One set of organs does not appear to belong to either of these categories and their structure suggests an auditory function, but, in the absence of evidence that bees hear, the purpose of these organs must be regarded as problematical.

3. THE MANDIBLES AND THEIR GLANDS.

The mandibles (fig. 9 A, *Md*) are the dark, strongly chitinous appendages of the head, commonly called the jaws, situated at each side of the mouth, anterior to the base of the proboscis. In all insects with biting mouth parts the jaws work sidewise, each being attached to the head by an anterior and a posterior articulation. They can thus swing in and out on a longitudinal axis in such insects, as the bee, that carry the head with the mouth directed downward, or in the same way on a vertical axis in those that carry the head with the mouth forward.

Both mandibular articulations are of the ball-and-socket type, although in the bee the socket is a very shallow one, the anterior consisting of a condyle on the outer angle of the clypeus fitting against a facet on the mandible, and the position of a facet on the lower edge of the postgena receiving a condyle from the mandible. The motion of the mandible is thus reduced to a hinge-joint movement, and, on this account, insects can only bite and crush their food; they can not truly chew it, since their jaws are incapable of a grinding motion. Each mandible is, of course, as pointed out in the introduction, really suspended from the head by a continuous membrane between its base and the cranium, being simply a modified saclike outgrowth of the head wall. The two articulations are productions of the chitin on the outside of this membrane.

Figure 9 A shows the location and shape of the mandibles (*Md*) of the worker as seen in a facial view of the head. Figure 11 A

shows the appearance of the left mandible in side view, while the right one is shown detached from the head in figure 13 A. The mandibles differ conspicuously in size and shape in the three forms of the bee as already described and as shown in figure 10 A, B, and C. That of the worker is hollowed out somewhat on the distal half of its inner face (fig. 13 A, *Md*) forming a spoon-shaped organ, the edge of which is smooth and rounded. The mandibles of both the queen (fig. 10 B) and the drone (C), however, are pointed at the apex and have a conspicuous subapical notch. Those of the drone

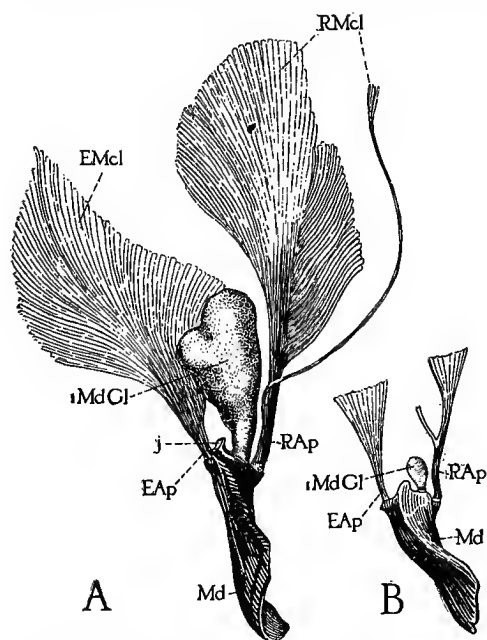


FIG. 13.—A, right mandible of worker, anterior view, with extensor and flexor muscles (*EMcl* and *RMcl*) and mandibular glands (*iMdCl*) attached; B, corresponding view of mandible of drone, with muscles cut off a short distance from their bases.

are smaller than those of either form of the female, but appear to be especially small on account of the great size of the drone's head. The mandible of the worker is undoubtedly to be regarded as the specialized form, since the notched mandible of the drone and queen is of the ordinary Hymenopteran type. Both the drone and the queen are, under normal circumstances, fed almost entirely by the workers, and they probably never have any use for their jaws as feeding organs. The queen needs her large, sharp-pointed mandibles for biting her way out of the thick wax cell in which she is reared, but the drone, on the other hand,

being reared in an ordinary cell resembling that of a worker, except in size, is easily able to cut through the thin cell cap with his comparatively weak jaws. The workers, however, have numerous uses for their mandibles, such as biting through the cell caps, eating pollen, and modeling wax. The last is the especial function of the worker mandible, and probably it is to accommodate this purpose that it has acquired its specialized spoonlike shape.

Each mandible is moved by two sets of muscles within the head. The outer one constitutes the *extensor muscle* (fig. 13 A, *EMcl*) and the inner the *flexor muscle* (*RMcl*). The latter is the stronger of

the two, since all the work of the mandible falls upon it, the extensor being used simply to open the jaw. While these muscles have their origins on the walls of the head, they are not inserted directly upon the mandibles, but on large apodemes (fig. 13 A, *EAp* and *RAp*) attached to the edges of the mandible.

A gland opens at the inner margin of each mandible between the anterior articulation and the base of the apodeme of the flexor muscle (fig. 13 A and B, *1MdGl*). In the worker it consists of a large sac covered with secreting cells lying within the front part of the head between the clypeus and the compound eye (fig. 10 A, *1MdGl*). These mandibular glands may be most easily studied by removing the front as shown in figure 10 A, B, and C. In order to do this, pull the head from the thorax and allow the prothoracic legs, which will usually come off with the head, to remain attached to it. Next melt a small hole in the bottom of a paraffin dish with a heated needle and fasten the head face upward into this, the attached legs helping to anchor the head in the paraffin. Cover the specimen with weak alcohol and by means of sharp needles remove the part of the front on either side between the clypeus and the lower half of the compound eye in the worker and drone and the entire front of the queen. In figure 10 the whole front is removed in all three forms in order to expose other internal parts of the head.

The mandibular gland (*1MdGl*) is of greatest size in the queen (fig. 10 B), though it is large in the worker (fig. 10 A and fig. 13 A), but it is reduced in the drone (fig. 13 B) to a very small oval sac, which is hidden by another gland (*2Gl*) in front (fig. 10 C). It was first described by Wolff (1875) as an olfactory mucous gland (*Riechschleimdrüsen*) and was supposed by him to secrete a liquid which was poured upon the roof of the mouth in order to keep this surface, on which Wolff thought the olfactory organs were located, in a moist condition capable of absorbing odor particles. There is absolutely no evidence, however, of the presence of organs of smell in the mouth, and furthermore, as pointed out by Schiemenz (1883), the gland varies in the three forms of the honey bee according to the size of the mandible, which is proportionately largest in the queen and smallest in the drone. Of the three, we should expect the drone or the worker to have the sense of smell most highly developed, and hence, even if we did not know that the sense of smell is located in the antennæ, it would seem more reasonable to suppose that the glands of the mandibles are connected in some way with the functions of these organs themselves.

The mandibles, as already stated, are used for eating pollen and as tools for manipulating and modeling wax. Therefore, according to Arnhart (1906), since the queen does not eat raw pollen, the product

of the mandibular glands must be intended for softening the wax when it is worked in the jaws. The secretion of the glands is said to be very volatile and strong smelling and to have an acid reaction. It is probably entirely possible that it may have a solvent effect upon the wax, or even, when mixed with it, change somewhat the chemical composition of this substance; in fact, some investigators claim that the wax of the comb differs chemically from that freshly taken from the wax plates. Even this explanation, however, does not seem entirely satisfactory, for the only occasions on which the queen has anything to do with wax is when she gnaws her way out of her cell after hatching or bites her way into the cells of young queens in order to sting them. However, these occasional uses by the queen of her mandibles appear to be important enough to maintain the large size of these organs in the queen, and it may be reasonable to assume that the demand upon their glands is likewise a large one when it does occur. Yet the mandibles of the queen are toothed and sharp pointed, which should provide her with sufficient cutting power both to emerge from her own cell and to enter the cells of other queens, and so, on the whole, the opinion of Schiemenz that the secretion of the mandibular glands is merely salivary in function would seem to be the simplest explanation and the most logical one. However, an actual test should certainly be made to determine whether the worker's

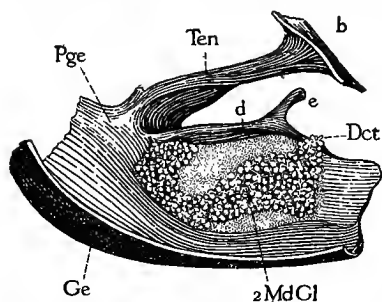


FIG. 14.—Internal mandibular gland (*2MdGl*) of worker, lying against inner wall of postgena (*Pge*) and opening (*Dct*) at inner edge of base of mandible.

manipulation of the wax with her mandibles produces any change in it, and to discover whether the queen simply bites her way mechanically through the wall of the cell or at the same time softens the wax by a secretion from her mouth. The male in any case has little use for his mandibles, and the glands are so small that they must certainly be functionless.

A second mandibular gland (fig. 14, *2MdGl*) is present in the worker. It consists of a delicate, flattened, racemose mass lying against the internal face of the wall of the fossa of the proboscis, whose duct opens into the mouth cavity at the posterior inner edge of the mandible. This gland was first described by Bordas (1895) as the *internal mandibular gland*. According to him, it corresponds with a similar gland in the *Bombidæ* (bumblebees) and in the *Vespidæ* (yellow jackets) and to the maxillary glands of other *Hymenoptera*. Nothing is known of its secretion.

4. THE PROBOSCIS.

The conspicuous group of mouth appendages in the honey bee, forming what is commonly known as the *proboscis* (fig. 9 A, *Prb*),

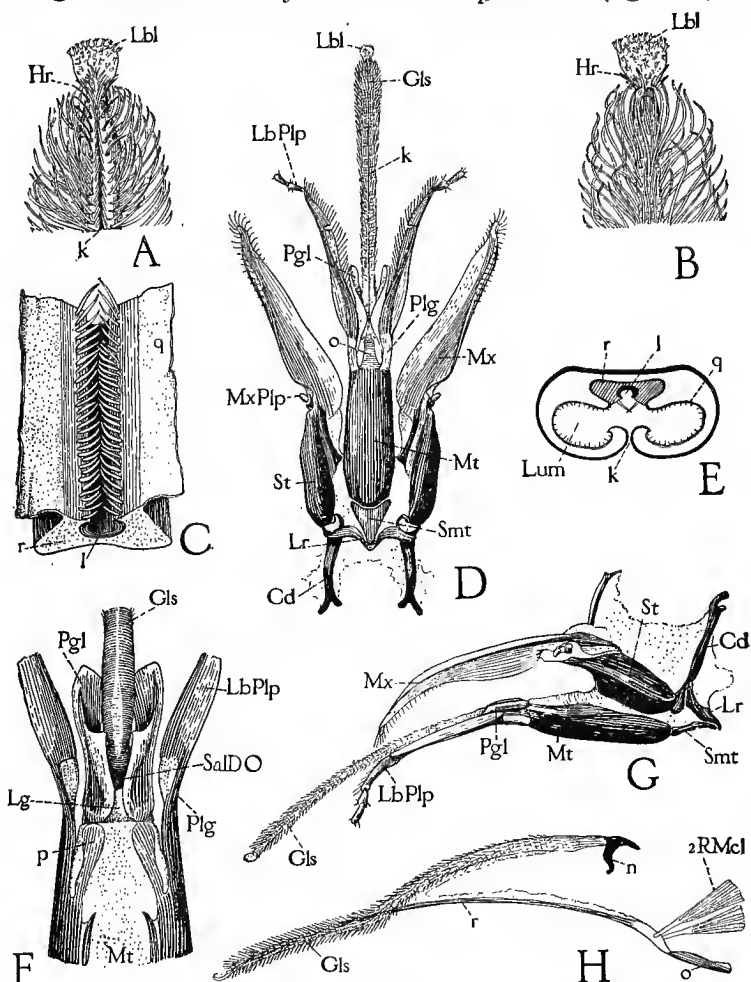


FIG. 15.—Mouth parts of the worker: A, tip of glossa, showing labellum (*Lbl*), guard hairs (*Hr*), and ventral groove (*k*); B, same, from above; C, small piece of glossal rod (*r*) with adjoining parts of walls (*q*) of glossal canal attached, showing ventral channel (*l*) guarded by rows of hairs. D, parts forming the proboscis, labium in middle and maxillae at sides, flattened out, ventral view; E, cross section of glossa showing its invaginated channel (*Lum*) and position of rod (*r*) along its dorsal wall, and likewise position of channel (*l*) of rod along median line within the glossal channel; F, end of mentum (*Mt*) and bases of ligula (*Lg*) and labial palpi (*LbPlp*), showing opening of salivary duct (*SalDO*), dorsal view; G, lateral view of proboscis showing parts on left side; H, lateral view of glossa (*Gls*) with its rod (*r*) torn away at base showing attachment of retractor muscles (*2RMcl*).

by means of which the bee takes up liquid food, consists of what correspond with the maxillae and the labium of insects that feed on solid

food alone. By separating the parts of the proboscis a little (fig. 9 B) it will be seen that, while there are five terminal pieces present, three of them arise from one median basal sclerite (*Mt*), the two wider lateral appendages (*Mx*) being carried each by a separate lateral basal piece (*St*). The median group constitutes the *labium* and the separate lateral parts the *maxillae*.

If the reader will now turn again to figure 3 C (p. 17), which may represent any generalized insect labium, and compare with it the drawing of the bee labium, forming the median series of parts in fig. 15 D, he will at once be able to identify the parts of the latter. The principal elongate median basal plate is the *mentum* (*Mt*), the small triangular plate at its base is the *submentum* (*Smt*), and the two jointed lateral appendages of the mentum are the *labial palpi* (*LbPlp*), each carried by a basal *palpiger* (*Plg*). It is only the parts of the bee's labium that lie between the palpi which are actually different from those in the generalized diagram where they consist of the four lobes of the *ligula* (*Gls* and *Pgl*). But even here it will be seen that the two small lobes (*Pgl*) in the bee's labium, partly concealed within the bases of the palpi, correspond with the *paraglossæ*. Hence we have only the long median appendage to account for and it is unquestionably the representative of the *glossæ* (*Gls*) which are here fused together and drawn out into this flexible tonguelike organ. In fact, a comparison with the mouth parts of other Hymenoptera in which the elements are much less modified leaves no doubt of this being the true interpretation of the bee's labium. It is simply an example of how nature constantly prefers to modify an already existing part to serve some new purpose rather than to create a new organ.

If, then, we bear in mind that the slender median appendage of the bee's labium represents the glossæ of other insects, we may for convenience call it the "tongue," as it is popularly termed, or, since it is a single organ, there is probably no grammatical objection to calling it the *glossa*. The word "tongue," however, to use it properly, should be applied to the true *lingua* or *hypopharynx* (fig. 3 C and D, *Hphy*) which arises from the upper surface of the labium. Many of the older entomologists, adopting the notion from Kirby and Spence, who defined the term in 1826, regarded the glossa of the bee as the homologue of the lingua in other orders. Even Packard in his Text-book of Entomology calls the glossa the "hypopharynx." Cheshire named it the "ligula," and his mistake has been perpetuated by several other writers on bee anatomy, including Cook and Cowan. The term *ligula* properly includes both the glossa and the paraglossæ, or should signify the basal piece from which these four lobes arise (fig. 3 C, *Lg*), so that it can not be applied to the glossa alone.

The derivation of anatomical names counts for nothing in their application—this must be determined by scientific usage and priority. Thus, *glossa* is the Greek word for “tongue,” but it was first applied in entomology to the median lobes of the labium; *lingua* is its equivalent in Latin and was first given to the true tongue or hypopharynx in insects; *ligula* is a diminutive derivative from “lingua” and has come to be applied collectively to the terminal parts of the labium beyond the mentum but not including the palpi. Hence, all these words mean the same thing by their origins, but their anatomical applications should be carefully distinguished. In this paper therefore the slender median appendage (*Gls*) of the labium will be called the *glossa*, or, for convenience, the *tongue*, but with the strict understanding that the organ in question is not the true tongue. This latter should be called the “hypopharynx,” but, as will be shown later, it is absent in the bee.

The glossa of the bee (figs. 9 B; 11 A and B, and 15 D, F, and G, *Gls*) is covered with long hairs which increase in length toward the end. The tip is formed of a small spoon-shaped lobe, the *labellum* or *bouton* (*Lbl*), which is covered by short delicate processes branched at their ends (fig. 15 A and B, *Lbl*). The long hairs of the glossa are arranged in circles and the transverse rows of hair bases give the tongue a multiarticulate appearance. Surrounding the dorsal side of the base of the labella and forming two short subterminal rows on the ventral side of the glossa are a number of stiff, outwardly curved, spinelike hairs (*Hr*). These hairs have been described as taste organs, but their appearance would suggest that they are simply protective spines guarding the delicate tip of the tongue. Between the two ventral rows of these spines is the termination of a groove (*A*, *k*) which extends along the midline of the under surface of the glossa (*D*, *k*) to its base (fig. 9 B, *k*). The cleft of this groove is covered by two fringes of converging hairs whose tips are inclined also toward the tip of the tongue.

Let us now return to a study of figure 15 D. The series of lateral pieces as already explained are the maxillæ. A comparison with figure 3 B representing a generalized maxilla will show that these organs in the bee have suffered a greater modification than has the labium, but the parts can yet be quite easily made out. The main basal plate (*St*) is the combined *stipes*, *subgalea*, and *palpifer*, the basal stalk is the *cardo* (*C'd*), and the little peglike process (*MxPlp*) at the outer end of the stipes is the greatly reduced *maxillary palpus*. Hence, we have left only the terminal bladelike lobe (*Mx*) to account for, and it is evident that it must be either the galea or the lacinia (see fig. 3 B, *Ga* and *Lc*) or these two lobes combined. Here again a comparative knowledge of the mouth parts of Hymenoptera comes

to our aid and shows clearly that the part in question is the outer lobe or *galea*, for the inner one becomes smaller and smaller in the higher members of the order and finally disappears.

The base of the submentum is connected in the bee with the upper ends of the cardines by a flexible, widely V-shaped band, the *lorum* (*Lr*). The posterior angle of the submentum rests in the apex of the lorum, while the tips of the loral arms are movably articulated with the distal ends of the cardines. The name "lora" was given to this structure by Kirby and Spence, but "lorum" is more correct, since this is the Latin form of the word (meaning a thong or lash). Some recent entomologists have spoken of the structure as consisting of two rods, thus making the word do duty as a plural, but the thing itself is all one piece. Cheshire and some others have incorrectly applied the name to the submentum.

The lorum is peculiar to the Hymenoptera, and the reason for it is clear when we examine the attachments of the parts of the proboscis to the head. As already stated, the maxillæ and labium are suspended in a large cavity on the back of the head which may be called the *fossa of the proboscis* (fig. 9 B, *PrbFs*). The maxillæ are articulated by their cardines (*Cd*) to the maxillary suspensoria (fig. 11 A, *e*) at the upper edges of the side walls of the fossa. The labium, on the other hand, is not attached to the solid walls of the cranium but is suspended in the membranous floor of the fossa. This is to afford it freedom of movement during feeding, but, in order to give it more substantial support and to make the regulation of its motions possible, the submentum is slung to the ends of the cardines by the lorum.

The terminal lobes of the labium and maxillæ when not in use are ordinarily folded down beneath the head against the mentum and stipites (fig. 19). When, however, the bee wishes to imbibe a thick liquid such as honey or sirup in large quantity, these parts are straightened out and held close together so as to form a tube between them leading into the mouth, the terminal joints of the labial palpi alone diverging from the rest (fig. 11 A).

The action of the mouth parts while feeding may be observed quite easily if some bees are given a small amount of honey and then watched through a lens while they are eating. A most convenient method is to put a few workers in a small screen-covered cage, such as are used for queen nurseries, spread a small drop of honey on the wire, and then place the cage under a simple microscope. It will be seen that the maxillæ are held almost stationary but that the base of the labium slides back and forth between the maxillary bases with a very regular to-and-fro movement as if the honey were being either pumped or sucked up into the mouth. It is probable that there is a sucking force exerted by the pharynx (fig. 11 B, *Phy*) but not

by the honey stomach (fig. 44, *HS*), which latter, as Cheshire remarks, could no more suck honey through the oesophagus than a balloon could suck gas from a pipe. The liquid undoubtedly runs up the temporary tube between the blades of the mouth parts first by capillary attraction, but it must be greatly assisted along its way to the mouth by the retraction of the labium. The load brought up when this is pulled back is then sucked into the mouth by the pharynx while the labium immediately goes out again after more. It acts thus as a sort of mechanical feeder and this function is probably derived from the lapping motion of the under lip in wasps and hornets.

The mentum (fig. 15 D and G, *Mt*) is hinged freely upon the submentum (*Smt*), the latter, as already described, is set into the socketlike angle of the lorum, while, finally, the arms of the lorum are articulated to the distal ends of the cardines of the maxillæ. Now, when the labium is retracted by means of muscles attached to the mentum, the submentum turns in the loral socket and assumes a position at right angles to the mentum while the lorum itself turns somewhat on its articulations with the cardines. This great freedom of motion is permitted by the loose membrane of the fossa in which both the maxillæ and the labium are suspended.

The observer, however, can not fail to note that beside this motion of the entire labium the tongue itself, or glossa (*Gls*), performs a conspicuous independent movement of its own. It is by far the most active member of the mouth parts during feeding, being actively thrust out and retracted while its tip is constantly moved about in a way suggestive of its being delicately perceptive of taste or touch or perhaps to both of these senses. So great is the retractile power of the tongue that its tip, which normally extends far beyond the end segments of the labial palpi, can be drawn back entirely within the latter. This contractile activity appears at first sight to be due to elasticity, but a closer examination will show that the entire ligula, i. e., the paraglossæ (*Pgl*) as well as the glossa (*Gls*), moves back and forth and that the action is due to a retraction of the base of the ligula (fig. 15 F, *Lg*) into the anterior end of the mentum (*Mt*). The ligula is supported on a membranous cone at the end of the mentum whose walls are strengthened by three thin chitinous plates, two above (F, *p*) and one below (D, *o*). By the contraction of muscles situated within the mentum (fig. 16, *IRMcl*) and inserted upon the base of the ligula the latter is pulled into the end of this cone whose walls, including the chitinous plates, simply turn inward.

But the tongue does possess also a contractile power of its own by means of which it actually shortens its length. A flexible rod arising from the median ventral supporting plate (fig. 15 D, *o*) of the ligula extends throughout its length. The base of this rod is curved down-

ward and has two muscles attached to it. This is shown by figure 15 H, where the rod (*r*) is torn from the glossa (*Gls*) basally so as to show the muscles (*2RMcl*) inserted upon it and its connection with the plate (*o*). By the contraction of the muscles the rod bends at its base and is drawn back into the mentum. The glossa thus shortens and becomes bushy just as does a squirrel's tail when one attempts to pull the bone out of its base.

The protrusion of the parts is due to the pressure of blood driven into the ligula from the mentum, while probably the glossa extends also by the straightening of its rod as the muscles relax. Wolff described a protractor muscle at the base of the ligula. The rod of the tongue is certainly not in itself contractile, as supposed by Cheshire, who looked for evidence of muscular striation in it. It has mostly a transparent and cartilaginous appearance, but is presumably chitinous.

The mouth parts, their action in feeding, and the muscular mechanism by which they are moved have been elaborately described and illustrated by Wolff (1875) in his monograph on the organs of smell in bees. Most unfortunately, however, Wolff's paper was written to show that the seat of the sense of smell is in the mouth, a most erroneous notion, and the title of his paper based on this notion has caused little attention to be paid to this work on the mouth parts of the bee, which is one of the best anatomical treatises ever produced on the mouth parts of any insect.

It still remains for us to describe the details of the glossa and its particular function in feeding. The tongue is not a solid appendage nor yet is it truly tubular. A compromise is effected by the longitudinal groove (fig. 15 A and D, *l*) on its ventral surface which expands within the tongue into a large cavity occupying half of its interior (E, *Lum*). The glossal rod (*r*), which has already been mentioned, lies in the dorsal wall of this channel and is, hence, really not an internal but an external structure. The rod is itself grooved along its entire ventral length (E, *l*) and this groove again is converted into a tube by two rows of short hairs which converge from its margins. The lips of the ventral groove of the glossa are so deeply infolded that its cavity is almost divided along the midline. Hence, the glossa might be described as containing three channels—a small median dorsal one (*l*) and two large latero-ventral ones (*Lum*).

The glossal rod (fig. 15 C, *r*) is very flexible but not contractile, as already stated, and is mostly clear and cartilaginous in appearance, its ventral groove (*l*) alone being lined by a deposit of dark chitin (fig. 15 C and E). Its shape in section is sufficiently shown by the figures. The walls of the large channels of the proboscis consist of a delicate membrane (C and E, *q*) covered with very small hairs.

The entire ventral cavity (*Lum*) with the rod (*r*) can be evaginated through the ventral cleft (*k*) by blood pressure from within. As Cheshire points out, this permits of the channels being cleaned in case of clogging by pollen or any foreign matter.

It is supposed that these glossal tubes are of especial service to the bee by enabling it to take up the smallest drops of nectar—quantities that would be lost in the clumsy tube formed between the parts of the labium and the maxillæ. The suction must be in large part capillary attraction, but here again the shortening of the glossa by the retraction of its rod must squeeze the contained nectar out of the upper ends of the channels where it is received upon the ventral flaps of the paraglossæ (fig. 15 F, *Pgl*), from which it runs around the base of the tongue (*Gls*) within the paraglossæ to the dorsal side of the mentum (*Mt*) and so on to the mouth.

The maxillæ and labium of both the queen and the drone (fig. 11 B) are smaller and weaker than those of the worker, and neither of these two forms is capable of feeding itself to any extent. If a hungry queen be given some honey she attempts to eat it and does imbibe a small quantity, but at the same time she gets it very much smeared over her head and thorax.

The mouth is hard to define in insects; practically it is the space surrounded by the bases of the mouth parts, but strictly speaking it is the anterior opening of the alimentary canal situated behind the bases of the mouth parts (fig. 19, *Mth*). Yet the enlargement of the alimentary canal (*Phy*) immediately following this opening is never spoken of as the mouth cavity but is called the pharynx. On the other hand the so-called epipharynx (*Ephy*) and hypopharynx (absent in the bee) are located in front of this opening and are consequently not in the pharynx at all, the former being attached to the under surface of the labrum and clypeus, while the latter is situated on the upper surface of the base of the labium. These and numerous other inconsistencies in the nomenclature of insect morphology have to be endured because the parts were originally named for descriptive purposes by entomologists who were not familiar with scientific anatomy. In this paper the term *mouth* will be applied to the true oral opening (fig. 19, *Mth*). The space in front of it between the bases of the mouth parts may be called the *preoral cavity*.

The duct of the salivary glands of insects in general opens upon the base of the labium in front of the hypopharynx. In the honey bee the salivary opening is on the dorsal side of the base of the ligula between the paraglossæ (fig. 15 F, *SalDO*). This alone would show that the glossa is not the hypopharynx of the bee, as many authors have supposed, for otherwise the opening of the salivary duct should be ventrad to the base of the glossa. In fact, this makes it clear that

the bee does not possess a hypopharynx. There is, however, a conspicuous chitinous plate located on the anterior part of the floor of the pharynx (fig. 19, *s*) having two terminal points hanging downward over the lower lip of the oral aperture, but, although this plate is truly hypopharyngeal in position, it is not the homologue of the organ called the hypopharynx in other insects. It is variously developed in all Hymenoptera, being simply a chitination of the floor of the pharynx, and should be called the *pharyngeal plate* (*Schlundbein* of Wolff). It will be more fully described in connection with the alimentary canal. If a hypopharynx were present it should be situated on the upper side of the labium (see fig. 3 D, *Hphy*) but there is here present only a plain arched membranous surface in the honey bee and other typical Hymenoptera.

The external location of the salivary opening enables the saliva to be mixed with the food before the latter enters the mouth. This is necessary in insects since the jaws are also on the outside of the

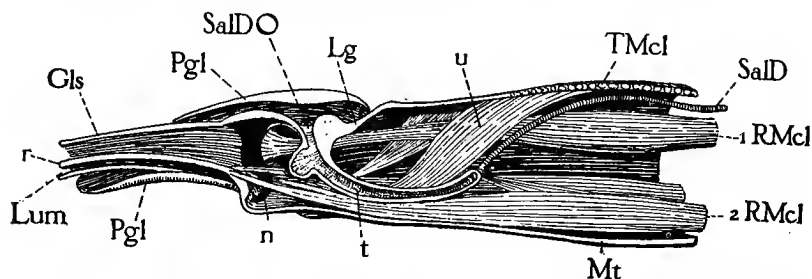


FIG. 16.—Median section through distal half of mentum (*Mt*) and base of ligula (*Lg*) of worker, showing opening of salivary duct (*SalDO*), and muscles connected with ligula and the "salivary syringe" (*t*).

mouth, and whatever chewing or crushing the food receives from them is consequently done in the preoral cavity.

In some insects the saliva is used for other purposes than digestion. For example, the saliva of some predaceous insects with piercing mouth parts belonging to the order Hemiptera is poisonous, and when one of these insects "bites," the saliva is injected into the wound by a special pump. The bite of the mosquito is made painful likewise by an irritant secretion from a part of the salivary glands. Bees appear to have the power of letting their saliva run down the tongue when necessary to dissolve a hard substance like sugar and render it capable of being taken up in solution, for they do not eat sugar with their mandibles. Moreover, there is even a sort of pump or so-called "salivary syringe" at the termination of the salivary duct in the ligula, by means of which the secretion can be forcibly ejected from the opening.

The salivary opening on the base of the ligula (fig. 15 F, *SalDO*) leads into a deep transverse pit with collapsible cartilage-like walls having its deepest part turned horizontally toward the base of the

labium (fig. 16, *t*). The salivary duct (*SalD*) bends downward in the anterior part of the mentum (*Mt*) and opens into the posterior end of the pit (*t*). When the retractor muscles (*1RMcl*) of the ligula pull the latter back into the mentum the lips of the salivary pit must necessarily be closed. The simultaneous contraction of the elevator muscle (*u*) attached to the roof of the horizontal part of the pit must expand the latter and suck the saliva from the salivary duct. When, finally, these muscles relax and the ligula is driven out by blood pressure in the mentum, probably produced in part by the contraction of its dorsal transverse muscles (*TMcl*), the saliva in the temporarily formed bulb must be squirted out upon the base of the tongue. Wolff (1875) calls each dorsal longitudinal muscle of the mentum (*1RMcl*)—the two inserted upon the basal hooks (*n*) of the glossa (fig. 15 H and fig. 16)—the *retractor linguae longus*. The large ventral retractor muscle of each side (*2RMcl*) he calls the *retractor linguae biceps* since its anterior end divides into two parts, one of which is inserted by a tendinous prolongation upon the base of the glossal rod (fig. 15 H and fig. 16, *r*) and the other upon the base of the ligula. The use of the word “lingua” in these names is objectionable because, as already explained (page 45), the lingua is properly the true tongue or hypopharynx. “Ligulae” should be substituted for “linguae.” The dilator muscle (fig. 16, *u*) of the salivary pit (*t*) is termed the *protractor linguae* by Wolff because, as he supposes, when the ligula is pulled back into the mentum the position of this muscle is reversed, so that a contraction of its fibers would help to evert the ligula.

The glands that furnish the saliva lie within the head and the thorax and will be described later in connection with the alimentary canal and the process of digestion.

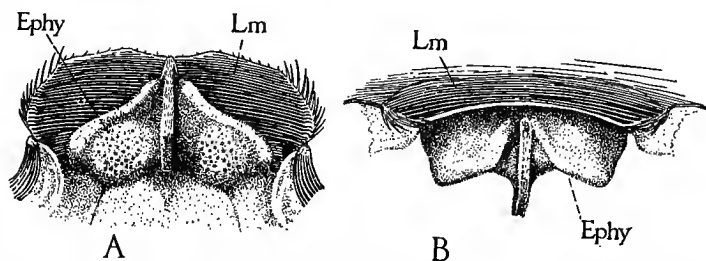


FIG. 17.—Epipharynx (*Ephy*) and labrum (*Lm*) of worker: A, ventral view; B, anterior view.

5. THE EPIPHARYNX.

The epipharynx of insects in general may be described as a dorsal tongue, it being a median lobe developed on the roof of the preoral cavity from the under surface of the clypeus or labrum and situated opposite the hypopharynx.

The epipharynx of the bee is a large three-lobed appendage depending from the roof of the preoral cavity just in front of the mouth (fig. 19, *Ephy*). Seen from below it is triangular (fig. 17 A) with the apex forward. Its median lobe has the form of a high, vertical, keel-like plate, while the lateral lobes are rounded but have prominent elevated edges converging toward the front of the keel. The appearance in anterior view is shown by figure 17 B. Situated on the posterior parts of the lateral lobes are a number of sense organs, each consisting of a small cone with a pit in the summit bearing a small hair (fig. 18). These are regarded as organs of taste.

Wolff (1875) made a most thorough study of the epipharynx, which he called the "palate sail" (*Gaumensegel*) on account of the high median crest. His drawing is the standard illustration of the organ found in nearly all books on the anatomy of the honey bee

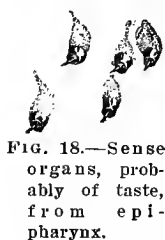


FIG. 18.—Sense organs, probably of taste, from epipharynx.

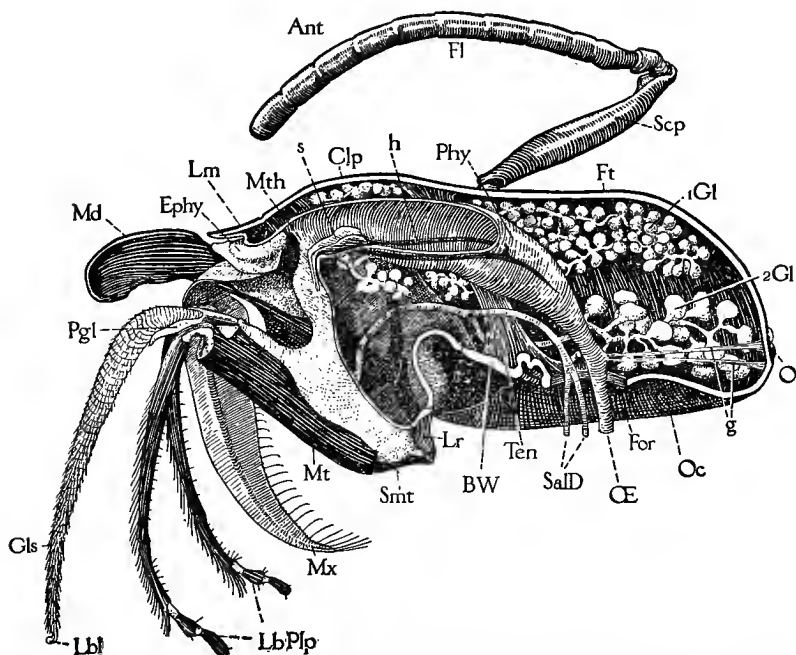


FIG. 19.—Median longitudinal section of head of worker, but with entire labium attached, showing internal organs except muscles and brain.

and in most works on general insect anatomy and the sense organs. Wolff, however, regarded the sensory cones as having an olfactory function, and this led him to erroneous conclusions regarding the functions of several other organs. For example, he thought that the mandibular glands poured a liquid upon the surface of the

epipharynx which kept it moist and capable of absorbing odor particles, while he explained the inhalation of the latter into the preoral cavity as brought about through the contraction of the air sacs situated about the mouth. Wolff's anatomical researches are without doubt some of the best ever made on the bee, and it is due to his mistaken idea of the location of the sense of smell, which, as already explained, is on the antennæ, that we have received from him a most excellent account and detailed drawings not only of the epipharynx but of the mandibular glands, the mouth parts, the salivary "pump," and the respiratory organs.

IV. THE THORAX AND ITS APPENDAGES.

1. THE STRUCTURE OF THE THORAX.

The apparent thorax of the bee (fig. 20, T_1 - IT , and fig. 21) and of most other Hymenoptera is not exactly the equivalent of the thorax in other insects. The middle division of the body, so conspicuous in this

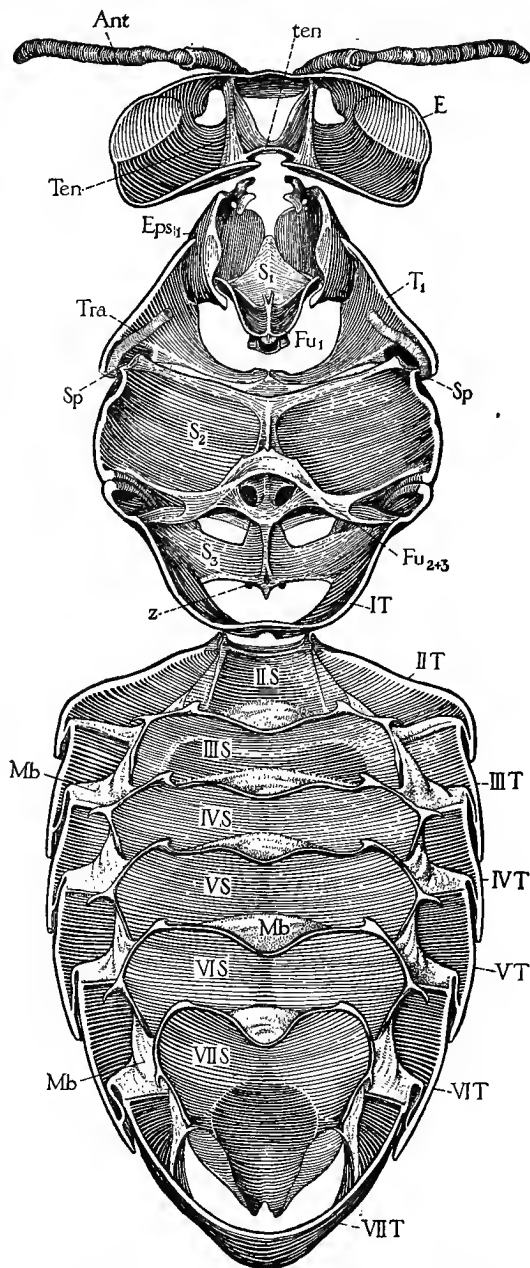


FIG. 20.—Dorsal view of ventral walls and internal skeleton of body of worker.

order, consists not only of the three leg-bearing segments, which alone

constitute the thorax of all other insects, but also of the first abdominal segment. The conspicuous necklike constriction posterior to the base of the hind legs (fig. 21, *Pd*) is, therefore, between the first and the second abdominal segments (fig. 1, *IT* and *IIT*).

The thorax of the honey bee at first sight looks entirely different in structure from that of all other insects except related Hymenoptera, in the higher families of which group it is more highly modified than in any other order of the whole series of insects. When, however, we examine the thorax of one of the lowest members of the Hymenoptera, such as a sawfly, we are surprised to find that, in each segment, the structure agrees very closely with our ideal diagram of a general-

ized thoracic segment (fig. 4).

The three segments are perfectly distinct, and the first abdominal segment, while it may be clearly separated from the rest of the abdomen, is not fused into the thorax so as to appear to be a part of it. If, now, we examine representatives of several families intermediate between the sawflies and

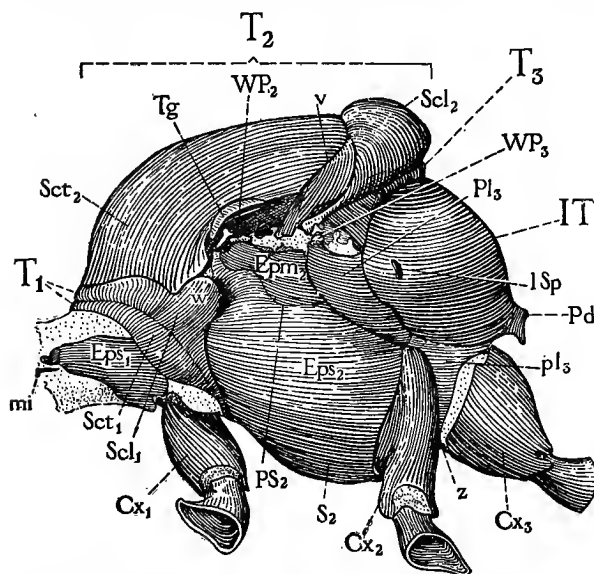


FIG. 21.—Thorax of worker, left side, with intersegmental lines somewhat exaggerated, showing prothorax (*T*₁, *Eps*₁, *Cx*₁), mesothorax (*T*₂, *Eps*₂, *Epm*₂, *S*₂, *Cx*₂), metathorax (*T*₃, *Pl*₃, *pl*₃, *Cx*₃) and propodeum or first abdominal segment (*IT*).

the bees, the line of specialization that has produced the bee thorax becomes perfectly evident. The principal features in these modifications are the following:

(1) The lateral and ventral parts of the prothorax (figs. 20 and 21, *Eps*₁ and *S*₁) are suspended loosely in a large membranous area which is continuous anteriorly as the neck. They thus form a sort of suspensorium for the front legs, which appears detached from the rest of the thorax. (2) The protergum (*T*₁) is solidly attached to the anterior edge of the mesothorax and its lateral parts extend downward till they meet on the venter behind the prosternum (figs. 20 and 21). (3) The postnotum (postscutellum) of the mesothorax (figs. 22, *PN*; 23 A, *PN*₂) is entirely invaginated into the cavity of the thorax and is reduced to the form of two lateral arms of the large

internal postphragma (*Pph*) which has no median tergal connection at all. (4) The metatergum (figs. 21 and 23 A, T_3) consists of a single narrow plate. (5) The metapleurum (fig. 21, Pl_3 and pl_3) shows no trace of a division into episternum and epimerum, but is divided into an upper (Pl_3) and a lower (pl_3) pleural plate. (6) The first abdominal tergum (fig. 21, *IT*) is solidly attached to the metathorax and forms an intimate part of the thoracic mass.

We shall now proceed with a more detailed account of the thorax, and the reader should occasionally turn back to figure 4 (p. 19) in order to keep clearly in mind the parts that make up a generalized thoracic segment.

The parts of the **prothorax** are so separated from each other that they appear to belong to different segments. The protergum (fig. 21, T_1) forms a collar completely encircling the front of the mesothorax. On each side a large lobe (*w*) projects posteriorly as far as the base of the front wing and constitutes a protective shield over the first thoracic spiracle. The tergum presents a median transverse groove, dividing it into an anterior and a posterior part, which parts may be called the scutum (fig. 23 A, T_1 , *Scut*) and scutellum (*Scel*). The propleurum (figs. 20, 21, Ep_{s1}) consists of a large plate presenting both a lateral surface (fig. 21) and a ventral surface (fig. 20). On account of the position of the coxal articulation (fig. 21) this plate would seem to be the anterior pleural plate alone (see fig. 4), which is the episternum. In some Hymenoptera the epimerum is represented by a very small plate on the rear edge of the episternum. The anterior ends of the two episterna form knobs which loosely articulate with the occipital region of the head (figs. 11 B, 20, and 21). Lying just ventrad of each is a slender cervical sclerite (fig. 21, *mi*). The prosternum (S_1) is shown by figure 20. It carries a large entosternum (Fu_1), forming a bridge over the nervous system behind the prothoracic ganglion (fig. 52).

The **mesotergum**, as seen in its natural position (fig. 21, T_2), consists of a large anterior scutum (Sc_{t_2}) and of a smaller but very prominent posterior scutellum (Sc_{l_2}), separated by a very distinct suture (*v*). The scutellum has two latero-anterior areas partially separated from the median area by sutures. When the mesotergum is detached from the rest of the thorax (fig. 22) it is discovered that there is attached laterally to the scutellum a large posterior internal part, which does not show on the surface at all. This is the representative of the postscutellum (*Pscel*) and its phragma (*Pph*) constituting the postnotum (*PN*) of our diagrammatic segment (fig. 4). The proof of this, again, is to be derived from a study of the lower Hymenopteran families. In some of the horntails (Siricidæ) the postnotum or postscutellum is a prominent plate on the surface of the dorsum behind the scutellum. In *Sirex* (Siricidæ) this plate is sunken below

the general surface and mostly concealed between the mesothorax and the metathorax. In higher families such as the Pompilidæ the postnotum of the mesotergum is entirely concealed by invagination, but it still carries a very large phragma. When, now, we come to the highest members of the order we find that the median part of the postnotum in the mesothorax is gone entirely and that it is represented only by the lateral arms (figs. 22, *PN*; 23 A, *PN*₂) carrying the large, purely internal postphragma (*Pph*).

The **mesopleurum** is large and consists principally of the episternum (fig. 21, *Eps*₂), which, however, is continuously fused with the mesosternum (figs. 20 and 21, *S*₂). The pleural suture (fig. 21, *PS*₂) is short and sinuous and does not reach more than half way from the wing process to the base of the middle leg. The epimerum is reduced to a small double plate lying above the episternum and posterior to the wing process (figs. 21, *Epm*₂, and 24 A, *Epm* and *Epm*). The

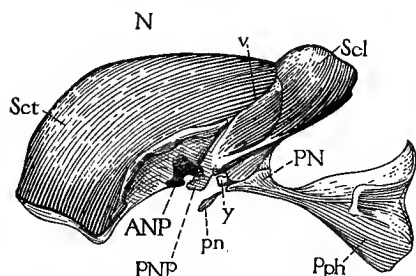


FIG. 22.—Lateral view of mesotergum of worker, removed from the rest of thorax to show large internal postscutellum (postnotum, *PN*) and its phragma (*Pph*) not visible normally in the bee from exterior.

pleural ridge (fig. 24 B, *PR*) is weak, but the wing process (*WP*) is well braced by a number of accessory internal ridges. One preapapterum (*2P*) and one postapapterum (*3P*) are present. Lying behind the postapapterum is another larger sclerite (fig. 24 A and B, *pn*), whose anterior end is articulated to the edge of the epimerum and whose posterior tapering end is loosely associated with the terminal arms

of the postnotum (fig. 22, *PN* and *pn*). This sclerite might be regarded as the fourth apapterum, but it is much more probably the representative of a small terminal bar of the postnotum present in other Hymenoptera, such as *Pepsis*, which connects this tergal plate with the epimerum, though in this genus it is not detached from the main postnotal sclerite.

Both the **mesosternum** (fig. 20, *S*₂) and the **metasternum** (*S*₃) contribute to the formation of a large entosternum (*Fu*₂₊₃), which forms a protecting bridge over the combined mesothoracic and metathoracic ganglia (fig. 52) and affords attachment for the ventral longitudinal muscles of the thorax (fig. 27, *lmcl*).

The **metathorax** consists of a very narrow series of plates (fig. 21, *T*₃, *Pl*₃, and *pl*₃) compressed between the mesothorax and the first abdominal tergum (*IT*). Its back plate is a single, narrow, transverse sclerite (figs. 21 and 23A, *T*₃) widening on the sides, where it carries the wings by the two wing processes (fig. 23 A, *ANP* and *PNP*). The

ordinary tergal divisions seem to be entirely obliterated. The metapleurum consists of a dorsal plate (fig. 21, Pl_3) supporting the hind wing and of a ventral plate (pl_3) carrying the hind leg. These two functions certainly identify these two plates as constituting together the metapleurum, but there is absolutely no trace of a division into an episternum and an epimerum. Once more, therefore, we have to go back to the generalized Hymenoptera to find out what has happened.

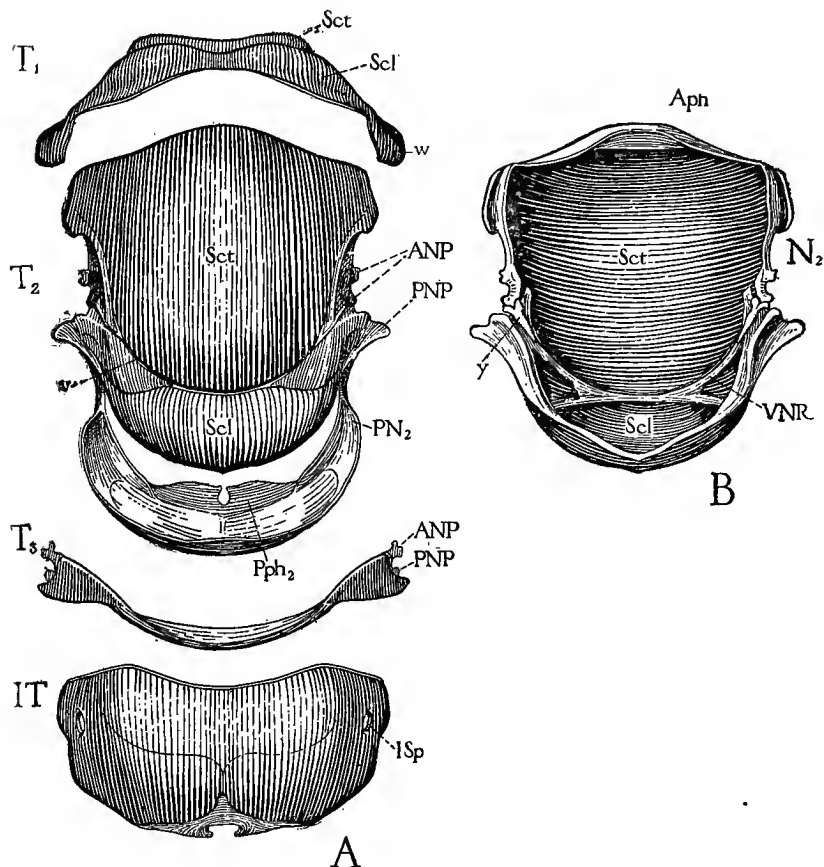


FIG. 23.—A, thoracic terga of worker separated from one another, showing protergum (T_1), mesotergum (T_2) and its internal postscutellum (postnotum PN_2) and phragma (Pph_2), metatergum (T_3) and propodeum or first abdominal tergum (IT); B, ventral view of principal or notal plate of mesotergum.

The answer is simple. *Sirex* has a typical metapleurum consisting of an episternum and epimerum separated by a complete pleural suture. In the higher forms this suture simply disappears, and consequently the pleurum shows no traces of its original component plates. The division into a wing-bearing and a leg-bearing plate is, therefore, a purely secondary one.

None of the Hymenoptera has separate trochantinal sclerites (see fig. 4, Tn), but, since the coxæ are articulated ventrally to knobs

(figs. 20 and 21, *z*) apparently belonging to the sterna, it might be supposed that the trochantins have fused with the latter plates.

The posterior part of the thoracic mass (fig. 21) consists of the first abdominal tergum (*IT*), which fits into the deeply concave posterior edges of the metathorax and forms the peduncle (*Pd*) that carries the rest of the abdomen (fig. 32). It consists of a single large, strongly convex sclerite (figs. 21 and 23 A, *IT*) bearing the first abdominal spiracles laterally (*ISp*) and having its surface divided into several areas by incomplete sutures.

Many entomologists find it difficult to believe that this plate, which so apparently belongs to the thorax, is really derived from the abdomen. But the proof is forthcoming from a number of sources. In the first place, the thorax is complete without it and the abdomen is incomplete without it, the latter having otherwise only nine segments. Again, if the plate is reckoned as a part of the thorax we

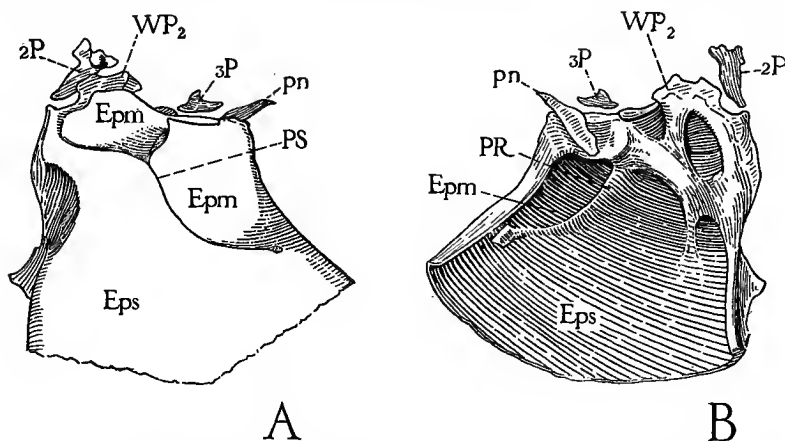


FIG. 24.—A, upper part of left mesopleurum of worker, external; B, inner view of same.

should have the anomaly of a thorax with three pairs of spiracles—there being the normal two on each side situated, as they always are, between the true thoracic segments. Furthermore, comparative anatomy shows us that in some of the sawflies (*Tenthredinidæ*) the first abdominal tergum, while separated by a wide membranous space from the second, is not at all incorporated into the thorax. In a horn-tail such as *Sirex* (*Siricidæ*) the entire first abdominal segment is fused to the posterior edge of the metathorax and is only loosely joined to the next abdominal segment by membrane. This insect affords, therefore, a most complete demonstration of the transference of this segment from the rest of the abdomen to the thorax. Finally, we have absolute proof of its abdominal origin based on a knowledge of development, for it has been shown by Packard from a study of the bumblebee that the first abdominal segment of the larva is transferred during the pupal metamorphosis to the thorax and forms the

part under discussion. We hence see that not only the first abdominal tergum but the entire segment has undergone transposition, though the ventral part has disappeared in all the higher families. This transferred part has been named both the *median segment* and the *propodeum* by writers who recognize it as belonging to the abdomen and not to the thorax.

The names current among systematists for the back plates of Hymenoptera afford an excellent example of the errors that entomologists may be led into through an ignorance of the comparative anatomy of insects. They recognize the protergum as such and then, knowing that there are yet two segments to be accounted for, they call the mesoscutum the "mesonotum," the mesoscutellum the "scutellum," the metatergum the "postscutellum" (being unaware that the true postscutellum is deeply concealed within the thorax), while the first abdominal tergum is called the metathorax. Such a nomenclature assigns both pairs of wings to the mesothorax. Too many systematists working in only one order of insects do not care whether their names are applied with anatomical consistency or not.

2. THE WINGS AND THEIR ARTICULATION.

In the study of insects the wings always form a most interesting subject because by them insects are endowed with that most coveted function—the power of flight. It has already been stated that the wings are not primary embryonic appendages, but are secondary outgrowths of the body wall from the second and third thoracic segments. Therefore it is most probable that the early progenitors of insects were wingless, yet for millions of years back in geological time they have possessed these organs in a pretty well developed condition. Nearly all of the insect orders have some characteristic modification of the **wing-veins** and their branches. None of them, however, departs nearly so far from the normal type as do the Hymenoptera, even the lowest members of this group possessing a highly specialized venation. Before beginning a study of the Hymenopteran series which leads up to the bee the student should first turn back to figure 6 (p. 22) and again familiarize himself with the generalized condition of the veins and the articular elements of the wing. By comparing, now, with this diagram the basal parts of the wing of a sawfly (*Itycorsia discolor*, fig. 26 A) it will be easy to identify the parts of the latter. Vein *C* has two little nodules (*C*, *C*) cut off from its basal end which lie free in the axillary membrane. Vein *Sc* articulates by an enlarged and contorted base (*Sc*) with the first axillary (*1Ax*), while vein *R* is continuous with the second (*2Ax*). The next two veins that come to the base and unite with each other are apparently not the media and cubitus but the first and third anals (*1A* and

3A), since they are associated with the third axillary (3Ax). In this species the subcosta (Sc) is entirely normal, but in the related horntail (*Sirex flavicornis*, fig. 26 B) the enlarged basal part of the subcosta is almost separated from the shaft of the vein, while the latter (fig. 25A, Sc) is short and weak. A study of the venation of this wing leads us to believe that the vein which arises from the radius a short distance from its base is the cubitus (Cu). Therefore the basal part

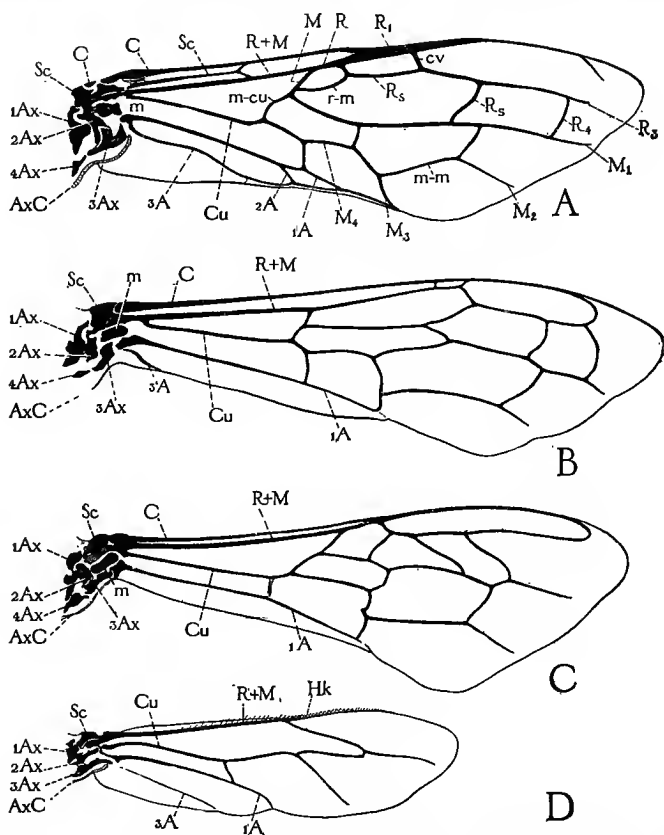


FIG. 25.—Wings of Hymenoptera and their basal articular sclerites (1Ax–4Ax): A, *Sirex flavicornis*, front wing; B, *Pepsis* sp., front wing; C, honey bee, front wing; D, honey bee, hind wing.

of the media is either gone or is fused with the radius. Since we discover its branches in the distal field of the wing, arising from the trunk of the radius, we conclude that the latter is the case. By this sort of reasoning we may arrive at the Comstock and Needham interpretation of the wing illustrated at A, fig. 25. From this it is evident that the branches of both the radius and the media have been bent back toward the posterior margin of the wing.

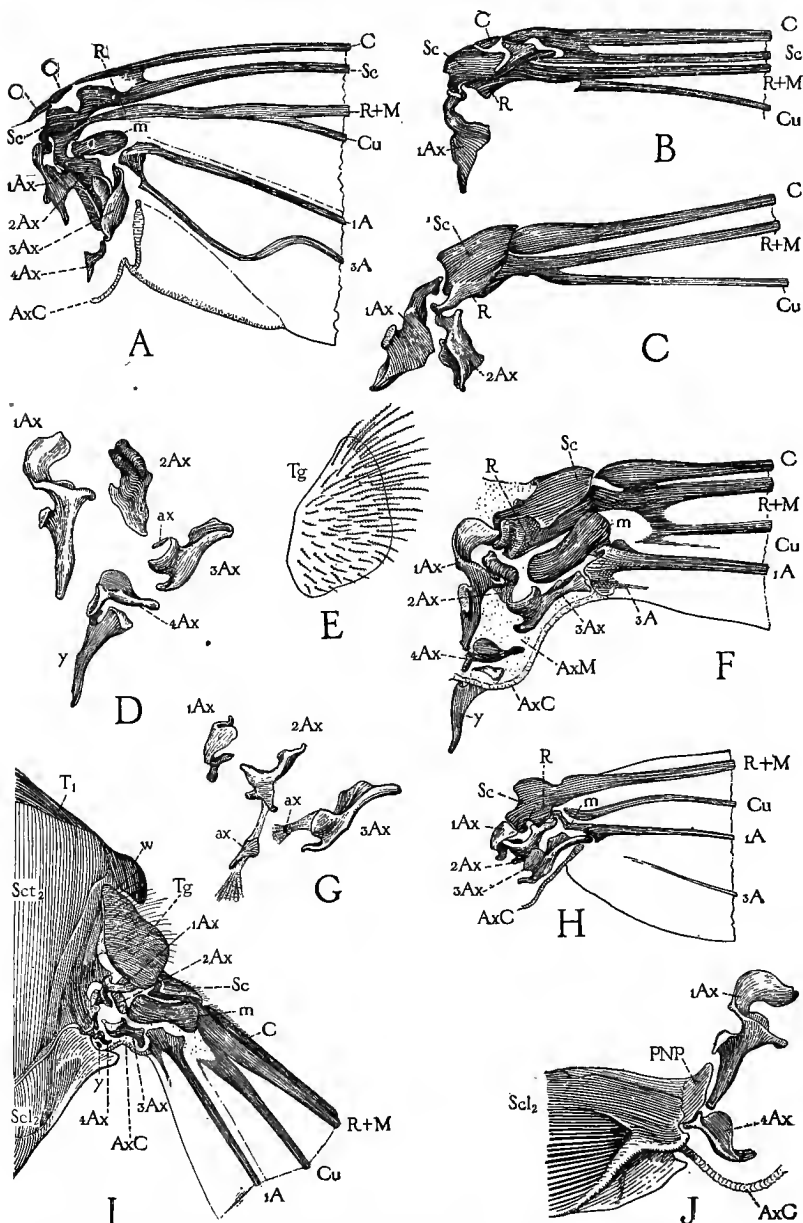


FIG. 26.—Basal elements of wings of Hymenoptera: A, base of front wing of a sawfly (*Itycorsia discolor*) showing comparatively generalized arrangement of veins and axillaries; B, bases of anterior veins of front wing of a horn-tail (*Strea flavicornis*), showing detachment of base of subcostal vein (Sc) from its shaft; C, corresponding view of anterior veins in front wing of a tarantula-killer (*Pepsis* sp.), showing complete absence of shaft of subcosta, but presence of basal part (Sc) fused with base of radius (R); D, axillaries of anterior wing of honey bee worker; E, tegula of worker; F, base of anterior wing of worker showing absence of shaft of subcosta but presence of scale (Sc) derived from its base; G, axillaries of hind wing of worker, the fourth absent in bee; H, base of hind wing of worker, showing absence of costal and subcostal veins and fusion of bases of subcosta (Sc₂) and radius (R) into large humeral mass; I, attachment of front wing to scutum (Sct₂) and scutellum (Scl₂) of mesotergum (J, under view of end of mesoscutellum (Scl₂) showing attachment of both first (1Ax) and fourth axillaries (4Ax) to posterior wing process (PNP), an unusual connection for first axillary.

Taking this wing of *Sirex* as a foundation let us proceed a little higher and examine the wing of a Pompilid, such as *Pepsis* (figs. 26 C and 25 B). We observed that in *Sirex* (fig. 26 B) the basal part of vein *Sc* is almost separated from the distal shaft. In *Pepsis* (fig. 26 C) it is entirely a separate piece, to which is fused also the base of vein *R*. Moreover, the shaft of *Sc* has disappeared entirely (fig. 25, B). Thus there is at the humeral angle of the wing a large chitinous mass (fig. 26 C, *Sc* and *R*) representing the fused bases of both the subcosta and the radius, which is associated with both the first axillary (1*Ax*) and the second axillary (2*Ax*).

If now we proceed to a study of the front wing of the bee we find that its basal characters (fig. 26 F) are more similar to those of *Sirex* (B), while its venation (fig. 25 C) resembles more closely that of *Pepsis* (B). The subcostal scale at its base (fig. 26 F, *Sc*) is not fused with the base of the radius, but the distal part of the subcosta is gone (fig. 25 C), as in *Pepsis*. In the hind wing of the bee (fig. 26 H) the bases of the subcosta and radius are fused into one large humeral mass articulating with the first two axillaries (1*Ax* and 2*Ax*). The third axillary (3*Ax*) is well developed but the fourth is absent. The venation (fig. 25 D) is reduced to a very simple condition, but to one just the opposite from primitive.

The details of the axillaries in the two wings are shown by figure 26 D and G. The fourth (4*Ax*) is well developed in the front wing (D) and has a large accessory sclerite (*y*) connected with it, upon which is inserted a long slender muscle (fig. 28, *cc*). A very small accessory sclerite (*ax*) occurs close to the muscle plate of the third axillary (3*Ax*). These are called "accessory" sclerites because they are of irregular occurrence in the wing bases of insects generally and are developed in connection with the muscle attachments. Similar ones occur in the hind wing (G, *ax*) in connection with the second (2*Ax*) and third axillaries (3*Ax*).

The front wing is attached to the posterior half of the side of the mesonotum. The anterior notal wing process is bilobed (figs. 22, 23 A, *T*₂, *ANP*) and is carried by the scutum, while the posterior process (*PNP*) is carried by the scutellum and is mostly hidden beneath the anterior wing process. The two wing processes, in fact, are so close together that the first axillary articulates not only with the first but also with the second (fig. 26 J). The axillary cord (fig. 26 F, *AxC*) arises from a lobe of the scutellum overlapped by the lateral margin (I and J, *AxC*). In the hind wing, where the fourth axillary is absent, the third articulates directly with the posterior notal wing process of the metatergum (fig. 23 A, *T*₃, *PNP*).

The base of the front wing is overlapped by a large scale (fig. 26, E and I, *Tg*) called the tegula. It is carried by the axillary mem-

brane, to which it is attached between the humeral angle of the wing base and the edge of the notum. The tegulæ are present in most insects, generally on the base of each wing, but they usually have the form of small inconspicuous hairy pads, as shown in the diagram (fig. 6, *Tg*). In the flies, moths, butterflies, and Hymenoptera, however, the tegulæ of the front wings develop into large conspicuous scales overlapping the humeral angles of the bases of these wings.

The motion of the wing in flight consists of both an up-and-down movement and a forward-and-backward movement, which two combined cause the tip of the wing to describe a figure-eight course if the insect is held stationary. Corresponding with these four movements are four sets of muscles. In the dragonflies nearly all of the wing muscles are inserted directly upon the base of the wing itself, but in other insects, excepting possibly the mayflies, the principal muscles are inserted upon the thoracic walls and move the wing secondarily. In the lower insects, such as the grasshoppers, crickets, stoneflies, net-winged flies, etc., the two wing-bearing segments are about equal in their development and each is provided with a full equipment of muscles. In these insects the wings work together by coordination of their muscles, although each pair constitutes a separate mechanism. In such insects, however, as the true flies and the wasps and bees the metathorax, as we have seen in the case of the bee, is greatly reduced, and what is left of it is solidly attached to the mesothorax. In the flies the hind wings are reduced to a pair of knobbed stalks having no function as organs of flight, while in the bees the hind wings, which are very small, are attached to the front wings by a series of hooklets on their anterior margins (fig. 25 D, *Hk*) which grasp a posterior marginal thickening of the front wings. Moreover, when we examine the interior of the bee's thorax we find that the muscles of the metathorax are greatly reduced or partly obliterated and that the great mesothoracic muscles serve for the movement of both wings, thus assuring a perfect synchrony in their action. Hence, it is clear that the union and consolidation of the thoracic segments in the higher insects is for the purpose of unifying the action of the wings.

The muscles of flight in the bee may be very easily studied by cutting the thorax of a drone into lateral halves. The cavity of the thorax is occupied almost entirely by three great masses of muscles. One of these is longitudinal, median, and dorsal (fig. 27, *LMcl*₂), extending from the mesoscutum (*Sc*₂) and the small prephragma (*Aph*) to the large mesothoracic postphragma (*Pph*₂). A small set of muscles (*LMcl*₃) then connects the posterior surface of this phragma with the lower edge of the propodeum (*IT*). On each side of the

anterior end of this great longitudinal muscle is a thick mass of dorso-ventral fibers (*VMcl*) extending from the lateral areas of the mesoscutum (*Sct₂*) to the lateral parts of the mesosternum (*S₂*). A contraction of the vertical muscles must depress the tergal parts, at the same time expanding the entire thorax in a longitudinal direction and stretching the longitudinal muscles. A contraction, then, of the latter muscles (*LMcl*) restores the shape of the thorax and elevates the tergal parts. Remembering, now, that the wings are

supported from below upon the pleural wing processes and that each is hinged to the back by the notal wing processes, it is clear that a depression of the dorsum of the thorax must elevate the wings and that an elevation of the dorsum depresses them—the pleural wing processes acting as the fulcrum. Hence, the chief up-and-down movements of the wings are produced by these great thoracic muscles acting upon the shape of the thorax as a whole and not directly upon the wings

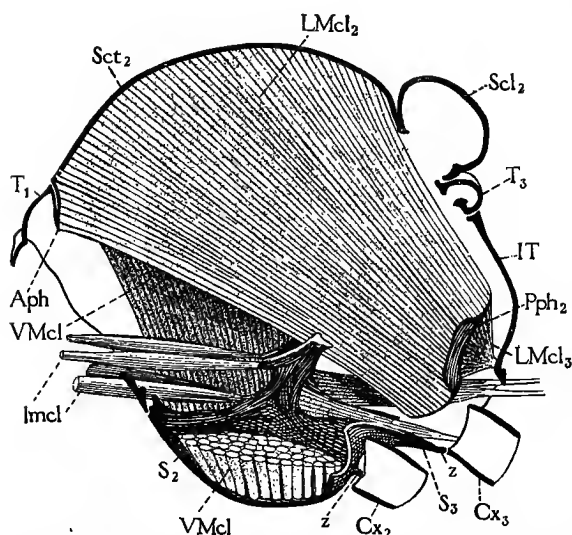


FIG. 27.—Median section through thorax of drone, showing longitudinal muscles (*LMcl₂*) of mesothorax going from mesotergal scutum (*Sct₂*) and small anterior phragma (*Aph*) to posterior phragma (*Pph₂*) of internal postscutellum (postnotum) of same segment, also showing vertical mesothoracic muscles (*VMcl*), and ventral longitudinal muscles (*Imcl*), and longitudinal muscles of metathorax (*LMcl₃*) going from postphragma of mesothorax (*Pph₂*) to posterior edge of propodeum or first abdominal tergum (*IT*). By alternate contraction of dorsal longitudinal muscles and vertical muscles, roof of thorax is elevated and depressed, causing wings to beat downward and upward respectively, being supported on fulcrum formed by pleural wing processes (fig. 28, *WP₂*) of side walls of thorax.

themselves. The vertical muscles are the *elevators* and the longitudinal the *depressors*.

But besides being moved up and down the wings can also, as before stated, be extended and flexed, i. e., turned forward and backward in a horizontal plane upon the pleural wing process. The muscles which accomplish these movements lie against the inner face of the pleurum (fig. 28), and each wing is provided with a separate set. The extensor muscle (*PMcl*) is the most anterior and is inserted by a long neck upon the preparapertum (*2P*). The latter is closely

connected with the anterior part of the base of the wing so that a contraction of the muscle turns the wing forward and at the same time depresses its anterior margin. For this reason the parapterum and the extensor muscle have been called the *pronator apparatus*, and the muscle is known also as the *pronator muscle*. In some insects which fold the wings back against the body this muscle is a great deal larger than in the bee. The *flexor muscle* (*RMcl*) consists of three parts situated upon the anterior half of the pleurum and inserted upon the third axillary (*3Ax*) by long tendonlike necks. These muscles are antagonistic to the extensor and by their contraction pull the wing back toward the body.

The mechanism which produces the wing motion thus seems to be a very simple one and may be summarized as follows: Each wing rests and turns upon the wing process of the pleurum (figs. 24 and 28, *WP*) by means of the pivotal sclerite or second axillary in its base (figs. 26 F and 28, *2Ax*). It is hinged to the back by the first and fourth axillaries (fig. 26 F, *1Ax* and *4Ax*) which articulate with the anterior and posterior notal wing processes (fig. 23 A, *T₂*, *ANP* and *PNP*), respectively. The large vertical muscles (fig. 27, *VMcl*) of the thorax depress the tergum, which pulls down with it the base of the wing and hence elevates the distal part—

the fulcrum being the pleural wing process. The dorsal longitudinal muscle (*LMcl*) restores the shape of the thorax, elevates the tergum, and consequently depresses the wing. Extension and flexion of the wing are produced by special muscles (fig. 28, *PMcl* and *RMcl*) acting upon its base before and behind the pleural wing process, respectively.

Besides these muscles there are several others (fig. 28) associated with the wing whose functions are less evident. Most conspicuous of these is a muscle occupying the posterior half of the mesopleurum (*aa*) and inserted upon the outer end of the scutellum. This may

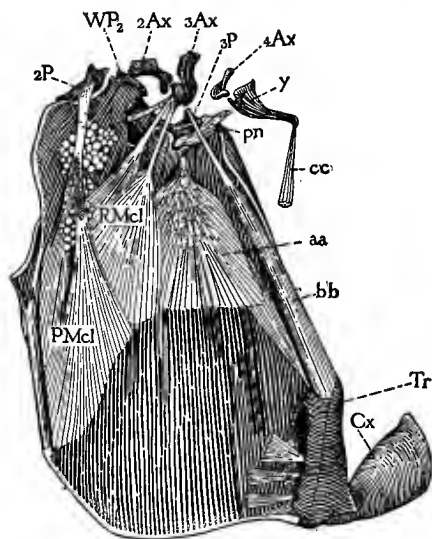


FIG. 28.—Internal view of right pleurum of mesothorax of drone, showing muscles inserted upon parapteral plates (*2P* and *3P*) and upon third axillary (*3Ax*). The wing rests upon wing process of pleurum (*WP₂*) by second axillary (*2Ax*); it is turned forward and downward by the pronator muscle (*PMcl*), inserted upon anterior parapterum (*2P*) which is attached to costal head of wing, and is turned back toward body by flexor muscle (*RMcl*) inserted upon third axillary (*3Ax*).

be simply accessory to the large vertical sterno-scutal muscle (fig. 27, *VMcl*). Another is a long slender muscle (*bb*) attached to the upper end of the mesocoxa and inserted upon the postparapterum (*3P*). This is sometimes termed the *coxo-axillary muscle*. A third (*cc*) is inserted upon the tip of the accessory sclerite (*y*) of the fourth axillary and is attached to the lateral arm of the large entosternum of the mesothorax and metathorax.

3. THE LEGS.

The legs of the honey bee are highly modified for several special purposes besides that of walking, but they are so well known and have been so often described that it will not be necessary to devote much space to them here.

The **front legs** (fig. 29 A) have a structure formed by the adjoining ends of the tibia and the first tarsal joint, which is called, on account of its use, the *antenna cleaner*. It consists (fig. 29 C) of a semi-circular notch (*dd*) in the base of the first tarsal joint provided with a comblike row of bristles. A specially modified, flat, movable spur (*ee*), shown in ventral view at B, is so situated on the end of the tibia (*Tb*) that it closes over the notch when the tarsus is bent toward the tibia. By grasping an antenna between the notch and the spur and drawing it through the inclosure the bee is able to remove from this sensitive appendage any pollen or particles of dirt that may be adhering to it.

The **middle legs** (fig. 29 D) present no special modifications of any importance. It will be observed, however, that they, as well as the other legs (A and F), have the first joint of the tarsus (*1Tar*) very greatly enlarged.

The **hind legs** of all three forms, the worker (F), the queen (E), and the drone (H), have both the tibia and the large basal segment of the tarsus very much flattened. In the queen and drone there seems to be no special use made of these parts, but in the worker each of these two segments is modified into a very important organ. The outer surface of the tibia (F, *Tb*) is fringed on each edge by a row of long curved hairs. These constitute a sort of basket (*Cb*) in which the pollen collected from flowers is carried to the hive. The structures are known as the *pollen baskets*, or *corbicula*. The inner surface of the large, flat, basal segment of the tarsus (*1Tar*) is provided with several rows of short stiff spines (G) forming a brush by means of which the bee gathers the pollen from its body, since it often becomes covered with this dust from the flowers it visits for the purpose of getting nectar. When a sufficient amount is accumulated on the brushes it is scraped off from each over the edge of the tibia of the opposite hind leg and is thus stored in the pollen baskets. Hence the worker often flies back to the hive with a great mass of

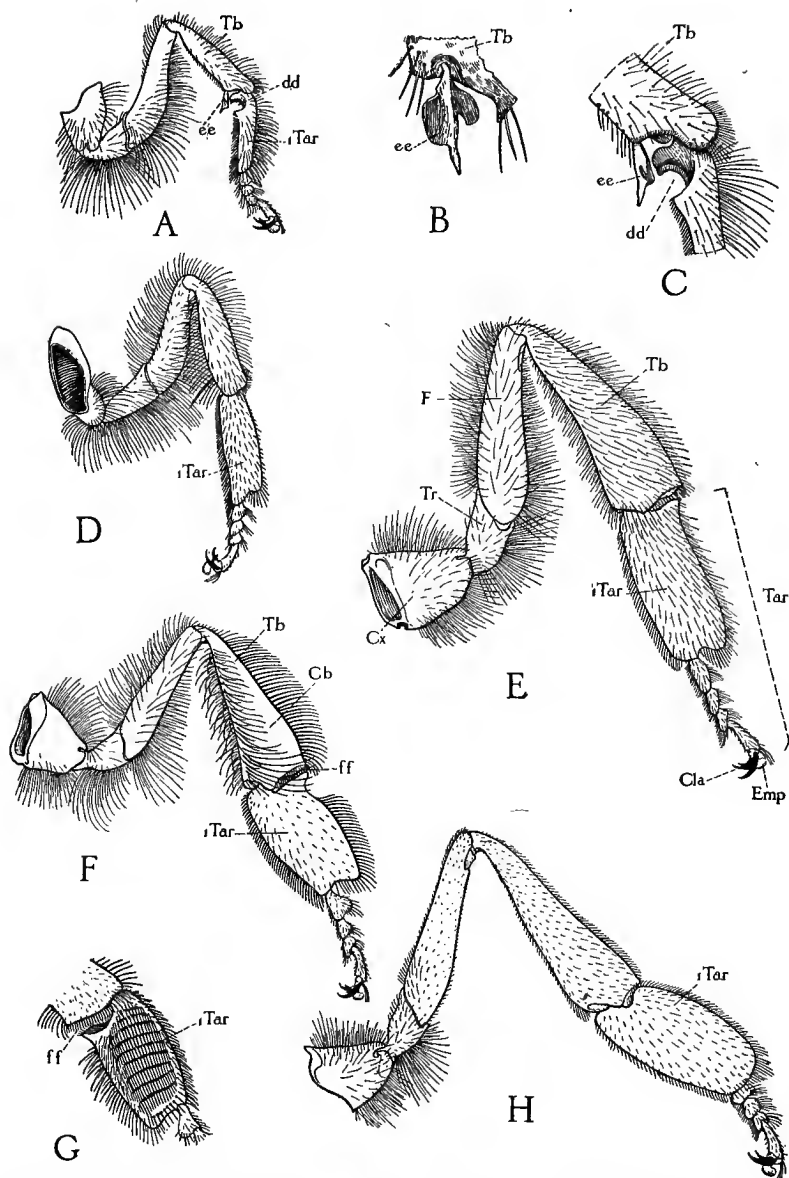


FIG. 29.—A, left front leg of worker, anterior view, showing position of notch (*dd*) of antenna cleaner on base of first tarsal joint (*ITar*), and of closing spines (*ee*) on end of tibia (*Tb*); B, spine of antenna cleaner (*ee*) in flat view; C, details of antenna cleaner; D, left middle leg of worker, anterior view; E, left hind leg of queen, anterior or outer view; F, left hind leg of worker, anterior or outer view, showing the pollen basket (*Cb*) on outer surface of tibia (*Tb*); G, inner view of first tarsal joint of hind leg of worker showing rows of pollen-gathering hairs and the so-called "wax shears" (*ff*); H, left hind leg of drone, anterior or outer view.

pollen adhering to each of its hind legs. The pollen baskets are also made use of for carrying propolis.

Between the ends of the hind tibia (*Tb*) and the first tarsal joint (*1Tar*) is a sort of pincerlike cleft (F and G, *ff*) guarded by a row of short spines on the tibial edge. This is popularly known as the "wax shears" and it is supposed to be used for picking the plates of wax out of the wax pockets of the abdominal segments. The writer, however, has watched bees take the wax from their abdomen and in these observations they always poked the wax plates loose

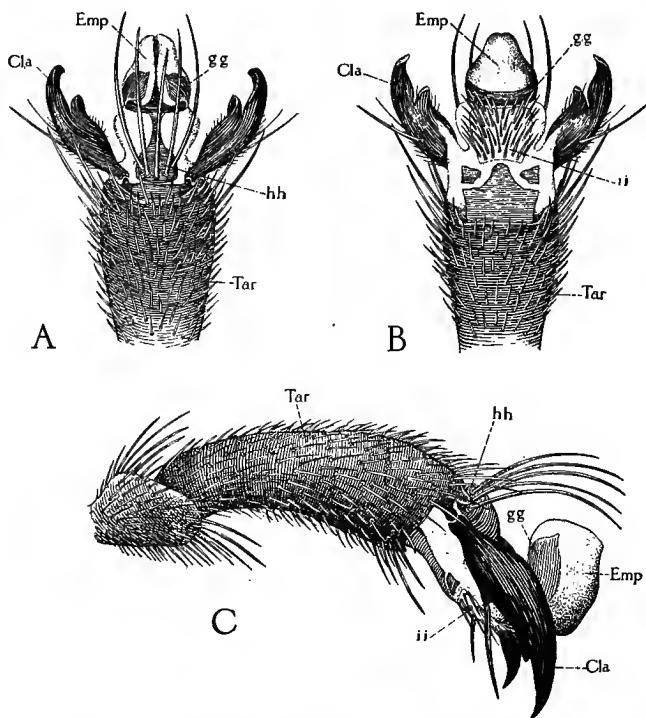


FIG. 30.—A, dorsal view of end of last tarsal joint of first foot (*Tar*), the claws (*Cla*), and empodium (*Emp*) of worker; B, ventral view of same; C, lateral view of same, showing empodium in ordinary position when not in use.

with the ordinary hairs or spines of the tibiae or tarsi and then by means of the feet passed them forward beneath the body to the mandibles.

The last tarsal joint of each leg bears a pair of *claws* (*E, Cla*) and a single median *empodium* (*Emp*). Each one of the claws is bilobed, consisting of a long tapering outer point and a smaller inner one (figs. 30 and 31). The claws of the worker (fig. 31 A) and the queen (B) are only slightly different in details of outline, although the claws of the queen are much greater in size than those of the

worker, but the drone's claws (C) are large and very strikingly different in shape from those of either the worker or the queen.

The empodium (fig. 30 A, B, and C, *Emp*) consists of a terminal lobe bent upward between the claws (C) and deeply cleft on its dorsal surface (A), and of a thick basal stalk whose walls contain a number of chitinous plates. One of these plates is dorsal (A and C, *hh*) and bears five very long, thick, curved hairs projecting posteriorly over the terminal lobe, while a ventral plate (B and C, *ii*) is provided with numerous short thick spines. A third plate (A, B, and C, *gg*) almost encircles the front of the terminal lobe, its upper ends reaching to the lips of the cleft.

When the bee walks on any ordinary surface it uses only its claws for maintaining a foothold, but when it finds itself on a smooth, slippery surface like glass the claws are of no avail and the empodia are provided for such emergencies as this. The terminal lobe is pressed down against the smooth surface and its lateral halves are flattened out and adhere by a sticky liquid excreted upon them by glands said to be situated in front of them. On the relaxation of the muscle that flattens the empodial lobes the latter spring back into their original position by the elasticity of the chitinous band (*gg*) in their walls.

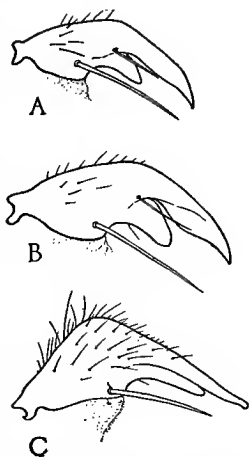


FIG. 31.—A, outer view of hind claw of worker; B, same of queen; C, same of drone.

V. THE ABDOMEN, WAX GLANDS, AND STING.

The abdomen of the worker and queen appears to consist of six segments (figs. 1, 32, 33, *II-VII*), but it must be remembered that, as has already been explained, the thoracic division of the body in the Hymenoptera includes one segment, the propodeum or median segment, which really belongs to the abdomen and is its true first segment according to the arrangement in all other insects. Hence, counting the propodeum (figs. 21 and 32, *IT*) as the first, we find seven exposed abdominal segments in the worker and queen and nine in the drone. Each one except the first consists of a tergum (*T*) and a sternum (*S*), the former reaching far down on the side of the segment, where it carries the spiracle (*S ρ*) and overlaps the edge of the sternum. The two plates of the last or seventh segment in the worker and queen are separated by a cleft on each side, and if they are spread apart it is seen that the tip of the abdomen

incloses a cavity which lodges the sting and its accessory parts. The end of the abdomen of the male (fig. 56 D) is quite different from that of the female, while in it parts at least of nine segments are

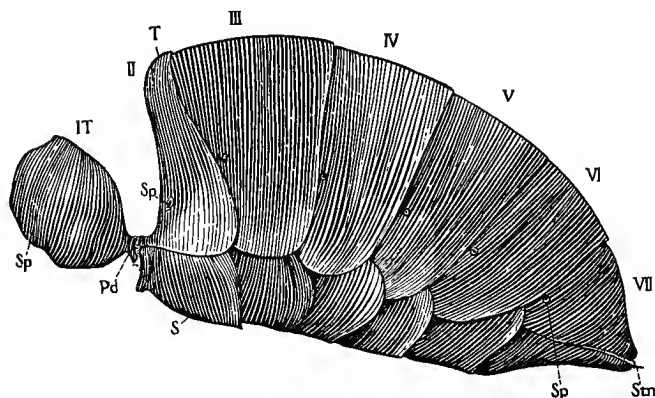


FIG. 32.—Lateral view of abdomen of worker, showing the propodeum (*IT*) as a part of the abdomen, of which it is the true first segment.

visible, the last is very much modified and is exposed only on the sides and below.

An internal view of the ventral plates and the lateral parts of the

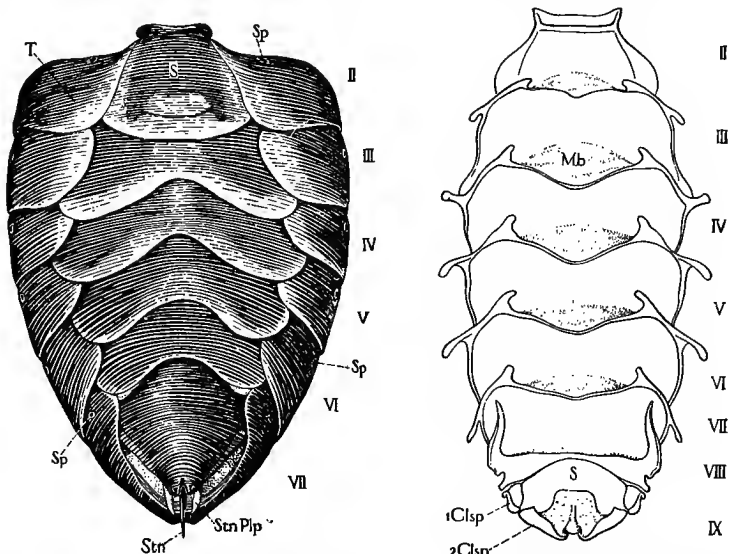


FIG. 33.—Ventral view of abdomen of worker, showing tip of sting (*Stn*) and palpuslike appendages (*StnPlp*) projecting from sting chamber within seventh segment (*VII*).

FIG. 34.—Dorsal view of abdominal sterna of drone, showing clasp-like appendages (*1Clsp* and *2Clsp*) of ninth segment.

terga in the worker is shown by figure 20, while a corresponding view of the male sterna is shown by figure 34. It will be seen that each sternum is very widely underlapped (viewed from above) by the

one next in front of it and that the intersegmental membrane (*Mb*) is reflected from the middle of the dorsal surface of each to the anterior edge of the following sternum. By removing an individual plate (fig. 35 A) this is more easily shown. It is also clearly seen that the transverse line of attachment of the membrane (*Mb*) divides the sternum into a posterior part (*Rd*), which is merely a prolonged reduplication underlapping the following sternum, and into an anterior part underlapped by the preceding sternum. The posterior half is, hence, purely external while the anterior half forms the true ventral wall of the segment, its dorsal face being internal and its ventral face external. The anterior part is also very smooth and shiny and somewhat bilobed and for this reason it is sometimes called the "mirrors." Its edge is bounded by a thickened ridge giving off a short apodeme (*Ap*) on each side. The mirrors of the last four sterna are also, and more appropriately, called the wax plates because the wax is formed by a layer of cells lying over them. It accumulates on the ventral side in the pocket between the wax plates and the posterior underlapping prolongation of the preceding sternum. Wax is formed only on the last four visible segments, i. e., on segments IV-VII, inclusive.

In studying any part of the body wall of an insect it must always be borne in mind that the chitin is originally simply an external cuticular layer of a true cellular skin or epidermis (erroneously called "hypodermis" in insects), but that in the adult stage the latter almost everywhere disappears as a distinct epithelium. Thus the chitin comes to be itself practically the entire body wall, the cell layer being reduced to a very inconspicuous membrane. However, in certain places the epithelium may be developed for special purposes. This is the case with that over the wax plates which forms a thick layer of cells that secrete the wax and constitute the so-called *wax glands*. The wax is first secreted in a liquid condition and is extruded through minute pores in the wax plates of the sterna, hardening on their under surfaces into the little plates of solid wax with which every bee keeper is acquainted.

The secretion of the wax has been studied by Dreyling (1903), who made histological sections through the glands at different times in the life of the bee. He found that in young, freshly emerged workers the epidermis of the wax plates consists of a simple layer of ordinary epithelial cells. As the activities of the bee increase, however, these cells elongate while clear spaces appear between them and, when the highest development is reached, the epithelium consists of a thick layer of very long cells with liquid wax stored in the spaces between them. In old age most of the cells become small again and in those bees that live over the winter the epithelium degenerates to a simple sheet of nucleated plasma showing no cell boundaries. It is thus evident that the secretion of wax is best performed during the prime

of life, which in bees is at about 17 days of age or before, and that old bees can only gather honey and pollen. Bees do not normally secrete wax while performing the other more ordinary duties of their life. When comb is needed a large number of young bees or bees that have not passed their prime hang together in vertical sheets or festoons within the hive and are fed an abundance of honey. After about twenty-four hours they begin to construct comb. During this time the wax is excreted through the wax plates and accumulates in

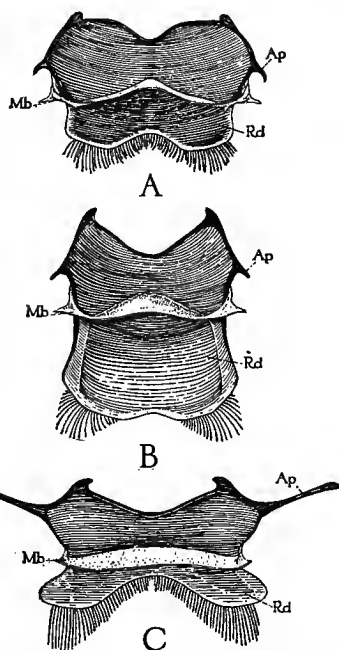


FIG. 35.—Dorsal surface of sixth abdominal sternum: A, worker; B, queen; C, drone; showing division of plate by line of attachment of intersegmental membrane (*Mb*) into anterior part with polished internal surface, in worker bearing wax glands, and into large posterior external part (*Rd*) underlapping anterior half of succeeding sternum.

the external wax pockets below. It is poked out of these pockets by means of the spines on the feet and is passed forward beneath the body to the mandibles. By means of these organs it is manipulated into little pellets and modeled into the comb. Dreyling describes the pores of the wax plates as excessively fine, vertical, parallel canals only visible in very thin sections and under the highest power of the microscope.

Corresponding abdominal sterna present quite different shapes in the three forms of the bee (fig. 35 A, B, and C). In the queen (B) the sterna are much longer than in the worker (A), while in the drone (C) they are shorter and have very long lateral apodemes (*Ap*).

The last three abdominal segments—the eighth, ninth, and tenth—are very different in the two sexes on account of their modification in each to accommodate the external organs of re-

production and egg laying. In the female these segments are entirely concealed within the seventh, but, in the male, parts of both the eighth and ninth segments are visible externally.

The seventh segment of the drone (counting the propodeum as the first) is the last normal segment, i. e., the last one having a complete tergum and sternum resembling those of the anterior part of the abdomen (fig. 56 D, *VIIIT* and *VIIS*). Behind the seventh tergum and partly concealed within it is the eighth tergum (*VIIIT*) carrying the last abdominal spiracles (*Sp*). The eighth sternum is

almost entirely concealed within the seventh. It is very narrow below, but is expanded at the upper parts of its sides (*VIIIS*), where it is partly visible below the eighth tergum and behind the seventh sternum. The dorsal part of the ninth segment is membranous except for a small apodeme-bearing plate on each side hidden within the eighth tergum. The ninth sternum, on the other hand, is a well-developed semicircular band (*IXS*) forming the ventral and ventrolateral parts of the ninth segment. It bears on each side two conspicuous lobes—one a small, darkly chitinized, dorsal plate (*1Clsp*) carrying a large bunch of long hairs, the other a large, thin, ventral plate (*2Clsp*). Between these four appendicular lobes is ordinarily a deep cavity, which is the invaginated penis (fig. 56 E), but in figure D this organ is shown partly evaginated (*Pen*). While the penis is really an external organ, the details of its structure will be described later in connection with the internal organs of reproduction. The tenth segment is entirely lacking in segmental form. The anal opening is situated in a transverse membrane beneath the eighth tergum (*VIIIT*), and below it is a thin chitinous plate, which may belong to the tenth segment.

In many insects the modification of the terminal segments of the males in connection with the function of copulation is much greater than in the bee. The ninth segment often forms a conspicuous enlargement called the *hypopygium*, which is usually provided with variously developed clasping organs in the form of appendicular plates and hooks.

The development of the external genital parts of the drone has been described by both Michaelis (1900) and Zander (1900). A small depression first appears on the under surface of the ninth segment of the larva shortly after hatching. Soon two little processes grow backward from the anterior wall of this pouch and divide each into two. The part of the larval sternum in front of the pouch becomes the ninth sternum of the adult, while the two processes on each side form the upper and lower appendicular lobes (the *valva externa* and the *valva interna* of Zander). The penis at first consists of two little processes which arise between the valvæ internæ, but is eventually formed mostly from a deep invagination that grows forward between them. These four processes arising on the ventral side of the ninth segment of the male larva are certainly very suggestive of the similar ones that are formed in the same way on the same segment of the female and which develop into the second and third gonapophyses of the sting. If they are the same morphologically we must homologize the two clasping lobes of the ninth sternum in the male with the two gonapophyses of this segment in the female. Zander (1900) argues against such a conclusion on the ground that the genital pouch is situated near the anterior edge of the segment in the female and

posteriorly in the male, while the parts in the two sexes develop later in an absolutely different manner. These arguments, however, do not seem very forcible—in the earliest stages the processes certainly look alike in the two sexes.

The sting of the bee is situated in the sting cavity at the end of the abdomen, from which it can be quickly protruded when occasion demands. This sting chamber contains also the reduced and modified sclerites of the eighth, ninth, and tenth abdominal segments. In fact, the sting chamber is formed by an infolding of these three segments into the seventh. It is consequently not a part of the true interior of the body or body cavity which contains the viscera, but is simply a sunken and inclosed part of the exterior, in the same sense that the oven of a stove is not a part of the real inside of the stove. Consequently the parts of the sting, though normally hidden from view, are really external structures.

A very gentle pull on the tip of the sting is sufficient to remove it from its chamber, but a sting thus extracted brings along with it the ninth and tenth segments, most of the eighth segment, the poison glands, and the terminal part of the alimentary canal. This is due to the fact that the inclosed segments are attached to the surrounding parts by very delicate membranes. For the same reason they so easily tear from the living bee as the latter hurriedly leaves its victim after stinging. The worker thus inflicts a temporary wound and pain at the cost of its own life. Undoubtedly, however, nature regards the damage to the enemy as of more importance to the bee community as a whole than the loss of one or a dozen of its members. The entire stinging apparatus with a bag of poison attached is thus left sticking in the wound while the muscles, which keep on working automatically, continue to drive the sting in deeper and deeper and at the same time pump in more poison. Such a provision certainly produces much more effective results than would a bee giving a thrust here and another there with its sting and then rapidly flying away to escape from danger.

The sting itself, when extracted from its chamber, is seen to consist of a straight tapering shaft with its tip directed posteriorly and its base swollen into a bulblike enlargement. In superficial appearance the shaft appears to be solid, although we shall presently show that it is not, but the bulb is clearly hollow and is open below by a distinct median cleft. Several plates of definite shape and arrangement always remain attached to the sting and overlap its base. The entire apparatus, including the base of the large poison sac, is shown somewhat diagrammatically in side view by figure 36. The bulb of the sting (*ShB*) is connected with the lateral plates by two arms which curve outward and upward from its base. (Only the left side is shown in the figure.) Between these arms the two poison glands

(*PsnSc* and *BGI*) open into the anterior end of the bulb. From the posterior ends of the plates two whitish fingerlike processes (*StnPlp*) project backward. When the sting is retracted these lie at the sides of the shaft (figs. 33 and 37), but in figure 36 the sting is shown in a partly protracted position. These appendages, often called the sting palpi, undoubtedly contain sense organs of some sort by means of which the bee can tell when her abdomen is in contact with the object upon which she desires to use her sting.

A close examination of the sting shows that it is a much more complicated structure than it at first sight appears to be. The shaft, for example, is not a simple, solid, tapering, spearlike rod, but is a hollow organ made of three pieces which surround a central canal. One of these pieces is dorsal (fig. 36, *ShS*) and is the true prolongation of the bulb (*ShB*), while the other two (*Lct*) are ventral and slide lengthwise on tracklike ridges of the dorsal piece. Moreover, each basal arm of the sting is double, consisting of a dorsal or posterior piece (*ShA*), which is likewise a prolongation of the bulb, and a ventral or anterior piece (*Lct*), which is continuous with the ventral rod of the shaft on the same side. Hence the sting may be analyzed into three elements, which

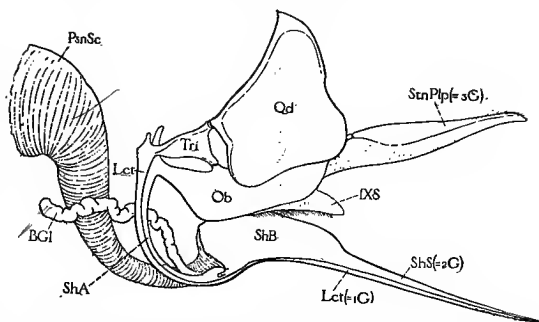


FIG. 36.—Semidiagrammatic view of left side of sting of worker, accessory plates (*Tri*, *Ob*, *Qd*), sting palpus (*StnPlp*), alkaline poison gland (*BGI*), and base of large poison sac (*PsnSc*) of acid gland.

are characterized as follows: The dorsal piece, known as the *sheath*, consists of a prominent basal swelling or *bulb* (*ShB*) containing a large cavity, of a terminal tapering *shaft* (*ShS*), and of two curved *basal arms* (*ShA*). The ventral part consists of two long slender rods, called the *lancets* or *darts* (*Lct*), which slide freely upon two tracks on the ventral edges of the sheath and diverge upon continuations of these tracks along the basal arms of the latter (*ShA*). The bulb is hollow, containing a large cavity formed by invagination from below, where it is open to the exterior by a lengthwise cleft. This cavity continues also through the entire length of the shaft of the sting as a channel inclosed between the dorsal sheath and the latero-ventral lancets. This channel, as will be explained later, is the *poison canal* of the sting.

Each arm of the sheath (*ShA*) is supported at its end farthest from the bulb by an *oblong plate* (fig. 36, *Ob*), which normally over-

laps the side of the bulb, and which carries distally the *palpi* of the sting (*StnPlp*). Each lancet is attached at its base to a *triangular plate* (*Tri*) which lies latero-dorsad to the base of the oblong plate and articulates with a knob on the dorsal edge of the latter by its ventral posterior angle. By its dorsal posterior angle the triangular plate is articulated to a much larger *quadrate plate* (*Qd*) which overlaps the distal half of the oblong plate. A thick membranous lobe (*IXS*), concave below, where it is thickly set with long hairs, overlaps the bulb of the sting and is attached on each side to the edges of the oblong plates. All of these parts are shown flattened out

in ventral view by figure 37.

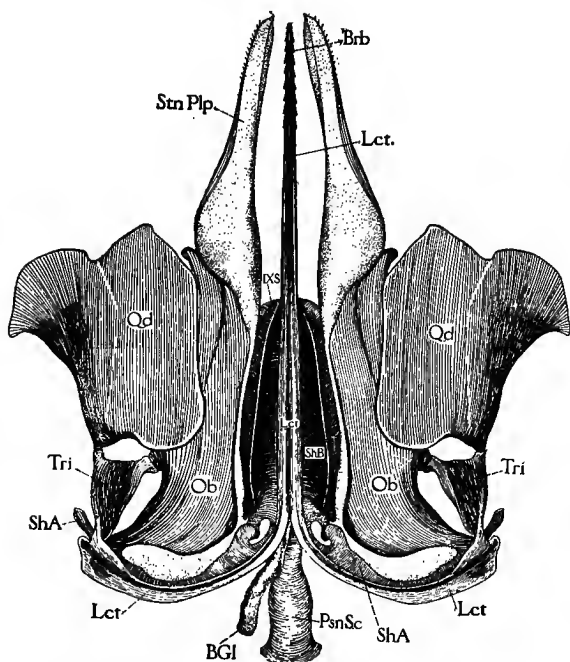


FIG. 37.—Ventral view of sting of worker and accessory parts, flattened out.

The presence of the two basal arms of the sheath might suggest that this part is to be regarded as made up of fused lateral halves. In this case we should have six appendicular elements, viz, the two lancets, the two halves of the sheath, and the two palpuslike organs. If now we turn back to figure 8, showing the component parts of the ovipositor of a longhorned grasshopper, we can not fail to be struck at

once by the great similarity between this organ and the sting of the bee (fig. 36). The first gonapophyses (*1G*) of the ovipositor are identical with the lancets (*Lct*) of the sting, and their sliding connection, by means of longitudinal tracks, with the second gonapophyses (*2G*) suggests at once that the latter represent the sheath of the sting (*ShS*). The identity is still more strongly suggested when we observe the small bulb (*ShB*) formed by the fused bases of these gonapophyses. The third gonapophyses (*3G*), which inclose between them the other parts of the ovipositor, represent the palpi of the sting (*StnPlp*). If, finally, we study the development of the parts of the sting we are convinced that this similarity between the sting and an ovipositor means something more than an accidental resemblance

between two different organs—in fact we can not doubt that the sting is simply an ovipositor which, being no longer needed for egg-laying purposes, has been modified into a poison-injecting apparatus. Zander (1899, 1900) and others have shown that the sting of the bee arises from six little abdominal processes of the larva, two of which arise on the eighth segment and four on the ninth. Those of the first pair develop into the lancets, those of the middle pair on the ninth segment fuse to form the sheath, while those of the outer pair become the palpi. The ovipositor, it will be remembered, develops in the lower insects from two pairs of processes arising on the eighth and ninth abdominal sterna, the second pair of which very soon splits into four processes. The simultaneous appearance of six on the bee larva is simply an example of the hurrying process or acceleration that the embryos and young of most higher forms exhibit in their development.

It is only the higher members of the Hymenoptera, such as the wasps and the bees and their close relatives, that possess a true sting. The females of the lower members have ovipositors which closely resemble those of such insects as the katydids, crickets, and cicadas, but which, at the same time, are unquestionably the same as the sting of the stinging Hymenoptera. It is said that the queen bee makes use of her sting in placing her eggs in the cells, but both the wasps and the bees deposit their eggs in cells or cavities that are large enough to admit the entire abdomen, and so they have but little use for an egg-placing instrument. But the females of the katydids and related forms like *Conocephalus* (fig. 8) use their ovipositors for making a slit in the bark of a twig and for pushing their eggs into this cavity. The cicada and the sawfly do the same thing, while the parasitic Hymenoptera often have extremely long and slender piercing ovipositors for inserting their eggs into the living bodies of other insects.

An examination of the sting in place within the sting chamber, as shown by figure 41, will suggest what the accessory plates represent in other less modified insects. It has already been explained that the last external segment of the female abdomen (fig. 32, VII) is the seventh. Within the dorsal part of the sting chamber is a slight suggestion of the eighth tergum (fig. 41, VIIIT), which laterally is chitinized as a conspicuous plate bearing the last or eighth abdominal spiracle (*Sp*). The triangular plate (*Tri*), as Zander has shown by a study of its development, is a remnant of the eighth sternum, and the fact that it carries the lancet (*Lct*) shows that even in the adult this appendage belongs to the eighth segment. The quadrate plate (*Qd*), since it is overlapped by the spiracle plates of the eighth tergum, might appear to belong to the eighth sternum, but Zander has shown that, by its development, it is a part of the ninth tergum. In many other adult Hymenoptera, moreover, the quadrate plates are undoubtedly tergal,

for they are sometimes connected by a bridge behind the eighth tergum. The oblong plate (*Ob*) and its stalk represent the ninth sternum, and since it carries both the arm of the sheath (*ShA*) and the palpus (*Plp*) it still maintains its original relationships to the gonapophyses. The membranous lobe arising from between the oblong plates and overlapping the bulb of the sting (figs. 36 and 37, *IXS*) must belong to the median part of the ninth sternum.

The tenth segment (fig. 41, *X*) consists of a short, thick tube having the anus (*An*) at its tip. It takes no part in the formation of the sting, but is entirely inclosed in the dorsal part of the sting chamber beneath the seventh tergum.

In the accessory plates of the bee's sting we have a most excellent illustration of how the parts of a segment may become modified to meet the requirements of a special function, and also an example of how nature is ever reluctant to create any new organ, preferring rather to make over some already existing structure into something that will serve a new purpose.

There are four glands connected with the sting, two of which are known to secrete the poison, which is forced through the canal between the sheath and the lancets and ejected into the wound made by the latter. It is this poison that causes the pain and inflammation in the wound from a bee's sting, which would never result from a mere puncture. The other two glands have been described as "lubricating glands," being supposed to secrete a liquid which keeps the parts of the sting mechanism free from friction. They lie within the body cavity, one on each side against the upper edge of the quadrate plate, where they are easily seen in an extracted sting, each being a small oblong or ovate whitish cellular mass. Transverse microtome sections through this region show that each of these glands opens into a pouch of the membrane between the quadrate plate and the spiracle-bearing plate of the eighth tergum. Each gland cell communicates with this pouch by a delicate individual duct. The secretion of the glands is thus poured upon the outer surfaces of the quadrate plates and might easily run down upon the bases of the lancets and the arms of the sheath, but, for all that, the notion that it is lubricative in function is probably entirely conjectural.

The large, conspicuous poison sac (figs. 36, 37, 41, and 57, *PsnSc*) that opens by a narrow neck into the anterior end of the bulb of the sting is well known to everyone at all acquainted with bees. The poison which it contains comes from the delicate branched thread attached to its anterior end (fig. 57), a minute tube which, if traced forward a short distance from the sac, will be seen to divide into two branches, which are long and much coiled and convoluted, each terminating finally in a small oval enlargement (*AGL*). These terminal swellings are generally regarded as the true glands and the tubes

(*AGL*) as their ducts, but the epithelium of the tubes appears to be of a secretory nature also, and, if it is not, it is hard to see any reason for their great length. It also does not look probable that the two little end bodies could form all the poison that fills the comparatively enormous sac.

The walls of the poison sac (fig. 38) are lined by a thick coat of laminated chitin (*Int*) thrown into numerous high folds. In the neck part of the sac the folds are arranged very regularly in a transverse direction and form interrupted chitinous rings, holding the neck rigidly open. The epithelium (*Epth*) contains nuclei (*Nu*), but the cell boundaries are very slightly marked. There is a distinct basement membrane (*BM*), forming a tunica propria externally, but there are no muscle fibers of any sort present except a few which are inserted upon the sac from some of the surrounding organs and which apparently act as suspensoria.

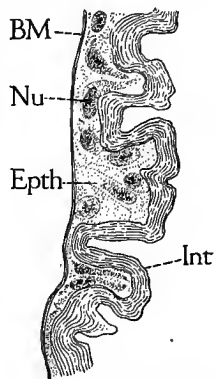


FIG. 38.—Section of small piece of wall of poison sac of sting.

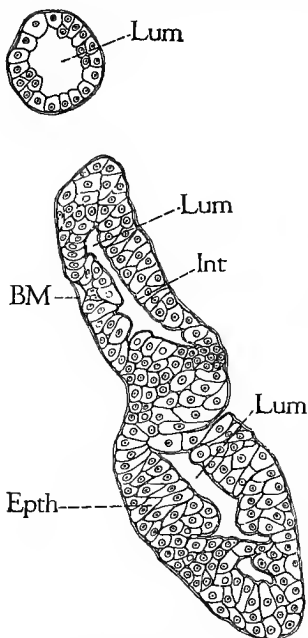


FIG. 39.—Sections of alkaline gland of sting.

The poison found in the sac has an acid reaction and is supposed to consist principally of formic acid. Hence its gland is known as the *acid gland* (*AGL*) of the sting.

The other sting gland is a short, very inconspicuous, and slightly convoluted whitish tube (figs. 36, 37, 41, and 57, *BGL*) opening directly into the base of the bulb ventrad to the opening of the poison sac. Its walls consist of a thick epithelium of distinct cells (fig. 39, *Epth*) lined with a thin chitinous intima (*Int*) and surrounded by a distinct basement membrane (*BM*), but, as in the other gland, there are no muscles present. The secretion of this gland is said to be alkaline and the gland is therefore known as the *alkaline gland* (*BGL*) of the sting.

Experiments made by Carlet (1890) show that it is only the mixture of the products from the two poison glands that is fully effective in stinging properties. Carlet's experiments were made upon houseflies and blowflies. He shows (1) that flies stung by a bee die almost instantly, (2) flies artificially inoculated with the secre-

tion of either gland alone do not die for a long time even in spite of the necessary mutilation, while (3) successive inoculations of the same fly first from one gland and then from the other produce death in a much shorter time than when inoculated from one gland alone—presumably as soon as the two liquids mix within the body.

The two secretions, one acid and the other alkaline, are poured together into the base of the sting bulb and mix within the cavity of the latter. The resulting poison is then driven through the channel in the shaft to near the tip of the latter, where it makes its exit into the wound. Since the large poison sac is not muscular, the poison is not forced through the sting by it, as is often supposed. A glance at figure 57 (see p. 135) will show that the accessory plates of the sting support several very compact sets of muscles on their inner faces. These muscles so act during the process of stinging that the triangular plates (figs. 36 and 37, *Tri*) turn upon their hinge-joint articulations with the oblong plates (*Ob*). By this motion of the triangular plates the attached lancets (*Lct*) are moved back and forth along the tracks on the lower edges of the sheath and its arms (*Sha*). Each of these tracks consists of a ridge with a constricted base which dovetails into a correspondingly shaped groove on the dorsal surface of the lancet. This structure, as seen in cross sections through the shaft and bulb of the sting, is shown by fig. 40 A, B, and C. The lancets are thus held firmly in place, while at the same time they may slide back and forth with perfect freedom. The figures show also that all three parts of the sting are hollow, each containing a prolongation (*bc*) of the body cavity. Between them, however, is inclosed another cavity through which the poison flows. This is the *poison canal* (*PsnC*). In the bulb (fig. 40 C) the body cavity is reduced to a narrow cleft (*bc*) by the great size of the invaginated poison canal (*PsnC*).

It will now be most convenient to describe the apparatus by means of which the poison is ejected from the sting. As before pointed out, the large poison sac can have no functions in this connection because its walls are entirely devoid of muscle fibers. On the other hand, there is an actual pumping apparatus situated within the bulb. This consists of two pouchlike lobes, having their concavities directed posteriorly, attached to the upper edges of the lancets (fig. 40 D and G, *Vlv*) on the anterior ends of the parts of the latter which slide within the lower edges of the bulb chamber. The lobes lie side by side within the bulb (fig. 40 C, *Vlv*), when the lancets are in the same position, and each has an accessory lamina against its own inner wall. When the lancets are pushed backward the walls of the lobes flare apart against the poison contained in the bulb and drive this liquid before them into the channel of the shaft, while at the same time they suck more poison into the front of the bulb from the glands. When,

on the other hand, the lancets are retracted the pouches collapse so that they may be drawn back through the poison-filled bulb without resistance, but they are ready for action again as soon as the movement of the lancets is reversed. The whole apparatus thus constitutes an actual force pump in which the lobes on the lancets alternately act as a piston and as valves. The lancets need not work together; in fact, they more often perhaps work alternately, the lobes being of such a size as to be effective either when acting together or separately.

The reader acquainted with other works on the anatomy of the bee, such as those of Cheshire (1886), Cook (1904), Cowan (1904), and Arnhart (1906), will see often repeated the statement that the poison leaves the sting both by a ventral opening between the lancets near their tips and by several lateral pores near the ends of the lancets opening from the poison canal upon

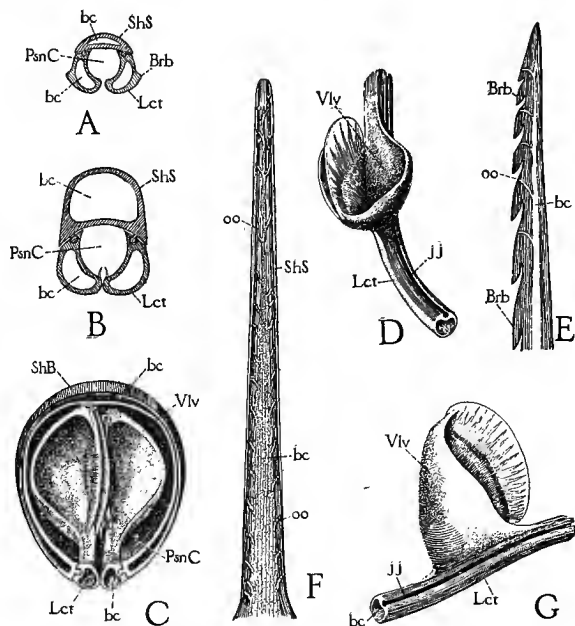


FIG. 40.—Details of sting of worker: A, section through tip of sting showing lancets (*Lct*) and shaft of sheath (*ShS*) surrounding central poison canal (*PsnC*), and each containing a prolongation of the body-cavity (*bc*); B, section of same near base of bulb; C, section of sting through basal bulb, showing poison canal as large invaginated cavity (*PsnC*) in bulb of sheath (*ShB*) containing the two valves (*Vlv*) of lancets (*Lct*); D, part of left lancet carrying valve (*Vlv*), dorsal view; E, tip of lancet showing pores opening on bases of barbs (*oo*) coming from body-cavity (*bc*) of lancet—not from poison canal; F, dorsal view of shaft of sheath showing lateral series of pores (*oo*) from prolongation of body-cavity (*bc*); G, lateral view of left valve and part of lancet.

the bases of the barbs. The writer, however, has never been able to observe the exit of the poison from any such lateral pores, while, on the other hand, it is very easy to watch it exude from between the lancets on the ventral side of the sting near the tip. If an excited bee is held beneath a microscope and the tip of the sting observed, the poison will be seen to accumulate in little drops near the tip on the ventral side. If, also, the bulb of an extracted sting

strongly decurved beyond the bulb. The lancets have fewer and smaller barbs than those of the worker, but the two poison glands are well developed (fig. 57, *AGl* and *BGl*), while the poison sac (*PsnSc*) is especially large.

A number of minute unicellular glands open upon the intersegmental membrane between the seventh and eighth terga of the abdomen. These are sometimes called the glands of Nassanoff, after their discoverer. Nassanoff suggested that they are sweat glands, while Zoubareff thought that they form small drops of liquid said to be excreted by bees during flight derived from the excess of water in the newly collected nectar. Their function, however, has been much more carefully investigated by Sladen (1902), who found that they are scent organs producing a strong odor even when the part of the back to which they are attached is removed from the rest of the abdomen. He furthermore identified this smell as the same that bees give off when a lot of them are shaken from a frame on the ground close to the front of the hive. Under such circumstances also, as in natural swarming or during the first flights in the spring or after a period of bad weather, bees are well known to produce a peculiar sound called the "joyful hum." Sladen observed that this was produced, in the case of bees shaken before the hive, by those individuals who first found the hive entrance, then by those next to them, until very soon all the others were informed of the location of the entrance and proceeded to make their way in. Also, when a swarm loses sight of its queen, those that find her first set up this "joyful hum" and immediately the rest of the swarm is attracted to the spot. In the springtime the young bees seem to be guided in their flights by this same hum of the old ones. Sladen, however, observing the odor emitted at the same time, thinks that this and not the sound is the real means of information, the sound being simply incidental to the special movement of the wings produced for the purpose of blowing the odor away from the body. He argues that we have no evidence of an acute sense of hearing in bees, while it is well known that they possess a delicate sense of smell located on the antennæ. This argument certainly seems reasonable, and we may at least accept Sladen's theory as the best explanation of the function of the glands of Nassanoff.

VI. THE ALIMENTARY CANAL AND ITS GLANDS.

1. THE GENERAL PHYSIOLOGY OF DIGESTION, ASSIMILATION, AND EXCRETION.

It is no exaggeration to say that eating is the most important thing that any animal does and that its alimentary canal is the most important organ it possesses. The entire system suffers when there is a deficiency in the food supply or an impairment in the digestive apparatus. Every other function is either subservient to or dependent upon that which furnishes nourishment to the cells. The senses of sight, smell, and taste are all more or less concerned in the acquisition of food. The muscular system enables the animal to hunt for it, to dig for it, to climb for it, or to chase living prey either on the ground, in the water, or in the air, and to kill, tear, and chew it when obtained. The blood is the servant of the stomach, for its entire function in insects is to carry the products of digestion to the body cells. The heart furnishes the motor power of the blood. The respiratory function is accessory to that of digestion, inasmuch as it furnishes the oxygen which unites with the waste materials ejected from the cells and renders them capable of being removed from the blood. This removal is accomplished partly by the respiratory system itself and partly by special excretory organs. Thus we see that the sense organs and the muscular system are the agents that cooperate in obtaining the raw food, the digestive tract is the kitchen of the body in which the food is prepared for use, the blood is the waiter that distributes it, while the respiratory and excretory systems are the refuse gatherers that remove waste products. The nervous system holds the controlling power over all these organs. It regulates them in the performance of their duties and coordinates their actions so that they all work together. It makes a unified organism out of what would otherwise be simply a complex mass of variously specialized cells.

The reproductive function alone contributes nothing to the individual. In fact, the production of spermatozoa by the male and of eggs by the female and the nourishing of the embryo and the young create a demand upon all the other organs for material which is separated from the individual that produces it. But this is what the organism exists for; this is its reason for being. At least this is what it amounts to in the case of the individual, though from a wider philosophical standpoint the real truth is probably just the reverse, viz, any species exists because its individuals reproduce themselves.

The writer has already made frequent use of the word "cell," assuming that the reader is familiar with the meaning of this word as used in anatomy and physiology. The entire body of an animal or plant is made up of *cells* or their products. The word, however, is misleading, for a cell is not a small sac or empty space, as was at

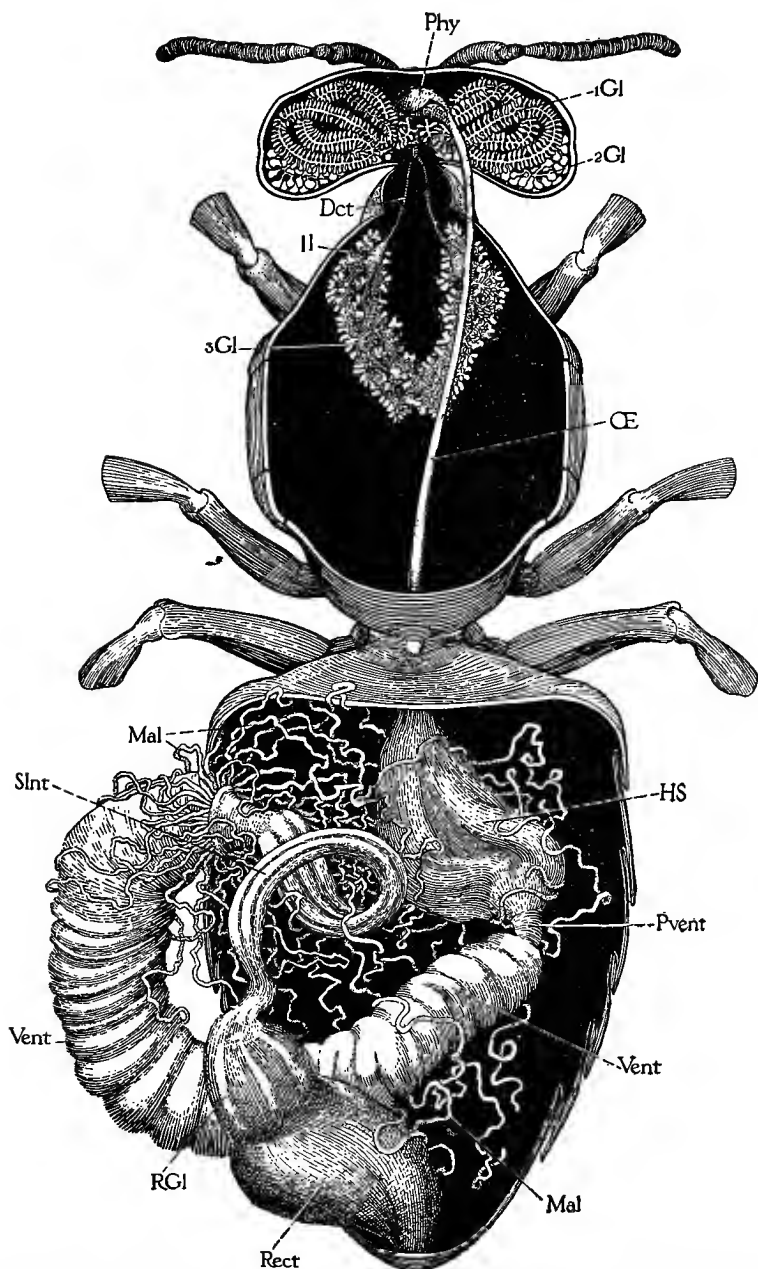


FIG. 42.—Alimentary canal of worker (*Phy-Rect*), together with pharyngeal glands (*1Gl*), and salivary glands of head (*2Gl*) and of thorax (*3Gl*), as seen by cutting body open from above and pulling the ventriculus (*Ventr*) out to left.

first supposed from the study of plants, but is a little protoplasmic body or corpuscle, visible only under the microscope, surrounded by a membranous cell wall and containing a small internal body called the nucleus. The different cells of the body are specialized in groups to do some one particular thing—the salivary cells secrete saliva, the muscle cells contract, the excretory cells pick out waste substances from the blood, and so on. But this specialization does not signify that each cell does not perform its own vital processes in addition to its specialty. The fact that it remains alive and works means that the complex chemical components of its body substance or *protoplasm* are constantly being reduced to simpler compounds which are expelled, while new protoplasm is built up from the supply of food material brought by the blood. This double process of destruction and reconstruction is known as *metabolism*, while its two phases, the breaking-down process and the building-up process, are known as *katabolism* and *anabolism*, respectively.

Now, while all the cells of the body must have nourishment, none of them, except those of the alimentary canal, is capable of utilizing the raw food materials that an animal obtains in a state of nature. These materials must therefore be changed into some other form in order that they may be *assimilated* by the cells. This change is called *digestion*.

The single cell composing the body of a Protozoan, living free in nature, digests its own food and then assimilates the products of its own digestion. But, of the cells constituting the body of any multicellular animal, only those of the alimentary canal are capable of digesting *raw* foodstuffs, and, moreover, as digestion is the specialty of these cells, they have also to digest the food for all the other cells of the body.

The two most important changes that must be brought about in the natural food by digestion are those which make it soluble in the blood and which render it capable of passing through animal tissues. In the first place, the food must diffuse through the walls of the alimentary canal as a liquid which mixes with the blood, for there are no pores or openings of any sort from the alimentary canal into the body cavity; and in the second place, it must pass through the walls of the cells themselves. The digestive changes result chiefly in a breaking down of the complex molecules of the raw food materials into more simple chemical substances. These are taken up by the cells and reconstructed into complex protoplasmic molecules which can not escape through the cell membrane until they are again broken down into simpler forms.

The waste products of the cells consist principally of carbon, hydrogen, and nitrogen. These are converted by the oxygen supplied by the respiratory system into carbon dioxid, water, and compounds of

urea. The first, being a gas, mixes with the air in the tracheal tubes and so reaches the exterior during exhalation. Much of the water is also given off through the tracheal system in the form of vapor which exhales from the spiracles, but, since insects are covered by their hard chitinous shell, it is probable that they do not "sweat." The compounds of urea, and probably also some water, are separated from the blood by the excretory glands, called Malpighian tubules in insects, which empty their products back into the alimentary canal, whence they are discharged with the fæces from the intestine.

Digestion is brought about by substances called *enzymes* which are contained in the various liquids mixed with the food in the alimentary canal. These liquids are secreted by the salivary glands and by the cellular walls of the stomach.

2. THE SALIVARY GLANDS.

The opening of the salivary duct on the base of the proboscis has already been described (see pp. 49-51). The true salivary glands, or those corresponding with the salivary glands of other insects, are arranged in two pairs, one situated within the head (figs. 19 and 42, *2Gl*) and the other within the thorax (fig. 42, *3Gl*). The four ducts unite into one median tube, which enters the base of the labium (fig. 19, *SalD*) and opens upon the upper surface of the ligula (fig. 15 F, and fig. 16, *SalDO*). The large and conspicuous glands lying within the anterior and upper parts of the head and opening into the pharynx will be described later in connection with this organ. They are special pharyngeal glands in no way homologous with the salivary glands of other insects, and are by many supposed to secrete the brood food instead of a digestive liquid like saliva.

The salivary glands of the head (*System No. 2* of Cheshire, *post-cerebral glands* of Bordas) lie against the posterior walls of the cranium. In the worker each consists of a loosely arranged mass of pear-shaped follicles or acini whose individual ducts unite irregularly with one another and eventually form a common duct on each side (figs. 19, 42, and 43 F, *2Gl*). Their two ducts unite with the median duct from the thoracic glands just before the bases of the mesocephalic pillars (fig. 19). In the drone these glands have a quite different appearance from those of the female, each consisting of a compact mass of very small follicles connected by minute ducts and flattened against the posterior walls of the head (fig. 43 B and C, *2Gl*). A large lobe of this gland in the drone extends forward on each side against the face, between the compound eye and the clypeus (fig. 10 C, *2Gl*), thus occupying the position of the large mandibular gland in the worker (A, *1MdGl*) and in the queen (B, *1MdGl*). There is also a prominent triangular mass of glandular cells in the drone situated just above the ocelli (fig. 10 C, *2Gl*) which has been

described by Bordas (1895) as a separate gland opening by two ducts into the œsophagus just behind the pharynx. The writer, however, has been utterly unable to discover any such ducts, though two suspensorial ligaments of the anterior end of the œsophagus are attached to the wall of the head at the posterior ends of these glands (fig. 11 B, *g*) and might easily be mistaken for ducts. These "post-ocellar glands" of Bordas, moreover, appear to be simply detached lobes of the postcerebral glands. They are prominent also in the queen (fig. 10 B, *2Gl*) and are represented by a few follicles in the worker.

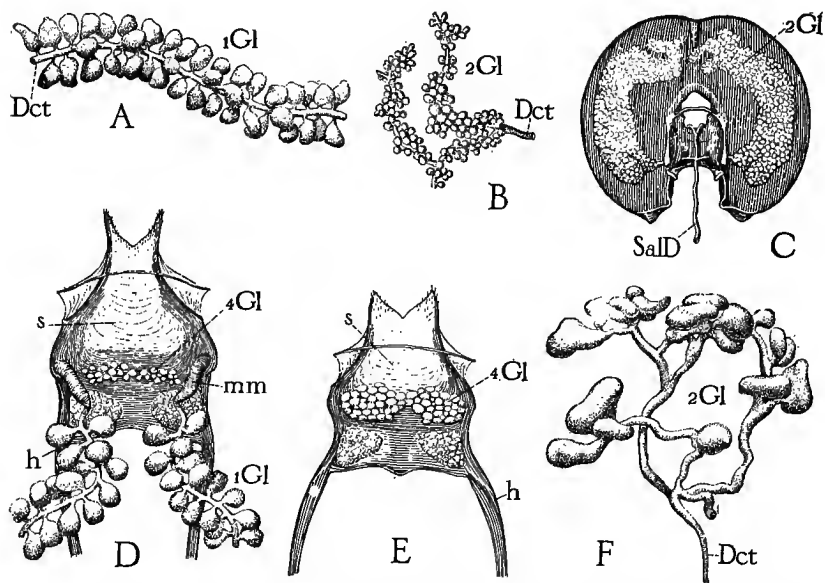


FIG. 43.—A, small piece of large lateral pharyngeal glands in head of worker; B, piece of postcerebral salivary glands in head of drone; C, postcerebral glands (*2Gl*) in normal position against posterior wall of head in drone; D, pharyngeal plate (*s*) of worker, ventral view, showing bases of lateral pharyngeal glands (*1Gl*) and their receptacula (*mm*), and median ventral pharyngeal gland (*4Gl*); E, corresponding view of pharyngeal plate of drone, showing entire absence of lateral pharyngeal glands, and greater development of small median glands (*4Gl*); F, part of postcerebral gland of worker.

Bordas describes the follicles of the postcerebral glands in the worker as hollow sacs, each having a large lumen lined with a chitinous intima. Their secretion, he says, is a thin viscid liquid, pale yellow in color and having a slightly alkaline reaction. According to Schiemenz (1883) each gland is developed as an outgrowth from the common duct of the thoracic glands.

The salivary glands of the thorax in the bee (*System No. 3* of Cheshire, *thoracic salivary glands* of Bordas) are the ones that correspond with the ordinary salivary glands of other insects. They are described by Schiemenz (1883) as being formed inside of the

outer covering (tunica propria) of the first part of the larval silk glands. But it is of common occurrence in insects that the salivary glands are temporarily specialized as silk-producing organs in the larva. In the adult worker these glands lie in the ventral part of the anterior half of the thorax (fig. 42, *3GI*). The two are widely separated anteriorly, but their posterior ends are contiguous. Each consists of a mass of small, many-branched, glandular tubes opening into several collecting ducts which empty into a sac near the anterior end of the gland (*U*). From each of these reservoirs, then, a duct (*Det*) runs forward and fuses with the one from the opposite side just within the foramen magnum of the head. The common duct thus formed turns downward within the head, receiving the two ducts of the postcerebral salivary glands and then enters the base of the mentum (figs. 19 and 43 C, *SalD*), to open as already described on the upper side of the ligula at the root of the glossa and between the bases of the two paraglossæ (fig. 15 F and 16, *SalDO*). The secretion of the thoracic glands is said also to be weakly alkaline. Therefore the entire salivary fluid poured out upon the labium is alkaline, and it must be designed to act especially upon the food taken through the proboscis. This action, furthermore, on account of the location of the salivary opening, may take place before the food enters the mouth.

The food of the bee consists normally of pollen, nectar, and honey. The first is eaten entirely with the mandibles, while the other two are taken through the proboscis. The pollen is to the diet of the bee what meat is to ours; that is to say, it contains the *proteid* or nitrogen-containing ingredient of the food which is necessary to the support of any animal, and also substances comparable with fat, called in general *hydrocarbons*. The nectar and honey consist principally of grape sugar, fruit sugar, and cane sugar, which belong to the class of chemical substances known as *carbohydrates*. Now, all of these foodstuffs, except the grape and fruit sugars, have to be changed chemically by the digestive process before they can be absorbed into the blood. The pollen, which contains the proteids and hydrocarbons of the food, is taken directly into the mouth by means of the mandibles and apparently is not digested until it reaches the small intestine, and therefore it would seem that it is the cane sugar which must be affected by the saliva. The change, or inversion, as it is called, of cane sugar, which has a very large molecule ($C_{12}H_{22}O_{11}$), consists of its reduction to grape and fruit sugars which have smaller molecules ($C_6H_{12}O_6$). Starch ($C_6H_{10}O_5$) must also be reduced to simpler and more soluble compounds before it is capable of absorption. Its inversion is effected in us partly by the saliva, but starch appears to form a very inconsiderable element in the bee's diet.

3. THE ALIMENTARY CANAL.

The alimentary canal is a tube which extends through the entire length of the body and, on account of being more or less coiled, it is generally considerably longer than the length of the body in insects. It has no openings of any sort into the body cavity. The internal organs are packed closely about it, and the interstices are filled with the blood, there being no special arteries or veins in insects. The amount of space occupied by the alimentary canal varies according to the amount of food it contains, and for this reason it seldom looks exactly alike in any two individuals examined.

The part of the canal immediately following the mouth forms an enlargement (fig. 42, *Phy*) called the *pharynx*. Succeeding this is a slender tube which leaves the head by the foramen magnum above the small transverse tentorial bar and traverses the entire length of the thorax. This is the *œsophagus* (*Æ*). In the anterior part of the abdomen the *œsophagus* expands into a large thin-walled sac which is ordinarily called the *crop* or *ingluvies*, but which, in the bee, is known as the *honey stomach* (*HSt*). Behind this is a short, narrow, necklike division, with rigid walls constituting the *pro-ventriculus* (*Prvent*). Then comes a large U-shaped part, with thick, spongy-looking walls containing numerous annular constrictions. This is the *ventriculus* (*Vent*), or stomach, of the bee, frequently referred to as the "chyle stomach." Following the ventriculus is a short, narrow, coiled *small intestine* (*SInt*) having a circle of about one hundred long, greatly coiled, blind, threadlike tubes opening into its anterior end. These latter are called the *Malpighian tubules* (*Mal*). Functionally they do not belong to the digestive tract, since they are excretory organs, corresponding with the nephridia of other invertebrates and with the kidneys of vertebrates. Following the small intestine is the *large intestine*, or *rectum* (*Rect*), which is often distended by its contents into a great sac occupying a large part of the abdominal cavity. Six whitish bands on its anterior end are called the *rectal glands* (*RGL*). The rectum opens to the exterior through the anus, which is situated, as already described, at the end of the rudimentary tenth or last segment of the abdomen (fig. 41, *An*).

After this brief general survey of the parts of the alimentary canal, we shall proceed with the description of each in detail, and at the same time give what is known of the rôle each plays in the process of digestion. What is known, however, about digestion in the bee, or in any insect, for that matter, really amounts to nothing, but the views of various writers on the subject must be discussed briefly, in order to show how little has actually been demonstrated.

The *pharynx* (figs. 11 B, 19, and 42, *Phy*) lies in the anterior part of the head close behind the clypeus, extending from the mouth

dorsally to above the antennæ, where it turns posteriorly and contracts into the much narrower œsophagus (\mathcal{E}). Attached to its walls are numerous suspensorial muscles, whose contraction must expand the pharyngeal cavity, while the latter may be contracted by the sheet of muscles surrounding its walls. In this way the pharynx is undoubtedly able to perform a sucking action, by means of which the liquid foods are taken into the mouth. Its lateral walls are strengthened by two long, chitinous rods (figs. 11 B and 19, h), which arise from a median anterior plate in its floor (fig. 19, s). The anterior end of this plate is prolonged into two free, tapering lobes which hang down over the lower rim of the mouth. The plate, in the worker, and the bases of the rods are shown in ventral view, removed from the pharyngeal wall, in figure 43 D. Near where the rods join the plate are two long, chitinous pockets (mm), opening above, which receive the ducts of the two large glands ($1Gl$) lying within the anterior part of the head. Between these two pockets is a transverse row of cells ($4Gl$), which have been described by Bordas (1895) as the "sublingual glands," but this name is not appropriate in insects, for, while the gland in question may be suggestive of the sublingual salivary gland of vertebrates, it does not lie beneath the tongue or lingua of the bee. Although the pharyngeal plate lies upon the floor of the true mouth, it is not, as already explained (p. 44), the equivalent of what is properly called the tongue, lingua, or hypopharynx in other insects—this organ being absent in most Hymenoptera. The only suggestion the writer can make, however, is to call this group of cells the *ventral* or *médian ventral pharyngeal gland* in distinction to the large lateral glands. A comparative view of the pharyngeal plate and its accessory parts in the drone is given in figure 43 E. The plate itself (s) is shorter than in the worker, and its anterior lobes are smaller. The lateral glands and their receptacula are entirely absent, but the median glands ($4Gl$) are much larger than those of the worker. Bordas says that each acinus of the latter glands in both the worker and the drone is provided with a fine, sinuous canaliculus, and that these tiny ducts open separately in two bundles on the lateral parts of the pharyngeal plate. The lateral glands are present in the queen, but are very small and rudimentary.

Especial interest attaches to the large lateral pharyngeal glands of the worker (*System No. 1* of Cheshire, the *supracerebral glands* of Bordas), because they are regarded by many as the source of the brood food and the so-called "royal jelly," which is fed to the larvæ and to the adult queens and drones by the workers. Each consists of a long coiled string of small ovate follicles attached to one median duct (fig. 43 A) and the two are intricately packed into the anterior and upper parts of the head (figs. 10 A, 19, and 42, $1Gl$). Each

acinus consists of a solid mass of several small cells, which are penetrated by a large number of fine, chitinous ducts, arising in the neck of the acinus from the common duct of the gland. These follicular ducts can be very clearly shown by treating a part of the gland with weak caustic potash, which dissolves the protoplasm of the cells and brings out the bunch of ductules very clearly.

The fact that these glands are entirely absent in the drone and at best rudimentary in the queen shows that they must in some way be connected with the special functions of the worker. Schiemenz (1883) and Cheshire (1886) have shown that their development in the different species of bees is in proportion to the social specialization. They vary from a group of cells opening by separate ducts upon the pharyngeal plate to the highly developed condition they present in the honey bee. The writer questions, however, whether these authors did not mistake the median pharyngeal glands of these lower genera of bees for rudimentary representatives of the lateral glands. Bordas states that the former occur in all Hymenoptera, but Schiemenz and Cheshire did not seem to recognize them. The bumblebees (*Bombus*) have them almost as well developed as the honey bee (*Apis*), especially the large females. In the genus *Psithyrus* they are similar to those of *Bombus* but are smaller, while in such genera as *Andrena* and *Anthophora* they are rudimentary or consist of a few scattered cells. Both Schiemenz and Cheshire have thus argued strongly that these glands of the pharynx are the organs that produce the brood food. On the other hand, Schönfeld (1886) has made an equally strong plea in favor of the ventriculus as the producer of this important material. He believes that the brood food, especially royal jelly, is regurgitated chyle. Both Schönfeld and Cook (1904) fed bees in a hive some honey containing powdered charcoal and later found this in the brood food in the comb cells, thus apparently confirming its ventricular origin. However, the charcoal that got into the cells might have come from the mouth, the œsophagus, or the honey stomach. It, of course, could not have gone through the stomach walls and entered the pharyngeal glands, as proved by Dr. J. A. Nelson, of this Bureau, from microtome sections of bees fed on lampblack. The arguments, then, in favor of the stomach and the pharyngeal glands seem equally strong, and perhaps the truth is, as occurs in so many such cases, that both sides are right—that the brood food is a mixture of chyle from the stomach and of secretion from the pharyngeal glands.

Arnhart (1906) seems to adopt the position that the brood food is chyle which has been acidified by the addition of an acid from the glands. He states that the acid reaction of the royal jelly is due to the presence of three-fourths of 1 per cent of tartaric acid. The contents of the ventriculus, on the other hand, and for that matter

of all the parts of the alimentary canal, are alkaline. Hence, it seems very logical to suppose that if the brood food comes from the stomach, its acid constituent is furnished by the glands in the head. But the difference between the brood food found in the cells and the contents of the ventriculus is so great that it would seem as if a very substantial addition of something more than a mere preservative acid must be made to the latter.

The brood food given to the queen larvæ, known as royal jelly, is a gummy paste of a milky-white color when fresh, but when taken out of the cell it soon acquires a darker tone with a yellowish tint. Under the microscope it appears to be a homogeneous, very minutely granular mass. It is very acrid and pungent to the taste, and must be strongly acid. Samples examined by the writer taken from cells containing queen larvæ two and four days old contained a number of fresh undigested pollen grains but no bits of hairs such as occur in the stomach.

The possible ventricular origin of a part of the brood food and its regurgitation will be further discussed when we treat of the stomach (page 98). The writer does not advocate any personal view regarding the origin of this larval food—the fact is, there is not enough known about it to enable one to formulate any opinion worth while. We know only that the whitish paste comes out of the mouths of the workers, but we *know* nothing of where it is made or of how it is made. Hence we can but await the evidence of further investigation.

The brood food is fed to the larvæ by the workers and is produced in greatest abundance by the younger individuals. The larvæ of the queens are said to receive nothing but pure royal jelly throughout their entire developmental period, while the larvæ of the drones and the workers are given the pure product only during the first three days of their life. From the beginning of the fourth day on, honey is said to be mixed with the diet of the drones and workers and, in the case of the former, undigested pollen also. Moreover, the adult queens and the drones receive a certain amount of prepared food throughout their lives; if they do not get it they become weak. While they can feed themselves with honey they apparently can not eat pollen, and consequently are not able to obtain the proteid element of diet unless fed this in a predigested condition by the workers. During egg-laying activity the queen especially demands this food, and by furnishing or withholding it the workers probably have the power of stimulating or inhibiting her production of eggs. Arnhart (1906) says that the workers feed it to weak or starved members of their own class, the material being accumulated upon the upper surface of the mentum of one bee whence it is sucked up through the proboscis by the other. All of these statements, however, concerning the feeding of the brood and the differences in the diet need to be verified. They

are based chiefly on the work of Planta, published in 1888. Cheshire (1886) states that the stomachs of queens contain a substance which is "microscopically indistinguishable from the so-called royal jelly," scarcely a pollen grain being discoverable in it. If this is so, it would seem to prove that the queen is fed this substance by the worker, for the stomach of the latter is invariably filled with a dark-brown slime

containing a varying amount of pollen and in no way resembling royal jelly. Cheshire further says that before impregnation the stomachs of the queens always contain pollen, the royal jelly being found in them two or three days after impregnation, when all traces of pollen have disappeared.

The narrow *œsophagus* (fig. 42, *Æ*) is a simple tube with a thick chitinous lining and muscular walls. The epithelium (fig. 45) is very rudimentary, its cell boundaries being lost and its nuclei (*Nu*) appearing as if imbedded in the lower layers of the thick transparent

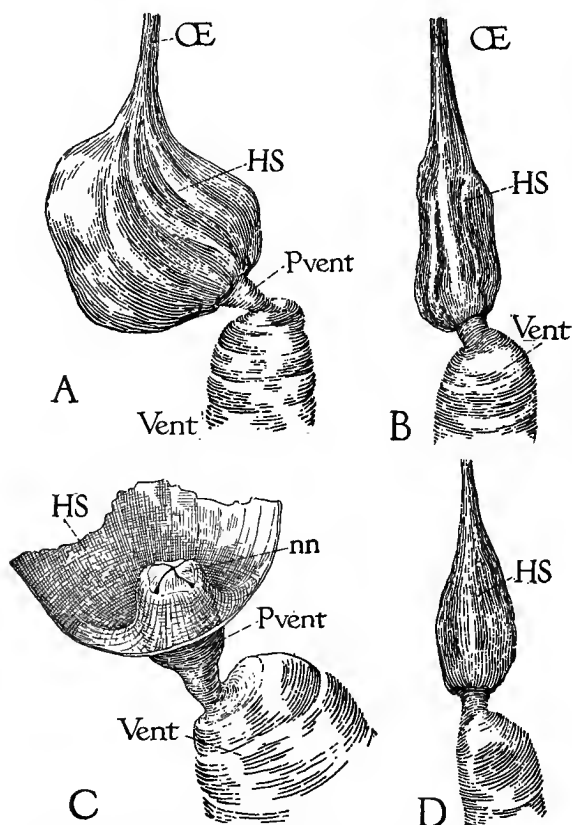


FIG. 44.—A, honey stomach (*HS*) of worker with posterior end of *œsophagus* (*Æ*), proventriculus (*Pvent*), and anterior end of ventriculus (*Vent*); B, same of queen; C, honey stomach (*HS*) of worker mostly cut away exposing the stomach-mouth (*nn*) of proventriculus (*Pvent*) leading into ventriculus (*Vent*); D, honey stomach of drone.

intima (*Int*). The muscles are disposed in an outer layer of transverse fibers (*TMcl*) and an inner layer of longitudinal ones (*LMcl*).

The **honey stomach** (fig. 42, *HS*) is simply an enlargement of the posterior end of the *œsophagus* lying within the anterior part of the abdominal cavity. It is best developed in the worker (fig. 44 A), but is present also in the queen (B) and in the drone (D). The organ should perhaps have been named the nectar stomach, for its

principal function in the bee is to hold the nectar as it is collected from the flowers and to allow the worker to accumulate a considerable quantity of this liquid before going back to the hive. Hence, since the honey stomach is a sac with very distensible walls, its apparent size varies greatly. When empty it is a small flabby pouch, but when full it is an enormous balloon-shaped bag with thin tense walls. The histological structure of the honey stomach (fig. 45, *HS*) is exactly the same as that of the œsophagus. The numerous high folds into which its epithelium (*Epth*) is thrown permit the enormous expansion of which the sac is capable. When a worker with its honey stomach filled with nectar reaches the hive, the nectar is either stored directly in a cell or is given up first to some other worker, who places it in a cell.

It would appear that all the food swallowed by a bee must go first into the honey stomach, and since the bee's diet consists of pollen and honey as well as nectar, one would suppose that in regurgitating the latter the bee would also disgorge the pollen it might have recently eaten. Honey which is made from the regurgitated nectar does indeed contain some pollen, but most of the pollen eaten by the bee is undoubtedly retained in the stomach as food. The apparatus by means of which the pollen is supposed to be separated from the nectar belongs to the following division of the alimentary canal, but it is not known that the worker takes nectar, and pollen for food, into its honey stomach at the same time.

The **proventriculus** (figs. 42 and 44, *Pvent*) forms the necklike stalk between the honey stomach (*HS*) and the true stomach or ventriculus (*Vent*), but a very important part of it also projects up into the honey stomach (fig. 44 C). If the honey stomach be slit open, a short, thick, cylindrical object will be seen invaginated into its posterior end and having an X-shaped opening at its summit (fig. 44 C, *nn*). This opening is the mouth of the proventriculus, and its four triangular lips, which are thick and strong, mark four longitudinal ridges of the proventricular tube. This structure is commonly known as the "stomach-mouth" and is supposed to be an apparatus designed especially to enable the worker to pick out pollen grains from the honey stomach and swallow them on down into the true stomach or ventriculus, while the nectar is left to be stored in the hive. Cheshire says: "While the little gatherer is flying from flower to flower her stomach-mouth is busy separating pollen from nectar." This notion is so prevalent among bee writers in general that it passes for a known truth. Yet it has really never been shown that the worker eats pollen while she is gathering nectar. Probably no more pollen is ever mixed with the nectar in the honey stomach than is found in the honey itself. Furthermore, under normal conditions pollen never accumulates in the honey stomach, even when the bee

is not collecting nectar—or, at least, the writer has not observed it—while, finally, both the proventriculus and its mouth are just as well developed in the queens and drones as in the workers, though neither of the former are known to eat pollen, and they certainly do not gather nectar.

If the honey stomach be cut open in a freshly killed bee, the proventricular mouth may be seen still in action. The four lips spasmodically open wide apart with a quivering motion and then tightly roll together and sink into the end of the proventricular lumen. This, of course, suggests their picking pollen out of the nectar, but it is probably simply the ordinary process by means of which the proventriculus passes any of the food in the honey stomach on to the ventriculus. Nearly all insects have some such proventricular apparatus, which simply takes the stored food from the crop as it is needed by the stomach. In some insects it forms apparently a straining apparatus, which prevents coarse, indigestible fragments from entering the stomach, while in some the proventriculus may be a triturating organ comparable with a bird's gizzard. Bees, however, do not crush the pollen either in their mandibles or in the proventriculus, for it occurs in perfect condition in the ventriculus.

Hence, before the current notion that the "stomach-mouth" is for the special purpose of taking pollen out of the nectar in the honey stomach can be accepted it must be first demonstrated that the workers eat pollen while the honey stomach contains nectar to be stored in the cells, i. e., any more than is disgorged along with the nectar; and, secondly, a reason must be shown why the queens and drones should have a "stomach-mouth" as well developed as that of the worker. In the meantime it appears most logical to regard the proventricular mouth as simply the ordinary apparatus, possessed by insects in general, by means of which all of the food is passed from the crop to the stomach.

A longitudinal section through the honey stomach, the proventriculus, and the anterior end of the ventriculus is shown in figure 45, which is made from a queen. The proventriculus does not differ from that of a worker, but the honey stomach is smaller and not so much turned to one side (cf. fig. 44 A and B). The two muscle layers of the œsophagus continue down over the walls of the honey stomach (*TMcl* and *LMcl*). The outer layer of transverse fibers, however, ceases at the posterior end of this organ, while the longitudinal fibers continue posteriorly over the proventriculus and the ventriculus as an external layer (*LMcl*). A new layer of internal transverse fibers begins on the proventricular walls and extends backward on the ventriculus (*TMcl*) beneath the longitudinals. Hence the muscles on the œsophagus and crop are in reverse order from those of the proventriculus and ventriculus. The proventriculus is deeply in-

vaginated into the posterior end of the honey stomach. Each lobe of its mouth forms a thick triangular ridge on the walls of its lumen, in which lies a special mass of longitudinal muscle fibers (*LMcl*). The epithelium of the lumen is lined by a thick, smooth, chitinous intima (*Int*), while the lobes of the mouth (*nn*) are provided with bristles pointing inward and backward into the mouth opening.

The posterior opening of the proventriculus into the ventriculus is guarded by a long tubular fold of its epithelium (fig. 45, *PventVlv*), the *proventricular valve*. This would appear to constitute an effective check against the escape of any food back into the proventriculus. It looks like one of those traps which induces an animal to enter by a tapering funnel but whose exit is so small that the captive can not find it from the other side. Yet Schönfeld has elaborately described experiments by means of which he induced the ventriculus to discharge its contents through the proventriculus into the honey stomach and even into the end of the oesophagus. He says that he did this by gently tapping on the honey stomach and the ventriculus at the same time. The experiment

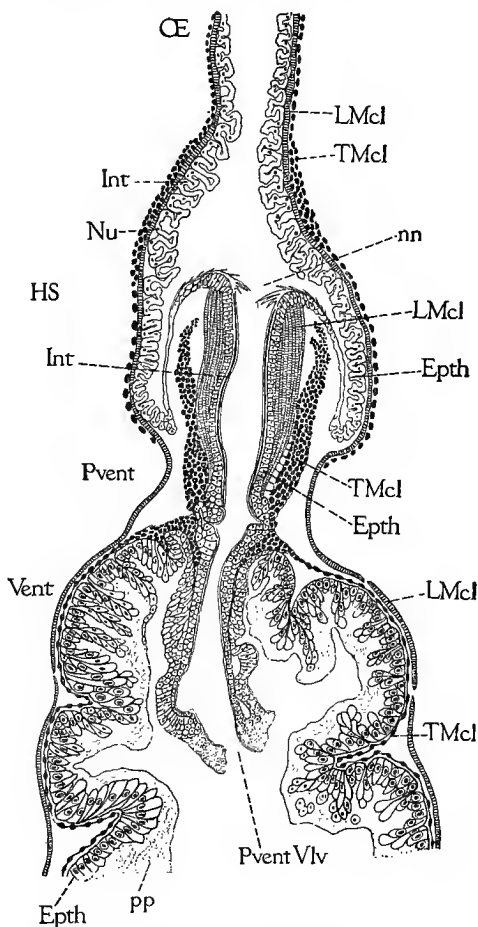


FIG. 45.—Longitudinal median section of base of oesophagus (*OE*), honey stomach (*HS*), proventriculus (*Pvent*) and ventriculus (*Vent*) of a queen.

was repeated many times with unvarying results and Schönfeld describes so minutely what happened that we can not disbelieve his statements. From these experiments he argues that the larval food-stuff is prepared in the stomach and regurgitated through the proventriculus directly into the ventriculus by a contraction of the honey stomach which brings the stomach-mouth against the base of the oesoph-

agus. We shall have to postpone a further discussion of this subject to page 99, after the ventriculus and its contents have been described.

The **ventriculus** (fig. 42, *Vent*) is the largest part of the alimentary canal in the bee and is bent into a U-shaped loop of which the posterior arm is dorsal. It is cylindrical and does not vary so much in shape and diameter according to its contents as do the other parts of the canal, although the numerous transverse constrictions which give it a segmented appearance are not at all constant. When examined under alcohol the ventriculus has an opaque whitish appearance, but in the natural condition—that is, as seen when examined in a freshly killed or asphyxiated bee—it is of a dark-brown color with lighter rings corresponding to the constrictions. The latter represent internal folds where the walls are really thicker than elsewhere, the color being due to the contents which naturally show more plainly through the thin parts.

The contents of the ventriculus invariably consist of a dark brown mucilaginous slime and generally also of a varying amount of pollen. The latter is most abundant in the posterior arm of the ventricular loop and is often densely packed in its rear extremity, while the anterior arm may be almost entirely free from it. The pollen in the ventriculus is always fresh-looking, the native color showing distinctly through the enveloping slime while most of the grains yet retain all of their contents. The writer has examined many samples of pollen from the stomachs of workers and, in all, the great mass of it showed no evidence of digestion, the color being fresh and the contents perfect—only a few had the latter shrunken and seldom was an empty shell observed. On the other hand, the pollen contained in the small intestine has invariably lost its bright color, the contents of the majority of the grains are more or less shrunken, while a number of empty shells are to be found. That in the rectum, finally, consists in large part of empty shells or of grains having the contents greatly shrunken and apparently mostly dissolved out, although a few perfect and bright-colored grains are always present, looking as if entirely unaffected by the digestive liquids. From these observations the writer would conclude that the digestion of pollen takes place principally in the intestine. In all parts of the alimentary tract there occur numerous bits of feathered bee-hairs, but these seem to be especially numerous in the ventriculus.

We are now in a position to discuss the possibility of the **production of the brood food** in the stomach. Schönfeld (1886), as has already been stated, argues that this substance is regurgitated “chyle” from the ventriculus. Arnhart (1906) adopts this view and elaborates considerably upon the chemical process by means of which the transformation of “chyle” into this larval food is effected through the addition of tartaric acid from the pharyngeal glands of the head.

The ventricular contents do become slightly milky when treated with a solution of tartaric acid, but they are not changed into anything at all resembling royal jelly. Moreover, a transformation of the brown slimy contents of the ventriculus into the white gummy paste on which the larvæ are fed does not seem possible without the addition of much other material. In fact the added material must make up the conspicuous part of the larval foodstuff and, from a purely argumentative standpoint, it would not seem necessary to assume that it contains any "chyle" at all. Again, if it were not for Schönfeld's experiments one could not easily believe that the food could be disgorged through the proventricular valve. The conspicuous action of the proventricular mouth is a swallowing motion, and the writer has not been able to induce the ventriculus to disgorge its contents through it in the way that Schönfeld describes, although perhaps sufficient care was not observed in exposing the organs. Cheshire states that the proventricular tube (fig. 45, *PventVlv*) in the ventriculus "rather makes regurgitation improbable than impossible," while he argues that the down-pointing bristles of the stomach-mouth would further interfere with this process. Cowan adopts the view of Dufour and Schönfeld that the brood food is of ventricular origin, and says in this connection: "Although saliva from the glands (especially System I) is probably added to the food, this can not, from its great variability, be entirely a secretion, as stated by Schiemenz. The work of Doctor Planta, we think, conclusively proves that the food is not a secretion, and that the nurses have the power of altering its constituents as may be required for the different bees." If the variation of the food is under the control of the workers producing it, it does indeed look impossible that it should be produced entirely by glands. Cowan illustrates by a diagram how regurgitation through the proventriculus may be possible in spite of the proventricular tube projecting into the ventriculus. Since this tube is simply a cylindrical fold its walls, as shown in figure 45, *PventVlv*, consist of two layers, and Cowan says that "when the bee wishes to drive the chyle food from the chyle-stomach (*Vent*) into the cells it forces the stomach-mouth (*nn*) up to the œsophagus (*Æ*) and the prolongation (*PventVlv*) unfolds, extending the chyle-stomach to the œsophagus, making a direct communication through which the food is forced by compression of the chyle-stomach by its muscles." The honey-stomach of the worker is much larger than that of the queen, shown by figure 45, in which there is not enough space for the unfolding of the proventricular tube. This mechanism suggested by Cowan looks simple and conclusive in a diagram, but when one attempts to unfold the proventricular tube by grasping the stomach-mouth in a pair of fine forceps and pulling the top of the proventriculus upward it is found that, while the tube *can* be entirely straightened out, doing

so involves the tearing of all the fine muscle fibers and tracheal branches uniting the honey-stomach to the upper end of the ventriculus (fig. 45). If, then, the organ itself can not be made to work according to this scheme, it might be supposed that the inner wall of the proventriculus and the tube are evaginated through the stomach-mouth (*nn*), but the walls of the former certainly appear to be entirely too rigid to permit of any such performance as this. Finally, it is not clear how *any* eversion of the tube could be produced by the proventricular muscles as they exist.

The various facts and arguments bearing on the origin of the brood food may be summarized as follows:

1. The brood food itself is a milky-white, finely granular, and gummy paste having a strong acid reaction said to be due to the presence of tartaric acid.

2. The pharyngeal glands of the head are developed in proportion to the social specialization of the various species of bees; they are always largest in those individuals that feed the brood, and they reach their highest development in the workers of the honey bee. From this it would seem that they are accessory to some special function of the worker.

3. The contents of the stomach in the workers consist of a dark brown, slimy, or mucilaginous substance in no way resembling the brood food, even when acidulated with tartaric acid. Pollen is present in varying quantity, mostly in the posterior end of the stomach, and shows little or no evidence of digestion. Since the brood food is highly nutritious, it must contain an abundance of nitrogenous food material which is derived only from pollen in the bee's diet. Therefore it is not clear how the stomach contents can alone form brood food.

4. The constituents of the food given to the different larvæ, at different stages in their growth, and to the adult queens and drones show a constant variation apparently regulated by the workers producing it. A variation of this sort can not be explained if it is assumed that the brood food is produced by the glands alone.

5. Powdered charcoal fed to a hive of bees appears after a short time in the brood food in the cells, and this has been urged as proof that the latter is regurgitated "chyle." But it is certainly entirely possible that the charcoal found in the food might have come only from the honey stomach or even from the œsophagus or mouth.

6. We have Schönfeld's word for the statement that a regurgitation of the stomach contents may be artificially induced by irritation of the honey stomach and ventriculus in a freshly dissected bee, but all explanations offered to show how this is mechanically possible in spite of the proventricular valve are unsatisfactory when the actual anatomical structure is taken into consideration.

The only conclusion, then, that we are really warranted in drawing concerning the origin of the royal jelly or of any of the larval food paste is that we do not know anything about it. Cheshire is probably responsible for the widespread opinion that it is formed by the pharyngeal glands, though Schiemenz (1883) published a large paper containing this theory three years before Cheshire's book was printed. The "chyle" theory, which also has many advocates, originated with Dufour but was principally elaborated by Schönfeld. Arnhart would derive the brood food from both the stomach and the glands. But we are still absolutely in the dark, since we lack definite and conclusive information. A satisfactory study of the subject would involve the chemical investigation of very minute quantities of substances, and it may be a long time before any interested person is found capable of undertaking a work of this sort. The writer of the present paper is professedly preparing an account only of the structure of the organs, but is doing this with the hope that it may furnish a basis for some future investigator who shall have time to devote himself to a study of the chemistry and physiology of the digestive organs and their glands.

In vertebrate animals the digestive secretion of the stomach is acid and its enzymes bring about especially the digestion of proteids. The resulting acid mixture is called *chyme*. In the intestine the contents are flooded with various alkaline liquids whose enzymes then take up the digestion of the other food elements. The final prepared product, which is absorbed by the lacteals, is called *chyle*. These names have been applied to the contents of the alimentary canal in insects—especially by Arnhart (1906), who speaks of the material undergoing digestion as "chyme" and the completed products as "chyle." But absolutely nothing is known of the digestive process in insects beyond the fact established by Plateau (1874) that the contents of all parts of the alimentary tract are alkaline during digestive activity and either neutral or weakly alkaline at other times. Hence, if we make use of these words in insect physiology, it must be with the understanding that no chemical significance is implied. The ventriculus is very commonly called the "chyle stomach" but there is probably no reason for calling it a "chyle stomach" any more than a "chyme stomach," and likewise there is no reason for supposing that the intestine does not contain chyle—in fact, it almost certainly does. The word "chyle" may be used with entire propriety in insect physiology to signify the completed products of digestion, but to designate a part of the alimentary tract as the "chyle stomach" is applying the term without an adequate basis of facts.

The contents of the ventriculus are surrounded by several concentric layers of thin filmy membrane which form an interior tube extending the entire length of the stomach and reaching down into the

anterior end of the intestine. This tube can be very easily seen by carefully cutting open the outer walls of the ventriculus, but it is best demonstrated by transverse microtome sections of a specimen prepared for histological purposes. Such a section is shown by figure 46 A. A small amount of solid food matter (*qq*) is seen in the center of the specimen, surrounding which are numerous irregular concentric rings of membrane (*Pmb*), some adhering to each other in places, others entirely free, most of them structureless, but others partly cellular. These are known as the *peritrophic membranes* (*Pmb*). They keep the solid contents of the stomach away from the epithelial walls, from which, as will be presently explained, they are given off from time to time.

The walls of the ventriculus (fig. 46 A) are thick and consist of numerous cells (*Epth*) apparently very irregularly arranged. On their inner surfaces is a thin intima (*Int*) and on their outer surfaces a still finer basement membrane (*BM*). Outside of the last are two layers of muscles, the external layer consisting of longitudinal fibers (*LMcl*) and the inner of transverse ones (*TMcl*). Numerous annular depressions of the walls form internal folds (fig. 45), but any part of the ventricular wall can be stretched out into a flat sheet, which is then seen to be full of little pits, giving the whole a screenlike appearance. Sections show that the pits result from circular invaginations of the basement membrane (fig. 46 B, *BM*), and that at the bottom of these pockets the cells are very small and convergent, while those on their lips are very large. Figure 46 B is a very perfect example of this structure of the epithelium, which is usually more or less obscured, as in figure 46 A, by a great proliferation of small cells from the lips of the cups—and then a large section seldom gives a symmetrical view of all the parts. The cups are all filled to overflowing by a gelatinous mass (*pp*) which fuses over their edges into a continuous coating beneath the intima over the entire inner surface of the epithelium. This mass appears to be formed mostly by the cells at the bottoms of the cups, for the outermost of these (fig. 46 B, *rr*) often insensibly fade into it.

Figure 46 E shows an opposite condition of the epithelial cells. Here the lip cells of the cups appear to be very actively dividing, and proliferating a great number of small cells (*Enz*) which float off into the gelatinous covering. These discharged cellules are all nucleated, but their protoplasm does not stain in preparations and consequently they appear clear and transparent as compared with the cells they apparently come from. The writer has not been able to find any of these cells actually in the process of division, but a comparison of figures B and E (which are camera lucida drawings and not diagrams) would certainly suggest that the condition of the cells in E has resulted from a very active division of the cells of the walls and

lips of the cups, which are quiescent in B. Comparing this with what is known to take place in other insects during digestion, there is every reason for believing that the proliferated cells are filled with the digestive secretion, and that E represents a stage immedi-

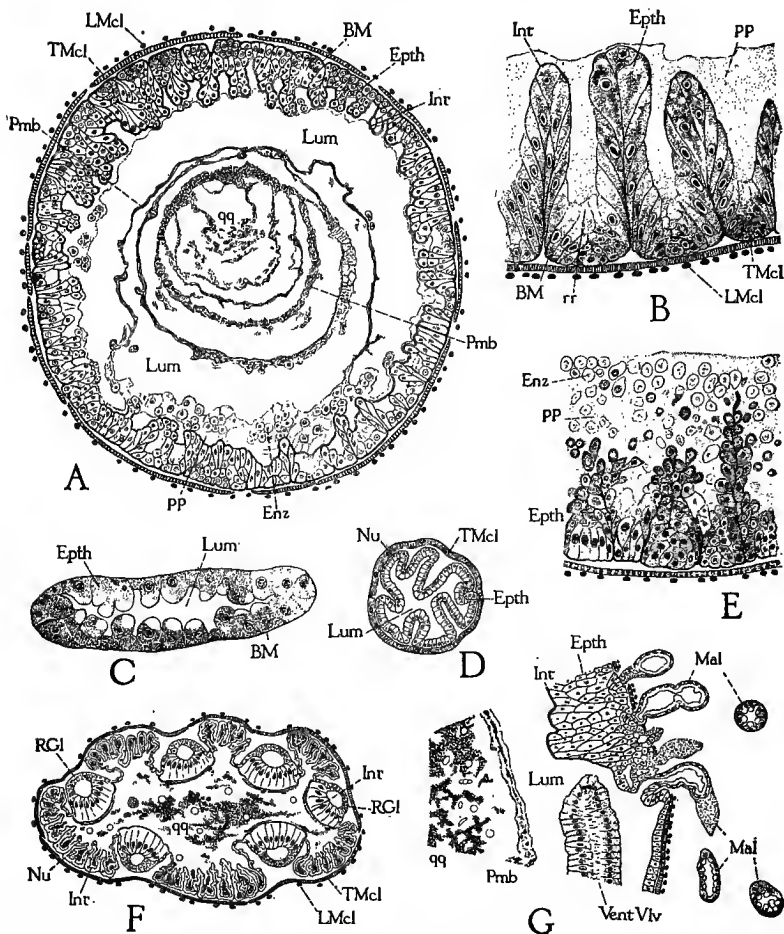


FIG. 46.—Histological details of alimentary canal of worker: A, cross section of ventriculus showing peritrophic membranes (*Pmb*); B, section of wall of ventriculus showing epithelial cups with cells in resting condition and covered by gelatinous mass (*pp*); C, section of Malpighian tubule; D, cross section of small intestine; E, section of ventricular epithelium after formation of numerous small digestive or enzyme cells (*Enz*) given off into gelatinous matrix (*pp*); F, section of anterior end of rectum through rectal glands (*RGI*); G, part of slightly oblique section through posterior end of ventriculus and anterior end of small intestine, showing openings of Malpighian tubules (*Mal*) into the latter.

ately subsequent to one of greatest secretive activity, in which there is a large number of little cells (*Enz*) highly charged with the enzyme-containing digestive juices imbedded in a gelatinous matrix covering the inner surface of the epithelium. This matrix next

separates itself from the ends of the remaining epithelial cells, which at the same time secrete a new intima over their inner surfaces. The lower part of figure 46 A shows this indisputably. The whole thing, then, finally contracts about the food and, as the digestive cellules give up their contents, shrivels and shrinks and becomes a peritrophic membrane. In figure A the outermost peritrophic layer is still in both conditions—its dorsal part is shrunken to a thin membranous form, while its lower part is gelatinous and filled with secretion cellules, though it is separated from the epithelium by a new intima and is detached at intervals from the latter. Beneath the new intima, furthermore, is seen at places the formation of a new gelatinous mass. Some of the inner peritrophic layers shown in A also retain remnants of cells.

Figure 46 A is drawn from a specimen which is typical of all in several series of sections through the ventriculus. The peritrophic layer partly adhering to the epithelium is no artifact, because the same condition may often be directly observed in dissections of fresh specimens. In the opposite end of the series from which the specimen was selected this layer is entirely free from the epithelium.

The peritrophic membrane has been described in some insects as being a prolongation from the intima of the proventriculus, the ventriculus itself being supposed never to secrete an intima. It is perfectly conceivable that the anterior end of the membranes might be generated by the outer cellular layer of the proventricular funnel and remain attached to it after the rest of it had become free from the ventricular wall, and thus give the appearance of belonging to the proventriculus. The writer, however, has several sets of longitudinal sections through these parts in the bee, but none of them nor any dissections made show such a condition.

Absorption is commonly supposed to take place largely in the ventriculus. If so, the food must pass through the several peritrophic membranes and then through the thick epithelium. It is entirely possible that it may do so, but the pollen contained in the ventriculus, as already stated, shows little or no evidence yet of digestion and does not begin to do so until it reaches the small intestine. On the other hand, the dark mucilaginous slime of the ventriculus does not appear in any quantity in the much drier contents of the small intestine. Therefore it may be supposed that this slime contains the sugar elements of the food and that the latter are principally digested in, and absorbed from, the ventriculus. The absorption of the proteids and hydrocarbons must take place in the intestine and rectum since these food elements in the bee's diet are derived only from the pollen. However, these conclusions are purely tentative, being based on the writer's observation of the contents of the different parts of the alimentary tract, which, while fairly extensive and continued through

most of a year, are confessedly not nearly adequate to serve as a basis for conclusive statements on the digestive process. They are sufficient, however, to show the utter lack of a basis in facts for many other opinions on this subject.

Cheshire (1886) describes two kinds of cells in the ventricular epithelium, "one secreting a digestive fluid (gastric juice) from the surrounding blood into the stomach, so that the pollen grains may be made fit for assimilation by a transformation not unlike that liquefying gluten in our own case; the other absorbing the nutrition as prepared and giving it up to the blood." Though Cheshire refers to his figures to show these two kinds of cells, he does not point out which are which—in fact, he does not even designate two different kinds in his drawings nor even represent two kinds.

The **small intestine** (fig. 42, *SInt*) forms a loop upon itself and constitutes a narrow tube connecting the stomach (*Vent*) with the large intestine or rectum (*Rect*). Its anterior end is somewhat enlarged and carries the circle of malpighian tubules (*Mal*). Its epithelium (fig. 46 D, *Epth*) is very simple and is thrown into six longitudinal folds that project into its lumen. On the outside is a thick sheath of transverse muscle fibers (*TMcl*) with distinct nuclei (*Nu*). The latter are designated by Cheshire (1886) as "longitudinal muscles" (see his figure 14 D), but this is a very evident mistake—the small intestine has no longitudinal muscles at all. It is evident that the folds of the epithelium permit the ordinarily narrow tube to expand very considerably when necessary to allow the passage of a large amount of food. The contents of the small intestine are usually drier than those of the ventriculus, consisting principally of masses of partly digested pollen, that is to say, the contents of the grains are partly dissolved out—presumably signifying that they are undergoing digestion. There is usually only a small amount of the brown slime present such as fills the ventriculus.

The **Malpighian tubules** (fig. 42, *Mal*) are wrapped and coiled about one another and about the viscera of the abdominal cavity. There are about 100 of them in the honey bee and they all open separately into the anterior end of the intestine. Each is a very long thread-like tube consisting of a single layer of epithelial cells provided with a very delicate basement membrane and intima (fig. 46 C). The ends of many of the cells are clear and bulge into the lumen. Figure 46 G shows a section through the junction of the ventriculus and the intestine where the tubules open by narrow necks penetrating the epithelium. The wall of the ventriculus forms a short double-layered fold (*VentVlv*) projecting backward into the anterior end of the intestine, behind which are the orifices of the Malpighian tubules. The section from which figure G was drawn is cut somewhat obliquely and takes in this fold only on one side.

The Malpighian tubules are regarded as excretory in function and are supposed to remove from the blood the nitrogenous waste products resulting from metabolism. Minute crystals of urates are often to be found in them and they probably perform the work of the kidneys in vertebrate animals.

The large intestine (fig. 42, *Rect*), called the rectum in insects, is an enormous sac which may lie limp and flabby in the rear part of the body or it may be so immensely distended by the amount of its solid and liquid contents as to occupy a large part of the abdominal cavity. The recognizable elements of the material within it consist mostly of the empty shells of pollen grains or of grains having their contents greatly shrunken and distorted—presumably as a result of the absorption of the protoplasm, although a considerable number are usually present which are only slightly digested, while there are always to be observed a few perfect and fresh-looking grains showing no evidence at all of digestion. The rest of the indefinite mass of solid rectal material consists of some unrecognizable, finely triturated substance, probably derived in part from fragments of the peritrophic membranes. There are always present a few bits of feathered bee hairs.

The epithelium of the rectum is, like that of the œsophagus, rudimentary, being distinguishable only by the nuclei (fig. 46 F, *Nu*) remaining in the outer layer of the thick transparent intima (*Int*). Outside of this is an external layer of longitudinal muscle fibers (*LMel*) and an inner layer of transverse fibers (*TMel*). The intima (*Int*) is thrown into numerous folds whose edges converge, forming pocketlike grooves between them in which are lodged small masses of the rectal contents. This is very suggestive that absorption takes place in this part of the alimentary tract, although it is not commonly supposed to do so, but if the pollen is not fully digested until it reaches the rectum, how can it be absorbed by the anterior part of the alimentary canal?

The so-called rectal glands (fig. 42, *RGL*) consist of six hollow epithelial tubes (fig. 46 F, *RGL*) and are the only parts of the rectal epithelium in which the cells are well developed. The cells on the outside of each "gland" are small, but the inner ones are very large and are covered by a thick layer of dark chitin (*Int*). The lumen is intercellular and does not communicate with that of the rectum. When the rectum is distended the "glands" bulge out on the surface as six short opaque ridges (fig. 42, *RGL*), but when it is empty they sink into the walls as in figure 46 F. Nothing is known of the function of these organs, and their glandular nature is entirely conjectural. If they are glands, it is not clear why the intima should be so especially dense on their inner faces.

VII. THE CIRCULATORY SYSTEM.

The liquid medium that distributes the digested food from the alimentary canal to the cells of the body tissues is called the *blood*, and the contractile organ that keeps the blood in motion is the *heart*. In vertebrate animals the blood is contained entirely within tubes called arteries and veins, but in insects and most other invertebrate animals the blood simply fills the empty spaces between the viscera of the body-cavity, which spaces may, however, constitute definite channels or *sinuses*, and may even be shut in by special membranes. Besides carrying and distributing the digested food that is absorbed into it in solution, the blood of animals generally has also to distribute oxygen to the tissue cells and carry off their waste products. Oxygen is obtained from the air and, like any other gas, is soluble in liquids. Hence it is present in the blood not in the form of small bubbles of gas but in solution, just as it is in all water exposed to the air. The respiratory system (see page 116) is simply a special contrivance for bringing air into close proximity to the blood so that its gases may diffuse into the latter, but many soft-bodied animals like earthworms absorb air directly through the skin. Vertebrate animals have a substance in their blood called hemoglobin which is contained in the red corpuscles and has a great capacity for absorbing oxygen. It, therefore, enables the blood to carry much more of this gas than could be dissolved simply in its plasma. Invertebrate animals do not need so much oxygen as vertebrates, and, therefore, most of them can get along with that which dissolves in the colorless blood plasma without the special aid of hemoglobin. Most insects, however, being excessively active creatures, must have a rapid metabolism in their cell tissues, and consequently they need much oxygen to consume the product of this metabolism, but they belong to the class of animals without red blood and, hence, nature has provided them with another means of obtaining a special supply of air, namely, a set of air-tubes branching minutely over nearly all the internal organs, the tissues, and even most of the cells in the body. (See "The Respiratory System," page 112, for discussion of oxidation and removal of waste products.)

The blood of insects is usually a colorless liquid containing opaque granular cells or corpuscles floating in it. There are no special blood vessels, but there are very definite channels between the muscles and viscera through which the blood flows, while conspicuous membranes stretched across the dorsal and ventral walls of the abdomen (fig. 1, *DDph* and *VDph*) inclose special dorsal and ventral sinuses which play an important part in the circulation. These membranes, called *diaphragms*, are rhythmically contractile, and contribute much to

maintaining the circulation of the blood. The heart (fig. 1, *Ht*) is located in the dorsal sinus, which latter is therefore often called the *pericardial chamber*. The pulsations of the diaphragms are produced by fine muscle fibers lying in their walls. These are usually arranged in a number of fan-shaped bunches on each side radiating from the edges of the diaphragm (fig. 47, *DphMcl*) toward the middle, where most of them are continuous with the fibers from the opposite side. It used to be supposed that those of the dorsal diaphragm produced the expansion of the heart, and they were for this reason called the "wing muscles of the heart," but the latter organ is now known to be a muscular tube and to contract and expand by its own

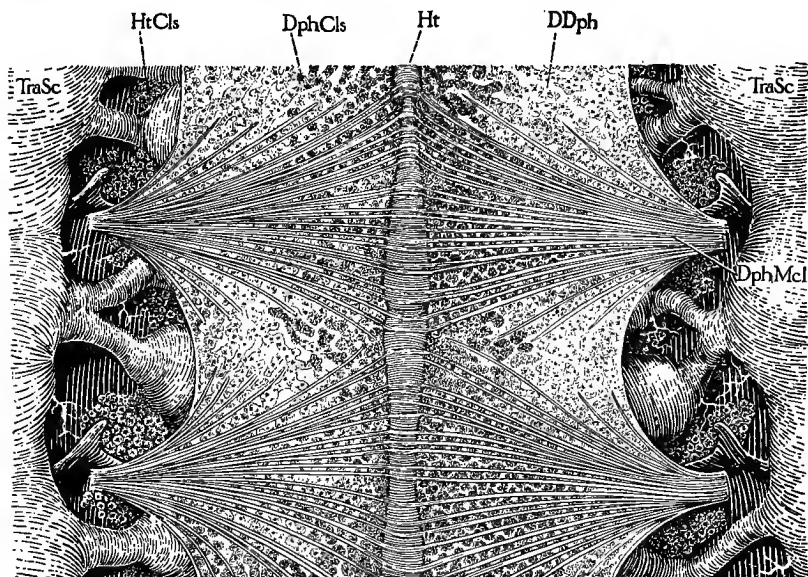


FIG. 47.—Dorsal diaphragm of drone, from one segment and adjoining parts of two neighboring segments, showing median heart (*Ht*) as seen through transparent diaphragm (*DDph*), fan-shaped bunches of diaphragm muscles (*DphMcl*), and lateral tracheal sac (*TraSc*) giving off sac-bearing trunks into pericardial chamber above diaphragm.

power. In some insects the muscles of the dorsal diaphragm form a meshwork of fine fibers surrounding numerous large and small holes in the membrane, which probably permit the entrance of blood into the sinus above, but in most species the diaphragm is imperforate and the blood enters the pericardial chamber above its scalloped edges (figs. 1 and 47).

The heart of insects in general is a long narrow tube (fig. 1, *Ht*) situated in the dorsal sinus or pericardial chamber of the abdomen along the midline of the body. It is swollen toward the middle of each segment into a *heart chamber* (*ht*) which presents a vertical slitlike opening or *ostium* (*Ost*) on each side. Theoretically, in

generalized insects, there should be a chamber to each segment, but the heart is variously shortened from both ends so that the chambers are always fewer than the segments. The posterior end of the heart is closed, but its anterior end is produced into a long narrow tube called the *aorta* (fig. 1, *Ao*) which extends through the thorax and opens by a few simple branches into the cavity of the head.

The heart of the bee (fig. 1, *Ht*) consists of only four chambers (*1ht-4ht*) lying in the third, fourth, fifth, and sixth segments of the abdomen. In the front of this part of the body it bends downward and forms a large convoluted loop (*i*) of about 18 folds where it passes through the abdominal constriction. All of this convoluted part really belongs to the abdomen, since it lies in the propodeal part of the apparent thorax, which is the true first abdominal segment. The aorta (*Ao*) extends forward from here as a very fine tube making a large arch between the muscles of the thorax and then enters the back of the head. According to Pissarew (1898) the convolutions of the anterior end of the heart are peculiar to the honey bee, being absent in its nearest relatives such as *Bombus* and *Megachile*. The heart walls, as before stated, are muscular and produce a rhythmical contraction of the tube whose pulsations follow each other from behind forward. Thus the contained blood is driven out of the anterior end of the aorta into the head, where it bathes the brain and the other organs of this region, and then flows backward, percolating through the spaces between the organs of the thorax.

From the thorax it enters the cavity of the ventral sinus—not the general abdominal cavity, at least in the bee—and is pumped backward by the pulsations of the ventral diaphragm and dorsally over the inner walls of the thorax and through definite channels about all the viscera, finally collecting in the dorsal sinus where it again enters the heart through the lateral ostia. The lips of the ostia are provided with small membranous lobes which project inward and constitute valves that prevent the expulsion of the blood. A similar valve is placed at the anterior end of each chamber of the heart to prevent a possible backward flow.

In the bee, both the dorsal and the ventral diaphragms are well developed, the former (fig. 1, *DDph*) extending from the third abdominal segment to the seventh, inclusive, while the latter (*VDph*) extends from the abdominal constriction to the eighth segment. The ventral diaphragm is much more muscular than the dorsal and its pulsations, which are very strong, follow each other from before backward. They may easily be observed by removing the top of the abdomen from an asphyxiated bee. The ventral sinus is very ample, inclosing the nerve cord of the abdomen, and receives into its anterior end the blood channels of the thorax, so that the latter

communicate with the general cavity of the abdomen only through the ventral sinus.

The dorsal diaphragm (fig. 1, *DDph*) ends by a free transverse edge near the front of the third abdominal segment. A part of it is shown by figure 47 extending across one segment and the adjoining parts of two others. The fan-shaped bunches of muscle fibers (*DphMcl*) are seen radiating from the anterior edges of the terga toward the midline, where they are mostly continuous with those from the opposite side, only a few of the anterior and posterior ones ending free in the membrane of the diaphragm. The latter is imperforate, but its edges are deeply scalloped between the points where the muscles are attached, allowing free entrance to the blood from the intervisceral channels of the abdomen. The dorsal surface of the diaphragm is covered by a network of cells (figs. 47 and 48, *DphCls*) arranged in flat branching and fusing bands. These cells

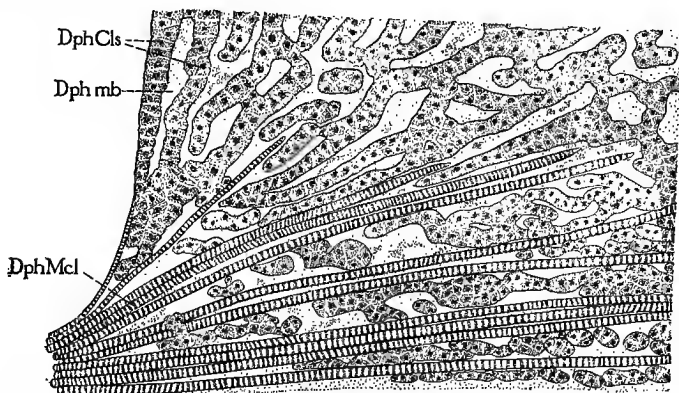


FIG. 48.—Small part of dorsal diaphragm of drone, showing bands of flat diaphragm cells (*DphCls*), the diaphragm membrane itself (*Dphmb*), and the muscle fibers (*DphMcl*).

may be called the *diaphragm cells* to distinguish them from the pericardial cells to be described later.

The abdominal circulation is very easy to observe in a living bee. The best way to demonstrate it is to pin an asphyxiated bee to a block of cork or paraffin and remove the top of the abdomen by making an incision with a small pair of scissors clear around it. Gently pull the alimentary canal to one side so as to expose the ventral diaphragm, which will be observed pulsating strongly backward. Next cut a small hole in the top of the thorax and insert into it a drop of some stain in a water solution (the writer used carmalum). Almost immediately this will appear in the ventral sinus of the abdomen, in which it is pumped backward by the diaphragm, and from which it goes upward through invisible channels between the air sacs and the alimentary canal and especially up

wide channels against the lateral walls of each segment. It does not run out free into the abdominal cavity, however, unless through a rent, nor does it enter the latter from the thorax except by way of the ventral sinus. The dorsal circulation of course can not be observed in this specimen because the back is removed. Therefore, take another bee and fasten it in the same manner, but make simply a shallow median slit along the back, thus exposing the dorsal sinus and the heart from above. Now insert a drop of stain into the thorax as before. After about two minutes this will appear in perceptible amount in the dorsal sinus, very much diluted, to be sure, with the blood, but there will be enough to give white blotting paper a distinct red tint. In a short time the heart becomes filled with the stained blood and appears as a red tube along the median line.

The dorsal sinus contains not only the heart but also two pairs of pericardial air sacs in each segment. These are seen entering the

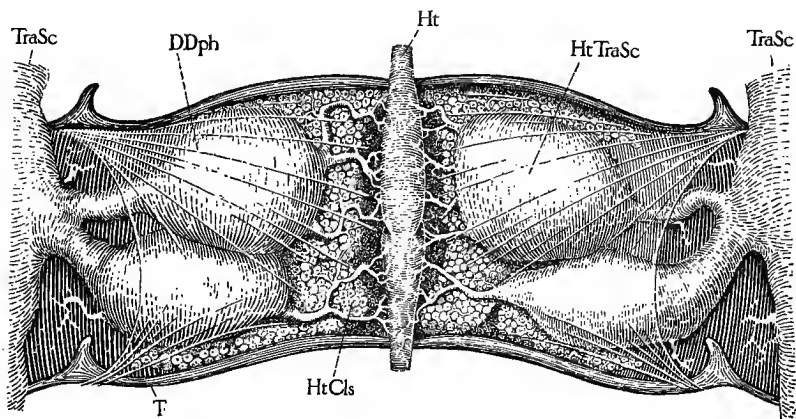


FIG. 49.—Pericardial chamber of one segment in worker, seen from below looking through transparent dorsal diaphragm (*DDph*), showing median heart (*Ht*), lateral pericardial air sacs (*HtTraSc*) given off from large lateral sacs (*TraSc*), and the padding of pericardial cells (*HtCls*) against inner surface of tergum (*T*).

sinus from the large lateral air sacs of the abdomen (*TraSc*) in figure 1 and also in figure 47. In the latter the heart (*Ht*) is seen along the median line as it shows through the diaphragm. Figure 49 gives a view of the pericardial sinus as seen from below, in one segment, by focusing through the transparent diaphragm (*DDph*). In the middle lies a chamber of the heart (*Ht*) with the slitlike ostium on each side. Laterally are the four pericardial air sacs (*HtTraSc*) giving off branches that ramify profusely upon the heart. Above the heart and the air sacs is a thick bed of large granular cells (*HtCls*) which make a soft padding between the hard tergal wall and the delicate organs of the sinus. These are called the *pericardial cells*. They may have some physiological function, as has often been supposed, but if so no one has decided what it is.

VIII. THE RESPIRATORY SYSTEM.

The lives of all animals depend upon a constant distribution of free oxygen gas throughout their bodies. This oxygen, continually inhaled and exhaled, is not used in the formation of tissues, it does not become a part of the living protoplasm of the animal—it is the physiological scavenger that eats up certain waste products of metabolism which are deadly to the system unless constantly removed or changed into less harmful compounds. The action of oxygen upon these waste substances within the body is comparable with ordinary combustion in that it results in the formation of carbon dioxid gas and water and in the generation of heat. Since the air, which is composed of both oxygen and nitrogen, is the source of the oxygen supply, the ordinary breathing processes involve an inhalation also of nitrogen gas, and the tissues become permeated with it as well as with oxygen. The nitrogen of the air, however, is not known to serve any physiological purpose in the body, its presence being simply unavoidably incidental to the inhalation of oxygen. While oxygen and nitrogen are two most important food elements, the tissues of animals can not make use of either in the gaseous condition, but must be supplied with substances containing these elements in combination with others in the form of solid and liquid food stuffs taken into the alimentary canal. Hence, air is not a food, and the respiratory system is to be regarded as chiefly excretory in function.

The means by which different animals receive oxygen into their systems are various. All aquatic breathers of course use that which is naturally dissolved in water. Many of the lower animals absorb air directly through their skins and into their tissues, while the carbon dioxid escapes the same way. Others that live in the water and whose bodies are covered by an impervious skin or shell have thin-walled, hollow, branching appendages, called *gills*, through which the blood circulates freely and through whose walls the necessary exchange of gases takes place. Land animals very commonly have some sort of an invagination from the exterior which allows the air to enter thin-walled tubes or cavities and be absorbed into the blood. Land vertebrates have a tube opening from the back of the mouth whose inner end branches profusely and forms a pair of organs called the lungs, through which the blood circulates freely in delicate tubes that allow the transfer of gases. Insects, finally, have a system of internal air tubes, called *tracheæ*, opening to the exterior by a number of small orifices, called *spiracles*, situated along the sides of the thorax and abdomen, which give off branches that ramify minutely to all parts of the organism, thus virtually making a lung of the entire body. The tracheæ are thin tubes made of flat epithelial

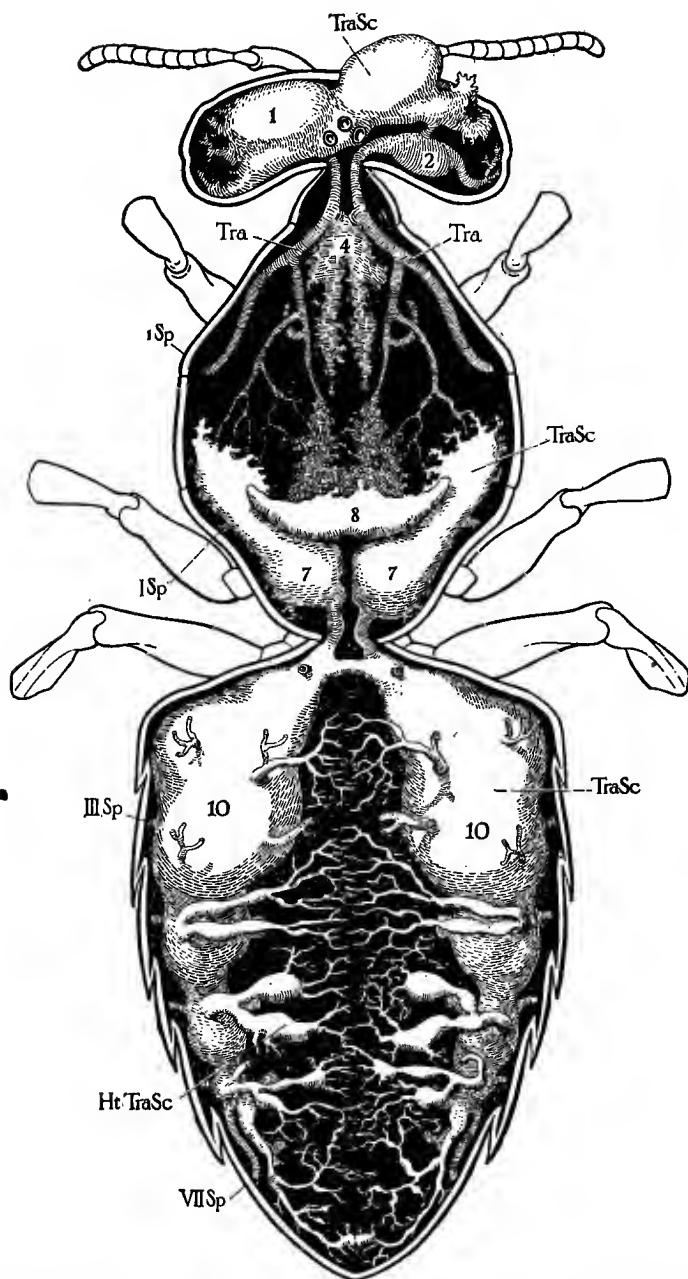


FIG. 50.—Tracheal system of worker as seen from above, one anterior pair of abdominal sacs (fig. 1, 9) removed and transverse ventral commissures of abdomen not shown.

cells lined with a delicate layer of chitin. The latter, however, is strengthened by circular thickenings which give the appearance of an internal spiral thread, but a closer examination shows that each thickening makes only a few turns and that several lie in parallel bands. This structure is for the purpose of maintaining an open passageway for the air through the very thin-walled tubes. The tracheæ branch into fine capillaries and these terminate in excessively delicate end-tubes. In some cases it is easy to see that a great number of capillary branches surround the cells of a tissue, if they do not actually enter the cell walls, but in others it can not be shown that the tracheæ really penetrate below the surface of a mass of cells.

Gases in solution, like solids, pass freely back and forth through moist animal membranes, going in the direction of the least pressure of each particular gas. By this simple method the gases go back and forth through the walls of the gills, lungs, or air tubes and permeate the tissues themselves. Vertebrate animals, as already explained, have a red substance in the blood called hemoglobin which has a very great oxygen-absorbing power and which greatly increases the oxygen-carrying power of the blood, but still a certain amount of oxygen is carried in solution by the liquid or plasma of the blood. Now, the blood of insects has none of this hemoglobin and all the oxygen it can carry is that which dissolves in its plasma, but, on account of the extensive ramification of the air tubes, it is not necessary for the blood to distribute the oxygen to the organs. It is usually stated that the blood in insects does not carry oxygen at all, except for its own use, but it would seem physically impossible that the gases should not diffuse out of the fine terminal air-tubes into the blood when they do so in all other cases. If the blood of a crab or crayfish is capable of carrying enough oxygen in solution to supply the wants of the body, there is no reason why that of an insect, which has much better facilities for obtaining air, should not do the same. Furthermore, we can not suppose that the products of katabolism have to accumulate about the end tracheæ in order to be oxidized. They are produced wherever metabolism is going on, which is everywhere in the living cell substance, and, hence, the latter must be permeated with oxygen in solution, which must also be in the blood along with the carbon dioxid formed. The carbon dioxid diffuses back into the end tracheæ from the blood. Therefore, while the great extent of the tracheal system in insects relieves the blood of the work of distributing the oxygen, the blood must nevertheless serve as an intermediary medium for both the oxygen and the carbon dioxid between the fine terminal tracheal branches and the cells.

It has sometimes been suggested that certain large cells called *œnocytes*, found especially in connection with the tracheal system,

function as intermediaries between the tracheæ and the cells, but Koschevnikov (1900) has shown that these cells appear to be temporary storehouses for waste products from the tissues—presumably uric acid compounds which have been already oxidized. Even the fat-body has been regarded as a sort of lung in which oxidation takes place, but there is no evidence to support this theory, although, for that matter, there is little evidence in favor of any theory in insect physiology.

The process of metabolism, or the vital activity of the cells themselves, results in a breaking down of the complex and highly unstable protoplasmic molecules into chemical substances of much simpler construction, and it is these by-products of metabolism that are attacked by the oxygen in the blood furnished by the respiratory system. Protoplasm consists principally of the elements carbon, oxygen, hydrogen, and nitrogen, and the oxidation process results, as before stated, in the formation of carbon dioxid (CO_2) and water (H_2O), while the residuary products are mostly organic compounds of nitrogen related to uric acid ($\text{C}_5\text{H}_4\text{N}_4\text{O}_3$) and urea (CON_2H_2). The carbon dioxid is a soluble gas which diffuses into the end tubes of the tracheæ and is exhaled. A part of the water at least is given off with the "breath" in the form of water vapor, for drops of it can be collected by inclosing bees or any insects in a tube for a short time. The nitrogen compounds and probably a part of the water are dissolved in the blood and removed by the Malpighian tubules, which are the kidneys of insects.

Besides this oxidation of waste products, which allows the process of metabolism to go on unhindered, the inhaled oxygen serves also another purpose, namely, that of maintaining the body heat. Although insects are usually classed as "cold-blooded" animals, they nevertheless maintain a temperature which is always higher than that of the surrounding air and is often a number of degrees above it. It is well known that the temperature of a beehive during the brood-rearing season is almost as high as that of the human body, and that even during winter it remains at nearly 80°F. ; but this is, of course, due to the accumulation and condensation of the warmth from the bodies of a great many bees, and is much higher than the temperature of any bee outside of the hive. In our own bodies certain substances are consumed by oxidation in the blood simply to produce the necessary heat energy for maintaining metabolism, and hence it seems reasonable to suppose that the same thing takes place in insects, although of course to a much less degree.

There are generally ten pairs of spiracles or breathing apertures in insects, two being situated on the sides of the thorax between the segments, but probably belonging to the mesothorax and the

metathorax (although the first is often regarded as prothoracic), while the other eight are situated on the sides of the first eight abdominal segments—in the bee on the lateral parts of the terga (figs. 32 and 33, *Sp*). The breathing apertures are usually provided with a closing apparatus of some sort consisting of the swollen lips of slitlike spiracles, of a small lid, or of a flexible and collapsible chitinous ring, each with special occlusor muscles attached. In the bee a chitinous band surrounds the tracheal tube opening at each spiracle, a short distance from the aperture, and has two opposite loops projecting on the same side, connected by a muscle whose contraction approximates the two halves of the band so as to close the lumen of the trachea.^a It is supposed that after an inhalation the spiracles are closed momentarily, so that the first force of the expiratory contraction of the abdomen is exerted against the air shut in the tracheæ, with the result of driving it into the extreme tips of the latter—the spiracles then opening, the rest of the contraction is expended in exhalation.

The internal tracheal system consists, among insects generally, of a large tracheal trunk lying along each side of the body, connected by short tubes with the spiracles and by transverse commissures with each other, while they give off segmental branches into the body cavity which ramify minutely upon the organs and tissues. In the thorax specially large tubes are given off on each side to the legs and to the bases of the wings, while in the head others go to the eyes, antennæ, and mouth parts. The whole body is thus virtually a lung with ten pairs of openings along the sides.

The tracheal system of the bee (figs. 1, 50, and 51) is best developed in the abdomen, where the longitudinal trunks are enlarged into two enormous lateral air sacs (*TraSc*), which are of greatest diameter in the anterior end of the abdomen. They are segmentally connected by large transverse ventral commissures (fig. 51, *TraCom*), most of which are themselves distended into small air sacs. Dorsally the lateral sacs give off in each segment a large tube which divides into two sacculated branches (figs. 49 and 50, *HtTraSc*) that enter the pericardial chamber and supply the heart and pericardial cells with tracheæ. In the thorax a large sac lies on each side of the propodeum (figs. 1 and 50, 7), which bears a short tube opening to the first abdominal spiracle (figs. 21 and 50, *ISp*). Above these sacs is a narrow transverse median one (figs. 1 and 50, 8) occupying the large cavity of the turgid mesoscutellum (fig. 21, *Sc₂*). In the ventral part of the thorax there is a large median posterior sac (figs. 1, 50, and 51, 5)

^a For a detailed description of the spiracles in the bee and their occlusor apparatus see Djathchenko (1906).

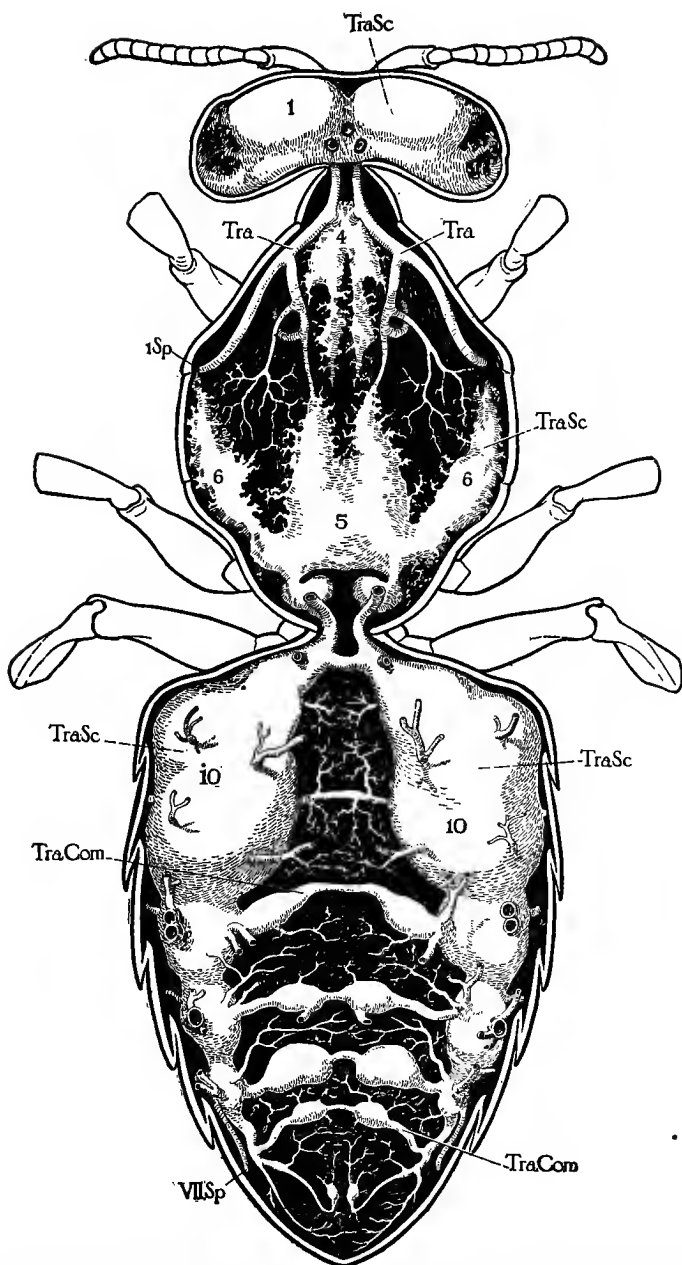


FIG. 51.—Tracheal system of worker showing lateral and ventral parts as seen from above, with dorsal sacs and trunks removed in both thorax and abdomen.

which gives off trunks to the middle and hind legs and a large sac on each side (fig. 51, 6 and 6) to the ventro-lateral walls of the thorax. Two large strong tubes (figs. 1, 50, and 51, *Tra*)—the only tracheæ in the bee's body well developed as tubes—extend backward from the head through the neck and prothorax to the first thoracic spiracles (figs. 50 and 51, *ISp*). Each of these gives off a branch which divides into the trachea for the first leg and into another that connects with the posterior ventral thoracic sac (5). An anterior median thoracic sac (4) is connected with the two large anterior tubes near where these enter the neck. In the head are a number of large sacs which are situated above the brain (see figs. 1, 50, and 51, 1), about the bases of the eyes and optic lobes (see figs. 1 and 50, 2), and above the bases of the mandibles (see fig. 1, 3).

Nearly all of the tracheæ in the bee's body are excessively delicate and their walls mostly lack the spiral thickening that ordinarily holds a tracheal tube open. They are consequently very distensible and, when inflated, they show as opaque glistening white vessels, which, however, when empty, are extremely difficult or actually impossible to see. The smaller branches are so numerous and flabby in the thorax and the legs (fig. 1, *LTra*) that they appear to form everywhere meshworks or sheets of tiny glistening air-cavities imbedded between the muscle fibers. Only the large trunks in the anterior part of the thorax have the normal tracheal appearance.

The body of the bee is thus most abundantly aerated, probably more so than that of any other insect. The numerous large and small sacs form great storehouses of air—tanks containing reserve supplies of oxygen. They are not present for the purpose of lightening the weight of the body, because inflation with air does not decrease the weight of any object surrounded by air.

The respiratory movements are limited to the abdomen in the bee on account of the solidity of the thorax. They vary a great deal according to the activity of the individual. While sitting quietly at the entrance of the hive or walking slowly about, bees usually exhibit almost no respiratory motion, only a very slight vibratory trembling of the abdomen being noticeable. Others that are walking hurriedly about lengthen and shorten the abdomen very perceptibly, the motion being specially pronounced at the tip. A bee that has just alighted after flying exhibits still more pronounced abdominal movements, not only a contraction and expansion but an up-and-down motion as well. When a bee is becoming asphyxiated in a killing bottle the extension and contraction of the abdomen is most pronounced, although much slower than in the ordinary breathing movements.

The muscles of the abdomen that produce respiration have been described by Carlet (1884), who distinguishes seven different sets of

them as follows: There are two dorsal sets: (1) The *internal dorsal*, going from the anterior edge of one tergum to the anterior edge of the next following tergum, and (2) the *external dorsal*, going from the lateral edge of one tergum to the corresponding edge of the following tergum. Both of these are expiratory, since their contractions bring the two segments together. On the sides are three sets: (3) The *external oblique*, going from the anterior edge of each tergum to the side of the corresponding sternum; (4) the *internal oblique*, crossing under the last from the anterior edge of each tergum to the side of the preceding sternum. These two sets are likewise expiratory, because their contractions approximate the terga and sterna. The third set of lateral muscles is (5) the *transverse*, lying between the overlapping surfaces of each tergum and its corresponding sternum and being, therefore, inspiratory, because the contraction separates the terga and sterna. Finally, there are two sets of ventral muscles: (6) The *external ventrals* and the *internal ventrals*, forming a letter *M* between the anterior edge of each sternum and the one following, and (7) the *interventral*, situated between the overlapping surfaces of consecutive sterna and causing their separation by contraction. These last are therefore also inspiratory.

It would thus seem that the abdomen is much better equipped with expiratory than with inspiratory muscles. Perhaps the expansion is partly due to elasticity, and perhaps, also, it is true that the abdomen contracts upon the full tracheæ and air sacs, before the spiracles open to allow exhalation, in order to drive the air into the farthest recesses and terminal tubes of the tracheal system, which necessitates an extra contractive force.

IX. THE FAT BODY AND THE CENOCYTES.

The fat tissue of insects is not miscellaneously distributed through the tissues, imbedded beneath the skin and packed between the muscles, but is disposed in sheets and strands within the body cavity, especially in the abdomen, or forms a definite mass, the *fat body*. The fat cells are large and extensively vacuolated with clear globules of fatty oils. In some insects the fat bodies have a brilliant yellow, golden, or orange color. Associated with the fat cells are other much larger and often gigantic cells, called *cenocytes*, attaining the largest size of all the cells in the body except the eggs. They were first discovered in segmental clusters attached to the tracheæ near the spiracles, but they are now known also to be scattered through the depths of the body cavity, where they occur imbedded especially between the fat cells. The term "*cenocyte*" signi-

fies merely that those cells first observed by Wielowiejski, who gave them this name, were slightly wine-colored.

Both the fat cells and the *œnocytes* of the honey bee have been specially studied by Koschevnikov (1900), who gives the history of the **fat body** as follows: In the larva it consists of gigantic lobes, the cells of which are in general all alike and so closely packed in 30 or more layers that, in the younger stages, most of them assume angular forms. Many of them are binucleate, and the protoplasm is strongly vacuolated except for a small area about the nuclei. In the full-grown larvæ the fat cells become globular and filled with a number of round granules, which, during the early part of the pupal stage, are set free by a dissolution of the cell walls and float free in the body cavity. In pupæ a little older, having even but a very thin chitinous covering, the adult fat body is fully formed, and yet neither the disappearance of the larval granules and nuclei nor the formation of new adult fat cells is to be observed. It seems that the granules of the larval fat cells, set free at the beginning of histolysis, are reassembled about the nuclei to form the fat cells of the adult. In the very young imago the cells of the fat body are very distinct, and each possesses a considerable amount of protoplasm, with enormous vacuoles which press upon all sides of the nucleus. In old bees the vacuolation is much reduced and may even be entirely lacking, while the cells become filled with a solid granular plasma. Old workers examined in the fall show the fat cells united into syncytia or masses in which the cell boundaries are lost, although the nuclei remain distinct. A queen does not appear to form these syncytia in old age.

The function of the fat body is still unsettled, but we do not know of any reason why it should not be comparable physiologically with the fat of vertebrate animals and constitute a reserve supply of materials which can be used both as food and as a source of heat oxidation. It has already been stated (p. 115) that insects maintain several degrees of body temperature. Some entomologists have supposed that the fat body gives rise to the corpuscles of the blood, others have believed it to be an excretory organ because concretions of uric-acid salts are often found associated with its cells, while still others have regarded it as the seat of the combustion of waste products by the tracheal oxygen.

The *œnocytes* of the bee are described by Koschevnikov (1900) as enormous cells imbedded in the fat bodies. He says that those of the larva persist into the pupal stage where they undergo dissolution and disappear, while new imaginal *œnocytes* are formed from proliferations of the ectodermal epithelium. The new ones are at

first small and increase about five times in diameter before reaching their adult proportions. The fat cells and the cenoctes, although closely associated with each other, are easily distinguishable by their size and by their reaction in life to staining solutions. Koschevnikov fed some bees honey or sugar sirup containing sesquichlorate of iron and then, after a few hours, removed the fat body, washed it in ferrocyanide of potassium, and placed it in alcohol acidulated with hydrochloric acid. He found a precipitate of Berlin blue in the fat cells while the cenoctes remained perfectly colorless. Thus he showed conclusively that the two classes of cells are physiologically different in life, although, he says, if a piece of dissected fat body be placed in the staining solution the color diffuses alike throughout all the cells.

The cenoctes have a golden brown pigmentation but no differentiated contents in young workers and queens. In old workers, toward the end of the summer, yellow granules begin to appear in them. During winter and especially in early spring the cenoctes of the workers contain a great number of these granules, but they are present in greatest quantity in queens several years old, while in the latter the fat cells also contain similar granules. Although Koschevnikov admits that the chemistry of these granules is entirely unknown, he thinks that they are undoubtedly excretory substances, that the waste products of metabolism are first taken up by the cenoctes and then delivered to the blood, and that the accumulation of the granules in the cells during old age means the loss of power to discharge them, which brings on the decline in the life activity of the bee. If this is so, then the cenoctes are, as he states, excretory organs without ducts—cells which serve as depositories for waste products.

According to this theory of Koschevnikov, the cenoctes might be likened in function to the liver of vertebrate animals, which, according to the present views of physiologists, is the seat of the splitting up of the immediate nitrogenous products of katabolism, discharged into the blood from the tissues, into those final compounds of nitrogen excreted by the kidneys.

Wheeler^a also describes the fat cells and cenoctes of insects as perfectly distinct in their origins, the fat cells arising from the mesoderm, which is the embryonic cell layer between that which forms the outer body wall and that which forms the embryonic alimentary canal, while the cenoctes are derived from internal proliferations of ectodermal cells.

^a Concerning the Blood Tissue of Insects. *Psyche*, VI, 1892, pp. 216-220, 233-236, 253-258, Pl. VII.

X. THE NERVOUS SYSTEM AND THE EYES.

We have learned so far that the bee is a complex animal made up of a large number of tissues and organs all definitely interrelated, and we speak of these tissues and organs as performing their own special functions. Yet, in itself, a mass of cells, even though a living mass, is incapable of doing anything—it is inert unless stimulated into action. The legs would not move, the heart would not beat, the glands would not secrete, the respiratory movements would not be produced, and the animal would cease to live were it not for a vital force that incites them all into activity. This force is generated by certain cells of the nervous system and is sent out to the other organs along the nerve cords, but we know nothing more about it than simply that it exists in living animals and is dependent upon the maintenance of the nerve cells.

Now, in order that an animal may be “alive,” it is not only necessary that the muscles should be made to contract, the glands to secrete, and all the other organs induced to perform their individual rôles, but it is equally important that they should all work together and accomplish definite results. The muscles must perform harmonious movements to produce walking, flying, breathing, or swallowing, the heart must beat in proper rhythm, the glands must secrete their juices at the right time and in needed amounts. Hence, the functions both of *stimulation* and *coordination* devolve upon the nervous system. The nerve-cells generate a force which, delivered through the nerve-fibers to the various organs, irritates the tissues into activity, but, at the same time, the cells send out this force in such a methodical manner that the activities produced in the different organs are definitely correlated and cooperate in maintaining the necessary condition for the life of the cells.

The nervous system, however, is more than simply the source of these physical and chemical processes that constitute the visible phenomena of life, for it is also the seat of all sense perceptions and, in the higher animals, of consciousness. We do not know, however, that insects possess consciousness—that they are actually aware of their own existence, and we therefore do not know that they have conscious sense perceptions. We do know that they are affected by external objects—by light, heat, taste, odor, pressure, and perhaps sound acting upon specially sensitized cells of the ectoderm called sense organs, but we do not know that the reaction of the individual is anything more than the exhibition of a very highly developed reflex nervous system. It is most probable that bees do all that they do—make the comb, store up honey and pollen, feed the young, attend to the wants of the queen, and so on—without knowing why, and we have no evidence that they are even conscious of the fact that they do

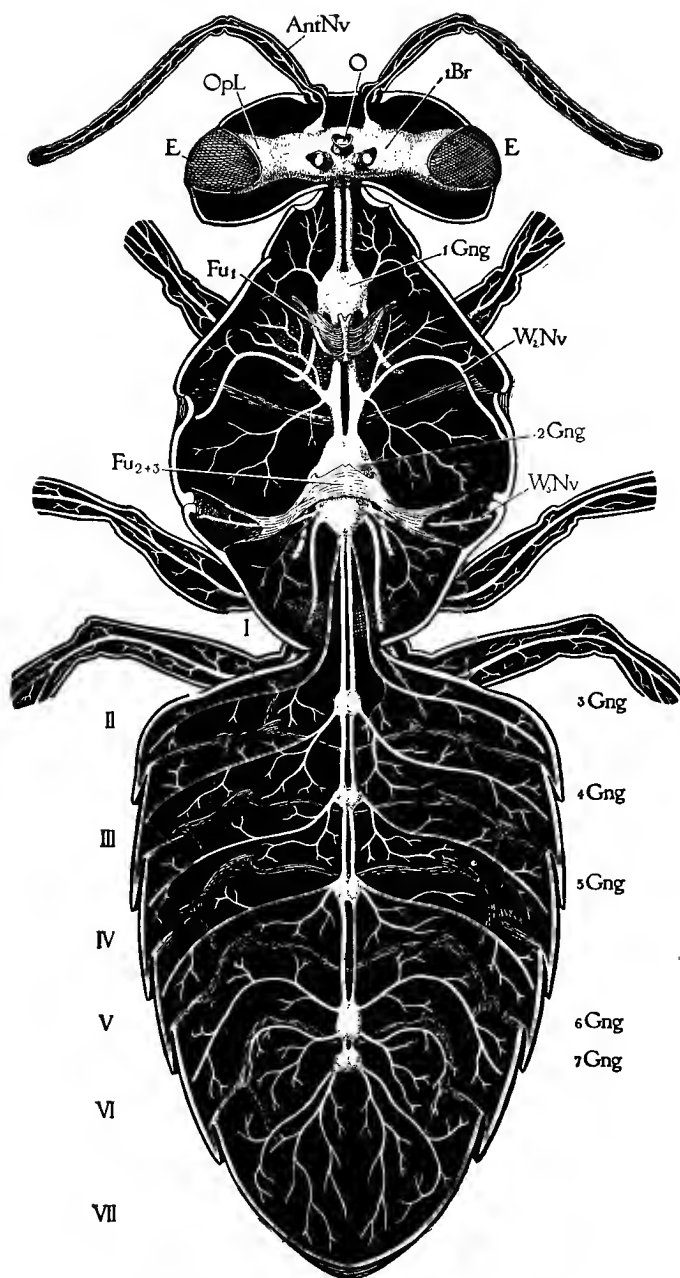


FIG. 52.—Nervous system of worker, dorsal view.

these things. Some authors have tried to prove that insects reason, but the burden of proof is still with them. We can admit that insects *may be* possessed of very slight conscious intelligence, but we can not admit that any one has ever *proved* it. Of course, a great deal of very interesting insect literature owes its readableness to the fact that the author endows his subjects with human emotions and some intelligence, or makes it appear that they consciously do things from a blind sense of obligation. The bee of literature is often quite a different creature from the bee of science.

If, then, we are forced to admit that we have no proof of intelligence or of conscious sensations in insects, we have, on the other hand, all the more evidence of a very high degree of nervous coordination. The body of a bee can be very greatly mutilated and the creature will still remain "alive" as long as the nervous system is left intact. The segments can be cut apart and each will yet be able to move its appendages as long as its nerve center is not destroyed. This shows that there are numerous vigorous centers of nervous stimulation, but proper coordination results only when all the parts are together and intact.

The nervous system of insects (figs. 1 and 52) is comparatively simple, consisting of a series of small nerve masses called *ganglia* (*Gn̄g*) lying along the mid-ventral line of the body, each two consecutive ganglia being connected by a pair of cords called the *commissures*. The ganglia contain the nerve cells, which are the source of the stimuli sent out to the other tissues, while they also receive the stimuli from the ectodermal sense organs. Thus there are incoming or *afferent* stimuli and outgoing or *efferent* stimuli. The commissures and the nerve-trunks that branch to all parts of the body consist of fibers which are fine prolongations of the nerve cells. These fibers are the electric wires that convey the stimuli to and from the nerve centers and are of two kinds, afferent and efferent, according to the direction of the stimulus each transports.

In a generalized embryo we should theoretically find a nerve ganglion developed from the ventral wall of each segment, making seven head ganglia, three thoracic, and at least ten abdominal ones. In the adult, however, many of these fuse with one another. In the head, for example, in place of seven ganglia there are only two, one situated above the œsophagus, called the *brain*, and one situated below it and called the *subœsophageal ganglion*. The connecting cords are known as the *circumœsophageal commissures*. The brain is composed of three embryonic ganglia, and in the adults of many lower insects these are still evident as three well-marked cerebral divisions or swellings, called the *protocerebrum*, the *deutocerebrum*, and the *tritocerebrum*. The first carries the *optic lobes* and innervates the compound and simple eyes, the second bears

two large *antennal lobes*, from which are given off the antennal nerves. The third innervates the lower part of the face and the labrum, while it gives off also a pair of nerves which unite in a small swelling, the *frontal ganglion*, that lies between the pharynx and the front of the head. A nerve runs posteriorly from this on the dorsal side of the pharynx or œsophagus to behind the brain, where it divides into several branches, some of which bear small ganglia while others extend backward on the œsophagus to the stomach. These nerves, originating in the frontal ganglion, constitute the *stomato-gastric system*, sometimes called also the “sympathetic system.”

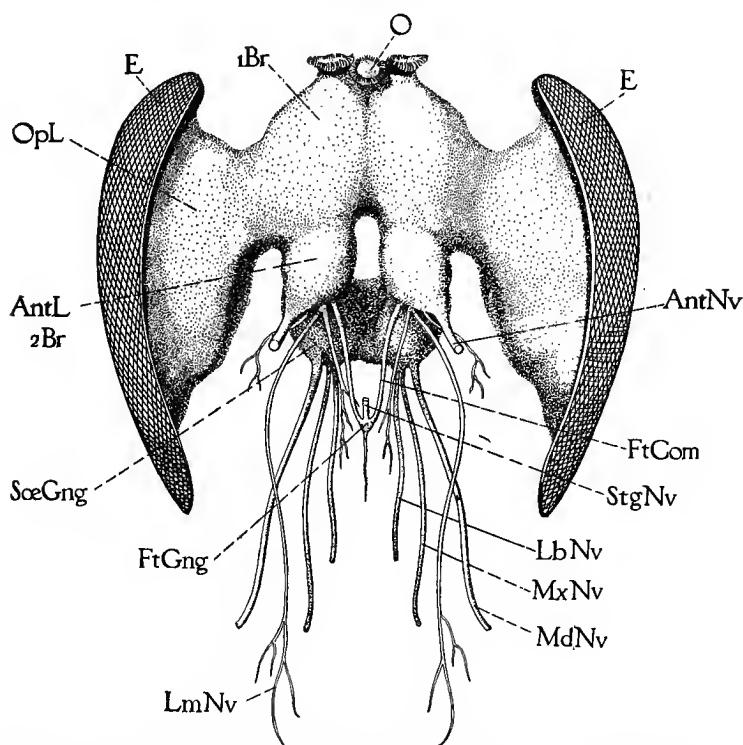


FIG. 53.—Brain and subœsophageal ganglion of worker and their principal nerves, anterior view.

The subœsophageal ganglion consists of at most four ganglia which innervate the mandibles, the hypopharynx, the first maxillæ, and the labium or second maxillæ. In adult insects the body ganglia also very commonly fuse with one another in varying combinations, for the number present is always less than the number of segments, varying from eleven to one.

The brain of the bee (fig. 53, *Br*) is distinctly composed of two parts, the protocerebrum (*1Br*), carrying the large optic lobes (*OpL*), and the deutocerebrum (*2Br*), which consists principally of the con-

spicuous antennal lobes (*AntL*) that give off the large antennal nerves (*AntNv*). The tritocerebrum is not present as a distinct brain division, and its nerves, the labral (*LmNv*) and the frontal (*FtCom*), appear to arise from the deutocerebrum at the base of the antennal lobes. The frontal ganglion (*FtGng*), formed at the union of the two frontal nerves, gives off a very small, anterior, median nerve and a much larger, posterior, stomatogastric trunk (*StgNv*, represented in the drawing as cut off a short distance behind the frontal ganglion) which goes backward on the dorsal side of the pharynx beneath the brain. Behind the latter, and just where the pharynx contracts to the tubular œsophagus, the stomatogastric nerve bears a pair of small ganglia which are connected by short nerves with the brain, and then it breaks up into branches that go posteriorly along the œsophagus but have not been traced.

The circumœsophageal commissures are so short in the bee that the subœsophageal ganglion appears to be attached directly to the lower ends of the brain, while the œsophagus appears to penetrate the latter between the antennal lobes. The three principal pairs of nerves from the lower ganglion (*MdNv*, *MxNv*, and *LbNv*) go to the mouth parts.

A most thorough study of the internal structure of the brain of the bee has been made by Kenyon (1896), to whose paper the reader is referred if interested in this subject. Kenyon's descriptions have never been verified, but his work has an appearance of thoroughness and carefulness. He applies the term "brain" to both of the nerve masses of the head, distinguishing the upper as the "dorsocerebrum" and the lower as the "ventrocerebrum," being led to do this from physiological considerations, the separation of the two being merely incidental to the passage of the œsophagus.

In the thorax of the bee (figs. 1 and 52) there are two large ganglia (*1Gng* and *2Gng*). The first is prothoracic, being situated above the prosternum, in front of the entosternum (fig. 52, *Fu₁*), and it innervates the prothorax and the first pair of legs. The second, which is situated in front of the middle legs and is protected above by the arch of the common entosternum of the mesothorax and metathorax (fig. 52, *Fu₂₊₃*), is a combination of the mesothoracic and metathoracic ganglia and the first two abdominal ganglia. This composite structure is evident from the fact that it innervates both the middle and the hind legs, the bases of both pairs of wings, the mesothorax, the metathorax, the propodeum, and the first abdominal segment behind the constriction (the true second segment). The first and second ganglia of the abdomen (fig. 52, *3Gng* and *4Gng*) lie in the first two segments (*II* and *III*) behind the constriction, which are the true second and third segments. But since the nerve trunks of these ganglia go, in each case, to the segments behind them, we

assume that they really belong to these latter segments, that is, to segments *III* and *IV*. The next three ganglia (*5Gng*, *6Gng*, and *7Gng*) lie in the segments they innervate (*V*, *VI*, and *VII*) and, hence, belong to the fifth, sixth, and seventh abdominal segments. The last, that is, the seventh ganglion, supplies all of the segments behind it with nerves and is therefore probably a compound of the ganglia originally belonging to the seventh, eighth, ninth, and tenth segments.

In connection with the nervous system it is most convenient to give a description of the simple and compound eyes. The other

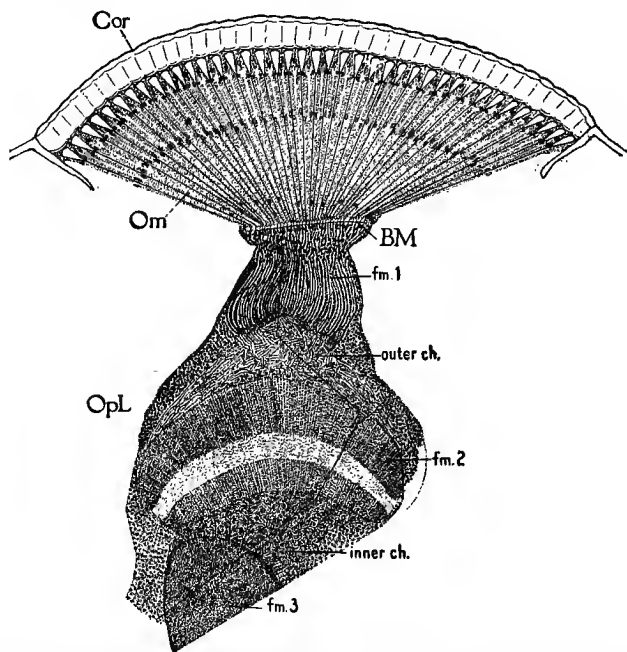


FIG. 54.—Horizontal section of compound eye and optic lobe of worker (after Phillips): *BM*, basement membrane; *Cor*, cornea; *fm*₁, *fm*₂, *fm*₃, outer, middle, and inner fibrillar bodies of optic lobe; *inner ch*, inner chiasma; *Om*, ommatidium; *OpL*, optic lobe; *outer ch*, outer chiasma.

sense organs will be found already described along with the parts on which they are located (see pp. 36 and 52). All the sense organs, to be sure, are of ectodermal formation and are only secondarily connected with the nervous system, but the eyes are so intimately associated with the optic lobes of the brain that their description here seems most appropriate.

The compound eye of the bee (figs. 9 A, 10, 52, and 53, *E*) has been specially studied by Phillips (1905) and figures 54 and 55 are reproduced from his drawings, while the following statements are based on his paper: The convex outer surface or *cornea* of the eye

presents a honeycomb appearance under the microscope, and each little hexagonal facet is the outer end of an eye tube called an *ommatidium*.

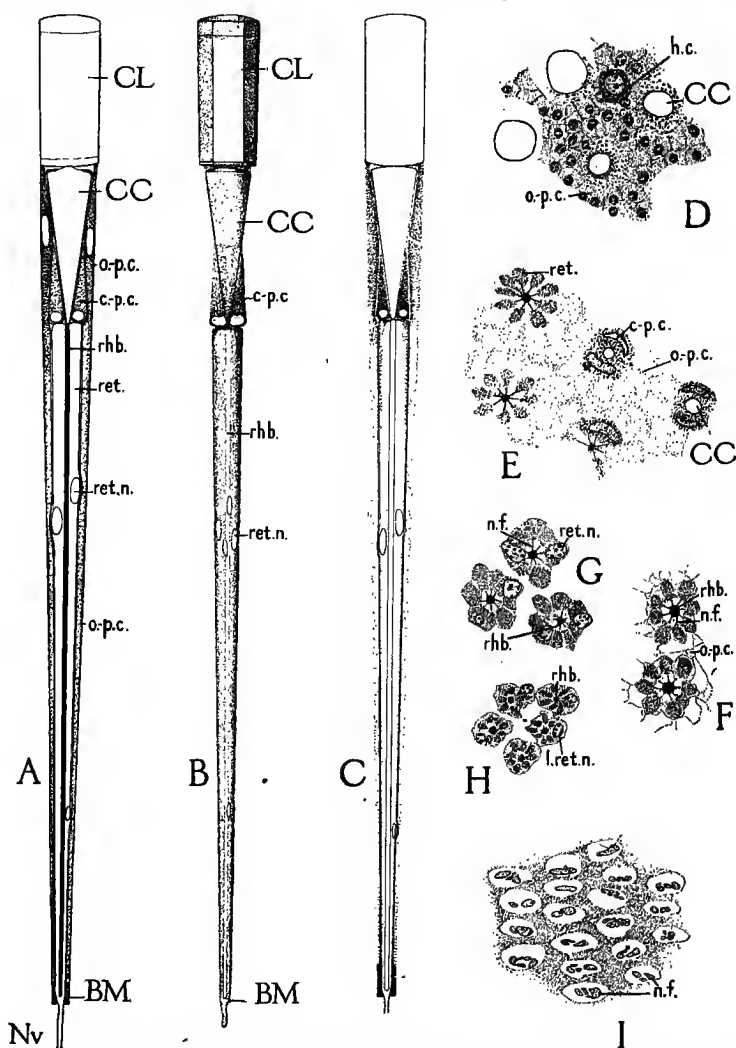


FIG. 55.—Histological details of compound eye of worker (after Phillips): A, entire ommatidium (somewhat diagrammatic), adult; B, entire ommatidium, as if dissected out, without outer pigment cells (diagrammatic), adult; C, section of entire ommatidium, showing distribution of pigment, adult; D, cross section just proximal to lens, slightly oblique; E, cross section through extreme distal ends of retinulae and proximal ends of cones, slightly oblique; F, cross section through retinulae, showing relation of outer pigment cells in this region; G, cross section through retinulae in region of nuclei; H, cross section through retinulae in region of proximal nucleus; I, cross section of eye, cutting basement membrane parallel (the distinctness of nerve fibers of each ommatidium is shown); BM, basement membrane; CC, crystalline cone; CL, crystalline lens; c.p.c., corneal pigment cell; h.c., hair-cell; l.ret.n., lower retinular nucleus; n.f., nerve fiber; Nv, uerve; o.p.c., outer pigment cell; ret., retinula; ret.n., retinular nucleus; rhb, rhabdome.

tidium, all of which converge toward the internal base of the eye, since each is vertical to the outer surface. Figure 54 is a horizontal

section through the eye and the optic lobe of the brain. The ommatidia (*Om*) are seen converging upon the *basement membrane* (*BM*) which is penetrated by the nerve fibers from the optic lobe (*OpL*). The outer ends of the ommatidia are transparent, forming the facets which together constitute the cornea (*Cor*) of the eye. The nerve fibers, by a complicated course through the optic lobe, reach the nerve cells of the brain, which are the true seat of sight perception, as of all other sensations, whether conscious or otherwise.

The ommatidia (*Om*), or eye tubes, are separated from one another by cells containing a dark coloring matter and known as the *pigment cells*. Each tube (fig. 55 A) consists of several parts, as follows: First, on the outside, is a clear six-sided, prismatic structure, with convex outer and inner surfaces, called the *crystalline lens* (*CL*), and which forms one of the facets of the cornea. Beneath the lens is a *crystalline cone* (*CC*) having its apex directed inward and followed by a *crystalline rod* or *rhabdome* (*rhb*) which extends to the basement membrane (*BM*) through the middle of the ommatidium. (The rhabdome is represented black for the sake of distinctness in figure 55 A; its natural appearance is more as shown in B and C.) Surrounding the rod is a circle of eight or nine long *retinulæ cells* (*ret*), each containing a conspicuous nucleus (*ret. n*) above its middle and continuing basally into an optic nerve fiber (*Nv*) penetrating the basement membrane. The arrangement of these cells about the rhabdome is shown in cross section at F and G. The inverted apex of the crystalline cone (A, B, and C, *CC*) is surrounded by the *corneal pigment cells* (*c.-p. c.*), while the entire ommatidium below the lens—the base of the cone, the corneal pigment cells, and the retinulæ—is surrounded by the long outer pigment cells (*o.-p. c.*), forming a packing between all the ommatidia, as shown in cross section at E.

The entire compound eye is simply a modified part of the epidermis (so-called "hypodermis" of insect histologists) in which the cuticle is transformed into the lenses or cornea, the cones, and the rods, the epithelium into the pigment and retinulæ cells, and the basement membrane into the floor of the eye perforated by the optic nerve fibers. According to Phillips the ommatidia arise from the ectoderm of the bee larva as groups of epithelial cells which become arranged in the form of spindles surrounded by smaller cells. The cells of the spindles become the retinulæ, while the surrounding small cells become the pigment cells and the cone cells. The cone cells come to occupy a position external to the retinulæ by an invagination of the latter, and, through a transformation of most of their protoplasm into a crystalline substance, they form the crystalline cone of the eventual ommatidium. The approximated edges of the retinulæ cells are

transformed into the crystalline rod. The cornea is secreted by the corneal pigment cells, which at first lie distal to the cone, and possibly also by the outer pigment cells. The nerve fibers are formed as differentiated parts of the retinulæ which penetrate through the basement membrane (fig. 54, *BM*) and enter the reticular ganglion beneath it at the outer end of the optic lobe of the brain. Hence the retinulæ are simply sense end-organs of the skin comparable at an early stage of their development with other sensory epidermal cells, and we thus see how a simple layer of epithelium may be transformed into such an immensely complex organ as the compound eye.

There has always been a great deal of discussion as to how insects see by means of the compound eyes. The weight of opinion now favors the theory that they see a part of the object or field of vision with each ommatidium. But it is most certain that, at best, most insects see very indistinctly, and, in fact, it is often questioned whether they really see the shape of objects at all or not. A few of them, however, such as dragonflies, appear to have a very acute vision. In the case of the honey bee there is yet much difference of opinion as to whether the workers discover nectar by the bright color of the flowers (i. e., by the sense of sight) or by the sense of smell. The sense of sight in bees and in insects generally, however, may be found elaborately discussed in many books dealing with the senses of insects.

The simple eyes or ocelli (figs. 9 A, 10, 52, and 53, *O*) are constructed on quite a different plan from that of the compound eyes, each consisting of a lenslike thickening of the cuticle back of which the epithelial cells are specially elongated, and sensitized by nerve connections. The ocelli of the bee, however, have never been carefully studied.

XI. THE REPRODUCTIVE SYSTEM.

The reproductive organs are those that produce the cells from which new individuals are formed. All animals grow from at least one cell called the *egg* and almost all from a combination of the egg with another cell called a *spermatozoon*. The uniting of these two cells is called the *fertilization of the egg*. In a few animals the two different kinds of reproductive cells are formed in the same individual, but in most of them, including all insects, the sperm and the eggs are produced in different individuals—the *males* and the *females*. In the honey bee the males are called *drones*, while the females are called *queens* or *workers*, according to their functions in the hive. The queens have the egg-producing organs or ovaries greatly developed, while these organs are rudimentary in the workers. The single active queen in each hive, therefore, normally produces all the eggs of the colony, while the work of rearing and providing for the brood

falls to the lot of the workers. Most other female insects lay their eggs at some place where the young will be able to find food when they hatch out, and the mother never in any way feeds or protects her offspring; in most cases she dies before her brood emerges from the eggs. But the wasps and bees are different in that nearly all of them make a nest of some sort for the protection of the young larvæ when they hatch, in which also they store up food for them to eat. In many species of wild bees all the work of constructing the nest, laying the eggs, and collecting and storing food for the young devolves upon the single female, as it naturally should, since insects do not ordinarily have servants, and the males of most species are utterly irresponsible in such matters. In some of the higher wasps, such as the hornets and yellow jackets, however, the first females that hatch out as adults in the spring help their mother provide for a still larger family by increasing the size of the house and collecting more provisions. Nature designed them for this purpose, moreover, by making them all sterile, allowing them to retain the maternal instincts, but depriving them of organs capable of producing offspring of their own. Thus there is here a beginning of that division of labor which reaches its highest development in the honey bee, where one form of the female is specialized entirely to produce the young and the other to rear the brood, keep the home in order, gather the food, and ward off enemies. The differences between the queens and the workers are supposed to result from the different diet on which larvæ designed to be queens are brought up, but a more thorough investigation of the food given to the different larvæ of the brood is yet needed before we can decide on the merits of this explanation. The work of numerous investigators seems to have demonstrated conclusively that the drone of the honey bee is always produced from an egg cell alone—that is, from an unfertilized egg—while the queens and workers are produced from fertilized eggs. The production of eggs that develop normally without the addition of the male element is called *parthenogenesis*. In a number of insects, such as some species of scales, a few beetles, and some of the gall-forming Hymenoptera, there are no males known, although the females are extremely abundant. Such cases are often regarded by entomologists as examples of parthenogenesis, and, if they are such, the result of the development of unfertilized eggs is here the formation of females only. A few other insects, such as some of the plant lice, produce eggs that develop without fertilization into females or into both males and females, but such cases nearly always occur in a cycle of alternating generations in which, at some stage, all the eggs are fertilized. As far as is known the production of males alone from parthenogenetic eggs is confined to the order Hymenoptera.

1. THE MALE ORGANS.

The reproductive organs of the drone are shown by figure 56 A. They consist of the *testes* (*Tes*), the *vasa deferentia* (*VDef*), the *vesiculæ seminales* (*Ves*), the *accessory* or *mucous glands* (*AcGl*), the *ductus ejaculatorius* (*EjD*), and the *penis* (*Pen*).

The *testes* of the bee (*Tes*) are said to be best developed in the pupa, at which stage they form the spermatozoa. Each consists of a large number of small tubules opening into a collecting reservoir at the end of the *vas deferens*. The spermatozoa pass down through the coiled *vas deferens* (*VDef*) and collect in the saclike enlargement of this duct, which constitutes the *vesicula seminalis* (*Ves*). In the mature adult drone these elongate sacs are densely packed with the active spermatozoa, while the testes that produced them become rudimentary. The *vesiculæ* when freshly dissected appear to be alive, for they bend and twist themselves about like small worms. Each opens by a short duct into the base of the *accessory mucous gland* (*AcGl*) of the same side. These organs have the form of two great sacs and are filled with a thick, white, homogeneous, finely granular liquid, which is supposed to mix with the spermatozoa as the latter are discharged. The two open at the bases into the single median *ejaculatory duct* (*EjD*) which opens into the anterior end of the *penis* (*Pen*). This last organ, shown in lateral view by figure 56 E, is an unusually large structure in the bee and is deeply invaginated into the cavity of the abdomen from the end of the ninth segment (*D, Pen*) as already described (see page 73). While the penis is simply an ectodermal tube, its walls present a number of very curious differentiations. The upper part is enlarged into a bulb (fig. 56 A and E, *B* and *PenB*) having two large irregular but symmetrical chitinous plates (*tt*) in its dorsal wall, beneath which is a large gelatinous thickening (*B, ss*). Near the base of the bulb is a double pinnate lobe (*A* and *E, uu*) projecting from the dorsal wall. Below this, on the ventral side, is a series of close-set, transverse plates (*E, vv*), followed again by large dorsal and ventral plates (*ww* and *xx*). The terminal part makes a thin-walled chamber (*A* and *E, yy*), from which project backward two very large membranous pouches (*zz*) ending in blunt points. The whole tube of the penis is capable of being turned inside out, and it is said that copulation is effected by its eversion into the oviduct of the queen, the basal pouches of the penis (*zz*) being forced into corresponding pouches of the oviduct, and the spermatozoa in the bulb placed near the opening of the spermatheca in the vagina. By their own activity probably the spermatozoa now make their way up into this receptacle of the female, the spermatheca, where they remain until ejected upon eggs passing down the oviduct. The spermatozoa received from one drone normally last the queen

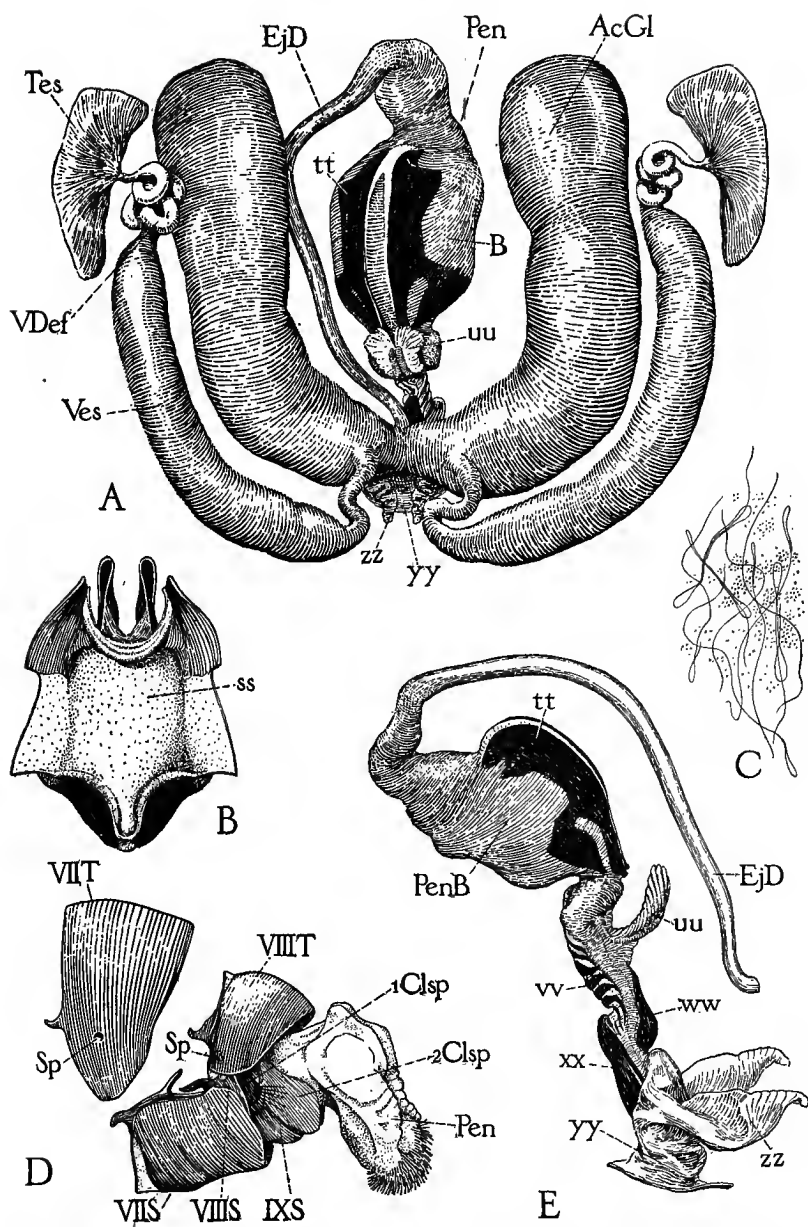


FIG. 56.—A, reproductive organs of drone, dorsal view, natural position; B, inner surface of dorsal wall of bulb of penis (E, *PenB*), showing gelatinous thickening (*ss*); C, group of spermatozoa and intermixed grauaules; D, terminal segments of male abdomen, showing the seventh tergum (*VIIT*) removed from its sternum (*VIIS*) and the penis (*Pen*) partly protruded; E, lateral view of penis as invaginated within abdomen, and ejaculatory duct (*EjD*).

throughout her life, so that after mating she goes into the hive never again to emerge except with a swarm, and her entire life is devoted to egg laying. The drone, on the other hand, dies immediately after mating, while those that do not mate are driven out of the hive in the fall and left to starve.

The *spermatozoa* (fig. 56 C) are minute threadlike cells, capable of a vibratory motion. As found in the vesiculæ, they are usually bent into closely compressed loops, although many are extended to their entire length. One end is blunt, but not noticeably enlarged, the other is tapering, while the half toward the tapering end seems to be the part chiefly endowed with the power of motion. The sperm threads are contained in a liquid within the vesiculæ, in which float also a great number of minute granules. The vibrations of the spermatozoa keep these granules in constant motion.

2. THE FEMALE ORGANS.

The organs of the female that produce the eggs are called the *ovaries* (fig. 57, *Ov*). In insects they consist of a varying number of egg tubules or *ovarioles* (*ov*) forming two lateral groups, in each of which the tubules converge at both ends, the anterior ends being drawn out into fine threads whose tips are connected, while the posterior ends are widened and open into the anterior end of the *oviduct* (*OvD*) on the same side of the body. An egg is simply a very large cell whose size is due to the great accumulation of yolk in its protoplasm, which serves as food for the future embryo. The eggs are formed in the terminal threads of the ovarioles and are at first apparently ordinary undifferentiated cells, but as they pass downward in the tubule they increase in size at the expense of some of the other ovarian cells. Hence the ovarioles usually have the form of a string of beads arranged in a graded series from very tiny ones at the upper end to others the size of the mature egg at the lower end. The two oviducts converge posteriorly and unite into the common median duct or *vagina* (*Vag*) which in most insects opens to the exterior upon the eighth sternum, as already described in the general account of the external anatomy of insects (see page 25), but in the bee and many other insects the eighth sternum is entirely lacking as a distinct sclerite, and the genital opening is therefore behind the seventh sternum and below the base of the sting. The posterior part of the vagina is very large, forming a *bursa copulatrix* (*BCpx*). In addition to these parts there is nearly always present in insects a special receptacle for the spermatozoa called the *spermatheca* (*Spm*). This, in most insects, opens directly into the vagina as it does in the bee, but in some it opens into the roof of the genital chamber above the eighth sternum, when this is present, by a separate orifice behind that of the

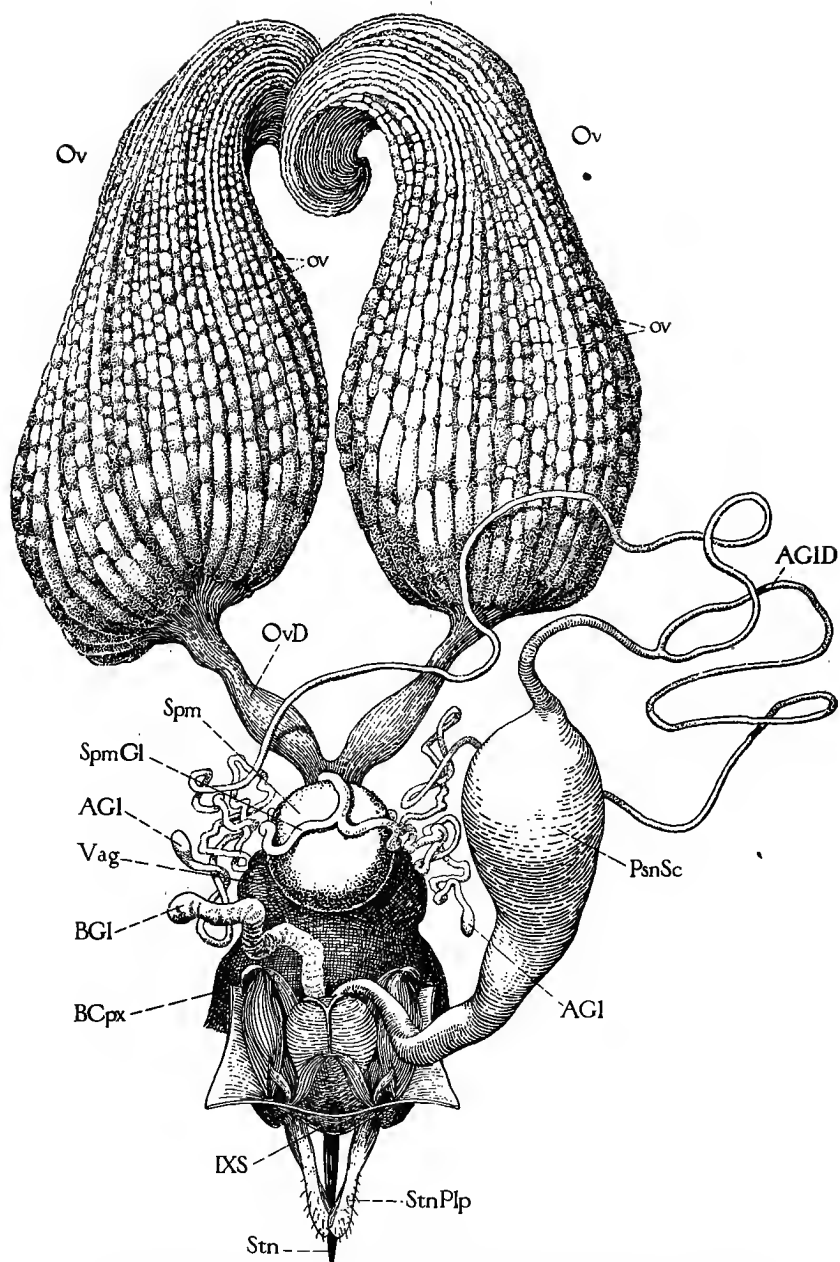


FIG. 57.—Reproductive organs, sting, and poison glands of queen, dorsal view.

vagina. In the bee the two poison glands (*AGL* and *BGL*) do not open into the vagina but, as already described, into the base of the sting. They are, hence, probably special organs having no homologues in nonstinging insects.

The ovaries of the queen bee form two large gourd-shaped masses (fig. 57, *Ov*) whose posterior or basal ends are enlarged and whose anterior ends are narrowed, curved, and attached to each other. Since the queen lays eggs continuously during her entire life the ovaries always contain eggs in all stages of growth, and consequently do not vary so much in appearance as they do in those insects that ripen only one lot of eggs and deposit these all at one time.

The structure of the ovarioles and the formation of the eggs in the bee have been specially studied by Paulcke (1900) and the following is a résumé of his paper: The terminal threads of the ovarioles are covered by a thin tunica propria and are filled with a protoplasmic mass containing transversely elongate nuclei in a single close series, but no cell outlines. Farther down, in the upper end of the ovariole proper, the nuclei become arranged in two rows, while here also the cell boundaries begin to appear; still farther along, where the cells are clearly defined, the latter become differentiated into epithelial cells and germ cells. Next, the germ cells themselves divide into egg cells and food or nurse cells. When first formed the egg cells occur in any part of the diameter of the tube, but they soon become arranged in a row down the middle of the ovariole and are separated by groups of nurse cells. The epithelial cells at this time arrange themselves on the periphery just within the tunica propria, but farther down they form a capsule or follicle about the egg and, less definitely, about the group of nurse cells at its upper end. The upper end of the egg becomes narrowed by a constriction of the epithelial capsule, which, however, does not shut it off from the nurse cells, a connection being retained with the latter in the form of a neck from the egg abutting against them. There are 48 of these nurse cells to each egg, which fact is accounted for by supposing that each original germ cell divides into 4, one of which ceases further division and becomes the egg cell, while each of the other 3 divides into 16 by four consecutive divisions. The latter are the nurse cells and their function is to nourish the egg cells. They persist down to the time when the egg is fully formed, when they suddenly disappear by being absorbed bodily into its yolk. Toward the end of the growth of the egg the follicle cells become thinner and thinner, so that when the egg is ready to go into the oviduct it has but a thin membrane to break through.

The organs of most especial interest to the student of the bee are the spermatheca and the apparatus by means of which the queen is able to dole out the spermatozoa to the eggs as she deposits the latter.

The spermatheca consists of a globular seminal sac (fig. 57, *Spm*), of a pair of tubular accessory glands (*SpmGl*), and of a duct whose upper end is connected with the sac and receives also the duct of the glands, and whose lower end opens into the anterior part of the dorsal wall of the vagina just caudad of the united bases of the oviducts.

The spermatozoa are discharged by the male into the upper end of the vagina, and in some manner they make their way up into the sperm sac through the duct. Cheshire (1885) described the latter as forking toward its lower end into an anterior branch which opens into the vagina and into a posterior branch which turns backward and becomes lost in the lower end of the vaginal wall. This second branch he believes is open in the young queen and is the one through which the spermatozoa enter the sac. Breslau (1906) has shown, however, that Cheshire was entirely wrong in his supposed observation of the forking of the duct, that the latter is a single tube, and that consequently the spermatozoa must both enter and leave the sac by the same conduit. It used to be supposed that the sperm sac had muscular walls and that it forced the spermatozoa out as from a compressed bulb, but Breslau has shown that this also is a mistaken notion, that the walls of the sac are entirely devoid of muscular fibers, and that the spermatozoa are sucked out by a muscular apparatus in the wall of the duct, which structure he names the *sperm pump*. Cheshire (1885) had previously described this apparatus in a very imperfect manner without recognizing any pumping function, for he supposed that by the relaxation of certain muscles the spermatozoa simply passed out of the sac and went down the tube. Breslau says, however, that the spermatozoa have not enough energy of their own to come out of the sac and, hence, do not need to be kept in by a special sphincter muscle, as described by Leydig.

The upper end of the spermathecal duct makes an **S**-shaped bend just beyond the opening of the sac, and a number of muscles disposed upon this part constitute Breslau's sperm-pump. Breslau shows that a contraction of certain of these muscles flattens the bend of the **S** and causes an enlargement of the lumen of the upper end of the loop. This, therefore, sucks into itself a small bundle of spermatozoa from the sac. The contraction then of other muscles forces the rest of the sperm-threads back into the mouth of the sac and drives the small bundle thus cut off down through the duct and into the vagina. Moreover, Breslau claims that this explanation is not theory only, for, by preparing histological sections from queens killed at different moments of egg-laying, he procured specimens showing the various stages in the pumping process and in the passage of the sperm through the duct. Cheshire calculated that a normal queen lays 1,500,000 eggs in her lifetime and that the spermatheca

holds about 4,000,000 spermatozoa, and therefore, allowing for drones, he concludes that there can not be more than four sperm-threads given to each female egg. But Breslau, figuring from the size of the sperm-bundle taken into the duct for each egg, states that each egg is actually given 75 to 100 spermatozoa. We feel that the latter calculation must be much more reliable than that of Cheshire because it is based on an actual observation of the size of the sperm mass delivered to the egg. Moreover, the myriads and myriads of tiny spermatozoa contained in the spermathecal sac make any attempt at a calculation of the number look absurd, and we can not believe that it is possible to even approximate the number present. Furthermore, as Breslau states, 100 spermatozoa make such an excessively small bundle that it requires a most effective and perfect apparatus to deliver even this number with anything like exactness—it is inconceivable that a mechanism could be perfect enough to give out only 4 or 5 or even 7 at a time.

On the floor of the vagina, opposite the opening of the spermathecal duct, is a free flap provided with muscles, which is so situated that when elevated its end fits into the opening of the duct above. Lenckart (1858) explained this flap as a contrivance for holding the passing egg tight against the upper vaginal wall so that its aperture through which the spermatozoa is received, called the micropyle, would come against the opening of the duct and thus insure fertilization. Breslau, on the other hand, does not think the flap in question has any such function and he regards it as a valve which by fitting into the orifice of the spermathecal duct closes the latter and so prevents the pump from sucking up the contents of the vagina at the same time that it sucks a bundle of spermatozoa out of the sac. Since, however, the flap is on the floor of the vagina and is pressed down by the passing egg it is not clear how it can at such a time act as a valve to close the orifice of the duct in the dorsal wall, since the pump is supposed to work by reflex action as the egg is entering the vagina, though, of course, it may so function before the egg has gone far enough to intervene between it and the duct opening; but it would certainly seem that a valve to close the latter, if needed at all, would be developed in the dorsal wall of the vagina in connection with the orifice itself. Furthermore, a collapsible tube like the spermathecal duct, even though lined with chitin, should automatically close at its lower end when a suction force is applied at the upper end.

Finally, Breslau attributes to the sperm pump not only the function of delivering a definite mass of spermatozoa to each egg, but also that of sucking the spermatozoa up from the vagina of a newly fertilized queen into the spermathecal sac. He does not seem now to see in the valve any obstacle to such an action. The spermatozoa are usually supposed to make their way up the duct by their own vibratory motion.

The anatomy of the spermatheca and the muscular apparatus of its duct for delivering the spermatozoa to the egg does not, as Breslau points out, throw any light on the determination of sex in bees. It is a common notion that all eggs of an unfertilized female develop into drones, but this is by no means proved; in fact, there is just as good reason for believing that, while no females develop, there are also no more than the normal number of drones produced—the eggs that might otherwise have developed into females, if laid by a fertile queen, all dying in the cells of the comb, from which they are removed by the workers. Modern investigation of the determination of sex shows that there is probably just as much reason in many cases for supposing that sex is established in the egg of the ovary before fertilization, as there is for believing it to result from fertilization or from subsequent environment of the egg or young embryo. Hence, it is not only very doubtful that the queen determines the sex of her offspring by controlling the fertilization of the eggs, but it is also very uncertain that fertilization itself has anything to do with it. Parthenogenesis in the bee may amount simply to this, that the male eggs, predetermined as such in the ovary, are capable of developing without fertilization, while the female eggs are incapable of such a development and die if they are not fertilized.

Each unlaidd egg of insects in general has a small hole in the upper end of its shell, called the *micropyle*, which admits the spermatozoa to its interior. One or several spermatozoa may enter the egg through this aperture, but the nuclear part of only one unites with the egg nucleus, this constituting the fertilization of the egg. After this the micropyle closes and the egg is deposited in a cell of the comb by the queen. The nucleus and a part of the protoplasm of the egg then begin to split up into a number of small cells which—but this is taking us into the development of the next generation, which is beyond the limits of our subject, and so here we must stop.

EXPLANATION OF THE SYMBOLS AND LETTERS USED ON THE ILLUSTRATIONS.

The writer has made an attempt to work out a set of convenient symbols for all the principal external and internal parts in the anatomy of an insect. It has been found, however, that entire consistency is incompatible with practicability, especially in making compound abbreviations, and, therefore, the latter has been given first consideration in many cases. For example, the symbol *Dct* suggests the word "duct" when standing alone much better than simply the letter *D*, but such combinations as *SalDct* and *OvDct* are unnecessarily long and the shortened forms of *SalD* and *OvD* are sufficiently suggestive of "salivary duct" and "oviduct." The abbreviation *Sc* is used in such compound symbols as *PsnSc* for "poison sac" and *TraSc*

for "tracheal sac," notwithstanding that *Sc* alone means "subcosta." The symbol *T* is used for "tergum," and *T*₁, *T*₂, etc., and *IT*, *IIT*, etc., indicate individual thoracic and abdominal terga, but *TMcl* is used to signify "transverse muscle." And so, in several other cases, it has been found expedient to sacrifice strict uniformity to practical considerations.

A combination of lower-case letters duplicating one entirely or partly of capitals signifies that the part so designated is a part or subdivision of the other. For example, *Ten* refers to the principal part of the tentorium and *ten* to a minor part; *Pl* and *pl* are subdivisions of the same pleurum; *Lmcl* and *lmcl* are both longitudinal muscles.

The most logical method of referring symbols to any particular segment of the body would be, perhaps, to prefix them with either a Roman or an Arabic numeral corresponding with the number of the segment. A common objection, however, to both would arise from the fact that entomologists are not at all agreed as to how many segments there are in any region of an insect's body. Furthermore, Roman numerals prefixed to all the symbols necessarily used on a drawing of the thorax, for example, would occupy entirely too much space. Finally, it is very desirable to have a method of referring to repeated structures without implying any segmental connection, and prefixed Arabic numerals are certainly most convenient and suggestive for such a purpose. A system often adopted to indicate the segment to which a part belongs, especially in the thorax, is the use of one, two, or three accents in connection with the abbreviation. But accented symbols lack artistic unity, and some of the accent marks are too easily lost in the engraving and printing. For these several reasons the writer has adopted the following system:

Numerical order of any repeated structure is indicated by an Arabic numeral placed before the abbreviation, and has no segmental significance. Thus *1P*, *2P*, etc., mean simply "first parapterum," "second parapterum," etc.; *1Gng*, *2Gng*, etc., mean "first ganglion," "second ganglion," etc., without implying that the ganglion belongs to any particular segment.

Symbols are referred to the prothorax, the mesothorax, or the metathorax, respectively, by the figures 1, 2, and 3 placed below and after them, except on the wings, where such numbers designate the branches of the veins according to the Comstock-Needham system.

The abdominal segments, counting the propodeum as the first, are indicated by the Roman numerals *I* to *X*, and, when any one of these is placed before an abbreviation, it refers the symbol to that individual segment.

The lower-case letters are used, singly and in pairs, to refer to miscellaneous parts having, in most cases, no individual or general anatomical names.

1. SYMBOLS.

<i>A</i> ,	anal vein; <i>1A</i> , first anal, <i>2A</i> , second anal, etc.
<i>AcGl</i> ,	accessory gland of male reproductive organs.
<i>AGl</i> ,	acid gland of sting, opening into poison sac (<i>PsnSc</i>).
<i>AGID</i> ,	duct of acid gland of sting.
<i>An</i> ,	anus.
<i>ANP</i> ,	anterior wing process of notum.
<i>ANR</i> ,	anterior marginal ridge of notum.
<i>Ant</i> ,	antenna.
<i>AntL</i> ,	antennal lobe of brain.
<i>AntNv</i> ,	antennal nerve.
<i>Ao</i> ,	aorta.
<i>Ap</i> ,	apodeme, any internal chitinous process of body-wall.
<i>Aph</i> ,	anterior phragma of any tergum, prephragma.
<i>Ax</i> ,	the axillaries or articular sclerites of the wing base, designated individually as <i>1Ax</i> , <i>2Ax</i> , <i>3Ax</i> , and <i>4Ax</i> .
<i>ax</i> ,	accessory axillary sclerites of irregular occurrence in connection with the principal axillaries (<i>Ax</i>).
<i>AxC</i> ,	axillary cord, or ligament-like thickening of posterior edge of basal membrane of wing, attached to posterior angle of scutellum.
<i>AxM</i> ,	axillary membrane, the thin membrane of wing base, containing the axillary sclerites and forming in some cases the lobes called alulae.
<i>B</i> ,	hulb (bulb of penis or of sheath of sting).
<i>BC</i> ,	body-cavity.
<i>bc</i> ,	any particular part of body cavity such as that prolonged into the mouth parts, legs or pieces of the sting.
<i>BCpæ</i> ,	bursa copulatrix.
<i>BGl</i> ,	alkaline gland of sting.
<i>BM</i> ,	basement membrane.
<i>Br</i> ,	brain.
<i>1Br</i> ,	protocerebrum.
<i>2Br</i> ,	deutocerebrum.
<i>3Br</i> ,	tritocerebrum.
<i>Brb</i> ,	barb.
<i>BW</i> ,	body-wall.
<i>C</i> ,	costa, first vein of wing.
<i>Cb</i> ,	pollen basket or corbiculum on hind tibia of worker.
<i>CC</i> ,	crystalline cone of compound eye.
<i>Cd</i> ,	cardo.
<i>Cer</i> ,	cercus.
<i>CL</i> ,	crystalline lens of compound eye.
<i>Cl</i> , <i>Cls</i> ,	cell, cells.
<i>Clæ</i> ,	claw.
<i>Clp</i> ,	clypeus.
<i>Clsp</i> ,	clasping lobes of ninth segment of male, perhaps equivalent to the four gonapophyses of ninth segment of female.
<i>1Clsp</i> ,	upper or outer clasper.
<i>2Clsp</i> ,	lower or inner clasper.
<i>Com</i> ,	commissure (of either nervous or tracheal system).
<i>Cor</i> ,	cornea.
<i>Ctl</i> ,	cuticle, the chitinous layer of the epidermis.
<i>Cu</i> ,	cubitus, fifth vein of generalized wing.

<i>Cv</i> ,	cross-vein.
<i>Cx</i> ,	coxa.
<i>CxP</i> ,	pleural coxal process.
<i>Dct</i> ,	duct.
<i>DDph</i> ,	dorsal diaphragm.
<i>Dph</i> ,	diaphragm.
<i>DphCls</i> ,	diaphragm cells.
<i>Dphmb</i> ,	membrane of diaphragm.
<i>DphMcl</i> ,	muscle fibers of diaphragm.
<i>E</i> ,	compound eye.
<i>EAp</i> ,	apodeme of extensor muscle.
<i>EjD</i> ,	ejaculatory duct.
<i>Em</i> ,	lateral emargination of notum.
<i>EMcl</i> ,	extensor muscle.
<i>Emp</i> ,	empodium.
<i>Enz</i> ,	digestive vesicles formed by ventricular epithelium.
<i>Ep</i> ,	epicranium.
<i>Ephy</i> ,	epipharynx.
<i>Epm</i> ,	epimerum.
<i>Eps</i> ,	episternum.
<i>Epth</i> ,	epithelium.
<i>F</i> ,	femur.
<i>Fl</i> ,	flagellum.
<i>For</i> ,	foramen magnum.
<i>Ft</i> ,	front.
<i>FtCom</i> ,	frontal commissure.
<i>FtGng</i> ,	frontal ganglion.
<i>FtNv</i> ,	frontal nerve.
<i>Fu</i> ,	furca or median entosternal apodeme of thoracic sterna.
<i>G</i> ,	gonapophysis.
<i>Ga</i> ,	galea.
<i>Ge</i> ,	gena.
<i>Gl</i> ,	gland.
<i>1Gl</i> ,	large pharyngeal gland in anterior part of head of worker.
<i>2Gl</i> ,	salivary gland in posterior part of head.
<i>3Gl</i> ,	thoracic salivary gland.
<i>4Gl</i> ,	small median gland below pharyngeal plate (<i>s</i>).
<i>Gls</i> ,	glossa.
<i>Gng</i> ,	ganglion.
<i>Gu</i> ,	gula.
<i>H</i> ,	head.
<i>Hk</i> ,	hooks on front edge of hind wing.
<i>Hphy</i> ,	hypopharynx.
<i>Hr</i> ,	hair.
<i>hr</i> ,	surface disk of "auditory" organ of antenna, probably modified base of sensory hair.
<i>HS</i> ,	honey stomach.
<i>Ht</i> ,	heart.
<i>ht</i> ,	individual chamber of heart.
<i>HtCls</i> ,	pericardial cells.
<i>HtTraSc</i> ,	pericardial tracheal sac.
<i>Int</i> ,	intima, the chitinous lining of any internal organ.
<i>IT</i> ,	tergum of first abdominal segment, the <i>median segment</i> , or <i>propodeum</i> , incorporated into thorax.

<i>L</i> ,	leg.
<i>Lb</i> ,	labium.
<i>Lbl</i> ,	labellum.
<i>LbNv</i> ,	labial nerve.
<i>LbPlp</i> ,	labial palpus.
<i>Lc</i> ,	lacinia.
<i>Lct</i> ,	lancet of sting, equivalent to first gonapophysis (<i>1G</i>).
<i>Lg</i> ,	ligula.
<i>LGl</i> ,	"lubricating" gland of sting (not shown in figures).
<i>Lin</i> ,	median lobe of lingua or hypopharynx.
<i>Lm</i> ,	labrum.
<i>LMcl</i> ,	longitudinal muscles.
<i>lmcl</i> ,	ventral longitudinal muscles of thorax.
<i>LmNv</i> ,	labral nerve.
<i>Lr</i> ,	lorum.
<i>LTra</i> ,	trachea of leg.
<i>Lum</i> ,	lumen, the cavity of any hollow organ, whether the glossa, sting, alimentary canal, or gland.
<i>M</i> ,	media, fourth vein of wing. M_1-M_4 , first to fourth branches of media.
<i>m</i> ,	median plate or plates of wing base.
<i>Mal</i> ,	Malpighian tubules.
<i>Mb</i> ,	intersegmental membrane.
<i>mb</i> ,	membrane.
<i>m-cu</i> ,	medio-cubital cross-vein.
<i>MD</i> ,	disclike muscle apodeme.
<i>Md</i> ,	mandible.
<i>1MdGl</i> ,	outer saclike mandibular gland.
<i>2MdGl</i> ,	inner racemose mandibular gland.
<i>MdNv</i> ,	mandibular nerve.
<i>Mes</i> ,	mesothorax, designated by figure 2 placed after and below any thoracic symbol.
<i>Met</i> ,	metathorax, designated by figure 3 placed after and below any thoracic symbol.
<i>Mi</i> ,	the chitinous plates of the neck collectively, the "microthorax," individually designated <i>mi</i> .
<i>mi</i> ,	cervical (microthoracic) sclerites.
<i>m-m</i> ,	median cross-vein.
<i>Mps</i> ,	mouth parts or trophi.
<i>Mt</i> ,	mentum.
<i>Mth</i> ,	month.
<i>Mx</i> ,	maxilla.
<i>MxPlp</i> ,	maxillary palpus.
<i>MxNv</i> ,	maxillary nerve.
<i>N</i> ,	notum.
<i>Nu</i> ,	nucleus.
<i>Nv</i> ,	nerve.
<i>O</i> ,	ocellus.
<i>Ob</i> ,	oblong plate.
<i>Oc</i> ,	occiput.
<i>Œ</i> ,	œsophagus.
<i>ŒCom</i> ,	circumœsophageal commissures.
<i>Om</i> ,	ommatidium.
<i>OpL</i> ,	optic lobe.

<i>Ost</i> ,	ostium or lateral aperture of heart.
<i>Ov</i> ,	ovary.
<i>ov</i> ,	ovariole, individual ovarian tube.
<i>OvD</i> ,	oviduct.
<i>OvO</i> ,	opening of vagina or median oviduct.
<i>P</i> ,	paraptera, small pleural plates below base of wing, typically two episternal paraptera or preparaptera (<i>1P</i> and <i>2P</i>) before pleural wing process (<i>WP</i>), and two epimeral paraptera or postparaptera (<i>3P</i> and <i>4P</i>) behind wing process.
<i>1P</i> , <i>2P</i> ,	episternal paraptera, preparaptera.
<i>3P</i> , <i>4P</i> ,	epimeral paraptera, postparaptera.
<i>PA</i> ,	arm of pleural ridge.
<i>Pcl</i> ,	postclypeus.
<i>PD</i> ,	muscle disc of episternal paraptera, giving insertion to pronator muscle (not present in the bee).
<i>Pd</i> ,	peduncle.
<i>Pen</i> ,	penis.
<i>PenB</i> ,	bulb of penis.
<i>Peps</i> ,	preepisternum.
<i>Pge</i> ,	postgena.
<i>Pgl</i> ,	paraglossa.
<i>Pgu</i> ,	pregula.
<i>Ph</i> ,	phragma.
<i>Phy</i> ,	pharynx.
<i>Pl</i> ,	pleurum.
<i>pl</i> ,	subdivision of pleurum.
<i>Plf</i> ,	palpifer, palpus-carrying lobe of maxilla.
<i>Plg</i> ,	palpiger, palpus-carrying lobe of labium.
<i>Plp</i> ,	palpus.
<i>Pmb</i> ,	peritrophic membrane.
<i>PMcl</i> ,	pronator muscle.
<i>PN</i> ,	postnotum or pseudonotum, the second or postalar tergal plate of the wing-bearing segments of most insects, the "postscutellum" of higher orders.
<i>pn</i> ,	small rod connecting postscutellum (postnotum <i>PN</i>) with upper edge of epimerum, probably a detached piece of the former (see figs. 22 and 24).
<i>PNP</i> ,	posterior notal wing process.
<i>PNR</i> ,	posterior marginal ridge of notum.
<i>Pph</i> ,	posterior phragma or postphragma of any tergum, carried by the second notal plate or postnotum (<i>PN</i>), the "postscutellum" of higher forms.
<i>PR</i> ,	internal pleural ridge, the entopleurum, marked externally by pleural suture (<i>PS</i>).
<i>Prb</i> ,	proboscis.
<i>PrbFs</i> ,	fossa of proboscis.
<i>PS</i> ,	pleural suture, external line separating episternum and epimerum, marking site of internal pleural ridge.
<i>Ps</i> ,	presternum.
<i>Psc</i> ,	prescutum.
<i>PscL</i> ,	postscutellum (postnotum).
<i>Psl</i> ,	poststernellum.
<i>PsnC</i> ,	poison canal of sting.
<i>PsnSc</i> ,	poison sac of sting into which opens the acid gland (<i>AGI</i>).

<i>Pt</i> ,	sensory pit.
<i>Ptr</i> ,	peritreme, spiracle-bearing sclerite.
<i>Pvent</i> ,	proventriculus.
<i>Pvent Vlv</i> ,	proventricular tube or valve in ventriculus.
<i>Qd</i> ,	quadrate plate of sting.
<i>R</i> ,	radius, third vein of generalized wing. R_1 – R_5 , first to fifth branches of radius. R_s , radial sector.
<i>RAp</i> ,	apodeme of flexor muscle.
<i>Rd</i> ,	posterior extension or reduplication of any tergal or sternal plate overlapping plate following it.
<i>Rect</i> ,	rectum, the large intestine of insects.
<i>RGl</i> ,	rectal glands.
<i>r-m</i> ,	radio-medial cross-vein.
<i>RMcl</i> ,	flexor muscle of mandible or wing.
<i>IRMcl</i> ,	dorsal retractor muscle of ligula.
<i>2RMcl</i> ,	ventral retractor muscle of ligula.
R_s ,	radial sector, or second branch of radius at first forking.
<i>S</i> ,	sternum.
<i>SalD</i> ,	salivary duct.
<i>SalDO</i> ,	external opening of salivary duct.
<i>Sc</i> ,	subcosta, second vein of generalized wing.
<i>ScI</i> ,	scutellum.
<i>Scp</i> ,	scape.
<i>Sct</i> ,	scutum.
<i>Sga</i> ,	subgalea.
<i>Sh</i> ,	sheath of sting, equivalent to the second gonapophyses (<i>2G</i>) or middle pair on ninth abdominal segment.
<i>ShA</i> ,	basal arm of sheath of sting.
<i>ShB</i> ,	hulb of sheath of sting or ovipositor.
<i>ShS</i> ,	shaft of sheath of sting.
<i>SInt</i> ,	small intestine.
<i>Sl</i> ,	sternellum.
<i>Slin</i> ,	superlingua, embryonic lateral lobes of hypopharynx, true appendages of fifth head segment.
<i>Smt</i> ,	submentum.
<i>SæGng</i> ,	subœsophageal ganglion.
<i>Sp</i> ,	spiracle.
<i>Spm</i> ,	spermatheca.
<i>SpmGl</i> ,	spermathecal gland.
<i>St</i> ,	stipes.
<i>StgNv</i> ,	stomatogastric nerve.
<i>Stn</i> ,	sting.
<i>StnPlp</i> ,	palpuslike appendages of the sting, equivalent to the third gonapophyses (<i>3G</i>) or the outer pair on ninth abdominal segment.
<i>T</i> ,	tergum.
<i>IT</i> ,	first abdominal tergum, the propodeum, incorporated into thorax.
<i>IIT</i> ,	second abdominal tergum.
<i>Tar</i> ,	tarsus.
<i>Tb</i> ,	tibia.
<i>Ten</i> ,	large tentorial arms of head, the mesocephalic pillars.
<i>ten</i> ,	slender tentorial arch over foramen magnum.
<i>Tes</i> ,	testes.
<i>Tg</i> ,	tegula.

<i>TMcl</i> ,	transverse muscle.
<i>Tn</i> ,	trochantin (not separated from sternum in bee).
<i>TnC</i> ,	coxal condyle of trochantin.
<i>Tr</i> ,	trochanter.
<i>Tra</i> ,	trachea.
<i>TraCom</i> ,	transverse ventral tracheal commissures of abdomen.
<i>TraSc</i> ,	tracheal sac.
<i>Tri</i> ,	triangular plate of sting.
<i>Vag</i> ,	vagina.
<i>VDef</i> ,	vas deferens.
<i>VDph</i> ,	ventral diaphragm.
<i>Vent</i> ,	ventriculus.
<i>VentVlv</i> ,	ventricular fold or valve in small intestine.
<i>Ves</i> ,	vesicula seminalis.
<i>Vlv</i> ,	valve of sting carried by lancet.
<i>VMcl</i> ,	large vertical muscles of thorax.
<i>VNR</i> ,	internal, median V-shaped notal ridge, the "entodorsum."
<i>Vx</i> ,	vertex.
<i>W</i> ,	wing.
<i>W₂Nv</i> ,	mesothoracic wing nerve.
<i>W₃Nv</i> ,	metathoracic wing nerve.
<i>WP</i> ,	wing process of pleurum.

2. ALPHABETICAL LETTERING.

<i>a</i> ,	clypeal suture.
<i>b</i> ,	anterior tentorial pit, in clypeal suture.
<i>c</i> ,	posterior tentorial pit, in occiput beside foramen magnum.
<i>d</i> ,	thickened posterior edge of lateral wall of fossa of proboscis.
<i>e</i> ,	process at upper end of <i>d</i> articulating with cardo of maxilla and forming maxillary suspensorium.
<i>f</i> ,	internal median keel of vertex in cranium of drone.
<i>g</i> ,	suspensorial ligaments of anterior end of œsophagus.
<i>h</i> ,	pharyngeal rod.
<i>i</i> ,	convolutions of dorsal blood vessel.
<i>j</i> ,	anterior articular knob of mandible.
<i>k</i> ,	ventral groove of glossa.
<i>l</i> ,	ventral groove of maxillary rod.
<i>m</i> ,	median plates of wing base.
<i>n</i> ,	basal hooks of glossa.
<i>o</i> ,	median ventral plate of ligula.
<i>p</i> ,	dorsal plates of anterior end of mentum, supporting ligula.
<i>q</i> ,	inner wall of canal of glossa.
<i>r</i> ,	chitinous rod of glossa.
<i>s</i> ,	pharyngeal plate, on anterior part of floor of pharynx.
<i>t</i> ,	salivary pouch opening on dorsal side of base of ligula, receiving common duct of salivary glands (<i>SalD</i>).
<i>u</i> ,	oblique muscles inserted upon dorsal side of salivary pouch of ligula.
<i>v</i> ,	transverse or V-shaped suture on surface of mesonotum or metanotum, formed by the internal V-shaped ridge or "entodorsum" (<i>VNR</i>).
<i>w</i> ,	lateral lobe of pronotum projecting posteriorly over the first spiracle.

<i>x</i> ,	thoracic plate lying laterad of anterior part of sternum, often regarded as a part of presternum.
<i>y</i> ,	accessory sclerite of fourth axillary (<i>4Ax</i>) of front wing, affording insertion for slender muscle (fig. 28, <i>cc</i>) attached below to common apodeme of mesosternum and metasternum.
<i>z</i> ,	coxal condyles of mesothoracic and metathoracic sterna, probably really the coxal condyles of trochantins (fig. 4, <i>TnC</i>) fused entirely with the sterna and episterna in each segment.
<i>aa</i> ,	muscle arising from inner wall of mesothoracic pleurum and inserted upon outer end of corresponding scutellum, probably accessory in function to the great vertical muscles (fig. 27, <i>VMcl</i>) between the mesothoracic sternum and scutum.
<i>bb</i> ,	coxo-axillary muscle, extending from upper end of coxa to third parapterum (<i>3P</i>).
<i>cc</i> ,	muscle inserted upon accessory sclerite (<i>y</i>) of fourth axillary (<i>4Ax</i>) from common presternum of mesothorax and metathorax.
<i>dd</i> ,	notch of antenna cleaner on first tarsal joint (<i>1Tar</i>) of front leg.
<i>ee</i> ,	spine of antenna cleaner situated on distal end of tibia (<i>Tb</i>).
<i>ff</i> ,	so-called "wax shears" or "wax pincers."
<i>gg</i> ,	transverse chitinous band of empodium (<i>Emp</i>), which compresses its two lobes when not in use and spread out by muscular effort.
<i>hh</i> ,	dorsal plate supporting empodium.
<i>ii</i> ,	ventral plate supporting empodium.
<i>jj</i> ,	dorsal groove of lancet interlocking with ventral ridge of sheath of sting.
<i>kk</i> ,	sting chamber within end of seventh abdominal segment, lodging sting whose accessory plates are derived from eighth and ninth segments.
<i>ll</i> ,	reservoir of thoracic salivary gland.
<i>mm</i> ,	receptacular chitinous pouches on ventral side of pharyngeal plate (<i>s</i>) receiving ducts of large lateral pharyngeal glands of head (<i>1Gl</i>).
<i>nn</i> ,	"stomach-mouth" at summit of proventricular projection within honey stomach (<i>HS</i>).
<i>oo</i> ,	pores on lancets (fig. 40 E) and shaft of sting sheath (F) opening to exterior from prolongation of body-cavity (<i>bc</i>) contained in each.
<i>pp</i> ,	gelatinous layer secreted upon inner surface of ventricular epithelium.
<i>qq</i> ,	food contents of alimentary canal.
<i>rr</i> ,	cells of ventricular epithelium apparently forming the internal gelatinous layer.
<i>ss</i> ,	cartilaginous mass on inner surface of dorsal wall of bulb of penis (fig. 56 E, <i>PenB</i>).
<i>tt</i> ,	dorsal plates of bulb of penis.
<i>uu</i> ,	fimbriated dorsal lobes of penis at base of bulb.
<i>vv</i> ,	ventral scalariform row of plates on tube of penis.
<i>ww</i> ,	dorsal basal plates of penis.
<i>xx</i> ,	ventral basal plates of penis.
<i>yy</i> ,	basal pouch of penis.
<i>zz</i> ,	copulatory sacs of penis.

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L. O. HOWARD, Entomologist and Chief of Bureau.

THE BEHAVIOR OF THE HONEY BEE
IN POLLEN COLLECTING.

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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY,
Washington, D. C., September 23, 1912.

SIR: I have the honor to transmit herewith a manuscript entitled "The Behavior of the Honey Bee in Pollen Collecting," by Dr. Dana B. Casteel, of this bureau. The value of the honey bee in cross pollinating the flowers of fruit trees makes it desirable that exact information be available concerning the actions of the bee when gathering and manipulating the pollen. The results recorded in this manuscript are also of value as studies in the behavior of the bee and will prove interesting and valuable to the bee keeper. The work here recorded was done by Dr. Casteel during the summers of 1911 and 1912 at the apiary of this bureau.

I recommend that this manuscript be published as Bulletin No. 121 of the Bureau of Entomology.

Respectfully,

L. O. HOWARD,
Entomologist and Chief of Bureau.

HON. JAMES WILSON,
Secretary of Agriculture.



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THE BEHAVIOR OF THE HONEY BEE IN POLLEN COLLECTING.

INTRODUCTION.

While working upon the problem of wax-scale manipulation during the summer of 1911 the writer became convinced that the so-called wax shears or pinchers of the worker honey bee have nothing whatever to do with the extraction of the wax scales from their pockets, but rather that they are organs used in loading the pollen from the pollen combs of the hind legs into the corbiculæ or pollen baskets (Casteel, 1912). Further observations made at that time disclosed the exact method by which the hind legs are instrumental in the pollen-loading process and also the way in which the middle legs aid the hind legs in patting down the pollen masses. During the summer of 1912 additional information was secured, more particularly that relating to the manner in which pollen is collected upon the body and legs of the bee, how it is transferred to the hind legs, how it is moistened, and finally the method by which it is stored in the hive for future use. In the present paper a complete account will be given of the history of the pollen from the time it leaves the flower until it rests within the cells of the hive. The points of more particular interest in the description of pollen manipulation refer to (1) the movements concerned in gathering the pollen from the flowers upon the body and legs, (2) the method by which the baskets of the hind legs receive the loads which they carry to the hive, and (3) the manner in which the bee moistens pollen and renders it sufficiently cohesive for packing and transportation.

THE STRUCTURES CONCERNED IN THE MANIPULATION OF POLLEN.

The hairs which cover the body and appendages of the bee are of the utmost importance in the process of pollen gathering. For the purposes of this account these hairs may be classified roughly as (1) branched hairs and (2) unbranched hairs, the latter including both long, slender hairs and stiff, spinelike structures.

Of these two classes the branched hairs are the more numerous. They make up the hairy coat of the head, thorax, and abdomen, with the exception of short sensory spines, as those found upon the antennæ and perhaps elsewhere, and the stiff unbranched hairs which

cover the surfaces of the compound eyes (Phillips, 1905). Branched hairs are also found upon the legs; more particularly upon the more proximal segments. A typical branched hair is composed of a long slender main axis from which spring numerous short lateral barbs. Grains of pollen are caught and held in the angles between the axis and the barbs and between the barbs of contiguous hairs. The hairy covering of the body and legs thus serves as a collecting surface upon which pollen grains are temporarily retained and from which they are later removed by the combing action of the brushes of the legs.

Although, as above noted, some unbranched hairs are located upon the body of the bee, they occur in greatest numbers upon the more distal segments of the appendages. They are quite diverse in form, some being extremely long and slender, such as those which curve

over the pollen baskets, others being stout and stiff, as those which form the collecting brushes and the pecten spines.

The mouth-parts of the bee are also essential to the proper collection of pollen. The mandibles are used to scrape over the anthers of flowers, and

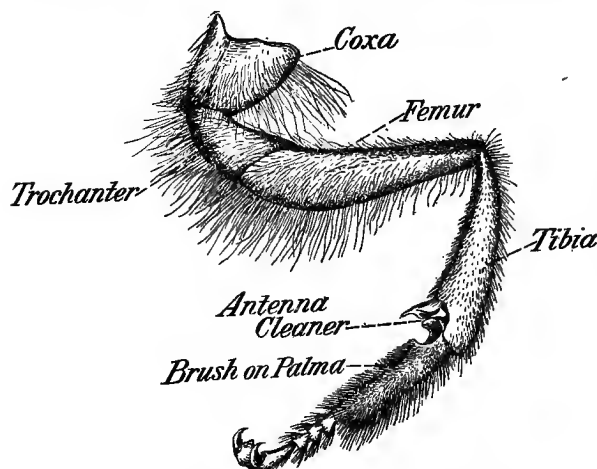


FIG. 1.—Left foreleg of a worker bee. (Original.)

considerable pollen adheres to them and is later removed. The same is true of the maxillæ and tongue. From the mouth comes the fluid by which the pollen grains are moistened.

The legs of the worker bee are especially adapted for pollen gathering. Each leg bears a collecting brush, composed of stiff, unbranched hairs set closely together. These brushes are located upon the first or most proximal tarsal segment of the legs, known technically as the palmæ of the forelegs and as the plantæ of the middle and hind pair. The brush of the foreleg is elongated and of slight width (fig. 1), that of the middle leg broad and flat (fig. 2), while the brush upon the planta of the hind leg is the broadest of all, and is also the most highly specialized. In addition to these well-marked brushes, the distal ends of the tibiæ of the fore and middle legs bear many stiff hairs, which function as pollen collectors, and the distal tarsal joints of all legs bear similar structures.

The tibia and the planta of the hind leg of the worker bee are greatly flattened. (See figs. 3, 4.) The outer surface of the tibia is marked by an elongated depression, deepest at its distal end, and bounded laterally by elevated margins. From the lateral boundaries of this depression spring many long hairs, some of which arch over the concave outer surface of the tibia and thus form a kind of receptacle or basket to which the name corbicula or pollen-basket is given. The lower or distal end of the tibia articulates at its anterior edge with the planta. The remaining portion of this end of the tibia is flattened and slightly concave, its surface sloping upward from the inner to the outer surface of the limb. Along the inner edge of this surface runs a row of short, stiff, backwardly directed spines, from 15 to 21 in number, which form the pecten or comb of the tibia. The lateral edge of this area forms the lower boundary of the corbicular depression and is marked by a row of very fine hairs which branch at their free ends. Immediately above these hairs, springing from the floor of the corbicula, are found 7 or 8 minute spines, and above them one long hair which reaches out over the lower edge of the basket.

The broad, flat planta (metatarsus or proximal tarsal segment of the hind leg) is marked on its inner surface by several rows of stiff, distally directed spines which form the pollen combs. About 12 of these transverse rows may be distinguished, although some of them are not complete. The most distal row, which projects beyond the edge of the planta, is composed of very strong, stiff spines which function in the removal of the wax scales (Casteel, 1912). The upper or proximal end of the planta is flattened and projects in a posterior direction to form the auricle. The surface of the auricle is marked with short, blunt spines, pyramidal in form, and a fringe of fine hairs with branching ends extends along its lateral edge. This surface slopes upward and outward.

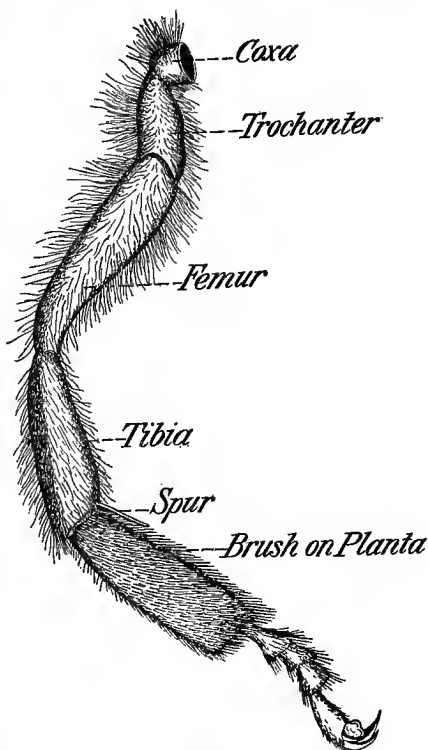


FIG. 2.—Left middle leg of a worker bee.
(Original.)

THE POLLEN SUPPLY.

When bees collect pollen from flowers they may be engaged in this occupation alone or may combine it with nectar gathering. From some flowers the bees take only nectar, from others only pollen; a third class of flowers furnishes an available supply of both of these substances. But even where both pollen and nectar are obtainable a bee may gather nectar and disregard the pollen. This is well illustrated by the case of white clover. If bees are watched while working upon clover flowers, the observer will soon perceive some which bear pollen masses upon their hind legs, while others will continue to visit flower after flower, dipping into the blossoms and securing a plentiful supply of nectar, yet entirely neglecting the pollen.

The supply of pollen which is available for the bees varies greatly among different flowers. Some furnish an abundant amount and present it to the bee in such a way that little difficulty is experienced in quickly securing an ample load, while others furnish but little. When flowers are small and when the bee approaches them from above, little, if any, pollen is scattered over the bee's body, all that it acquires being first collected upon the mouth and neighboring parts.

Very different conditions are met with when bees visit such

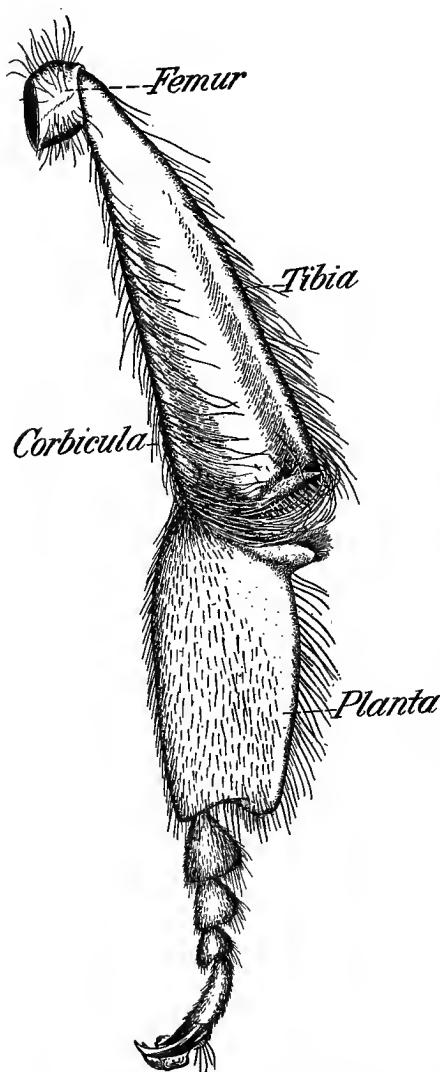


FIG. 3.—Outer surface of the left hind leg of a worker bee. (Original.)

plants as corn and ragweed. The flowers of these plants are pendent and possess an abundant supply of pollen, which falls in showers over the bodies of the bees as they crawl beneath the blossoms. The

supply of pollen which lodges upon the body of the bee will thus differ considerably in amount, depending upon the type of flower from which the bee is collecting, and the same is true regarding the location upon the body of a bee of pollen grains which are available for storage in the baskets.

Moreover, the movements concerned in the collection of the pollen from the various body parts of the bee upon which it lodges will differ somewhat in the two cases, since a widely scattered supply requires for its collection additional movements, somewhat similar in nature to those which the bee employs in cleaning the hairs which cover its body.

✓ GENERAL STATEMENT OF THE POLLEN-COLLECTING PROCESS.

A very complete knowledge of the pollen-gathering behavior of the worker honey bee may be obtained by a study of the actions of bees which are working upon a plant which yields pollen in abundance. Sweet corn is an ideal plant for this purpose, and it will be used as a basis for the description which follows.

In attempting to outline the method by which

pollen is manipulated the writer wishes it to be understood that he is recounting that which he has seen and that the description is not necessarily complete, although he is of the opinion that it is very nearly so. The movements of the legs and of the mouthparts are so rapid and so many

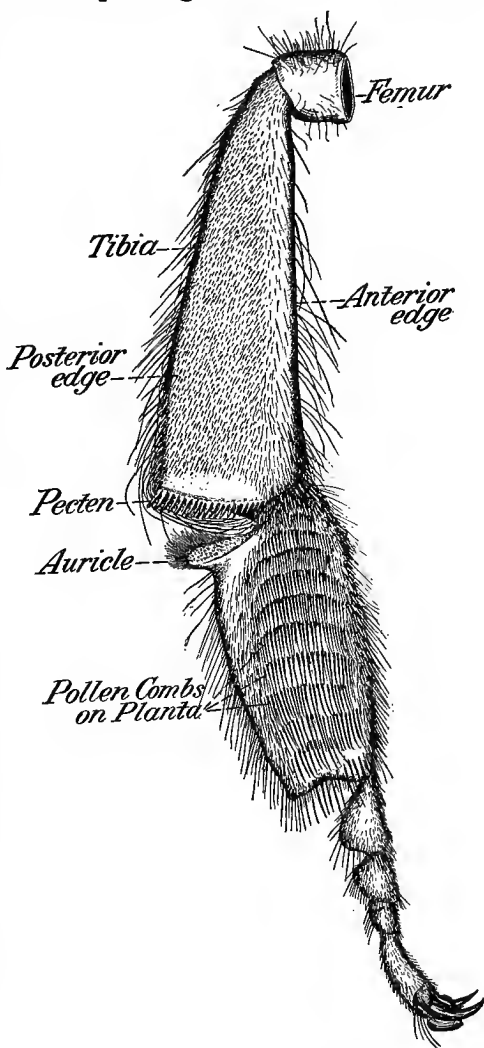


FIG. 4.—Inner surface of the left hind leg of a worker bee. (Original.)

members are in action at once that it is impossible for the eye to follow all at the same time. However, long-continued observation, assisted by the study of instantaneous photographs, gives confidence that the statements recorded are accurate, although some movements may have escaped notice.

To obtain pollen from corn the bee must find a tassel in the right stage of ripeness, with flowers open and stamens hanging from them. The bee alights upon a spike and crawls along it, clinging to the pendent anthers. It crawls over the anthers, going from one flower to another along the spike, being all the while busily engaged in the task of obtaining pollen. This reaches its body in several ways.

As the bee moves over the anthers it uses its mandibles and tongue, biting the anthers and licking them and securing a considerable amount of pollen upon these parts. This pollen becomes moist and sticky, since it is mingled with fluid from the mouth. A considerable amount of pollen is dislodged from the anthers as the bee moves over them. All of the legs receive a supply of this free pollen and much adheres to the hairs which cover the body, more particularly to those upon the ventral surface. This free pollen is dry and powdery and is very different in appearance from the moist pollen masses with which the bee returns to the hive. Before the return journey this pollen must be transferred to the baskets and securely packed in them.

After the bee has traversed a few flowers along the spike and has become well supplied with free pollen it begins to collect it from its body, head, and forward appendages and to transfer it to the posterior pair of legs. This may be accomplished while the bee is resting upon the flower or while it is hovering in the air before seeking additional pollen. It is probably more thoroughly and rapidly accomplished while the bee is in the air, since all of the legs are then free to function in the gathering process.

If the collecting bee is seized with forceps and examined after it has crawled over the stamens of a few flowers of the corn, its legs and the ventral surface of its body are found to be thickly powdered over with pollen. If the bee hovers in the air for a few moments and is then examined very little pollen is found upon the body or upon the legs, except the masses within the pollen baskets. While in the air it has accomplished the work of collecting some of the scattered grains and of storing them in the baskets, while others have been brushed from the body.

In attempting to describe the movements by which this result is accomplished it will be best first to sketch briefly the rôles of the three pairs of legs. They are as follows:

(*a*) The first pair of legs remove scattered pollen from the head and the region of the neck, and the pollen that has been moistened by fluid substances from the mouth.

(b) The second pair of legs remove scattered pollen from the thorax, more particularly from the ventral region, and they received the pollen that has been collected by the first pair of legs.

(c) The third pair of legs collect a little of the scattered pollen from the abdomen and they receive pollen that has been collected by the second pair. Nearly all of this pollen is collected by the pollen combs of the hind legs, and is transferred from the combs to the pollen baskets or corbiculae in a manner to be described later.

It will thus be seen that the manipulation of pollen is a successive process, and that most of the pollen at least passes backward from the point where it happens to touch the bee until it finally reaches the corbiculae or is accidentally dislodged and falls from the rapidly moving limbs.

ACTION OF THE FORELEGS AND MOUTHPARTS.

Although the pollen of some plants appears to be somewhat sticky, it may be stated that as a general rule pollen can not be successfully manipulated and packed in the baskets without the addition of some fluid substance, preferably a fluid which will cause the grains to cohere. This fluid, the nature of which will be considered later, comes from the mouth of the bee, and is added to the pollen which is collected by the mouthparts and to that which is brought into contact with the protruding tongue and maxillae, and, as will appear, this fluid also becomes more generally distributed upon the legs and upon the ventral surface of the collecting bee.

When a bee is collecting from the flowers of corn the mandibles are actively engaged in seizing, biting, and scraping the anthers as the bee crawls over the pendent stamens. Usually, but not always, the tongue is protruded and wipes over the stamens, collecting pollen and moistening the grains thus secured. Some of the pollen may possibly be taken into the mouth. All of the pollen which comes in contact with the mouthparts is thoroughly moistened, receiving more fluid than is necessary for rendering the grains cohesive. This exceedingly wet pollen is removed from the mouthparts by the forelegs (fig. 5), and probably the middle legs also secure a little of it directly, since they sometimes brush over the lower surface of the face and the mouth. In addition to removing the very moist pollen from the mouth the forelegs also execute cleansing movements over the sides of the head and neck and the anterior region of the thorax, thereby collecting upon their brushes a considerable amount of pollen which has fallen directly upon these regions, and this is added to the pollen moistened from the mouth, thereby becoming moist by contact. The brushes of the forelegs also come in contact with the anterior breast region, and the hairs which cover this area become moist with the sticky exudation which the forelegs have acquired in the process of wiping pollen from the tongue, maxillae, and mandibles.

ACTION OF THE MIDDLE LEGS.

The middle legs are used to collect the pollen gathered by the forelegs and mouthparts, to remove free pollen from the thoracic region, and to transport their load of pollen to the hind legs, placing most of it upon the pollen combs of these legs, although a slight amount is directly added to the pollen masses in the corbiculæ. Most of the pollen of the middle legs is gathered upon the conspicuous brushes of the first tarsal segments or plantæ of these legs.

In taking pollen from a foreleg the middle leg of the same side is extended in a forward direction and is either grasped by the flexed foreleg or rubbed over the foreleg as it is bent downward and backward. In the former movement the foreleg flexes sharply upon itself until

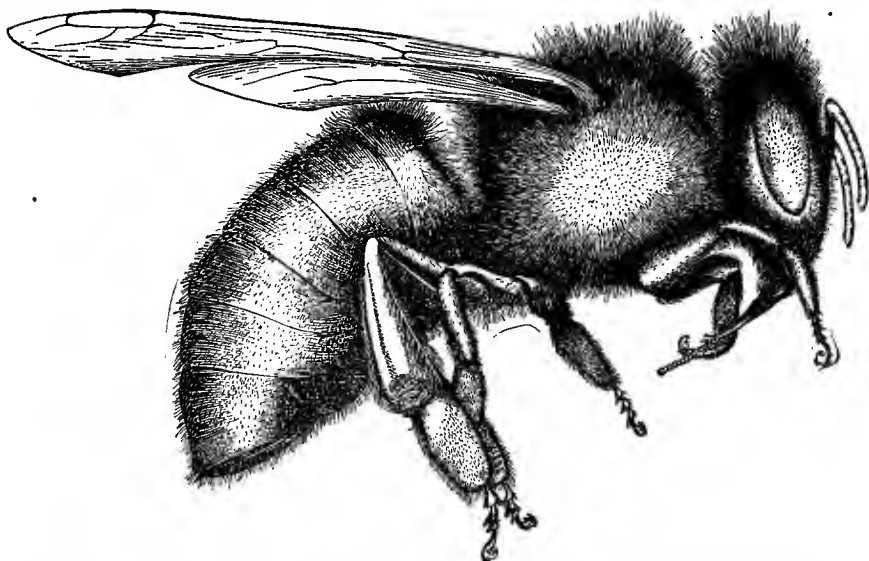


FIG. 5.—A flying bee, showing the manner in which the forelegs and middle legs manipulate pollen. The forelegs are removing wet pollen from the mouthparts and face. The middle leg of the right side is transferring the pollen upon its brush to the pollen combs of the left hind planta. A small amount of pollen has already been placed in the baskets. (Original.)

the tarsal brush and coxa nearly meet. The collecting brush of the middle leg is now thrust in between the tarsus and coxa of the foreleg and wipes off some of the pollen from the foreleg brush. The middle leg brush is then raised and combs down over the flexed foreleg, thus removing additional pollen from the outer surface of this leg. The middle leg also at times reaches far forward, stroking down over the foreleg before it is entirely flexed and apparently combing over with its tarsal brush the face and mouthparts themselves. When the middle leg reaches forward to execute any of the above movements the direction of the stroke is outward, forward, and then back toward the body, the action ending with the brush of the leg in contact with the long hairs of the breast and with those which spring

from the proximal segments of the forelegs (coxa, trochanter, femur). As a result of the oft-repeated contact of the brushes of the middle and forelegs with the breast, the long, branched hairs which cover this region become quite moist and sticky, since the brushes of these two pair of legs are wet and the pollen which they bear possesses a superabundance of the moistening fluid. Any dry pollen which passes over this region and touches these hairs receives moisture by contact with them. This is particularly true of the free dry pollen which the middle pair of legs collect by combing over the sides of the thorax.

The pollen upon the middle legs is transferred to the hind legs in at least two ways. By far the larger amount is deposited upon the pollen combs which lie on the inner surfaces of the plantæ of the

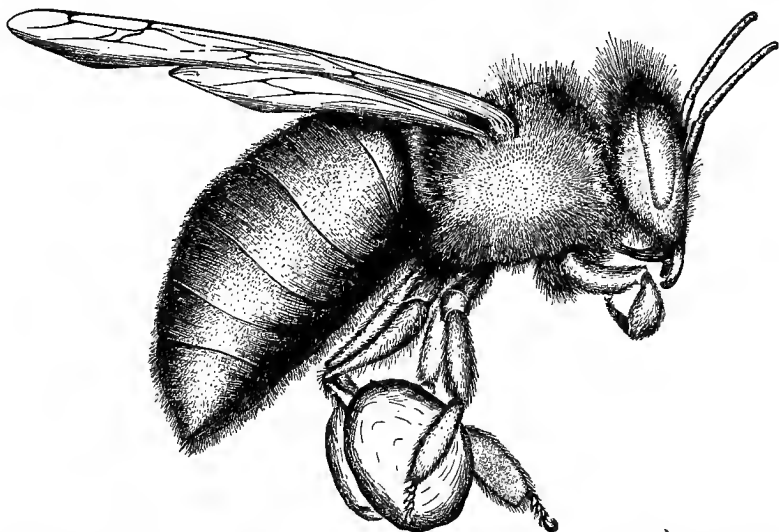


FIG. 6.—A bee upon the wing, showing the position of the middle legs when they touch and pat down the pollen masses. A very slight amount of pollen reaches the corbiculæ through this movement. (Original.)

hind legs. To accomplish this a middle leg is placed between the plantæ of the two hind legs, which are brought together so as to grasp the brush of the middle leg, pressing it closely between them, but allowing it to be drawn toward the body between the pollen combs of the two hind legs. (See fig. 5.) This action results in the transference of the pollen from the middle-leg brush to the pollen combs of the hind leg of the opposite side, since the combs of that leg scrape over the pollen-laden brush of the middle leg. This action may take place while the bee is on the wing or before it leaves the flower.

The middle legs place a relatively small amount of pollen directly upon the pollen masses in the corbiculæ. This is accomplished when the brushes of the middle legs are used to pat down the pollen masses and to render them more compact. (See fig. 6.) The legs are used

for this purpose quite often during the process of loading the baskets, and a small amount of pollen is incidentally added to the masses when the brushes come into contact with them. A misinterpretation of this action has led some observers into the erroneous belief that all or nearly all of the corbicular pollen is scraped from the middle-leg brushes by the hairs which fringe the sides of the baskets. The middle legs do not scrape across the baskets, but merely pat downward upon the pollen which is there accumulating.

It is also possible that, in transferring pollen from the middle leg of one side to the planta of the opposite hind leg, the middle-leg brush may touch and rub over the pecten of the hind leg and thus directly place some of its pollen behind the pecten spines. Such a result is, however, very doubtful.

ACTION OF THE HIND LEGS.

The middle legs contribute the major portion of the pollen which reaches the hind legs, and all of it in cases where all of the pollen first reaches the bee in the region of the mouth. However, when much pollen falls upon the body of the bee the hind legs collect a little of it directly, for it falls upon their brushes and is collected upon them when these legs execute cleansing movements to remove it from the ventral surface and sides of the abdomen. All of the pollen which reaches the corbiculae, with the exception of the small amount placed there by the middle legs when they pat down the pollen masses, passes first to the pollen combs of the plantae.

When in the act of loading pollen from the plantar brushes to the corbiculae the two hind legs hang beneath the abdomen with the tibio-femoral joints well drawn up toward the body. (See fig. 7.) The two plantae lie close together with their inner surfaces nearly parallel to each other, but not quite, since they diverge slightly at their distal ends. The pollen combs of one leg are in contact with the pecten comb of the opposite leg. If pollen is to be transferred from the right planta to the left basket, the right planta is drawn upward in such a manner that the pollen combs of the right leg scrape over the pecten spines of the left. By this action some of the pollen is removed from the right plantar combs and is caught upon the outer surfaces of the pecten spines of the left leg.

This pollen now lies against the pecten and upon the flattened distal end of the left tibia. At this moment the planta of the left leg is flexed slightly, thus elevating the auricle and bringing the auricular surface into contact with the pollen which the pecten has just received. By this action the pollen is squeezed between the end of the tibia and the surface of the auricle and is forced upward against the distal end of the tibia and on outward into contact with the pollen mass accumulating in the corbicula. As this act, by which the left

basket receives a small contribution of pollen, is being completed, the right leg is lowered and the pecten of this leg is brought into contact with the pollen combs of the left planta, over which they scrape as the left leg is raised, thus depositing pollen upon the lateral surfaces of the pecten spines of the right leg. (See fig. 7.)

Right and left baskets thus receive alternately successive contributions of pollen from the planta of the opposite leg. These loading movements are executed with great rapidity, the legs rising and falling with a pump-like motion. A very small amount of pollen is loaded at each stroke and many strokes are required to load the baskets completely.

If one attempts to obtain, from the literature of apiculture and zoology, a knowledge of the method by which the pollen baskets



FIG. 7.—A bee upon the wing, showing the manner in which the hind legs are held during the basket-loading process. Pollen is being scraped by the pecten spines of the right leg from the pollen combs of the left hind planta. (Original.)

themselves are loaded, he is immediately confused by the diversity of the accounts available. The average textbook of zoology follows closely Cheshire's (1886) description in which he says that "the legs are crossed, and the metatarsus naturally scrapes its comb face on the upper edge of the opposite tibia in the direction from the base of the combs toward their tips. These upper hairs * * * are nearly straight, and pass between the comb teeth. The pollen, as removed, is caught by the bent-over hairs, and secured. Each scrape adds to the mass, until the face of the joint is more than covered, and the hairs just embrace the pellet." Franz (1906) states that (translated) "the final loading of the baskets is accomplished by the crossing over of the hind-tarsal segments, which rub and press upon each other." Many other observers and textbook writers evidently believed that the hind legs were crossed in the loading process.

On the other hand, it is believed by some that the middle legs are directly instrumental in filling the baskets. This method is indicated in the following quotation from Fleischmann and Zander (1910) (translated):

The second pair of legs transfer the pollen to the hind legs, where it is heaped up in the pollen masses. The tibia of each hind leg is depressed on its outer side, and upon the edges of this depression stand two rows of stiff hairs which are bent over the groove. The brushes of the middle pair of legs rub over these hairs, liberating the pollen, which drops into the baskets.

A suggestion of the true method is given by Hommell (1906), though his statements are somewhat indefinite. After describing the method by which pollen is collected, moistened, and passed to the middle legs he states that (translated) "the middle legs place their loads upon the pollen combs of the hind legs. There the sticky pollen is kneaded and is pushed across the pincher (*à travers la pince*), is broken up into little masses and accumulates within the corbicula. In accomplishing this, the legs cross and it is the tarsus of the right leg which pushes the pollen across the pincher of the left, and reciprocally. The middle legs never function directly in loading the baskets, though from time to time their sensitive extremities touch the accumulated mass, for the sake of giving assurance of its position and size."

The recent valuable papers of Sladen (1911, 1912, *a, b, c, d, and e*), who was the first to present a true explanation of the function of the abdominal scent gland of the bee, give accounts of the process by which the pollen baskets are charged, which are in close accord with the writer's ideas on this subject. It is a pleasure to be able to confirm most of Sladen's observations and conclusions, and weight is added to the probable correctness of the two descriptions and interpretations of this process by the fact that the writer's studies and the conclusion based upon them were made prior to the appearance of Sladen's papers and quite independent of them. His description of the basket-loading process itself is so similar to the writer's own that a complete quotation from him is unnecessary. A few differences of opinion will, however, be noted while discussing some of the movements which the process involves. As will later be noted, our ideas regarding the question of pollen moistening, collecting, and transference are somewhat different.

ADDITIONAL DETAILS OF THE BASKET-LOADING PROCESS.

The point at which pollen enters the basket can best be determined by examining the corbiculae of a bee shortly after it has reached a flower and before much pollen has been collected. Within each pollen basket of such a bee is found a small mass of pollen, which lies

along the lower or distal margin of the basket. (See fig 8, *a*.) It is in this position because it has been scraped from the planta of the opposite leg by the pecten comb and has been pushed upward past the entrance of the basket by the continued addition of more from below, propelled by the successive strokes of the auricle. Closer

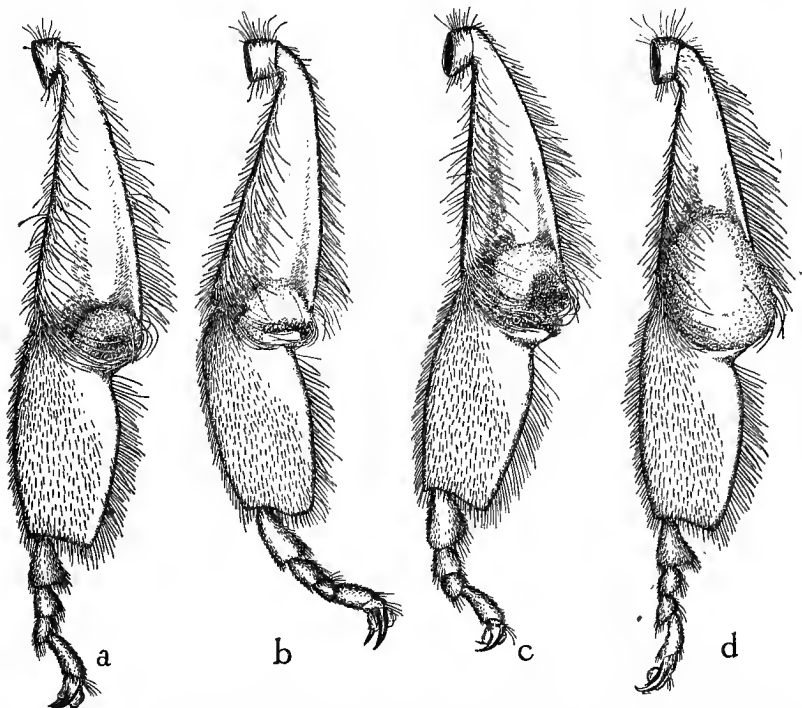


FIG. 8.—Camera drawings of the left hind legs of worker bees to show the manner in which pollen enters the basket. *a*, Shows a leg taken from a bee which is just beginning to collect. It had crawled over a few flowers and had flown in the air about five seconds at the time of capture. The pollen mass lies at the entrance of the basket, covering over the fine hairs which lie along this margin and the seven or eight short stiff spines which spring from the floor of the corbicula immediately above its lower edge. As yet the pollen has not come in contact with the one long hair which rises from the floor and arches over the entrance. The planta is extended, thus lowering the auricle; *b*, represents a slightly later stage, showing the increase of pollen. The planta is flexed, raising the auricle. The hairs which extend outward and upward from the lateral edge of the auricle press upon the lower and outer surface of the small pollen mass, retaining it and guiding it upward into the basket; *c*, *d*, represent slightly later stages in the successive processes by which additional pollen enters the basket. (Original.)

examination of the region between the pecten and the floor of the basket itself shows more pollen, which is on its way to join that already squeezed into the basket.

If the collecting bee is watched for a few moments the increase will readily be noted and the fact will be established that the accumulating mass is gradually working upward or proximally from the lower

or distal edge of the corbicula and is slowly covering the floor of this receptacle. (See fig. 8, *b*, *c*, and *d*.) In many instances the successive contributions remain for a time fairly separate, the whole mass being marked by furrows transverse to the long axis of the tibia.

Sladen (1912, *b*) notes the interesting fact that in those rather exceptional cases when a bee gathers pollen from more than one species of flowers the resulting mass within the corbicula will show a stratification parallel to the distal end, a condition which could result only from the method of loading here indicated.

As the pollen within the basket increases in amount it bulges outward, and projects downward below the lower edge of the basket. It is held in position by the long hairs which fringe the lateral sides of the basket, and its shape is largely determined by the form of these hairs and the direction in which they extend. When the basket is fully loaded the mass of pollen extends laterally on both sides of the tibia, but projects much farther on the posterior side, for on this side the bounding row of hairs extends outward, while on the anterior edge the hairs are more curved, folding upward and over the basket. As the mass increases in thickness by additions from below it is held in position by these long hairs which edge the basket. They are pushed outward and many of them become partly embedded in the pollen as it is pushed up from below. When the pollen grains are small and the whole mass is well moistened the marks made by some of the hairs will be seen on the sides of the load. (See fig. 9, *a*.) These scratches are also transverse in direction and they show that the mass has been increased by additions of pollen pushed up from below.

Even a superficial examination of a heavily laden basket shows the fallacy of the supposition that the long lateral fringing hairs are used to comb out the pollen from the brushes of either the hind or middle legs by the crossing of these legs over the lateral edges of the baskets. They are far from sufficiently stiff to serve this purpose, and their position with relation to the completed load shows conclusively that they could not be used in the final stages of the loading process, for the pollen mass has completely covered many of them and its outer surface extends far beyond their ends. They serve merely to hold the pollen in place and to allow the load to project beyond the margins of the tibia.

The auricle plays a very essential part in the process of loading the basket. This structure comprises the whole of the flattened proximal surface of the planta, except the joint of articulation itself, and it extends outward in a posterior direction a little beyond the remaining plantar edge. The surface of the auricle is covered over with many blunt, short spines and its lateral margin is bounded by a row of short rather pliable hairs, branched at their ends. When

the planta is flexed the auricle is raised and its surface approaches the distal end of the tibia, its inner edge slipping up along the pecten spines and its outer hairy edge projecting into the opening which leads to the pollen basket. (See fig. 8, *b*.) With each upward stroke of the auricle small masses of pollen which have been scraped from the plantar combs by the pecten are caught and compressed between the spiny surface of the auricle and the surface of the tibia above it. The pressure thus exerted forces the pasty pollen outward and upward, since it can not escape past the base of the pecten, and directs it into the entrance to the corbicula. The outward and upward slant of the auricular surface and the projecting hairs with which the outer edge of the auricle is supplied also aid in directing the pollen toward the basket. Sladen (1911) states that in this movement the weak wing of the auricle is forced backward, and thus allows the escape of pollen toward the basket entrance, but this appears both doubtful and unnecessary, since the angle of inclination of the auricular surface gives the pollen a natural outlet in the proper direction.

If the corbicula already contains a considerable amount of pollen the contributions which are added to it at each stroke of the auricle come in contact with that already deposited and form a part of this mass, which increases in amount by continued additions from below. If, however, the corbicula is empty and the process of loading is just beginning, the first small bits of pollen which enter the basket must be retained upon the floor of the chamber until a sufficient amount has accumulated to allow the long overcurving hairs to offer it effective support. The sticky consistency of the pollen renders it likely to retain contact with the basket, and certain structures near the entrance give additional support. Several small sharp spines, seven or eight in number, spring from the floor of the basket immediately within the entrance, and the entire lower edge of the corbicula is fringed with very small hairs which are branched at their ends. (See fig. 3.) One large hair also springs from the floor of the basket, somewhat back from the entrance, which may aid in holding the pollen, but it can not function in this manner until a considerable amount has been collected.

As the pollen mass increases in size and hangs downward and backward over the pecten and auricle it shows upon its inner and lower surface a deep groove which runs outward from the entrance to the basket. (See fig. 9, *b*.) This groove results from the continued impact of the outer end of the auricle upon the pollen mass. At each upward stroke of the auricle its outer point comes in contact with the stored pollen as soon as the mass begins to bulge backward from the basket.

Although the process is a rather delicate one, it is entirely possible so to manipulate the hind legs of a recently killed bee that the

corbiculæ of the two legs receive loads of pollen in a manner similar to that above described. To accomplish this successfully the operator must keep the combs of the plantæ well supplied with moistened pollen. If the foot of first one leg and then the other is grasped with forceps and so guided that the pollen combs of one leg rasp over the pecten spines of the other, the pollen from the combs will be transferred to the corbiculæ. To continue the loading process in a

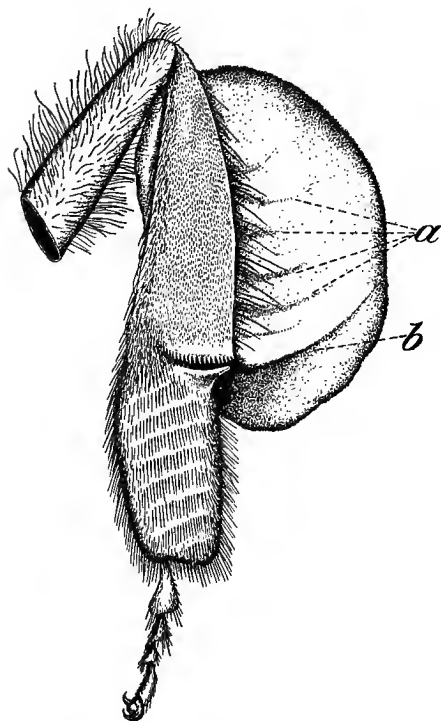


FIG. 9.—Inner surface of the right hind leg of a worker bee which bears a complete load of pollen. *a*, Scratches in the pollen mass caused by the pressure of the long projecting hairs of the basket upon the pollen mass as it has been pushed up from below; *b*, groove in the pollen mass made by the strokes of the auricle as the mass projects outward and backward from the basket. (Original.)

proper manner, it is also necessary to flex the planta of each leg just after the pollen combs of the opposite leg have deposited pollen behind the pecten. By this action the auricle is raised, compressing the pollen which the pecten has secured, and forcing some upward into the corbicula. Bees' legs which have been loaded in this artificial manner show pollen masses in their corbiculæ which are entirely similar in appearance to those formed by the labors of the living bee. Moreover, by the above method of manipulation the pollen appears first at the bottom of the basket, along its lower margin, gradually extends upward along the floor of the chamber, comes in contact with the overhanging hairs, and is shaped by them in a natural manner. All attempts to load the baskets by other movements, such as

crossing the hind legs and scraping the plantar combs over the lateral edges of the baskets, give results which are entirely different from those achieved by the living bee.

POLLEN MOISTENING.

Many descriptions have been written by others of the method by which pollen is gathered and moistened. Some of these are indefinite, some are incorrect, while others are, in part, at least, similar

to my own interpretation of this process. A few citations will here be given:

The bee first strokes the head and the proboscis with the brushes of the forelegs and moistens these brushes with a little honey from the proboscis, so that with later strokes all of the pollen from the head is collected upon these brushes. Then the middle-leg brushes remove this honey-moistened pollen from the forelegs and they also collect pollen from the breast and the sides of the thorax.—[Translation from Alefeld, 1861.]

In his account of the basket-loading process Alefeld assigns to the middle-leg brushes the function of assembling all of the pollen, even that from the plantar combs, and of placing it on the corbiculae, this latter act being accomplished by combing over the hairy edge of each basket with the middle-leg brush of the same side.

It appears probable that the bee removes the pollen from the head, breast, and abdomen by means of the hairy brushes which are located upon the medial sides of the tarsal segments of all of the legs, being most pronounced upon the hind legs. The pollen is thus brought together and is carried forward to the mouth, where it is moistened with saliva and a little honey.—[Translation from Franz, 1906.]

Franz then says that this moistened pollen is passed backward and loaded.

Since the pollen of many plants is sticky and moist it adheres to the surface of the basket. Dry pollen is moistened by saliva, so that it also sticks.—[Translation from Fleischmann and Zander, 1910.]

Pollen is taken from flowers principally by means of the tongue, but at times, also, by the mandibles, by the forelegs, and middle legs. The brushes of the hind legs also load themselves, collecting from the hairs of the body. The pollen dust thus gathered is always transmitted to the mouth, where it is mixed with saliva.—[Translation from Hommel, 1906.]

Sladen considers the question of how pollen is moistened by the honey bee, humblebee (bumblebee), and some other bees, but does not appear to reach definite conclusions. In one of his papers (1912, *c*) he states that the pollen of some plants may be found in the mouth cavity and in the region of the mouth, but he reaches the conclusion that this pollen is comparatively "dry," using the word in a "relative sense." He asserts that "nowhere but on the corbicula and hind metatarsal brushes did I find the sticky pollen, except sometimes on the tips of the long, branched hairs on the back (upper) edges of the tibiae and femora of the middle legs, and then only in heavily laden bees, where it is reasonable to suppose it had collected accidentally as the result of contact with the hind metatarsal brushes."

These and other considerations lead Sladen to think that, in the case of the bumblebee at least, the pollen "may be moistened on the hind metatarsus with the tongue." He states that the tongue of the bumblebee is of sufficient length to reach the hind metatarsus

(planta) and that it might rub over the brushes of the metatarsi or be caught between them when they are approximated and thus moisten the two brushes simultaneously. However, he has never seen the tongue of the collecting honey bee brought near to the hind legs, and it appears probable to him that it can not easily reach them. "Possibly the middle or front legs are used as agents for conveying the honey" (in the case of the honey bee). "In the humblebee the tongue is longer, and it could more easily moisten the hind legs in the way suggested."

In an earlier paper Sladen (1912, *a*) gives the following as his opinion of the "way in which pollen dust is moistened with nectar," although he states that this is one of the points "which still remains obscure":

The only satisfactory manner in which, it seems to me, this can be done is for the tongue to lick the tarsi or metatarsi of the forelegs, which are covered with stiff bristles, well suited for holding the nectar, the nectar being then transferred to the metatarsal brushes on the middle legs, and from these, again, to the metatarsal brushes on the hind legs. The latter being thus rendered sticky, the pollen dust would cling to them. The different pairs of legs were certainly brought together occasionally, but not after every scrape of the hind metatarsi, and their movements were so quick that it was impossible to see what was done. Still, several pollen-collecting bees that I killed had the tarsi and metatarsi of the forelegs and the metatarsal brushes of the middle and hind legs moistened with nectar, and I think it probable that the moistening process, as outlined, is performed, as a rule, during the flight from flower to flower.

Sladen (1912, *c*) also considers the possibility that the fluid which moistens the pollen might be secreted through the comb at the end of the tibia, through the tibio-tarsal joint, or from the surface of the auricle, but finds no evidence of glandular openings in these regions. A suggestion of a similar nature, apparently unknown to Sladen, was made by Wolff (1873), who describes "sweat-glands" which, he claims, are located within the hind tibia and the planta, and which pour a secretion upon the surface of the corbicula and upon the upper end of the planta through many minute openings located at the bases of hairs, particularly those which arise from the lateral margins of the corbicula. Wolff is convinced that the fluid thus secreted is the essential cohesive material by which the grains of pollen are bound together to form the solid mass which fills each fully loaded basket. He noticed that the mouthparts are used to collect pollen, and that some of it is moistened with "honey" or "nectar," but he does not consider that the fluid thus supplied is sufficient to explain adequately the facility with which the collecting bee brings together the scattered grains of pollen and packs them away securely in the baskets. Wolff's description of the basket-loading process itself is strikingly similar to that advocated later by Cheshire.

The writer is not prepared to deny the possibility that the surface of the chitin of the hind legs of worker bees may be moistened by the secretion of glands which lie beneath it, but he is convinced that any fluid thus secreted bears little or no relation to the cohesion of the pollen grains within the baskets. Sections and dissected preparations of the hind legs of worker bees show certain large cells which lie within the cavity of the leg and which may function as secreting gland cells; but similar structures occur in even greater numbers within the hind legs of the drone and they are found within the hind legs of the queen.

As has been noted, the extreme moisture of the plantar combs and of the tibio-tarsal articulation of the hind leg is readily understood when one recalls the manner in which moist pollen is compressed between the auricle and the tibial surface above it.

From the account already given it is evident that, in the opinion of the writer, the mouth is the source from which the pollen-moistening fluid is obtained. It is extremely difficult to determine with absolute accuracy the essential steps involved in the process of adding moisture to the pollen. In an endeavor to solve this problem the observer must of necessity consider a number of factors, among which may be noted (1) the location upon the body of the collecting bee of "moist" and of comparatively "dry" pollen, (2) the movements concerned in the pollen-gathering and pollen-transferring processes, (3) the relative moisture of those parts which handle pollen, (4) the chemical differences between the natural pollen of the flower and that of the corbiculæ and of the cells of the hive, and (5) the observer must endeavor to distinguish between essential phenomena and those which are merely incidental or accidental.

In the first place it should be noted that the relative dampness of pollen within the corbiculæ depends very largely upon the character of the flower from which the pollen grains are gathered. When little pollen is obtained it is much more thoroughly moistened, and this is particularly true in cases when the pollen is all, or nearly all, collected in the region of the mouth, the forelegs, and head. When a bee takes pollen from white or sweet clover practically all of it first touches the bee in these regions. It immediately becomes moist, and in this condition is passed backward until it rests within the baskets. There is here no question of "dry" and "wet" pollen, or of collecting movements to secure dry pollen from other regions of the body, or of the ultimate method by which such free, dry pollen becomes moist.

The sticky fluid which causes pollen grains to cohere is found upon all of the legs, in the region of their brushes, although the pollen combs and auricles of the hind legs are likely to show it in greatest abundance, since nearly all of the pollen within each basket has

passed over the auricle, has been pressed upward and squeezed between the auricle and the end of the tibia and the pollen mass above, and by this compression has lost some of its fluid, which runs down over the auricle and onto the combs of the planta. It is not necessary to invoke any special method by which these areas receive their moisture. The compressing action of the auricle squeezing heavily moistened pollen upward into the basket is entirely sufficient to account for the abundance of sticky fluid found in the neighborhood of each hind tibio-tarsal joint. As has been noted, the brushes of the forelegs acquire moisture directly by stroking over the proboscis and by handling extremely moist pollen taken from the mouthparts. The middle-leg brushes become moist by contact with the foreleg and hind-leg brushes, probably also by touching the mouthparts themselves, and by passing moist pollen backward. The hairy surface of the breast is moistened by contact with the fore and mid leg brushes and with the moist pollen which they bear.

The problem of the method of pollen moistening is somewhat more complicated in the case of flowers which furnish an excessive supply. Under such conditions the entire ventral surface of the collecting bee becomes liberally sprinkled with pollen grains which either will be removed and dropped or will be combed from the bristles and branching hairs, kneaded into masses, transferred, and loaded. The question naturally arises whether the movements here are the same as when the plant yields but a small amount of pollen which is collected by the mouthparts and anterior legs. In the opinion of the writer they are essentially the same, except for the addition of cleansing movements, executed chiefly by the middle and hind legs for the collection of pollen which has fallen upon the thorax, upon the abdomen, and upon the legs themselves. Indeed it is questionable as to just how much of this plentiful supply of free pollen is really used, in forming the corbicular masses. Without doubt much of it falls from the bee and is lost, and in cases where it is extremely abundant and the grains are very small in size an appreciable amount still remains entangled among the body-hairs when the bee returns to the hive. Yet it is also evident that some of the dry pollen is mingled with the moistened material which the mouthparts and forelegs acquire and together with this is transferred to the baskets.

In all cases the pollen-gathering process starts with moist pollen from the mouth region. This pollen is passed backward, and in its passage it imparts additional moisture to those body regions which it touches, the brushes of the fore and middle legs, the plantæ of the hind legs, and the hairs of the breast which are scraped over by the fore and middle leg brushes. This moist pollen, in its passage backward, may also pick up and add to itself grains of dry pollen with which it accidentally comes in contact. Some of the free, dry pollen

which falls upon the moist brushes or upon the wet hairs of the thorax is also dampened. Some of the dry pollen which is cleaned from the body by the action of all of the legs meets with the wet brushes or with the little masses of wet pollen and itself becomes wet by contact. Pollen grains which reach the corbiculæ either dry or but slightly moistened are soon rendered moist by contact with those already deposited. Little pollen gets by the sticky surfaces of the combs of the plantæ or past the auricles without becoming thoroughly moist.

Sladen (1912, *c*) very aptly compares the mixture of dry pollen with wet to the kneading of wet dough with dry flour and suggests that the addition of dry pollen may be of considerable advantage, since otherwise the brushes, particularly those of the hind legs, would become sticky, "just as the board and rolling pin get sticky in working up a ball of dough if one does not add flour." The addition of a considerable amount of dry pollen gives exactly this result, for the corbiculæ then rapidly become loaded with pollen mixed with a minimum supply of moisture and the brushes remain much dryer than would otherwise be the case. However, if too much dry pollen is added the resulting loads which the bees carry back to the hives are likely to be irregular, for the projecting edges of the masses may crumble through lack of a sufficient amount of the cohesive material by which the grains are bound together.

On the other hand, it does not appear at all necessary to mix much dry pollen with the wet, nor do the brushes become sufficiently "sticky" from the presence of an abundance of the moistening fluid to endanger their normal functional activity. I have observed bees bringing in pollen masses which were fairly liquid with moisture, and the pollen combs also were covered with fluid, yet the baskets were fully and symmetrically loaded.

Sladen's different interpretations of the pollen-moistening process are rather confusing, and it is difficult to distinguish between what he states as observed facts and what he puts forward as likely hypotheses. He agrees with me in his observation that all of the legs become moist in the region of their brushes and also in his supposition that this moisture is transferred to them from the mouth. In this moistening process my observations show that the fluid concerned is passed backward by the contact of the middle-leg brushes with the wet foreleg brushes and that the middle-leg brushes in turn convey moisture to the plantæ as they rub upon them. I am also convinced that the wet pollen grains furnish additional moisture to the brushes as they pass backward, and this is particularly true in the case of the extremely moist surfaces of the auricles and the pollen combs of the planta, since here moisture is pressed from the pollen upon these areas. The pollen upon the fore and middle leg brushes is not always "dry" even in "a relative sense."

In describing pollen manipulation several writers state that dry pollen is picked up by the brushes of the legs and is carried forward to the mouth, there moistened (according to some, masticated), and is then carried backward by the middle legs for loading. Obviously such accounts do not apply to cases in which all of the pollen is collected by mouthparts and forelegs. Do they apply in cases where much pollen falls on the body and limbs? Without doubt a certain amount of this free pollen is brought forward when the middle legs, bearing some of it, sweep forward and downward over the forelegs, mouthparts, and breast. However, it does not appear to the writer that this dry pollen is carried to the mouth for the specific purpose of moistening it, or that it is essential to its moistening that it be brought in contact with the mouth. Some of it touches the moist hairs on the forelegs and breast and is moistened by contact. All that remains on the brushes of the middle legs secures moisture from these brushes or from wet pollen which the brushes collect from the mouthparts or forelegs. The supposed necessity of carrying forward pollen to the mouth for moistening is a delusion. Some is accidentally brought forward and into contact with the mouth and gets wet, but the process is not essential.

If the pollen which bees transport to their hives has been moistened with some fluid substance which causes the grains to cohere, this addition should be indicated by differences in the results of an analysis of pollen from a plant as compared with that found in the corbiculæ of a bee which has been working on this plant. For the sake of determining this difference and in an endeavor to ascertain, if possible, the approximate nature of the added fluid, analyses were made of three kinds of pollen, as follows: (1) Pollen collected by hand from the corn plant itself; (2) pollen taken from the corbiculæ of bees which had secured their supply from corn; (3) pollen stored in the cells of the hive. In the first two cases pollen from the same species of plant (corn) was used. The material from the cells of the hive was composed largely of corn pollen, but contained an admixture of some other pollens.

The writer is indebted to Dr. P. B. Dunbar, of the Bureau of Chemistry, for the following analyses:

	Pollen direct from corn.	Corn pollen from corbicula.	Stored pollen from hive.
Total solids.....	53.47	66.94	79.66
Moisture.....	46.53	33.06	20.34
Reducing sugar before inversion.....	2.87	11.07	17.90
Sucrose.....	2.77	3.06	2.25
Total reducing sugar after inversion.....	5.79	14.29	20.27
Dry basis:			
Reducing sugar.....	5.37	16.54	22.47
Sucrose.....	5.18	4.57	2.82
	10.55	21.11

These analyses show conclusively that a very large amount of sugar has been added to the pollen by the time it reaches the corbiculæ. Calculated on a dry basis just about twice as much sugar is present in the basket pollen as in that from the corn plant. Not only is this so, but the additional fact is disclosed that over three times as much reducing sugar is present in the corbicular pollen as sucrose. This latter result indicates that honey (largely a reducing sugar) rather than nectar (containing more sucrose) is the chief sugar ingredient of the corbicular pollen. The additional amount of sugar (here again a reducing sugar) in the stored pollen of the hive is what might be expected, since it is supposed that the workers add honey and possibly other ingredients to the pollen within the storage cells.

The total solid percentages, corn 53.47, corbicula 66.94, stored pollen 79.66, also show that the fluid substance which is added is one highly charged with solids, a condition which honey amply fulfills.

In the descriptions which have been cited of the pollen-gathering process in which the mouth is supposed to supply the requisite fluid three substances are mentioned: Nectar, honey, and saliva. The analyses herein given indicate that reducing sugar is mingled with the pollen, and in the case of corn it is indicated that honey is used in greater abundance. Without doubt a certain amount of saliva also finds its way to the pollen, but the proportion of this substance has not been determined. This salivary fluid may have adhesive qualities, but this is scarcely necessary, since honey alone is amply sufficient for this purpose.

It appears probable that the fluid which a bee adds to the pollen which it is collecting varies somewhat in amount, since the pollen of different plants differs considerably in moisture content and that of the same plant will differ in this respect at different times. Pollen collected in the early morning before the dew has left the plant is much more moist than that found upon the same plant later in the day, and the grains, if taken when moist, have a natural tendency to become aggregated and form small masses. Moreover, this may explain the fact that bees make their pollen-collecting trips during the morning hours, rather than in the afternoon, although some may be seen upon the flowers throughout the whole day.

STORING POLLEN IN THE HIVE.

When the bee has fully loaded its baskets and before it returns to the hive it often spends a little time upon the plant from which it has been collecting, occupied with the task of cleaning scattered grains of pollen from its body and of patting down securely the loads which it has obtained. Upon its return to the hive it hurries within and seeks for a suitable place in which to deposit the pollen. Some

returning bees walk leisurely over the combs and loiter among their sister workers, while others appear to be greatly agitated, shaking their bodies and moving their wings as though highly excited. Many pollen-bearing bees appear eager to receive food upon their return to the hive, and they will solicit it from other workers or take it from the honey-storage cells. The workers of the hive at times take a little of the fresh pollen from the baskets of the laden bee, nibbling it off with their mandibles or rasping off grains with their tongues.

If the combs of a colony are examined, stored pollen will be found in various parts of the hive. In the brood frames the greatest amount is located above and at the sides of the brood and between this and the stored honey. Cells scattered through the brood from which young bees have lately emerged may also contain pollen. In the outer frames of the hive, where brood is less likely to be found, nearly all of the cells may be packed with pollen, or honey-storage cells may be found interspersed with those filled with pollen. As a rule pollen is not stored in drone comb, although this occasionally happens.

As the pollen-bearing bee crawls over the combs it appears to be searching for a suitable cell in which to leave its load. It sticks the head into cell after cell until finally one is located which meets its requirements, although it is an open question as to why any one of a group should be chosen rather than another. This selected cell may already contain some pollen or it may be empty. If partly filled, the pollen which it contains is likely to be from the same species of plant as that which the bee carries, although different kinds of pollen are often stored in the same cell.

In preparation for the act of unloading the bee grasps one edge of the cell with its forelegs and arches its abdomen so that the posterior end of the abdomen rests upon the opposite side of the cell. The body is thus held firmly and is braced by these two supports with the head and anterior thoracic region projecting over one of the neighboring cells. The hind legs are thrust down into the cell and hang freely within it, the pollen masses being held on a level with the outer edge of the cell, or slightly above it. The middle leg of each side is raised and its planta is brought into contact with the upper (proximal) end of the tibia of the same side and with the pollen mass. The middle leg now presses downward upon the pollen mass, working in between it and the corbicular surface, so that the mass is shoved outward and downward and falls into the cell. As the pollen masses drop, the middle legs are raised and their claws find support upon the edge of the cell. The hind legs now execute cleansing movements to remove small bits of pollen which still cling to the corbicular

surfaces and hairs. After this is accomplished the bee usually leaves the cell without paying further attention to the two pellets of pollen although some collecting bees will stick the head into the cell, possibly to assure themselves that the pollen is properly deposited. It has been stated by some (Cheshire, for example) that the spur upon the middle leg is used to help pry the pollen mass from the corbicula. This structure is in close proximity with the mass while the middle leg is pushing downward upon it, but its small size renders difficult an exact estimate of its value in this connection. It is certainly true that the entire planta of the middle leg is thrust beneath the upper end of the pollen mass, but the spur may be used as an entering wedge.

Pollen masses which have been dropped by the collecting bee may remain for some time within the cell without further treatment, but usually another worker attends to the packing of the pollen shortly after it has been deposited. To accomplish this the worker enters the cell head first, seizes the pollen pellets with its mandibles, breaks them up somewhat or flattens them out, probably mingles additional fluid with the pollen, and tamps down the mass securely in the bottom of the cell. As is shown by the analyses of corbicular pollen and of stored pollen, certain substances are added to the pollen after the collecting bee leaves it in the cell. Sugar is certainly added, and it is generally supposed that secretions from some of the salivary glands are mixed with the pollen after deposition. It appears probable that the stored pollen or "beebread" is changed somewhat in chemical composition through the action of the fluids which have been added to it, either during the process of collection, at the time of packing, or later.

SUMMARY.

Pollen may be collected by the worker bee upon its mouthparts, upon the brushes of its legs, and upon the hairy surface of its body. When the bee collects from small flowers, or when the supply is not abundant, the mouthparts are chiefly instrumental in obtaining the pollen.

The specialized leg brushes of the worker are used to assemble the pollen, collecting it from the body parts to which it first adheres and transporting it to the pollen baskets or corbiculae of the hind legs. In this manipulation the forelegs gather pollen from the mouthparts and head; the middle legs, from the forelegs and from the thorax; the hind legs, from the middle legs and from the abdomen.

The pollen baskets are not loaded by the crossing over of one hind leg upon the other or to any great extent by the crossing of the middle legs over the corbiculae. The middle legs deposit their loads upon the

pollen combs of the hind plantæ, and the plantæ, in turn, transfer the pollen of one leg to the pecten comb of the other, the pecten of one leg scraping downward over the pollen comb of the opposite leg. (See fig. 7.) A little pollen is loaded directly from the middle legs into the baskets when these legs are used to pat down the pollen masses. (See fig. 6.)

Aside from the foregoing exception, all of the pollen which reaches the baskets enters them from below, since it is first secured by the pecten combs, and is then pushed upward by the impact of the rising auricles, which squeeze it against the distal ends of the tibiæ and force it on into the baskets to meet that which has gone before.

The long hairs which form the lateral boundaries of the baskets are not used to comb out pollen from the brushes of any of the legs. They serve to retain the accumulating masses within the baskets and to support the weight of the pollen, as it projects far beyond the surfaces of the tibiæ.

Pollen grains are moistened and rendered cohesive by the addition to them of fluid substances which come from the mouth. Analyses show that honey forms a large part of this moistening fluid, although nectar and secretions from the salivary glands are probably present also.

In the process of pollen manipulation this fluid substance becomes well distributed over the brushes of all of the legs. The forelegs acquire moisture by brushing over the mouthparts, and they transfer this to the hairs of the breast and to the middle-leg brushes when they come in contact with them. The middle-leg brushes transmit their moisture to the pollen combs of the hind legs when they rub upon them. All of these brushes also transport wet pollen which has come from the mouthparts and thereby acquire additional moisture. The auricles and the plantæ of the hind legs become particularly wet from this source, since fluid is squeezed from the wet pollen when it is compressed between the auricles and the distal ends of the tibiæ. Dry pollen which falls upon the body hairs becomes moist when brought into contact with the wet brushes or with wet pollen.

During the process of manipulation pollen passes backward from its point of contact with the bee toward its resting place within the baskets.

Pollen which the collecting bee carries to the hive is deposited by this bee within one of the cells of the comb. As a rule, this pollen is securely packed in the cell by some other worker, which flattens out the rounded masses and adds more fluid to them.

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THE MANIPULATION OF THE WAX
SCALES OF THE HONEY BEE.

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II

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INTRODUCTION.

The particular form of bee activity with which this paper deals is that which results in the removal of the wax scales from the bodies of the worker bees and in the application to the comb of the wax thus obtained. A detailed presentation of the facts will be given and attention called to certain current conceptions of this process which are in error.

Since the bee is a very lively insect it is not surprising that the bodily movements upon which some of its activities depend are extremely difficult to follow and may easily be misunderstood. All of its highly specialized legs may be used at once in the performance of some intricate process, and the observer is in need of keenness of sight and patience if he would gain more than an approximate understanding of the parts taken by the several members.

In the more permanent literature of apiculture and of zoology will be found well-written accounts of the habits of bees, accounts which are founded upon a large amount of careful observation and which represent the work of many students of bees from the time of Huber on. As the years have gone by, errors of sight and of judgment have gradually been eliminated, so that at the present time our knowledge of bee life, so far as it goes, rests upon a fairly satisfactory foundation of authenticated facts. Yet many puzzling questions are still unanswered, and some supposed facts may still be doubted.

An examination of a number of bees from an active colony will show great variation in the appearance of the wax scales of differ-

ent members of the colony. In some cases no scales can be observed, even upon dissection. In others the scales will be found to be extremely thick and completely filling the wax pockets. Some bees will show scales in two or three pockets and none in others. Many of the workers will possess a complete supply of scales, either all of about the same thickness or varying considerably in thickness. These and other diverse conditions present themselves for explanation.

The present account is particularly concerned with the manipulation of the wax scales. By what process or series of processes are the scales of wax removed from their pockets and added to the comb? That the wax which forms the comb is produced by the bees themselves, being elaborated within their bodies and given out in the form of thin plates or scales, is a fact well known to all students of bees; but many differences of opinion have been expressed concerning the exact method of wax manipulation. It is also well known that the workers of the hive perform many duties—building the comb, gathering the stores of pollen and honey, caring for the brood and the queen, repairing, cleaning, ventilating, and guarding the hive—and it has been fairly well established that in some cases, at least, these duties vary with the age of the individual worker, although more accurate information on this point is much to be desired. Dreyling's¹ results, in particular, indicate that bees of certain ages are incapable of producing wax, since their glands are either undeveloped or atrophied. Do these bees use the wax secreted by others, taking it from them, manipulating it, and forming it into comb? By careful observation bees devoid of wax scales or with scales too thin for satisfactory removal may be discovered working with the wax. Do these bees procure their wax from other workers, or are they merely reworking the wax of the comb? Upon each hind leg of a worker bee is located a peculiar pincers-like structure long known as the wax shears. Do bees really use this instrument in extracting the scales from the pockets, and if so, does the owner of the scale perform this operation, or is the scale removed by another worker? Or may it not be that the wax scales drop from their pockets when they reach a suitable thickness, and are salvaged by other workers and added to the comb? All of the above interpretations of these processes have been advanced by various observers. It is the object of this paper to present a true account of the manner in which the scales of wax are transported from their pockets to the comb and to point out some of the causes which lead to diversity in scale number and scale form.

¹ Dreyling, L. 1903. Ueber die wachbereitenden Organe der Honigbiene. Zoologischer Anzeiger, Vol. 26.

Same.—1905. Die wachbereitenden Organe bei den gesellig lebenden Bienen. Zoologische Jahrbücher, Abtheilung für Anatomie u. Ontogenie d. Thiere, Vol. 22.

THE WAX-PRODUCING ORGANS.

The way in which the wax scales are formed, as secretion products arising from the surfaces of the wax plates on the ventral side of the abdomen of the workers, has been well described by others and with apparent accuracy. The accounts of Dreyling embody the results of a very considerable amount of work, and will, for the present, at least, be taken at their full value. The work of Snodgrass¹ upon the anatomy of the wax plates and wax glands may be relied upon. Only a brief statement will here be given of the structure of these organs and of the manner in which the scales are formed.

As is well known, wax is produced by the worker bees only. The location of the wax-secreting surfaces, or wax plates, may be readily determined by an examination of the ventral surface of a bee's abdomen. By stretching the abdomen somewhat it will be seen that each of the last four visible sternal or ventral plates is divided into two regions: A posterior projecting edge which is distinctly hairy, and a smooth anterior half which is usually covered by the next preceding plate. This anterior region is divided by a median ridge into two distinct, irregularly oval areas, which thus lie on either side of the midventral line. These areas are the wax plates, and upon them the wax scales are formed. Each one of the last four sternal plates bears two wax plates, making eight in all. (See fig. 1.)

The glands which secrete the wax lie on the floor of the abdomen immediately above and in contact with the wax plates, and their secretion is deposited upon the external surfaces of the plates, exuding through the many minute pores which perforate the plates. Upon coming in contact with the air the fluid wax hardens, forming a covering over the entire outer surface of the plate, which gradually increases in thickness with the continued addition of wax through the pores. In this way the wax scales are produced, and since they are

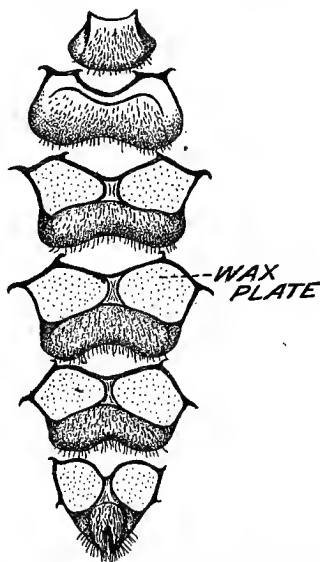


FIG. 1.—Ventral abdominal plates of a worker bee dissected to show the position of the wax plates. (Original.)

¹ Snodgrass, R. E., 1910. The Anatomy of the Honey Bee, Bur. Ent., Tech. Ser. 18, U. S. Dept. Agr.

molded upon the surfaces of the eight wax plates they correspond to them in number and in form.

In its natural position each wax scale lies between its wax plate and the overlapping edge of the next preceding sternal plate. The scale thus fits into a little crevice or wax pocket and is well protected from injury. If the bee extends its abdomen the rear edges of the scales can be seen protruding from their pockets, or if the scales become very thick they will push the covering sternal plates outward and will project from the pockets.

THE FORMATION OF THE WAX SCALES.

The problem of wax secretion has been extensively studied by Dreyling, who shows that the wax glands differ markedly in structure in bees of different ages. In the newly emerged bee the epidermis which underlies the wax plate is composed of epithelial cells nearly cubical in form. As the bee grows older these cells become elongated and are separated by clear spaces, and when the bee has reached the height of its activity as a wax producer these gland cells are elongated and show liquid wax stored in the spaces between them. When the wax-secreting period is over these cells degenerate, so that in sections through the glands of old field bees, or of bees that have lived over winter, the layer of cells beneath the wax plates appears greatly shrunken, and individual cells can be distinguished by their nuclei only. These histological data are given by Dreyling in support of the conclusion that the secretion of wax is much more abundant at a certain period in the bee's life and that old bees and very young bees are, as a rule, incapable of wax production. These conclusions are in harmony with the practical experiences of bee keepers.

METHODS OF OBSERVATION.

In a study of the behavior during scale removal and wax building it is necessary to watch the bees while they are working naturally within the hive. To accomplish this, observatory hives are used in which glass is substituted for wood in part of the construction. Most of the work is done upon colonies in modified nucleus boxes (fig. 2). The two sides are removed from each hive and are replaced with glass in the form of sliding doors, two to a side, and glass plates are fitted to the top. In all cases wooden shades cover both sides and top when the bees are not under observation. Although bees are somewhat disturbed when light is first admitted to the hive, they appear to become accustomed to it and work normally unless the hive is left open for too long a period.

When a hive is well crowded with bees, and when the frames are widely spaced, the workers are apt to extend the comb above the level of the top bars of the frames until it comes in contact with the glass. This gives the observer an excellent opportunity to study the comb

workers at close range, and it also obviates the necessity of placing glass ends in the hive against which comb might be built.

Even with the best of arrangements it is difficult to follow some of the movements of the workers during the act of scale removal. As an aid to vision a Zeiss binocular microscope is used, the tubes being removed from the stand and held to the eye after the manner of a field glass. By the use of this instrument a bee appears to acquire

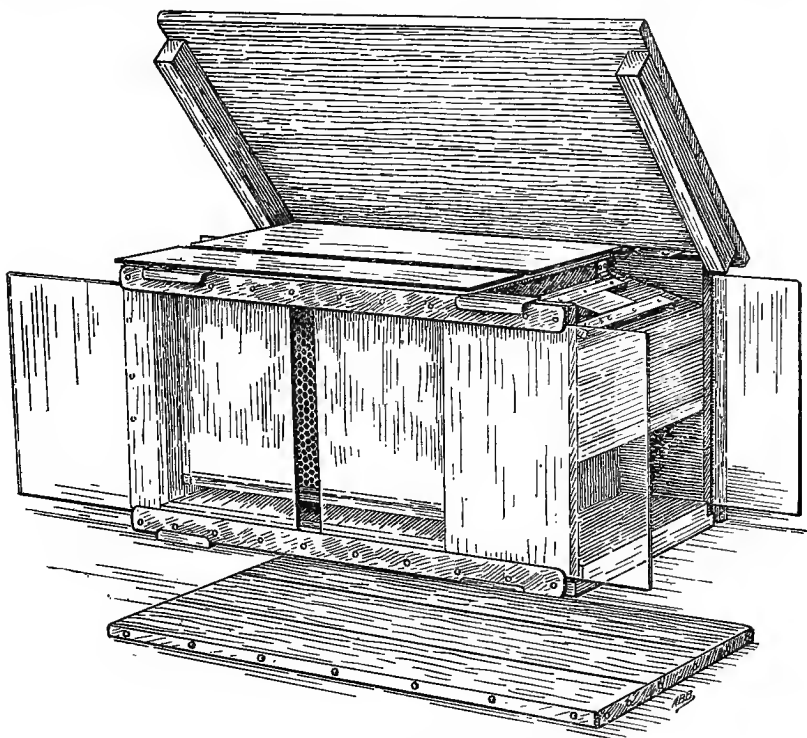


FIG. 2.—Observatory hive. The sides are fitted with sliding glass doors, and two pieces of glass cover the top. The sliding glass doors allow the observer to gain access to any small area of the outer comb without removing the glass from the entire side of the hive. Screens of wood cover the glass of the sides and top when the bees are not under observation. (Original.)

the dimensions of a large-sized rat, and the action of its legs and mandibles may be followed with great precision.

For the sake of later identification many of the bees are marked by painting different colors on their backs, and some are numbered. Such distinctive marks make it possible to follow the actions of an individual bee from day to day.

The observations here recorded were made during the summer of 1911 at the apiary of the Bureau of Entomology.

REMOVAL OF THE WAX SCALES.

The determination of the exact method by which the wax scales are removed either comes as the result of prolonged and patient

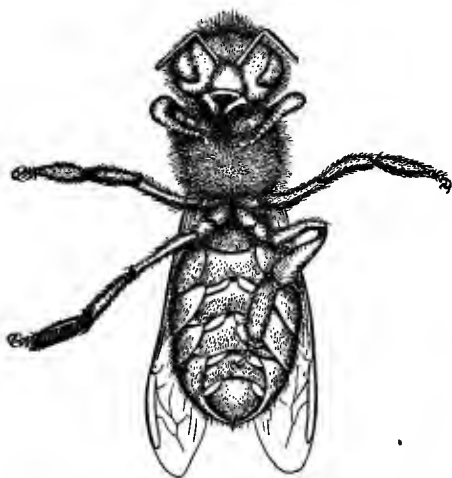


FIG. 3.—Ventral view of a worker bee in the act of removing a wax scale. The two middle legs and the right hind leg are used for support, while the left hind leg removes the scale. (Original.)

watching or is the product of good fortune. Long before the observer is able to decide upon all of the details of the process he becomes convinced that usually the scales are removed by the bee which secretes them and by this bee are masticated and added to the comb. The workers never assist each other in the process of removal, although, as will be mentioned later, free scales may, in some cases, be handled by other workers.

As a rule, the scales are removed while the bee is standing on the comb or its support, and the wax thus obtained is applied to the comb near the place where it is removed. Since the whole process of removal takes place beneath the worker's body it can be observed most satisfactorily when the bee is seen from the side or when it is building comb against a glass plate.

The posture of a bee in the act of removing a scale is rather characteristic and is at once recognized by one familiar with it. Immediately before the scale is to be removed the bee may



FIG. 4.—Side view of a worker in the same posture as that shown in figure 3. (Original.)

be busily engaged upon the surface of the comb, plying with its mandibles the wax of the scale last extracted or reshaping and polishing wax already deposited, its whole body somewhat agitated, moving

backward and forward or from side to side as it adapts its position to the work in hand. Suddenly its body becomes very quiet. The forelegs and mandibles are raised from the comb, and the head is held with the face inclined toward the comb. The hind leg of one side is now raised, and its flattened first tarsal segment or planta is slipped along the ventral surface of the extended abdomen and comes in contact with the protruding wax scales of the corresponding side (figs. 3 and 4). The weight of the bee is now supported upon three legs; upon the middle leg of the side from which the scale is to be removed and upon the middle and hind legs of the other side. The first tarsal segment of the leg which is to remove the scale is now pressed firmly against the abdomen, and the edge of a protruding scale becomes engaged with it. Steady, continuous pressure is now exerted both against the abdomen and toward the rear, with the result that the



FIG. 5.—Ventral view of a worker bee showing the position of the wax scale just before it is grasped by the forelegs and mandibles. The scale is still adhering to the spines of the pollen combs. The bee is supported upon the two middle legs and upon the hind leg which is not removing the scale. (Original.)

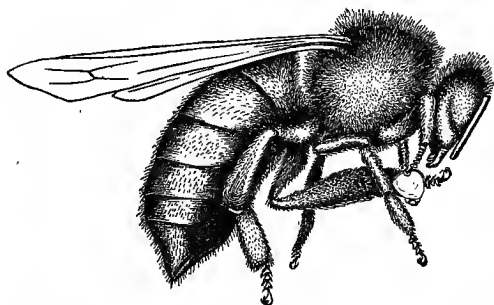


FIG. 6.—Side view of a worker bee in the same posture as that shown in figure 5. (Original.)

scale is drawn out of its pocket but remains attached to the leg which removed it. The hind leg bearing the scale is now quickly flexed toward the thorax and head, thus carrying the scale forward under the body of the bee and placing it in a position where it may be readily grasped by the forelegs

or the mandibles (figs. 5 and 6). Sometimes the scale is apparently removed from the hind leg by the mandibles alone, but usually the forelegs aid in this process and also manipulate the scale while

the mandibles are masticating it. After the scale has been thoroughly masticated the wax is applied to the comb.

THE SCALE-REMOVING ORGAN.

A point of particular interest in the process of wax scale removal is that which deals with the manner in which the scale is grasped by the hind leg which removes it. As is well known, each hind leg of the worker bee bears a pincerslike structure—the so-called wax shears—located at the juncture of the tibia and the flattened first tarsal segment or planta (fig. 7). According to the statements of numerous writers, the wax scales are grasped between the edges of the supposed pincers formed by the pecten above and the auricle below, and are either snipped off or are held by the jaws of the pincers and thus drawn from the pockets. Cowan's¹ account may be given as typical of others which are current in the literature of apiculture and of zoology.

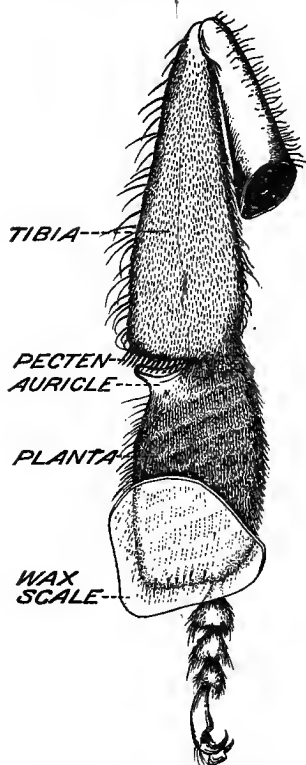


FIG. 7.—Inner surface of the left hind leg of a worker bee, showing the position of a wax scale immediately after it has been removed from the wax pocket. The scale has been pierced by seven of the spines of the pollen combs of the first tarsal segment or planta. The jaws of the so-called wax shears or pincers are formed by the pecten spines above and the surface of the auricle below. (Original.)

The articulation of the tibia and planta being at the anterior angle, and the absence of the spur on the tibia (which only the honey bee does not possess) give the pecten a freedom of action it would not otherwise have and enable it to be used together with the auricle on the planta, which is quite smooth, as a true pair of pincers, and as an instrument for laying hold of the thin flakes of wax, and for bringing them forward to be transferred by the other legs to the jaws for manipulation.

As a matter of fact, the wax shears have nothing whatever to do with the removal of the wax scales. They perform an entirely different function, being concerned with the gathering of pollen in a manner to be described in a future paper.

In coming to the above conclusions the writer was first convinced that the so-called wax shears are not used in removing scales by noting that the position of the tibio-tarsal joint at the time of scale

¹ Cowan, T. W., "The Honey Bee," 2d ed., London, 1904.

removal is such as to make it impossible for the pincerslike crevice to grasp the scale. Moreover, the open jaws of the shears point laterally and away from the scales rather than toward them, nor, indeed, is it possible for the shears to grasp even the projecting edges of any of the ventral or lateral body plates and thus steady or guide the leg as it seeks contact with the scales.

The transverse rows of spines upon the planta, called pollen combs, and not the wax shears are instrumental in the removal of scales. Snodgrass (1910), in discussing the anatomy of the hind leg and its functions, states that the wax is "poked out of" the "pockets by means of the spines on the feet"—"with the ordinary hairs or spines of the tibiae or tarsi," and the same general conclusions were reached independently by the writer, but with this exception; only the spines of the first tarsal segment (planta) function in this manner, and usually only certain large spines in the rows at the distal end of this segment.

It is exceedingly difficult to capture a bee at the very moment at which the scale is being drawn from its pocket and before it has been carried to the mouth, and even if this is accomplished the captive is very likely to drop the scale from the hind leg in its struggles to escape. If, however, one is successful, the scale-removing leg will show the little wax scale adhering to the distal end of the inner surface of the first tarsal segment, being pierced in several places by the strong spines which project from the lower rows of the pollen combs. (See fig. 7.)

It can also be shown experimentally that this method of removing the wax scales is entirely possible, for if the hind tarsus of a bee is mounted upon a small stick and is gently rubbed along the ventral side of a fully extended dead bee's abdomen, holding it in such a position that the pollen combs brush over the projecting edges of the scales, one of the scales will probably be removed and will be seen adhering to the spines in the manner above described.

In any hive where comb is being constructed rapidly many free scales will be found upon the bottom board and upon the lower bars of the frames. If these scales are examined microscopically some will be found without marks upon them, having evidently been loosened from their pockets accidentally during the movements of the workers over the comb and around the hive. Others will show certain marks and scratches upon them, indicating that they were voluntarily removed from the pockets, and in some cases they may bear the marks of the mandibles, showing that they were dropped during the process of mastication. Most of the scales which are marked at all are indented with several small punctures showing the places where the spines of the pollen combs have pierced them. These scars are exactly similar in appearance to those on the scale

shown in figure 7. Such free scales are not marked as they would be had they been extracted by such a structure as the so-called wax shears.

So far as can be determined there does not appear to be any regular order for the removal of scales. One may be taken from the left side and then one from the right, or the bee may remove two or three from one side in succession. An attempt to remove a scale is by no means always successful, the worker often trying first one side and then the other, pressing the pollen combs against the more anterior scales and running them down to the most posterior, until at last a scale is impaled upon the spines or the bee discontinues its efforts.

FURTHER MANIPULATION AND THE MASTICATION OF SCALES.

When a scale has become attached to the spines it is transferred to the mouth with great rapidity, so swiftly, in fact, that the eye can scarcely follow the action. This is not surprising, for it is necessary only to flex the leg toward the head to bring the scale in close contact with the forelegs and mandibles. The leg is rotated through the arc of a circle, downward, forward, and upward, while at the same time the head is slightly turned under to receive the scale. The process of mastication is more prolonged. It is usually supposed that the pure wax of the scale differs in chemical composition from the wax of the comb, this change being accomplished during mastication, by which process the wax is mixed with saliva, becomes translucent rather than transparent, changes somewhat in color, and becomes more pliable.

The behavior of a bee upon receiving a wax scale at its mouth is subject to considerable variation. On some occasions the scales are apparently manipulated by the mandibles alone, while at other times the forelegs are brought into requisition and assist the mandibles. When a scale is thin and small and has been firmly grasped by the mandibles little assistance is needed from the legs. But if a scale of medium or extra thickness is presented, or if the mandibles do not hold it securely and it is in danger of falling from the mouth, the two forelegs are used to great advantage in readjusting the scale and in so holding it that the mandibles may be applied to it most advantageously. If a scale is small and thin, it may be masticated entirely before any wax is applied to the comb; but if of considerable size a portion only may be prepared, this deposited upon the comb, and then the remainder treated in a similar manner.

As a rule the wax which is deposited upon the comb by the producing bee is first subjected to the action of the mandibles and mixed with saliva. Such, however, is not always the case, for some bees appear to be "careless" and will mingle small unchewed portions of scales with the masticated wax. Indeed, it is not uncom-

mon to find nearly perfect scales mixed with the wax of a newly made comb. The masticated wax itself is spongy and flaky when it is deposited by the producing bee and will later be reworked, thereby gaining greatly in compactness and smoothness.

The entire process of the removal of one scale, its mastication, and the application of the wax to the comb is completed in about four minutes, only a very small portion of this interval being consumed in the work of extracting the scale from its pocket and passing it to the mouth, except in cases in which scales appear to be removed with difficulty.

FREE SCALES.

When wax scales are voluntarily removed they are taken off by the bee which secretes them and in the manner above described. Many, however, are accidentally detached, being loosened from their pockets by movements of the abdomen, incidental cleansing movements of the legs, or by contact with objects both within and without the hive. Such scales, and also those which are dropped in the course of transference from the wax pocket to the mouth, may or may not be recovered later and added to the comb. Since old wax is used over and over again in the rebuilding of comb, it is but natural to expect that scattered scales would likewise be utilized by the colony and not be allowed to go to waste, and it is probably true that such is usually the case. Yet there appears to be no concerted action among the workers to salvage such particles of wax, no class of comb workers whose duty it is to pick such material from the bottom board of the hive and carry it to the comb. Scales which drop are likely to remain for a long time, and some may even be carried out through the entrance with waste material. If, however, scales accidentally dislodged or voluntarily removed fall on the comb among the comb workers they are often noticed by them, picked up, masticated, and built into the comb. If a scale slips from the pollen combs or is fumbled by the bee before being grasped by the mandibles, it is seldom recovered by the worker to which it belongs unless it falls very near her or she stumbles upon it accidentally.

PARTIAL REMOVAL OF SCALES.

Although a bee endeavors to remove an entire wax scale at one operation, the attempt is not always successful. A scale that has become very thick is difficult of removal, particularly so if the outer edge is broken or beveled. When the bee applies its pollen combs to such a scale the spines may fail to get a hold upon the wax, or they may not become sufficiently well fixed in it to make possible the removal of the entire scale. Instead of this, shreds and small pieces of wax are torn off and remain sticking to the bristles of the pollen

combs. These may be entirely disregarded by the bee, or they may be cleaned off by scraping the combs together, the shreds of wax dropping to the bottom of the hive. More usually, however, if a worker is actively engaged in the task of adding to the comb these bits of wax will be carried forward to the mouth, masticated, and applied.

In one case which came under observation a worker had removed all of its wax scales except a very large, thick one which was evidently sticking tightly in its pocket. Repeated efforts were made by the bee to accomplish the extraction of this scale, but with only partial success, since the main portion of the scale remained in the pocket. But as the result of its efforts the bee succeeded in beveling off the entire projecting edge of the scale, rasping it off bit by bit and carrying the small pieces forward to the mouth, masticating them, and disposing the wax upon the comb.

PRODUCERS AND BUILDERS.

The presence of well-developed scales protruding from the pockets of a worker does not necessarily indicate that this individual will shortly add this wax to the comb, even though the colony may at the time be producing comb at a rapid rate. Such a bee may be working upon the comb as a molder of wax rather than as a producer. One who is intent upon a study of the process of scale removal will often be disappointed after following for a time the movements of a worker that is evidently manipulating wax and which shows the protruding edges of scales beneath its abdomen, for the wax with which it is working is being picked up, little by little, from the comb and comes not from its own body. This reworking of wax is one of the most characteristic features of comb construction, for it goes on continually while new comb is being produced, and it is, of course, a necessary process in the reconstruction of old comb.

The claim has been made by several investigators and writers that the bees which sculpture the wax are not at the same time concerned with its secretion and deposition—that there are producing bees and building bees. In a sense this is true, but not entirely so. Without doubt many active comb workers are, at the time, nonproductive, for the wax glands of many are not functionally active. The results of Dreyling would indicate that the old bees, at least, might be considered as falling in this class, and the direct observations of the writer lead to the conclusion that old bees devoid of wax scales perform a considerable share of the labor of reworking newly deposited wax and of shaping and polishing the cells of the comb.

However, as noted above, bees with well-developed wax scales often busy themselves with wax working rather than with production. Moreover, a bee that is removing its scales may discontinue

this work and give its attention to the molding of wax laid down by others. This may occur immediately after a worker has removed the last of its scales, or the bee may turn to sculpturing while several scales yet remain in the pockets. It is thus evident that the producing bee may also be a worker of wax produced by others and that nonproductive bees do not monopolize the work of sculpturing and polishing the comb.

SUMMARY.

As is well known, the wax produced by the worker bee occurs in the form of scales, eight in number, which appear upon the surfaces of the eight wax plates. These wax plates are located upon the last four visible ventral plates of a worker bee's abdomen. The wax is secreted by glands which lie upon the inner surface of each wax plate. The liquid wax exudes through pores which perforate the wax plates, and it hardens to form the scales as it comes in contact with the air.

Unless accidentally dislodged the wax scales are always removed and manipulated by the bee which secretes them.

In the process of removal the scale is not grasped by the so-called wax shears, but it is pierced by a few of the stiff spines on the distal end of the first tarsal segment of the hind leg and is then drawn from its pocket and remains adhering to these spines until removed for mastication.

By flexing the hind leg the scale is brought forward beneath the bee's body and into proximity with the mouth. In the process of mastication the forelegs usually aid the mandibles by holding the scale in an advantageous position.

No definite sequence is observed by the bee in the order in which it removes its scales.

As a rule entire scales are removed at one operation, although it sometimes happens that a thin scale is broken in extracting it from its pocket or an extremely thick one is gradually beveled off by the continued rasping of the pollen combs.

Scales which are removed accidentally or which are dropped during manipulation may be recovered later and built into the comb, but the recovery of free scales is usually not accomplished by the bee which secreted them.

Bees which are producing wax may also rework the masticated wax laid down by others. Producing bees may turn to the work of building and sculpturing the comb either before all their scales are removed or immediately after this has been accomplished.

