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# ANATOMY AND PHYSIOLOGY OF THE HONEYBEE

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# ANATOMY AND PHYSIOLOGY
## OF THE
# HONEYBEE

BY
R. E. SNODGRASS
*U. S. Bureau of Entomology*

FIRST EDITION
SIXTH IMPRESSION

McGRAW-HILL BOOK COMPANY, INC.
NEW YORK AND LONDON
1925

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McGRAW-HILL BOOK COMPANY, INC.

PRINTED IN THE UNITED STATES OF AMERICA

THE MAPLE PRESS COMPANY, YORK, PA.

# PREFACE

During the course of preparing this volume, which began as a revision of *The Anatomy of the Honey Bee*, published as a bulletin by the U. S. Bureau of Entomology in 1910, friends of the writer frequently expressed surprise that the bee should have changed so much in fourteen years as to require such a considerable rewriting of its structure. Fortunately, however, the bee has not changed, but our knowledge of it has changed very much, and mostly by addition, though some, too, by subtraction.

Much of the new matter here presented has been taken from work done by the writer in his official connection with the Office of Bee Culture in the Bureau of Entomology. The work has been facilitated in every way by the help of those who are or have been connected with this office, and the writer is particularly indebted to Dr. E. F. Phillips, for nineteen years in charge of the office, whose constant interest in the anatomy of the honeybee and all subjects related to it has made the work possible. Nearly all the illustrations of the original bulletin are reproduced here by the permission of the Bureau of Entomology. So many important additions to a knowledge of the anatomy, physiology, and behavior of the bee are incorporated into the present text from the work of others that the writer must now share credit with all those whose names are given wherever abstracts or quotations are made from their papers. It is to be hoped that, as a result of our combined efforts, our ideas of the bee are placed on a surer scientific basis than ever before, and one on which future workers in all branches of bee science and bee culture may build securely.

The anatomy of any animal is a complex of what it receives from its remote progenitors and of that which it needs for its own purposes. Each species is housed in its ancestral dwelling remodeled to fit the needs of its present-day life, and the edifice shows in its structure its evolution from an earlier type. As a consequence, few of the parts or organs of an animal are constructed as they might have been had they been made expressely for their modern uses. It is not profitable, therefore, to study any form

of life as if it were a thing of itself; and the anatomy of the honeybee can be rightly understood only when seen as an adaptation of general insect structure to the special needs of the bee.

A plan of description following this principle necessarily involves a longer course than one that goes directly at its subject, especially when applied to the honeybee, which, in its bodily structure, has departed far from that of its ancestors. Though the ancestors of the bee have not been preserved, some other insects have retained ancestral characters, and consequently, in the following chapters, the student will be introduced first to one of these, such as a grasshopper or a cricket, or to some lower member of the bee's own order, or given a general review of the history of an organ, before he is brought at last to the subject of his chief interest. This method, though risking the impatience of the practical apiculturist, makes acquaintance with the bee, in the end, not only easier, but more interesting, since, to a knowledge of facts, it adds understanding.

R. E. SNODGRASS.

WASHINGTON, D. C.

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## EXPLANATIONS OF THE SYMBOLS USED ON THE FIGURES

It has become impossible to use a set of symbols representing all the named parts of the bee that will not ignore certain standardized abbreviations in different subjects without the few duplications given in the following list. Lower case letters are repeated on different figures without necessarily implying identity of parts so distinguished and are explained in connection with the figures.

Arabic numbers used alone on external parts designate segments of the thorax, subjoined to symbols they indicate the thoracic segments to which parts so designated belong, placed before symbols they mean numerical order in a series. Roman numerals designate segments of the head or of the abdomen, and cells of the wings; prefixed to a symbol they indicate the abdominal segment to which the part belongs.

*A*, anal vein.
*Ab*, abdomen.
*Ac*, precoxal bridge.
*AcGl*, accessory gland.
*AGl*, acid gland.
*AglD*, duct of acid gland.
*Alb*, albuminoid granule.
*Alv*, alveolus.
*Am*, amnion.
*Amp*, ampulla.
*AMR*, anterior mesenteron rudiment.
*AN*, alinotum.
*An*, anus.
*ANP*, anterior notal wing process.
*ANR*, anterior notal ridge.
*Ant*, antenna.
*AntL*, antennal lobe.
*AntNv*, antennal nerve.
*Ao*, aorta.
*Ap*, apodeme.
*Ar*, arolium.
*Aur*, auricle.
*Aw*, prealar bridge.
*Ax*, axillary sclerite.
*1Ax*, first axillary.
*2Ax*, second axillary.
*3Ax*, third axillary.
*4Ax*, fourth axillary.
*ax*, accessory axillary.
*AxC*, axillary cord.
*AxM*, axillary membrane.
*B*, bulb.
*BC*, body cavity.
*bc*, part of body cavity.
*BCpx*, bursa copulatrix.
*BGl*, alkaline gland.
*Bl*, blastoderm.
*BM*, basement membrane.
*BP*, bursal pouch.
*Br*, brain.
*1Br*, protocerebrum.
*2B* , deutocerebrum.
*3Br*, tritocerebrum.
*Brb*, barb.

*brg*, bridge.
*BW*, body wall.
*C*, costa.
*Can*, canal of scent gland.
*CB*, cephalo-dorsal body.
contraction band of muscle.
crystalline body.
*Cb*, corbiculum.
*CC*, crystalline cone.
*CCl*, cap cell.
cleavage cell.
*Cd*, cardo.
*Ce*, cervical sclerite.
*Cen*, centrosome.
*Cer*, cercus.
*Cho*, chorion.
*Chr*, chromosome.
*CL*, cortical layer.
crystalline lens.
*Cl*, *Cls*, cell, cells.
*Cla*, claw.
*Clp*, clypeus.
*Clsp*, clasper.
*CMcl*, closing muscle of spiracle.
*Com*, commissure.
*Cor*, cornea.
*Cst*, spermatocyst.
*Ct*, cuticula.
*Cu*, cubitus.
*Cv*, cross-vein.
*Cx*, coxa.
*CxC*, coxal cavity.
*CxP*, pleural coxal process.
*da*, dorsal arm of spiracle valve.
*DBl*, dorsal blastoderm.
*Dct*, *Dcts*, duct, ducts.
*DDph*, dorsal diaphragm.
*Dm*, dermis.
*Dph*, diaphragm.
*DphCls*, diaphragm cells.
*DphMb*, diaphragm membrane.
*DphMcl*, diaphragm muscles.
*DS*, dorsal strip of blastoderm.
*E*, compound eye.
end disc of muscle.
*EAp*, extensor apodeme.
*ECl*, enveloping cell.
*Ect*, ectoderm.
*EjD*, ejaculatory duct.
*EMcl*, extensor muscle.
*Enz*, digestive cell.
*Ep*, epicranium.
*Epd*, epidermis.
*Ephy*, epipharynx.
*Epm*, epimeron.
*epm*, subdivision of epimeron.
*Eps*, episternum.
*eps*, subdivision of episternum.
*Epst*, epistoma.
*Epth*, epithelium.
*F*, femur.
*FAp*, flexor apodeme.
*Fbl*, fibrilla, sarcostyle.
*Fbr*, fiber.
*FCl*, follicle cell.
*Fl*, flagellum.
*fm1*, outer fibrillar body.
*fm2*, middle fibrillar body.
*fm3*, inner fibrillar body.
*FMcl*, flexor muscle.
*For*, foramen magnum.
*Fr*, front.
*FrCom*, frontal commissure.
*FrGng*, frontal ganglion.
*FrNv*, frontal nerve.
*Ft*, fat.
*FtCls*, fat cells.
*Fu*, furca.
*G*, gonapophysis.
*Ga*, galea.
*GB*, germ band.
*GCls*, "ganglion" cells.
*Ge*, gena.
*Gl*, gland.
*1Gl*, pharyngeal gland.
*2Gl*, postcerebral gland.
*3Gl*, thoracic salivary gland.
*Gls*, glossa.
*Gng*, ganglion.
*GCls*, tibial "ganglion" cells.
*Gu*, gula.
*H*, head.
median disc of muscle.
*h*, humeral cross vein.
*Hk*, hook.
*Hphy*, hypopharynx.
*Hr*, hair, seta.
*HrCl*, trichogenous cell.

*HS*, honey stomach.
*Ht*, heart.
*ht*, chamber of heart.
*HtTraSc*, pericardial tracheal sac.
*Hy*, hypodermis.
*IB*, interzonal body.
*In*, intima.
*Int*, intestine.
*Ir*, iris
*IS*, first abdominal sternum.
*ISp*, first abdominal spiracle.
*IT*, first abdominal tergum.
*J*, light disc of muscle.
*L*, leg.
*Lb*, labium.
*Lbl*, labellum.
*LbNv*, labial nerve.
*LbPlp*, labial palpus.
*Lc*, lacinia.
*LCt*, larval cuticula.
*Lct*, lancet.
*Leu*, leucocyte.
*Lg*, ligula.
*Lin*, lingua.
*Lm*, labrum.
*LMcl*, dorsal longitudinal muscle.
*lmcl*, ventral longitudinal muscle.
*LmNv*, labral nerve.
*Ln*, lens.
*LP*, lateral plate of embryo.
*Lr*, lorum.
*LTra*, trachea of leg.
*Lum*, lumen.
*M*, media.
mesophragma of muscle.
*m*, median plate.
*m-m*, median cross vein.
*Mal*, Malpighian tubule.
*Mb*, *mb*, membrane.
*MC*, median cord.
*Mcl*, muscle.
*m-cu*, medio-cubital cross-vein.
*Md*, mandible.
*MdGl*, mandibular gland.
*MdNv*, mandibular nerve.
*Ment*, mesenteron.
*Mes*, mesothorax.
*Meso*, mesoderm.
*Met*, metathorax.
*Mir*, mirror.
*MrB*, mushroom body.
*mrb*, elevation of mushroom body.
*MP*, median plate of embryo.
*Mps*, mouth parts.
*Mt*, mentum.
*Mx*, maxilla.
*MxPlp*, maxillary palpus.
*MxNv*, maxillary nerve.
*N*, notum.
accessory disc of muscle.
*Nbl*, neuroblast.
*NCl*, nurse cell.
*Nk*, neck.
*NlG*, neural groove.
*Nu*, nucleus.
*Nv*, nerve.
*O*, ocellus.
*Ob*, oblong plate.
*Oc*, occiput.
*Œ*, œsophagus.
*ŒCom*, circumœsophageal commissure.
*Oen*, *Oens*, œnocyte, œnocytes.
*Om*, ommatidium.
*OMcl*, opening muscle of spiracle.
*Ooc*, oocyte.
*Oog*, oogonium.
*Op*, operculum.
*OpL*, optic lobe.
*OpMcl*, muscle of operculum.
*Ost*, ostium.
*Ov*, ovary.
*ov*, ovariole.
*OvD*, oviduct.
*P*, parapteron.
*1P*, *2P*, episternal paraptera, subalar plates.
*3P*, epimeral parapteron, basalar plate.
*PA*, pleural arm.
*Pa*, paracardial cells.
*Pc*, postcoxal bridge.
*Pcl*, postclypeus.
*PD*, disc of pronator muscle.
*Pd*, peduncle.
*Pen*, penis.
*PenB*, bulb of penis.
*Peps*, pre-episternum.

*Pg*, pigment.
*Pge*, postgena.
*PgGl*, postgenal gland.
*Pgl*, paraglossa.
*Ph*, phragma.
*1Ph*, anterior phragma.
*2Ph*, middle phragma.
*3Ph*, posterior phragma.
*Phy*, pharynx.
*Pi*, pit.
*Pl*, pleuron.
*pl*, subdivision of pleuron.
*Plf*, palpifer.
*Plg*, palpiger.
*Plp*, palpus.
*Pmb*, peritrophic membrane.
*PMcl*, protractor muscle.
*PMR*, posterior mesenteron rudiment.
*PN*, postnotum, phragmanotum.
*PNP*, posterior notal wing process.
*Po*, pore.
*PR*, pleural ridge.
*Pr*, protoplasmic substance.
*Prb*, proboscis.
*PrbFs*, fossa of proboscis.
*PrL*, protocerebral lobe.
*Proc*, proctodeum.
*PS*, pleural suture.
*Psc*, prescutum.
*Pscl*, postscutellum.
*PsnC*, poison canal of sting.
*PsnSc*, poison sac.
*Pt*, peritreme.
*Pv*, pulvillus.
*Pvent*, proventriculus.
*PventVl*, proventricular valve.
*Pw*, postalar bridge.
*Q*, dark disc of muscle.
*Qd*, quadrate plate.
*R*, radius.
$R_s$, radial sector.
*r*, radial cross-vein.
*Rd*, posterior fold.
*Rect*, rectum.
*Ret*, retinulæ.
*RGl*, rectal gland.
*Rhb*, rhabdom.
*Ri*, *ri*, ridge.
*r-m*, radio-medial cross-vein.
*RMcl*, retractor muscle.
*1RMcl*, dorsal retractor of ligula.
*2RMcl*, ventral retractor of ligula.
*Rt*, retinula.
*S*, sternum.
*1S*, first sternal sclerite.
*2S*, second sternal sclerite.
*3S*, third sternal sclerite.
*4S*, fourth sternal sclerite.
*s*, sectorial cross-vein.
*SalD*, salivary duct.
*SalDO*, opening of salivary duct.
*Sar*, sarcoplasm.
*Sarl*, sarcolemma.
*Sc*, subcosta.
*SCl*, *SCls*, sense cell, sense cells.
*Sco*, scolopala.
*Scp*, scape.
*Sct*, scutum.
*Sga*, subgalea.
*Sh*, sheath of sting.
*ShA*, arm of sheath of sting.
*ShB*, bulb of sheath of sting.
*SHr*, sensory hair.
*ShS*, shaft of sheath of sting.
*SInt*, small intestine.
*Slin*, superlingua.
*Smt*, submentum.
*SntGl*, scent gland.
*SNv*, sensory nerve.
*SO*, sense organ.
*SœGng* subœsophageal ganglion.
*Sp*, spiracle.
*Spc*, spermatocyte.
*SPg*, sensory peg.
*Spg*, spermatogonium.
*Spi*, spireme.
*SPl*, sensory plate.
*Spm*, spermatheca.
*SpmGl*, spermathecal gland.
*Spt*, functional spermatid.
*spt*, degenerate spermatid.
*sptB*, bud of degenerate spermatid.
*Srs*, sarcosome.
*St*, stipes.
*StgNv*, stomatogastric nerve.
*Stom*, stomodeum.
*Stn*, sting.

*StnPlp*, palpus of sting.
*T*, tergum.
*Tæ*, tænidia.
*Tar*, tarsus.
1*Tar*, first joint of tarsus, planta.
*Tb*, tibia.
*Ten*, tentorium.
*ten*, cross-bar of tentorium.
*Tes*, testis.
*Tfbl*, tonofibrillæ.
*Tg*, tegula.
*Th*, thorax.
*TMcl*, transverse muscle.
*Tn*, trochantin.
*TnC*, coxal condyle of trochantin.
*Tr*, trochanter.
*Tra*, trachea.
*tra*, tracheole.
*TraCom*, tracheal commissure.
*TraSc*, tracheal sac.
*Tri*, triangular plate.
*Tu*, tubercle.
*va*, ventral arm of spiracle valve.
*Vac*, vacuole.
*Vag*, vagina.
*VB*, vitreous body.
*VDef*, vas deferens.
*VDph*, ventral diaphragm.
*Vent*, ventriculus.
*VentVl*, ventricular valve.
*Ves*, vesicula seminalis.
*Vit*, vitelline membrane.
*Vl*, valve.
*Vlv*, valvula (gonapophysis).
*VMcl*, vertical muscles.
*VNC*, ventral nerve cord.
*VNR*, ventral notal ridge.
*VO*, opening of vagina.
*Vx*, vertex.
*W*, wing.
$W_2$, front wing.
$W_3$, hind wing.
$W_2Nv$, nerve of front wing.
$W_3Nv$, nerve of hind wing.
*WP*, pleural wing process.
*WxGl*, wax gland.
*Y*, yolk.
*Z*, telophragma of muscle.

# ANATOMY AND PHYSIOLOGY OF THE HONEYBEE

## CHAPTER I

## GENERAL EXTERNAL STRUCTURE

In insect anatomy the study of the external structure of the body is of special importance because the outer shell of the insect is at once its skin and its skeleton. It is modified in all the ways by which insects are adapted to their environment, it carries all the organs by means of which the creature keeps in touch with its surroundings; and in addition it supports the attachments of the body muscles, and protects the soft internal parts. The form of insects, therefore, has a two-fold significance—it represents an adaptation to the demands of external environment, combined with structural modifications to meet the needs of internal organization.

### 1. FORM AND COMPOSITION OF THE BODY OF AN INSECT

In examining a bee (Fig. 1) it is easily seen that it consists of a *body* and *appendages*, and that the body is divided by constrictions into three parts. These features are characteristic of all insects. The bee, however, is such a furry creature that further details of the structure of its parts are obscure in its natural condition. The hairs can either be rubbed off with a small brush, or more quickly removed by placing the bee in melted paraffin, allowing the latter to harden, and then carefully breaking the paraffin away. Most of the hairs come off with the wax and the body of the insect is thus left fairly bare and in good condition for study.



FIG. 1.—The worker honeybee.

**The Principal Parts of an Insect.**—On the naked bee (Fig. 2) the three parts of the body above noted are much more clearly defined. The middle division appears to be the most important one since it is supported by the legs, and in turn carries the wings and the other two parts of the body. It is known as the *thorax* (*Th*). The first division is the *head* (*H*), which is movably joined to the front end of the thorax by a narrow neck, and carries the antennæ, the eyes, and the organs of feeding. The third

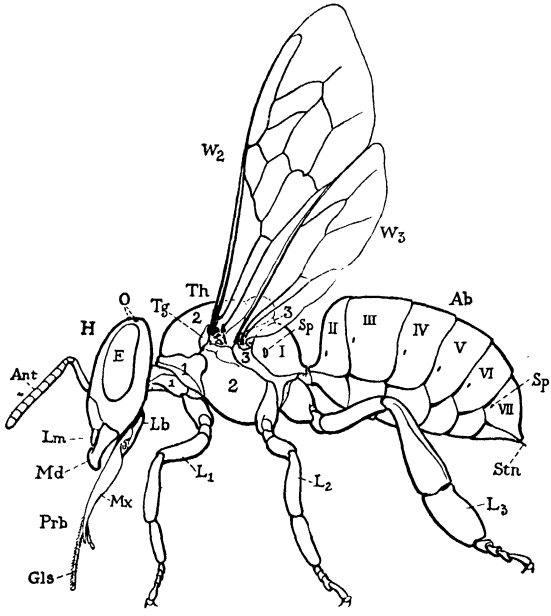



FIG. 2.—Lateral view of worker with hairs removed, showing divisions of body, and appendages of left side.

*H*, head, bearing ocelli (*O*), compound eyes (*E*), antennæ (*Ant*), jaws (*Md*), and proboscis (*Prb*); *Th*, thorax, composed of prothorax (*1*, *1*), mesothorax (*2*, *2*), metathorax (*3*), and propodeum (*I*), the first three segments each with a pair of legs ($L_1$, $L_2$, $L_3$), the second and third bearing each a pair of wings ($W_2$, $W_3$); *Ab*, abdomen, composed of six visible segments (*II-VII*), with tip of sting (*Stn*) projecting from rear end.

division is the *abdomen* (*Ab*), which is movably attached by a short basal stalk in the bee to the rear surface of the thorax and carries the sting mostly concealed in its posterior end. Further details may now be studied on each part.

*The Head.*—In the honeybee the head (Fig. 2, *H*) is triangular in facial view and is flattened in the direction of the lengthwise axis of the body, but it may have various forms in different

insects. It bears two large eyes (*E*) symmetrically placed on the upper parts of its sides, a group of three very small eyes (*O*) forming a triangle on top, a pair of jointed antennæ (*Ant*) movably inserted on the middle of the face, two strong jaws (*Md*) attached, one on each side, to the lower edges of the cheeks, and a long proboscis of several parts (*Prb*) projecting below from behind the mandibles or sometimes bent back under the neck. The mouth is situated between the bases of the jaws and the proboscis, concealed from in front by a broad upper or anterior lip (*Lm*) attached to the lower edge of the face. In the bee the walls of the head are but little divided into plates as they are in some other insects; only one subdivision is distinct, this being a large median plate on the lower part of the face, just above the front lip.

*The Thorax.*—The thorax of the bee (Fig. 2, *Th*) is a very compact and solid region of the body, being designed to support the wings ($W_2$, $W_3$) and the legs ($L_1$, $L_2$, $L_3$) and to give attachment internally to the muscles that move them; but it differs from the head in that its walls are cut by grooves into many irregular plates of various sizes and shapes like the pieces of a picture puzzle. In fact, the thorax of the bee is a puzzle, for, ordinarily, an insect's thorax consists of three distinct rings or *segments* placed one before the other and known as the *prothorax*, the *mesothorax*, and the *metathorax* respectively. Each segment carries one pair of legs, while the second and the third carry in addition each a pair of wings. The wall of each segment, furthermore, is subdivided into plates or sclerites, which are repeated with modifications on the three consecutive segments.

The thorax of the bee and of its relations in the Order Hymenoptera, however, consists of *four* segments; it comprises the usual three thoracic segments and another which in other insects is the first segment of the abdomen. Furthermore, the thoracic segments are so consolidated and their plates so modified that the study of the bee's thorax is a difficult subject, but for that reason the more interesting. The details of the thoracic structure in the bee will be described fully in a later chapter, but we may note here its more prominent features. The prothorax (Fig. 2, *1*, *1*) consists of a detached plate that appears to belong to the neck, although it supports the front legs, and of a second plate which forms a collar around the front of the rest of the thorax. The mesothorax (*2*, *2*) consists of a back plate and of a large plate

covering the sides and the lower surface of the segment, with the front wings ($W_2$) inserted between them, and the middle legs ($L_2$) attached to the lower plate. The metathorax is reduced to a narrow ring (*3*, *3*) which carries the hind wings ($W_3$) and the hind legs ($L_3$), and is also divided into a dorsal plate and a latero-ventral plate. The fourth segment consists of a back plate forming the sloping rear surface of the thorax (*I*) and of a ventral plate which is not visible from the side, but has no appendages. This fourth segment is known as the *propodeum*.

*The Abdomen.*—The abdomen is the simplest region of an insect's body. In the majority of insects it consists of ten or eleven segments, most of which are separated from one another by flexible membranes, though the rear margin of each usually overlaps the front margin of the segment next behind. Each segment has a dorsal and a ventral plate, the former typically overlapping the upper edge of the latter on each side.

In the honeybee the abdomen (Fig. 2, *Ab*) consists of six well-defined, visible segments (*II-VII*), and of three others hidden within the last visible one. The abdominal region of the bee's body is thus composed of only nine segments, but it must be remembered that the segment which is the first segment of the abdomen in other insects forms here a part of the thorax (*I*). The next segment (*II*), which in the bee is the first segment of the abdominal division of the body, is narrowed very abruptly in front to form the stalk or *peduncle* by which the abdomen is united to the thorax. The last exposed segment (*VII*) is cone-shaped and encloses the terminal three segments. Two of these bear the sting, the tip of which (*Stn*) may be seen projecting from the apex of the seventh segment.

**The Fundamental Structure of an Insect.**—This brief review of the external parts of the bee brings out two important facts regarding it: One is, that the thorax and abdomen consist of a series of segments; the other, that the head and thorax carry paired appendages. On the thorax, moreover, the appendages are segmentally arranged, which suggests that the presence of paired appendages on the head may mean that the head consists of a series of united segments. Furthermore, the segmentation of the abdomen suggests that this region also might have had appendages at some stage of its history. The abdomen of some of the lower insects, in fact, does have rudiments of segmental appendages, and many other insects have certain structures on

the terminal segments which, as we shall see later, are most likely modified appendages. From a study of anatomy we may infer, therefore, that, in the evolution of an insect, *segments may become fused and appendages may be lost.*

This conclusion is entirely confirmed by a study of the young embryos of some insects less specialized than the bee, which show that the head is composed of a series of segments at first almost as distinct as those of the thorax and abdomen, and that each segment of the entire body, except the first and the last, bears a pair of small lobes on its ventral surface, some of which develop into the appendages of the adult while the others disappear. Thus we conceive of an insect as consisting fundamentally of a body or trunk composed of a series of segments or *metameres*, each of which, except the two terminal ones, bears a pair of ventral appendages (Fig. 3). The wings of insects are regarded as secondary appendicular outgrowths and are not counted as true appendages.

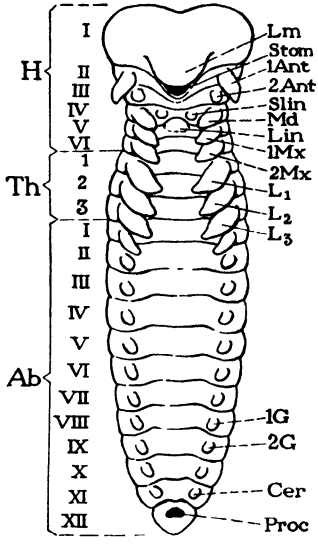



FIG. 3.—Diagrammatic representation of a generalized insect embryo, showing primitive segmentation of head (*H*), thorax (*Th*), and abdomen (*Ab*), and segmental appendages (1*Ant*-*Cer*).

1*Ant*, first antenna; 2*Ant*, second antenna; *Cer*, cercus; 1*G*, 2*G*, first and second gonapophyses; $L_1$, $L_2$, $L_3$, thoracic legs; *Lin*, lingua; *Lm*, labrum; *Md*, mandible; 1*Mx*, first maxilla; 2*Mx*, second maxilla; *Proc*, proctodeum; *Slin*, superlingua; *Stom*, stomodeum.

Other animals, such as the shrimps, the crabs and the lobsters, the centipedes, and the spiders have this same type of metameric construction with ventral segmental appendages. Together they constitute the zoological Phylum known as the Arthropoda, of which the insects form the Class Insecta. Spiders perhaps reach the highest degree of development amongst the arthropods, but the insects have attained a greater anatomical perfection.

## 2. THE STRUCTURE OF THE BODY WALL

The retaining wall of the body of an insect, which is continuous over all its external parts and enters into many of its internal parts, is known as the *body wall.* Most of its exterior is usually

hard and horny in adult insects; but this shell-like surface covering is not the entire body wall, it is merely an outermost coating over an underlying layer of cellular tissue that can be seen only in thin sections prepared for microscopic study. A piece of the body wall greatly magnified (Fig. 4 A) shows that it really consists of three superposed layers, the superficial hard part called the *cuticula* (*Ct*), the cellular layer called the *hypodermis* (*Hy*), and an innermost lining or *basement membrane* (*BM*).

**The Cuticula.**—The cuticula forms not only the covering over the external surface of the body, but also the hard parts of the interior of the body, since it lines all the infoldings of the body wall that produce various internal structures.

*The Structure of the Cuticula.*—The cuticula usually shows a division into an outer, dark-colored, denser layer, and an inner, pale, softer layer. The two parts are distinguished by some writers as the *exocuticula* and the *endocuticula*, but they are usually and more conveniently known as the *epidermis* (Fig. 4 A, *Epd*) and the *dermis* (*Dm*). The epidermis consists largely of a substance called chitin (pronounced ky̆-tin), while the dermis is said to be of a different chemical composition, consisting of a substance more related to cellulose. But in general the entire cuticula is usually spoken of as the chitinous layer of the body wall. The two layers of the cuticula differ much in relative thickness in different parts of the body wall, which is not everywhere continuously hard and solid; there are movable places such as at the neck, at the articulations of the legs, and between the segments of the abdomen, where the epidermis is very thin. At such places the cuticula is soft and flexible and is said to be *membranous*, or is called a *membrane* (Fig. 4 B, *Mb*).

The walls of the head and of the segments of the other parts of the body are divided by *sutures* into plate-like pieces called *sclerites*. Some of the sutures are mere grooves in the chitinous wall, while others are membranous. Where sutures have evidently been obliterated by the union of sclerites, the latter are said to be *fused*.

The cuticula is probably continuous over all the external surface of the body, and over the inner surface of all internal parts derived from the hypodermis. It often appears to contain fine canals or pores over glands or sense organs, but it has not been shown to be actually perforated in such cases.

*Cuticular Appendages.*—All the hairs, spines, scales and other surface structures of insects are outgrowths of the exoskeleton. Some hairs and spines are solid appendages of the cuticula (Fig. 4 D), while others are hollow outgrowths containing either a fold of the hypodermis (E) or a prolongation from a single cell (F). Hairs of the last sort are usually movably attached by a membranous base in a socket or *alveolus* (*Alv*) of the cuticula, which may be either flush with the surface (F) or

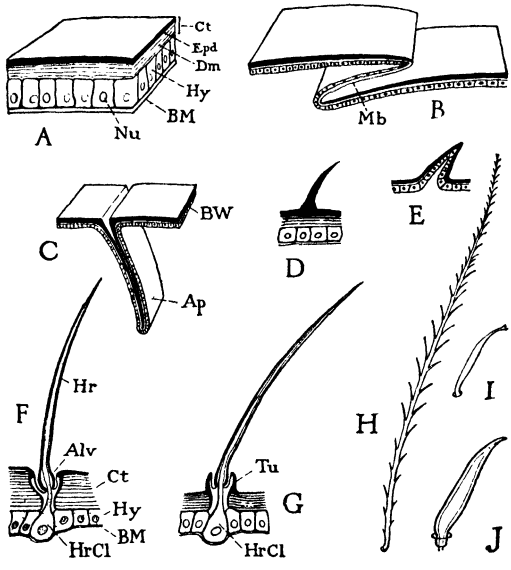



FIG. 4.—The body wall and its modifications.

A, piece of body wall, showing external cuticula (*Ct*) composed of epidermis (*Epd*) and dermis (*Dm*), the cellular hypodermis (*Hy*), and basement membrane (*BM*). B, intersegmental fold of body wall with membranous cuticula (*Mb*). C, chitinous infold of body wall forming an apodeme (*Ap*). D, a solid cuticular spine. E, a hollow cuticular spine. F, a hair or seta (*Hr*) and its relation to the body wall. G, a seta arising from a tubercle (*Tu*). H, a branched hair of the bee. I, specially modified hair from inner face of hind tibia of worker. J, spine-like hair of comb at end of hind tibia of worker.

elevated on a tubercle (G). Hairs of this kind are called *setæ*. Usually setæ are simple and bristle-like (F, G), but most of those of the bee are branched and plume-like (H), though others are smooth, while some have special forms such as those shown at I and J. The various special kinds of setæ of the bee, however, will be described in connection with the parts of the body on which they occur. Nearly all setæ of the honeybee are more or less bent at the base where they fit into the alveolus, and the

alveoli are generally of the sunken type (F); but the eyes are covered with smooth, bristle-like setæ that project straight out of their sockets.

*Apodemes.*—One important reason for the rigidity of the body wall of insects is that nearly all the muscles except those of the alimentary canal are attached to it. The strain on the wall is such that in many places it needs to be strengthened or braced by internal arms. In some cases, moreover, the muscle ends are so large that they have to be accommodated by infoldings of the body wall; in others their action is made more effective by their being attached to projecting rods or ridges. For these various reasons the body wall is infolded in the form of ridges, arms, or plates, which in general are termed *apodemes* (Fig. 4 C, *Ap*). Apodemes occur in all parts of the body and together constitute the *endoskeleton* of the insect, in distinction to the surface plates, which form the *exoskeleton.*

**The Hypodermis.**—The hypodermis (Fig. 4 A, *Hy*) consists usually of a single layer of contiguous cells suporting the cuticula. The cells have various shapes, being sometimes cubical, sometimes columnar, sometimes flat, varying with the region of the body and with the age of the insect. In certain parts of adult insects the hypodermis is often reduced to a thin sheet of nucleated tissue in which the cell boundaries have become lost. The hypodermal cells are modified in various ways and constitute the essential elements in many organs derived from the body wall. In general the following three classes of hypodermal cells may be distinguished:

*Chitinogenous Cells.*—The cuticula is a product of the underlying hypodermis, being either a secretion from the cells, or a direct modification of their outer ends. The cuticula-producing cells are known as *chitinogenous cells.* They form not only the normal cuticular layers, but also all of the cuticular modifications such as hairs, scales, sensory appendages, and the lenses of the eyes. The chitinogenous cells, therefore, become differentiated into cells of various sorts. Those that form hairs or hair-like structures are called *trichogenous cells*, those that form lenses are *lentigenous cells*, and others may be named according to their products.

*Hypodermal Gland Cells.*—Some cells of the hypodermis take on the function of secreting substances other than chitin, and these are distinguished as *gland cells.* In the honeybee they form

the wax glands and scent glands of the skin, the salivary and other glands of the mouth and mouth appendages, and the poison glands of the sting. In some insects gland cells have been described as penetrating into hollow hairs or spines, in addition to the chitinogenous cells that formed the hairs, and as discharging their products (poisons, scents, wax) from the hair tips. It is said also that some of these gland cells of hairs have a nerve fiber connected with their bases.

*Hypodermal Sense Cells.*—When a sensory nerve is connected with a cell of the hypodermis, the cell becomes a *sense cell.* In insects the known sense cells are always found in connection with an external cuticular structure (Fig. 19 B, *SCls*), and the complex of cuticular and cellular parts forms a *sense organ* or *sensillum.* The simpler sense organs have but one sense cell in each sensillum, though there may be one or two other associated hypodermal cells, but with some of the more complex organs the innervated hypodermis forms a mass of sense cells, as in the antennæ of the bee which are richly provided with sense organs of several kinds (Fig. 10 G, H, *SCls*). The sensory complex reaches its greatest development, however, in the eyes (Figs. 90, 91, 92), where there are highly specialized sense-cell structures beneath lens-like thickenings of the cuticula.

The many sense organs of the bee will be described in detail in connection with the parts of the body on which they occur, except the eyes which are given in the chapter on the nervous system. The sense organs are mentioned here, together with the apodemes, spines, hairs and glands formed from the cuticula and hypodermis, in order to show how important to the insect is its body wall, and how such various and complicated structures are formed by modifications of its three simple elements.

**The Basement Membrane.**—The basement membrane (Fig. 4 A, *BM*) is a thin inner lining of the body wall, covering the inner surface of the hypodermis and all the organs formed from the latter, including the hypodermal glands, the sense organs, and various other parts to be described later. The continuity of the basement membrane is interrupted at the points where muscles are attached to the body wall, since the fibrillar elements of the muscles are anchored into the inner layer of the cuticula by intervening tendons apparently derived from the hypodermal cells. The membrane appears to be perforated also by the

nerves of the sense organs, though possibly it forms an invaginated sheath over the nerve endings.

In adult insects the basement membrane is a thin layer of structureless tissue. It is usually believed to be a product of the inner ends of the hypodermal cells, but some investigators claim that it is cellular in its origin.

## CHAPTER II

## THE HEAD AND ITS APPENDAGES

The common differentiation of the forward end of the trunk into a head movably attached to the body gives an appearance of kinship amongst animals that may be in no wise related. We, for example, have no anatomical relationship with insects, but the head of an insect, with its mouth and prominent eyes, humanizes the creature to a large degree in our imagination. Yet, animals more closely related to insects, such as crabs and spiders, may have the head and thorax all in one piece.

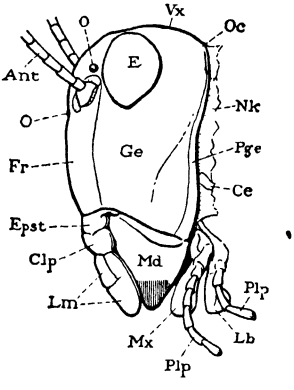



FIG. 5.—Head of a grasshopper, side view, showing structure of insect head and mouth parts of more typical form than in the bee.

*Ant*, antenna; *Ce*, cervical sclerite; *Clp*, clypeus; *E*, compound eye; *Epst*, epistoma or postclypeus; *Fr*, front; *Ge*, gena; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *Nk*, neck; *O*, ocellus; *Oc*, occiput; *Pge*, postgena; *Plp*, palpus; *Vx*, vertex.

### 1. THE GENERAL STRUCTURE OF AN INSECT'S HEAD

The head of an adult insect, as already explained, is an unsegmented cranium-like capsule, carrying the mouth, the eyes, the antennæ and the organs of feeding. The head and mouth parts of the bee are highly specialized; the head of a grasshopper (Fig. 5) is more representative of a typical insect head. The structure of the head in any case, however, can be rightly understood only by studying its development.

**The Development of the Head and Mouth Parts.**—In the insect embryo (Fig. 3) there are at least six head segments. The first segment carries the eyes but has no typical appendages. The appendages of the second segment (1*Ant*) become the antennæ of the adult (Fig. 5, *Ant*). Those of the third (2*Ant*) disappear in all insects before hatching but are the equivalent of the second antennæ of shrimps, lobsters and other crustaceans. The

appendages of the fourth segment (*Md*) form the strong, biting jaws or *mandibles* of the adult (Fig. 5, *Md*). The fifth pair (1*Mx*) becomes the second mouth appendages or *maxillæ* (Fig. 5, *Mx*). The last pair (2*Mx*), the second maxillæ of the young embryo, grow together in a later embryonic stage to form the single lower lip or *labium* (Fig. 5, *Lb*) of the adult. The *mouth* (*Mth*) is formed as an ingrowth of the body wall probably in the first embryonic segment, though it later enlarges until it occupies the ventral parts of all the segments between the first and the sixth. A large lobe (*Lm*) of the first embryonic segment grows downward in front of the mouth and becomes the front lip or *labrum* of the adult (Fig. 5, *Lm*). Three small ventral lobes of the embryo head that arise between the mouth and the second maxillæ grow together to form a single median tongue-like organ of the adult known as the *hypopharynx*, which usually appears to be attached to the anterior or dorsal surface of the labium (Fig. 13 D, *Hphy*). Of the three component lobes of the hypopharynx, the median one is the *lingua* (Fig. 3, *Lin*), and the two lateral ones are the *superlinguæ* (*Slin*) or *maxillulæ*. Probably none of these lobes are true segmental appendages, and entomologists do not agree as to the segment or segments on which they originate. The hypopharynx often preserves a three-lobed form in the adult, indicative of its triple origin. It may be rudimentary, as in some wild bees (Fig. 14 E, *Hphy*). It is entirely absent in the honeybee.

Before the insect hatches great changes take place in the head region and its appendages. The segments consolidate so thoroughly that it is difficult to define their limits in the mature head. The antennæ move to the upper parts of the cranium, but the other persisting appendages and lobes remain grouped around the mouth and together constitute the so-called *mouth parts*.

**The Structure of a Typical Insect Head.**—The head capsule of an adult insect is more or less divided by grooves or sutures into a number of plates, which, though seldom completely outlined, are characteristic of the different head regions. These are better shown on the head of a grasshopper (Fig. 5) than on that of a bee (Fig. 6) where nearly all of the sutures are obliterated. The top of the head is called the *vertex* (Fig. 5, *Vx*), the sides or cheek regions are known as the *genæ* (*Ge*), the face is the *front* (*Fr*), and the back of the head, surrounding the neck, is called the *occiput* (*Oc*) above and the *postgenæ* (*Pge*) at the sides. The front

and the genæ and the genæ and postgenæ are separated by sutures. Two plates intervene between the lower edge of the front (*Fr*) and the upper lip (*Lm*). The lower one (*Clp*) is the *clypeus.* The upper one (*Epst*) is called sometimes the *postclypeus,* sometimes the *epistoma.* The mandibles (*Md*) are attached along the lower edges of the genæ, but have special articulations in front with the angles of the epistoma, and behind with the lower ends of the postgenæ. The maxillæ (*Mx*) are also articulated to the postgenæ, but the labium (*Lb*) is suspended from the membrane at the base of the neck (*Nk*). The large lateral eyes (*E*) are called the *compound eyes,* because each is composed of a great number of separate eye elements forming little hexagonal *facets* visible on the surface. All of the facets together constitute the *cornea,* or transparent outer surface of the eye, the dark color being located in the deeper parts. The compound eyes are developed on the first embryonic segment. On the forehead of the grasshopper are three other small, simple eyes, called the *ocelli* (*O*). Two are placed just above the bases of the antennæ (*Ant*), the other median one is between and slightly below the antennal bases.

While the form of the head may vary much in different insects, the mouth parts undergo still greater modifications in their adaptation to the diversity of feeding habits which various groups of insects have adopted, and, in many cases, furnish characters distinctive of the orders.

### 2. THE HEAD OF THE HONEYBEE

A study only of the skeleton of the head is here included, but, since this comprises both external parts and internal parts, it is convenient to subdivide the subject accordingly.

**The External Structure of the Head.**—The general external appearance and structure of the head of a worker bee is shown from before and behind by Fig. 6. In facial view (A) the head is triangular, with the apex below. The side angles are rounded and capped by the great compound eyes (*E*). In the opposite direction the head is very much flattened, the face being convex, while the rear surface (B) is somewhat hollowed to fit snugly on the anterior end of the thorax. The three ocelli or simple eyes (A, *O*) are situated on top of the head with the median one in front of the others. The antennæ (*Ant*) arise close together from the face between the lower halves of the compound eyes, where each is inserted into a small circular membranous socket

of the head wall. The mouth parts are attached to the lower part of the head. The *labrum* is the wide, free, transverse flap (A, *Lm*) at the lower edge of the face. The *mandibles* are the strong jaw-like organs (*Md*) closing behind the labrum and hinged to the lateral parts of the head below the compound eyes. The *mouth* opens between the bases of the mandibles. Behind the mandibles is a composite organ with its terminal parts prolonged to form a *proboscis* (Fig. 2, *Prb*). In Fig. 6 the proboscis (A, *Prb*) is shown cut off near its base, but it is seen to consist of the *maxillæ* (*Ga*) and *labium* united at their bases (B). The

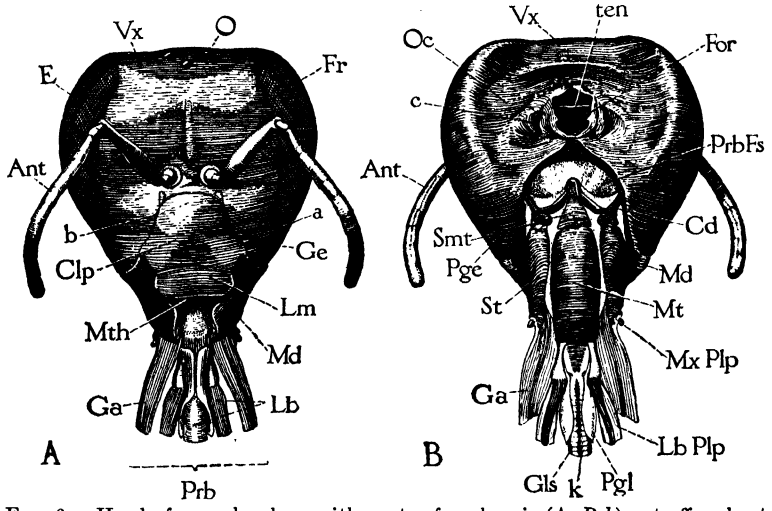



FIG. 6.—Head of a worker bee, with parts of proboscis (A, *Prb*) cut off a short distance beyond their bases.

A, anterior view. B, posterior view. *a*, clypeal suture; *b*, pit at origin of anterior tentorial arm; *c*, pit at origin of posterior tentorial arm.

single, long, slender, flexible member of the labium that extends beyond the tips of the maxillary lobes in the worker is commonly called the *tongue* or *glossa* of the bee (Figs. 2, 8 A, *Gls*). The details of the proboscis and its uses are described in section 5 of this chapter.

The walls of the head capsule of the bee are not marked by sutures to the extent that they are in some of the lower insects, but cranial regions may be distinguished and named as on the head of the grasshopper (Fig. 5). Thus the top of the head is the *vertex* (Fig. 6, *Vx*), the upper part of the face is the *front* (A, *Fr*), the antennæ being inserted much lower than in the

grasshopper, the cheeks are the *genæ* (*Ge*), shortened by the greater length of the eyes in the bee, and the area on the back of the head (B) consists of the *occiput* (*Oc*) above and the *postgenæ* (*Pge*) below. The only distinct sclerite in the cranium of the bee is the *clypeus*, the large median plate on the face (A, *Clp*) between the bases of the antennæ and the labrum. The sclerite is defined by a suture (*a*) which arches upward below the antennal bases and ends ventrally on the sides at the bases of the mandibles. Since it carries the anterior mandibular articulations the plate evidently comprises both clypeus and epistoma of the head of the grasshopper (Fig. 5, *Clp*, *Epst*). The upward curve of the suture in the bee enlarges the epistomal region of the sclerite. Two pits in the suture (*b*), near the upper transverse part, mark the anterior roots of the internal tentorium.

The posterior wall of the head (Fig. 6 B) is perforated by a large pentagonal hole, the *foramen magnum* (*For*), by means of which the head cavity communicates through the membranous neck with the cavity of the thorax, and through which pass the œsophagus, the blood vessel, and the air tubes and nerves that extend between the head and the thorax. A small transverse rod (*ten*) seen within the foramen is a part of the internal skeleton of the head, the posterior roots of which are marked by two large pits (*c*) in the occiput, one on each side of the foramen magnum.

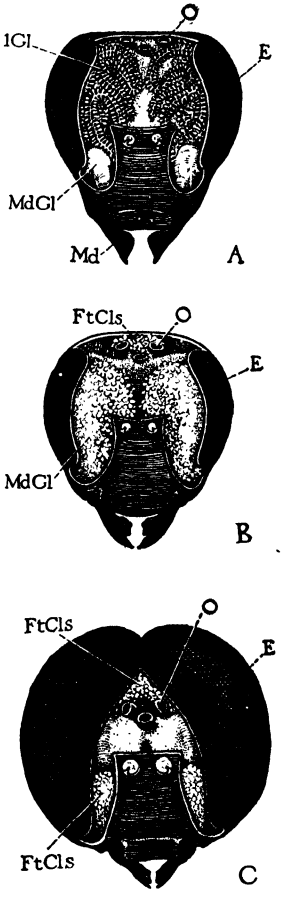



FIG. 7.—Head of worker (A), queen (B), and drone (C), facial view, with antennæ and proboscis cut off, and parts of the face removed to expose the pharyngeal glands (*1Gl*) in the worker, and the mandibular glands (*MdGl*) in the worker and queen.

*E*, compound eye; *1Gl*, pharyngeal gland; *Md*, mandible; *MdGl* mandibular gland; *FtCls*, fat cells; *O*, ocellus.

The base of the proboscis is loosely suspended in a large membranous cavity, the *fossa of the proboscis* (Fig. 6 B, *PrbFs*), forming a deep notch shaped like an inverted U in the posterior wall of the head between the postgenæ (*Pge*) and below the foramen magnum.

The heads of the worker, the queen, and the drone differ conspicuously in size and shape, as may be seen by comparing A, B, and C of Fig. 7. In these drawings the front has been removed in order to show various internal parts to be described later. While the head of a worker (A) is triangular in facial view, that of the queen (B) is more rounded on the sides and is wider in proportion to the length. The queen's head is somewhat smaller than the worker's head, but that of the drone (C) is much larger than the head of either of the female forms and is nearly circular in outline. The compound eyes (*E*) of the worker and the queen are about equal, but those of the drone are enormously enlarged and are broadly contiguous on the vertex, crowding the ocelli (*O*) down toward the bases of the antennæ. The antennæ of the drone consist of 13 segments, while those of the queen and worker have but 12 segments. The mandibles (*Md*) are largest in proportion to the size of the head in the queen, and are very small in the drone. Those of the worker have a smooth terminal edge, while this edge is notched and toothed in the queen and drone. The parts of the proboscis are much longer in the worker and capable of much more action than in the queen and the drone, which are almost wholly dependent on the workers for their food.

**The Internal Structure of the Head.**—The internal structure of the cranium may be best studied in longitudinal sections of the head. Figure 8 shows a vertical slice of the cranium of a worker (A) and of a drone (B) between the median plane and the outer edges of the antennal and mandibular bases. Such sections may be made by imbedding the head in paraffin and then cutting it as desired with a sharp knife or a razor. In the figure of the drone (B) the pharynx (*Phy*), œsophagus (*Œ*) and neck are retained. Figure 29 shows the inner skeleton of the lower half of the head wall.

The principal parts of the internal skeleton of the head, or *endocranium*, consists of two large, oblique, strongly chitinous bars forming braces between the front and the back walls of the head (Fig. 29, *Ten*, shown only on the left side in Fig. 8). These

bars in the bee were named by Macloskie (1881) the *mesocephalic pillars*. Their bases are connected by the slender transverse bar (*ten*) already noticed, arching across the foramen magnum (Fig. 6 B, *ten*). This bar and the two pillars represent a structure common to all insects and known as the *tentorium*. In the embryo the tentorium is formed from tubular ingrowths of the head wall, which, uniting across the middle, form the transverse

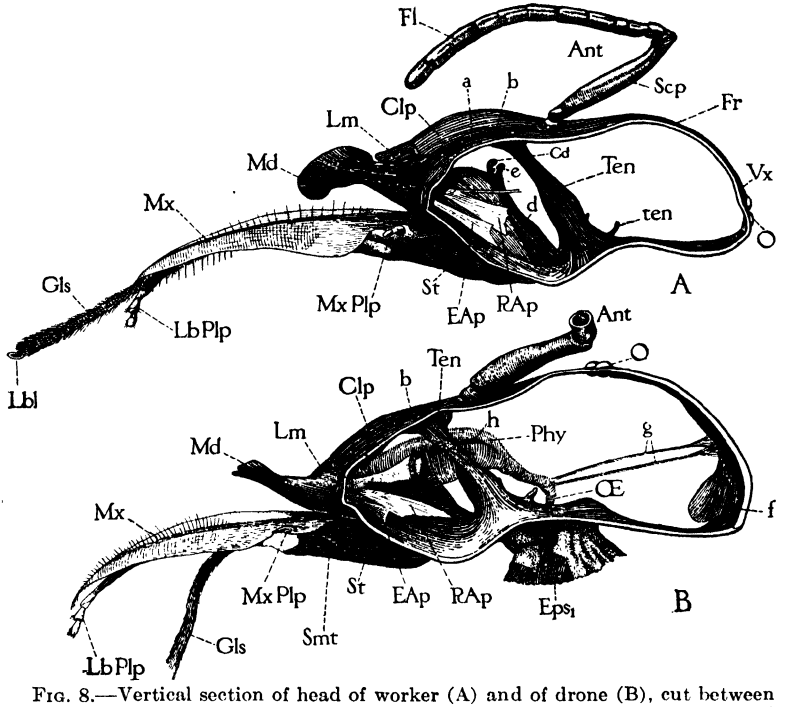



FIG. 8.—Vertical section of head of worker (A) and of drone (B), cut between median plane and bases of antenna (*Ant*) and mandible (*Md*) of left side. All soft parts removed except pharynx (*Phy*) and œsophagus (*Œ*) of drone.

*a*, clypeal suture; *b*, pit at anterior root of tentorium; *d*, posterior edge of wall of fossa of proboscis; *e*, articular knob of maxillary suspensorium; *f*, internal median crest on vertex of drone; *g*, suspensorial ligaments of œsophagus; *h*, pharyngeal rod.

part or body, which may be either a narrow bar as in the bee or a wide plate as in many other insects. The points of origin of the tentorial arms in the bee show externally as the pits already noted, those of the *anterior* arms being in the clypeal suture (Fig. 6 A, 8 A, B, *b*), those of the *posterior* arms being at the sides of the foramen magnum (Fig. 6B, *c*). In some insects a third or *dorsal* pair of arms arises near the bases of the antennæ.

The side walls of the fossa of the proboscis are inflected as two high, thin vertical plates, as seen from the interior of the head (Fig. 8 A, *d*) in front of the tentorial pillars (*Ten*). The free edge of each of these plates in the worker is so much thicker than the basal part that it appears at first sight to be a separate endocranial structure. The upper angle of each plate projects as a free process (*e*) to which is articulated the basal piece of the maxilla (Fig. 6 B, *Cd*). It thus constitutes the *maxillary suspensorium*. (Macloskie includes under this term both the process of the cranial wall and the basal piece or *cardo* of the maxilla.)

In the head of the drone (Fig. 8 B) the shape of the tentorial pillars and of the maxillary suspensoria are somewhat different from those of the worker (A), and there is a thin, internal ridge (*f*) along the midline of the vertex between the compound eyes, which is not present in the worker.

Besides these apodemes of the cranial wall there are others that project into the head cavity from near the bases of the mouth appendages for the attachment of muscles that move the appendages. Such apodemes are specially developed in connection with the mandibles and will be described in the discussion of these organs.

### 3. THE ANTENNÆ AND THEIR SENSE ORGANS

The antennæ are the two slender, jointed, movable appendages of the head (Fig. 6 A, *Ant*), attached near the center of the face in the bee, where each is inserted into a membranous socket just above the upper part of the clypeal suture (*a*).

**The Structure of the Antennæ.**—Each antenna consists of two parts that form a prominent elbow with each other, the two being usually so held in life that the first or proximal part extends outward, forward, and upward from the basal attachment and carries the other in a pendent position, from its distal end. The first part, called the *scape* (Figs. 10 A, 18, *Scp*), consists of a single long joint inserted into the antennal socket of the head by a prominent knob on its base turned toward the face. This articulating knob is attached to the rim of the socket by a circle of membrane, but it is also pivoted on a slender peg-like process projecting upward from the lower edge of the socket. Hence, the antenna is free to move in any direction but, at the same time, is held firmly in position by the pivot. The second or distal

division of the antenna, distinguished as the *flagellum* (*Fl*), is cylindrical and much longer than the first. It is composed of 11 small joints in the worker and queen, and of 12 in the drone. The first joint is somewhat thicker than the others and is slightly bent (Fig. 10 A, 1*Fl*). Its base is articulated freely to the end of the scape, but its distal end is attached to the second joint by a narrow ring of membrane which permits of but little motion. The second joint widens a little toward its distal end, but the rest are short cylinders of even diameter, except the last which is rounded and obliquely flattened at the end. These joints have deeply inflexed rims at their adjoining ends connected by short membranes.

Each antenna is a hollow outgrowth of the head wall and its cavity or lumen is continuous with the cavity of the head. Four muscles that move the antenna as a whole are inserted on the base of the scape and attached at their other ends to the inner face of the large tentorial arm (Fig. 29, *Ten*) of the same side. The muscles that move the flagellum independently are situated in the scape and are inserted on the base of the first joint of the flagellum. The flagellum itself, however, contains no muscles and consequently, though the nature of its articulations gives it much flexibility, its joints cannot be individually moved. The lumen of the antenna is traversed by tracheal trunks and by a double antennal nerve (Fig. 86, *AntNv*) arising from the corresponding antennal lobe of the brain (Fig. 87, *AntL*).

**The Senses of Insects.**—Popularly the antennæ of insects are known as "feelers" because they are constantly moved about in all directions with a nervous kind of motion as if the insect were feeling its way along by means of them, and there can be no doubt that the antennæ are the seat of perceptive senses of some sort by means of which insects acquire much "information" concerning their surroundings and their companions. Moreover, a minute examination of the antennæ shows that they contain a large variety of organs with nerve connections which can be explained only as sense receptors. The study of insect senses, however, is a most elusive subject and one that becomes more so the further we consider 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, for example, are perceived also by insects when placed near them, and likewise that they get impressions of objects and of movements, and perhaps distinguish the colors and in a vague way the shapes of different objects. Furthermore, it is known that some of their perceptions are more delicate than ours, and it has been claimed that certain insects see color where we see none. They may even possess senses of which we have no conception.

Hence, while it can be stated that insects perceive those differences in external things which we call touch, taste, smell, sound, color and shape, and act accordingly, we cannot say what the sensations they acquire from these same properties may be like. In fact, we do not know that insects have conscious sensations at all, for what looks like an action due to conscious perception may be purely a reflex one, unaccompanied by any sensation. The question of whether or not an insect is possessed of consciousness is one that cannot be answered one way or the other. Understanding, then, that our knowledge of insect senses amounts only to this, that many things which give us certain sensations make also impressions of some sort on the insect, which vary in kind and degree much as they do in us, we may proceed with a study of the sense organs located on the antennæ and with a review of the experiments made to determine their functions.

**Varieties of Antennal Sense Organs in the Honeybee.**—A close examination of a bee's antenna shows first that it is covered with many hairs of various kinds, though none of them are of the branched variety. The hairs on the scape (Fig. 10 A, *Scp*) are longer and scattered, those on the first joint of the flagellum (1*Fl*) are short and straight. All of these hairs are probably ordinary setæ containing prolongations from hypodermal cells but without nerve connections (Fig. 4 F, G). The rest of the flagellum is thickly covered with very small pale hairs, which give the flagellum a grayish, furry appearance. The hairs of this size on the second and third joints (Fig. 10 A) are thicker than the others and have their tips distinctly recurved. They are set in sockets of the cuticula but appear to have no connections with the hypodermis. The hairs of the last eight joints in the worker are more slender and mostly curved toward the tip of the antenna (B, *SHr*), and each contains an axial strand (C, *b*) from a group of

hypodermal sense cells that penetrates the cuticula by a channel or pore beneath the hair. Such hairs are, therefore, the outer parts of sense organs. At the distal end of each joint of the flagellum except the first and the last there is a fringe of longer, slightly recurved hairs (B, *Hr*). Between them, at the distal ends of the fourth to the tenth joints of the flagellum, are a few hairs of a different type which occur more abundantly on the end of the eleventh segment. These hairs (A, B, *SPg*) are thick and blunt, but have transparent walls through which may be seen a core of protoplasmic tissue that arises from sense cells beneath the cuticula. Sensory hairs of this shape are called *sense pegs* (B, C, *SPg*) to distinguish them from the more slender hairs. Finally, sections of an antenna reveal still other hairs of a sensory nature sunken into pits beneath the surface of the cuticula and therefore designated *pit hairs* or *pit pegs* according to their length (D, E). The more shallow ones on the antenna of the bee are called by some foreign writers the *champagne-cork organs* (D), while the deeper ones are distinguished as *flask-shaped organs* (E). In some insects there are organs of the last kind very deeply sunken with long tubular necks reaching to the exterior. These are known as *Forel's flasks*, but organs of this sort do not occur in the bee.

Besides the hair organs there are three other kinds of sense organs on the bee's antenna. One of these is the most characteristic and the most numerous of all the antennal organs, appearing externally as innumerable small elliptical plates closely distributed over the last eight joints of the flagellum except on a narrow band along the outer side (A, B, *SPl*). These are the *sense plates*, or "pore plates" of some writers. An organ of a different kind, known as the *organ of Johnston*, occurs in the basal segment of the flagellum (H, *SCls*), being indicated externally only by a circle of pits in the membrane between this segment and the next (A, *Pi*). Finally, on the inner surface of the base of the scape, are two sets of minute pores (I, *Po*) each receiving the end of a sense-cell prolongation (J).

**Classification of Antennal Sense Organs.**—In all, therefore, eight different varieties of sense organs have been distinguished on the antennæ of the honeybee. Five of them have the external part in the shape of a hair or peg, one is characterized by the plate-like form of its exposed part, and the other two appear only as pits or pores on the surface. In any case the true sense organ

is a complex of parts formed from the cuticula and from the hypodermis, limited internally by the basement membrane, and with one or more of the hypodermal cells sensitized by nerve connections. The entire sense organ is known as a *sensillum*. One having the external part in the form of a hair is distinguished as a *sensillum trichodeum* (Fig. 10 C, *SHr*), according to the commonly adopted classification of Schenk (1903); one in which the external part is peg-shaped or cone-shaped is a *sensillum basiconicum* (C, *SPg*); a hair, peg, or cone in a shallow pit is a *sensillum cœloconicum* (D); a deeper pit

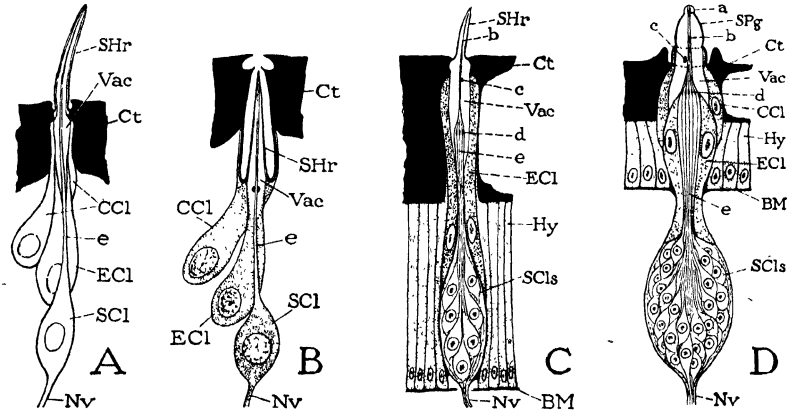



FIG. 9.—Diagrammatic structure of antennal sense organs of Hymenoptera.

A, the elements of a sensillum, comprising a sense hair (*SHr*) projecting from the cuticula (*Ct*), a distal enveloping cell or cap cell (*CCl*), a proximal enveloping cell (*ECl*), and a sense cell (*SCl*) with proximal nerve (*Nv*) and distal prolongation (*e*) through a vacuole (*Vac*) into the hair (*SHr*).

B, sensillum ampulaceum of the honeybee (*diagrammatic after Vogel*, 1923), the sense hair (*SHr*) sunken in a flask-shaped pit.

C, sensillum trichodeum of a wasp (*diagrammatic after Vogel*), with group of sense cells (*SCls*) in hypodermis (*Hy*) giving off a fasciculus of distal strands (*e*) containing sensory rods (*d*) and ending in terminal strand (*b*). *c*, "secretion body" in liquid of vacuole (*Vac*).

D, sensillum basiconicum of a wasp (*diagrammatic after Vogel*), in which the sense cells (*Scls*) form a group projecting into cavity of antenna beyond layer of normal hypodermis (*Hy*). *a*, cupola of thin membrane at end of sense peg or cone (*SPg*).

constitutes a *sensillum ampullaceum* (E); and a plate organ is a *sensillum placodeum* (F). The sensilla trichodea, or organs of the hair type, however, are not all alike. Amongst those on the antennæ of wasps and bees, Vogel (1923) distinguishes two kinds; in one the hair contains a prolongation from a single hypodermal sense cell, in the other it contains a compound strand from

a number of sense cells. The first, probably represented in the bee by the slender recurved hairs (B, *Hr*) at the distal ends of the joints of the flagellum, is the most simple of insect sense organs of the hair variety, and such sensilla are usually regarded as organs of touch. Many organs of this kind, described by McIndoo (1916), in which the hair takes on various shapes (Fig. 19) occur also on or near the mouth parts of the bee. The sensilla trichodea of the second kind are more allied in their internal structure to the sensilla basiconica and placodea and so far as known in the bee occur only on the antennæ. The organ of Johnston is perhaps to be classed as a *chordotonal organ*, a more typical example of which occurs in the leg (Fig. 43), while the pore organs either represent a distinct type of sense organ or possibly are to be regarded as a variety, of the sensilla placodea.

**General Structure of Insect Sense Organs.**—The student will probably find the various descriptions of insect sense organs given by different writers very confusing and unsatisfactory on account of their lack of uniformity. But he must not expect such definite statements in insect histology as he finds in textbooks on human histology, because the minute structure of insects is a very difficult thing to study and has been the subject of comparatively few careful investigations. Any of our present ideas, therefore, particularly those concerning the structure and function of the sense organs must he held subject to revision and possible rejection. Yet, it appears now that a large number of the sensilla of insects conform to one general plan of structure, involving an external cuticular part and internal cellular parts, the latter consisting of three sublying hypodermal cells or multiples of them (Fig. 9 A). The outermost of these cells, known as the *distal enveloping cell* or *cap cell* (*CCl*), is probably the original chitinogenous cell that formed the cuticular part of the organ, corresponding with the trichogenous cell of an ordinary seta (Fig. 4 F, G, *HrCl*). The next one within is the *proximal enveloping cell* (Fig. 9 A, *ECl*). The innermost cell is the *sense cell* (*SCl*). This last is not a "nerve cell" or "ganglion cell" as it was commonly called by earlier writers, but a hypodermal cell which has been penetrated at its base by a nerve fiber (*Nv*) and thus secondarily converted into a sense cell. In this respect the insect sense cell is comparable with the taste buds of vertebrate animals and not with the olfactory cells which are said to be true nerve cells. The distal end of the sense cell sends out

a long slender process (*e*) which penetrates the two enveloping cells and reaches to the tip of the hair or other external part. It is often surrounded by a vacuole (*Vac*), which is enclosed by one or both of the enveloping cells and continuous into the hollow of the hair when a hair is present. The vacuole appears to contain a liquid that bathes the terminal strand of the sense cell, and which perhaps in some cases exudes on the external surface of the organ. The sensilla cœloconica and ampullacea, as described by Vogel (Fig. 9 B), are constructed according to this simple type with the modification of having the external peg or hair (*SHr*) sunken into a pit of the cuticula.

**Structure of a Typical Hymenopteran Sensillum.**—The sensilla of the small curved hairs of the bee's antenna (Fig. 10 B, *SHr*) and those of the pegs (*SPg*) and the plates (*SPl*) are more complicated in their internal structure than the simpler type of organ just described (Fig. 9 A), but their cellular parts are still referable to the three fundamental cells or to multiples of them. The structure of the sensillum basiconicum of a wasp (Fig. 9 D) has been described in particular detail by Vogel and may be taken as typical of all organs of this sort. The external cone here has chitinous side walls (*SPg*), but it is capped by a membranous *cupola* (*a*). A delicate axial strand (*b*) prolonged from the sense cells traverses the cone and spreads out on the under surface of the cupola. Beneath the base of the cone the strand enlarges to a thick bundle or *fasciculus* of fibers (*e*) that springs directly from the deeper-lying sense cells (*SCls*). The terminal strand (*b*) is surrounded by a large vacuole (*Vac*) contained within the distal enveloping cell (*CCl*) which fills the cuticular cavity beneath the cone, and it is shut in below by two proximal enveloping cells (*ECl*) that surround the fasciculus (*e*).

In organs of this sort the multiple sense cells (Fig. 9 D, *SCls*) form a compact mass with a nerve branch (*Nv*) penetrating its base from one of the nerve trunks of the antenna. Vogel says it can be shown by the Golgi method of staining that the nerve branch to the sense organ consists of a bundle of minute nerve fibers each of which goes to a single sense cell and penetrates the base of the latter, not branching over its outer surface as claimed by Berlese, though the outer sheath or neurilemma of the nerve spreads over the base of the sense-cell mass. The fibers of the fasciculus (*e*), on the other hand, are slender prolongations

of the cells themselves, and are continued through the slender terminal strand (*b*) to the cupola (*a*) at the end of the cone. Each of these fibers, just where the strand enlarges into the fasciculus, contains a differentiation of some sort (*d*), noted by several investigators, but definitely described by Vogel as a clear elongate rod, about 3 microns in length, containing two dark-staining granules. The vacuole (*Vac*) surrounding the strand and continuing to the tip of the cone, Vogel says, is filled with a clear mucous secretion apparently formed by the two basal enveloping cells or also by the distal cell, and this fluid he thinks must diffuse upon the outer surface of the cupola since staining shows that liquids easily pass through the thin walls of the latter. Vogel believes, therefore, that sensilla of this type are olfactory in function, that the exuded liquid takes up the odor substance and carries it as a fine emulsion to the terminal fibers of the sense cells. Within the vacuole and usually close to the terminal strand Vogel finds a minute corpuscle (*c*) which he says stains in eosin, gold chloride, and iron hematoxylin and which he calls the *secretion body* on account of its position, though he can suggest nothing of its nature or function.

In the wasp the mass of sense cells belonging to each sensillum basiconicum (Fig. 9 D, *SCls*) projects below the general level of the basement membrane (*BM*) into the lumen of the antenna, but in the hair organs of this type (C) and in the plate organs the sense cells are enclosed between normal hypodermal cells (*Hy*) and do not bulge into the cavity of the antenna. In the honeybee (Fig. 10 G) the sense cells of all the antennal sense organs beyond the third joint of the flagellum form a thick layer (*SCls*) continuous around all the sensilla-bearing part of each joint but beneath an outer layer of ordinary hypoderm cells (*Hy*). The sense-cell layer presents an even inner surface limited by the basement membrane (*BM*), but on account of its absence along the outer side of the antenna, the lumen of the latter is eccentric. Cell boundaries are not distinct in the sense-cell layer of the bee, but the numerous oval nuclei are very prominent.

**Structure of Antennal Sensilla of the Honeybee.**—The external forms of the various sense organs found on the antennæ of the honeybee have already been described (page 20), and it has been shown that, with the exception of the organ of Johnston, they may be classified according to their cuticular parts as hair organs, plate organs, and pore organs.

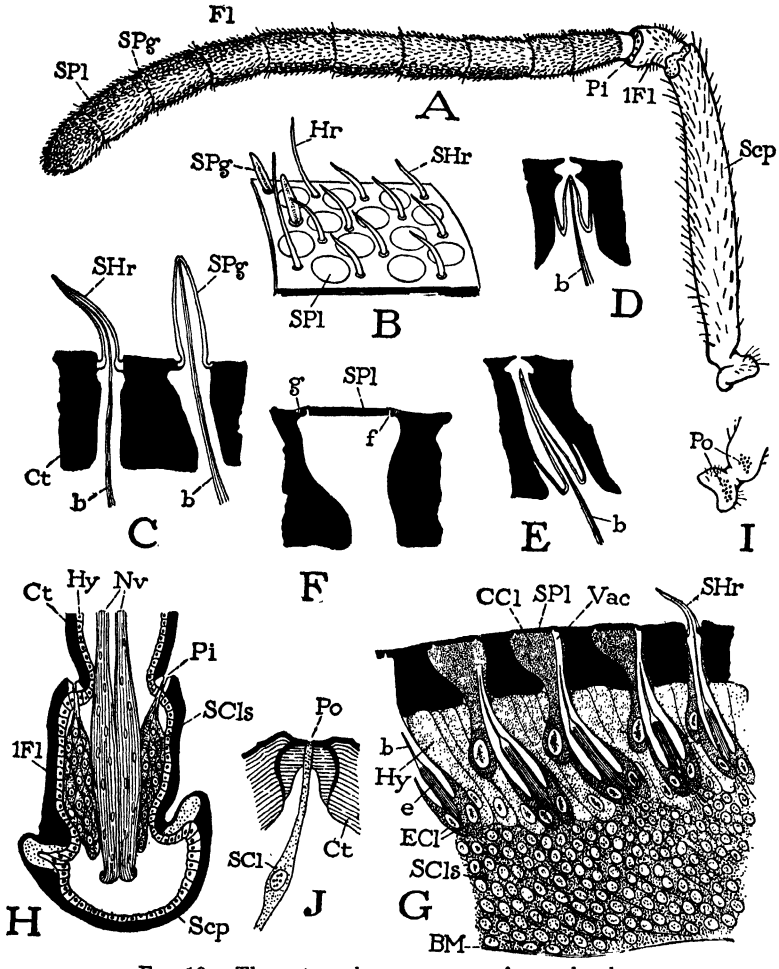



FIG. 10.—The antennal sense organs of a worker bee.

A, left antenna, outer surface, showing division into scape (*Scp*) and flagellum (*Fl*). *Pi*, pits of organ of Johnston (H) in membrane between first and second joints of flagellum, *SPg*, sense peg; *SPl*, sense plate.

B, part of surface of flagellum beyond third joint, showing recurved hairs (*Hr*), sense hairs (*SHr*), sense pegs; (*SPg*), and sense plates (*SPl*).

C, section through a sense hair (*SHr*) and sense peg (*SPg*) with sublying cuticula (*Ct*) and penetrating strands (*b*, *b*) from sense cells.

D, a shallow pit peg, or "champagne-cork organ." E, a deeper pit peg, or "flask-shaped organ"

F, vertical section through a sense plate (*SPl*) and supporting cuticula. *f*, circular groove on under surface; *g*, circle of thin chitin on outer surface.

G, vertical longitudinal section through part of wall of flagellum, showing sensilla placodea (*SPl*) and a sensillum trichodeum (*SHr*). *b*, terminal strand of sense cells; *BM*, basement membrane; *CCl*, distal enveloping cell or cap cell; *e*, fasciculus of sense cell processes; *ECl*, basal enveloping cells; *Hy*, hypodermis; *SCls*, sense cells; *SHr*, sense hair, *SPl*, sense plate; *Vac*, vacuole.

H, longitudinal section through organ of Johnston in first segment of flagellum (1*Fl*) with end of scape (*Scp*) at right angle to flagellum (see A).

I, group of sense "pores" (*Po*) on base of scape. J, section of "pore" organ (*from McIndoo*).

*The Hair Organs.*—Under this heading we may include all the sense organs in which the cuticular part has the form of a hair, whether the hair be slender or thick, exposed on the surface or sunken into a pit.

The most numerous sense organs of this type on the antenna of the honeybee are those of the small, pale, curved hairs that cover the last eight joints of the flagellum in the worker (Fig. 10 B, C, G, *SHr*). Each hair is about 30 microns in length and has very thin walls through which may be seen an axial protoplasmic strand from the sublying sense cells. Other sense organs with the external part in the form of a hair comprise those of the more slender recurved hairs found at the distal ends of the joints of the flagellum (B, *Hr*). These two forms of hair organs are usually distinguished as the sensilla trichodea. The external parts of the peg organs, or sensilla basiconica, of the bee (B, C, *SPg*) are merely thicker straight hairs of about the same length as the small curved ones. They lack the terminal membranous cap or cupola described by Vogel for the corresponding organs of the wasp (Fig. 9 D, *a*). The cuticular parts of the pit-peg organs, or sensilla cœloconica, of both varieties in the bee (Fig. 10 D, E) are likewise but hairs sunken into cavities of the cuticula.

The hypodermal elements in the organs of the slender recurved hairs (B, *Hr*) are said by Vogel to consist of but a single sense cell connected with each hair, as in the sense organs of the mouth parts (Fig. 19 F, D). The cellular parts in all the other hair-like sensilla of the antenna of the honeybee, however, are more complicated and are essentially the same as those of the sensilla placodea. In the following account of the plate organs, therefore, the description of the hypodermal parts will apply to the organs of the small curved hairs and the sunken hairs as well as to those of the plates.

*The Plate Organs.*—The sensilla placodea or sensory plate organs of the antennæ are so similar in their internal structure to the organs of the hair or peg type as to suggest that the plates are but basal remnants of hairs, or are hairs modified in some other way. The plates on the antenna of a worker bee (Fig. 10 B, *SPl*) are elliptical in form and about 12 to 14 microns in longest diameter, which is lengthwise on the antenna, and have plane, smooth exteriors. They are usually flush with the surface of the antenna, though in sections they are sometimes slightly

elevated or depressed. Each is surrounded by a narrow, pale line, and usually a second less distinct line closely encircles the first. Beneath the plate is a large cavity (F), which is clearly homologous with the hair canals of the other organs (C). The cavity is asymmetrically narrowed at its inner end, the wall toward the base of the antenna being approximately vertical while the opposite one slopes toward it. The under side of the plate has a narrow groove (*f*) all around its edge which shows on the surface as the inner pale line just noted. External to the groove and concentric with it there is usually a narrow, non-chitinized ring in the outer part of the cuticula (*g*) which forms the external pale line seen on the outer surface. McIndoo (1922) has described the outer ring as an external groove, but the writer does not see it as such, and the surface is often convex over it; sometimes it is not visible at all. The plate itself is very thin, about 1.5 microns thick, and is weakly chitinous, but the part over the groove is an extremely delicate film not more than .5 of a micron in thickness.

The cellular parts of the plate organs differ only in details of form or proportion from those of the hair and peg organs. The cavity beneath the plate is occupied by a large distal enveloping cell or cap cell (Fig. 10 G, *CCl*) having its basal end prolonged inward beneath the cuticula and containing a large nucleus. In longitudinal sections the nuclei of the cap cells form a very conspicuous row of large oval bodies through the middle of the layer of normal hypodermal cells (*Hy*). The part of each cap cell toward the base of the antenna is excavated by the neck of a long flask-shaped vacuole (*Vac*) which lies very close to the vertical wall of the cuticular cavity and ends beneath the groove at the basal end of the plate. The inner end of the vacuole lies in the lower half of the normal hypodermal layer (*Hy*) and is surrounded by the distal parts of two proximal enveloping cells (*ECl*). Each vacuole contains a cylindrical bundle of sense-cell processes (*e*) ending in a terminal strand (*b*). The latter extends into the neck of the vacuole, but in sections examined by the writer it was not seen in any case to reach as far as the plate—a condition which might be due to poor fixation, since both von Frisch (1921) and Vogel (1923) describe the terminal strand in the plate organs of the bee as attached to or very near the groove. In the wasp (*Vespa vulgaris*), according to Vogel, the strand attaches to a median longitudinal furrow of the plate, though Ruland (1888) claimed that it does not reach the plate. Schenk (1903) and

McIndoo (1922) evidently mistook the distal enveloping cell for a prolongation from the sense cells, for McIndoo (in his Fig. 13, 1922) shows a long stalk, which he calls a "nerve strand," arising from the sense cells and expanding at its distal end against the entire under surface of the plate. He entirely overlooks the vacuole and the true sensory processes. Such a mistake, however, might be made by examining cross-sections alone since the vacuoles and the bundles of sense-cell fibers slant distally from the base of each joint of the flagellum.

The thick parts of the bundles, or fasciculi, of sense-cell processes (*e*) stain deeply in hematoxylin and stand out prominently in their vacuoles. At their distal ends, however, where they contract to form the terminal strands, they are pale, and just within the darker part there is an appearance of a transverse layer of minute, transparent rods. Vogel has described and figured very definitely the presence here of sense rods in the sense-cell fibers of the plate organs similar to those he describes in the other organs, but specimens of both the plate and the hair organs of the bee examined by the writer, in which the fibers were frayed and separated at this point, suggest that the appearance of rods is due rather to clear spaces between the darkly stained fibers. At any rate there is some structural differentiation here which possibly needs closer investigation before we can be sure of its true nature.

The number of sense plates on the antennæ of the honeybee has been calculated by Schenk, McIndoo and Vogel, and from their figures, which are reasonably close, it appears that there are from 2,000 to 3,000 plates on the antennæ of the queen, 5,000 to 6,000 in the worker, and about 30,000 in the drone. The total number of sense cells for all the organs of one antenna of a drone bee has been estimated by Vogel at about 500,000.

*The Organ of Johnston.*—The organ supposedly of a sensory nature located in the first joint of the flagellum (Fig. 10 H) is of huge size as compared with the others but is of a simpler structure. It consists of a cylindrical sheath of sense cells (*SCls*) surrounding the antennal nerves (*Nv*) through nearly the entire length of the joint. The cells have long slender necks directed distally and attached in groups to the inner ends of small pits (A, H, *Pi*) in the articular membrane between the first and second joints. The basal ends of the cells are probably connected with branches of the antennal nerves in the distal end of the scape (*Scp*). This organ appears, therefore, to consist simply of groups of sense cells

attached directly to the cuticula, and is clearly a simplified example of that known as Johnston's organ which is present in many insects and most highly developed in the mosquitoes and gnats. Child (1894) has shown that the sense cells of the organ are developed from an involution of the hypodermis, and that in the mosquito each cell is prolonged distally into a slender strand containing a small rod-like differentiation in its base. This is very suggestive, therefore, that the organ has the same essential structure as the other antennal organs, and, if there are sense rods in the cell processes as described, there is suggested furthermore a comparison with the more highly developed sense organs in the tibia of the bee (Fig. 43) and the so-called chordotonal organs of other insects in which rods known as scolopalæ appear to be essential elements.

*The Pore Organs.*—The sense pores on the base of the antenna appear externally as two groups of minute pits on the inner surface of the proximal end of the shaft of the scape and its basal knob (Fig. 10 I, *Po*). Beneath each pit, as described and figured by McIndoo (1914), there is an inverted flask-shaped differentiation of the cuticula (J) set off by darkly chitinous walls from the rest of the cuticula. The center of this is perforated by a channel that receives a prolongation from a sublying sense cell (*SCl*). McIndoo calls this a "sense fiber," the end of which, he asserts, comes to the surface in the pit where it is actually exposed to the air. Insect anatomists, however, will not generally concede that protoplasmic tissue ever penetrates the cuticula, or that the cuticula itself is ever lacking at any point. Erhardt (1916), in describing similar organs on the wing base in other insects, says that the channel of the cuticula is closed by a very fine membrane, and that there is never a perforation in the membane. Furthermore, as in the other sense organs, the "nerve" is but a prolongation from a hypodermal sense cell. The pore organs are widely distributed on other parts of the body of the bee and occur in many other groups of insects.

**Résumé of Antennal Sense Organs of the Bee.**—Detailed studies of the bee's antennæ, then, have shown that these organs are richly provided with nerve-end organs of at least seven different kinds, most of which are confined to the antennæ, though some are much more numerous on other parts of the body. The structure of the organs is such that no one doubts their sensory nature, and from experiments we can be fairly sure that

insects get sensations of some sort from their surroundings, since they react to things that give us sensations. These two steps in the study of insect senses are easy, but the investigator is confronted by a difficult problem when he attempts to assign the different sense reactions of the insect to the various sense organs he finds distributed over its body. There is little unanimity of opinion yet as to what sense function belongs to any particular set of sense organs, except the eyes.

**The Nature of the Antennal Senses.**—All the organs of the flagella of the bee's antennæ, except perhaps the longer sensory hairs, have been regarded by one writer or another as olfactory in function. Schenk (1903), however, suggested that the plate organs, delicately hinged as they are to the encircling cuticula, are organs for registering air pressure, possibly giving information of the proximity of objects in the darkness of the hive. Their great numbers in the drone, however, and their presence in other insects does not conform with such an explanation. McIndoo does not believe that any of the organs of the antennæ except the pores on the base of the scape are organs of smell, and he discredits in particular the idea that the plate organs have an olfactory function both because he believed the sense-cell strands ended against the plate and because his experiments on live bees (to be outlined presently) indicated to him that bees smell but slightly if at all with the antennæ. Since, however, the vacuoles containing the true sense-cell strands of the plate organs end against the exceedingly thin cuticula of the grooves, which is but half a micron in thickness, the idea of odor substances penetrating the vacuoles is not so unreasonable. Though there is no evidence of a liquid being discharged on the outer surfaces of the plates as claimed by Berlese, a small amount sufficient to absorb odor particles might exude from the vacuoles into the grooves as suggested by Vogel.

We cannot here review all the experiments that have been made on the senses supposed to be located on the bee's antennæ, and, therefore, only the later and more important ones are given. In the matter of experiments, however, the worker is confronted by another difficulty, for while at first thought it seems very easy to hold some strong-smelling substance near the antenna of a beetle, an ant, or a 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 produce an irritation or a pain in the nerves of the sense organs or in those of the thin membranous parts of the skin, and the reaction of the insect might not indicate a perception of odor on its part any more than our blinking would indicate that we smell such things as formaldehyde or strong ammonia with our eyes if these substances are held close to our faces. Furthermore, irritant gases and volatile liquids affect the mucous membranes of our 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 long ago pointed out by Forel, experiments on the sense of smell should be made with odors that concern the insect in its natural habitat, which would be principally the odors of the things on which it feeds.

*Experiments by McIndoo.*—Two investigators recently have carried out large series of experiments first to find out if bees possess a sense of smell, and second to determine the location of the perceptive organs. McIndoo (1914) worked with bees confined in flat cages where their reactions to odors could be carefully noted. His cages were triangular in shape, 10 inches long on two sides, 6 inches at the other, and ½-inch deep. The bottoms were made of cheese-cloth and the tops covered with glass. First McIndoo determined that normal bees confined in these cages and supplied with queen candy, water, sirup or honey and a piece of honeycomb would live a considerable time. Middle aged workers lived an average of over 9 days, queens 16½ days, drones 3 days and 9 hours. In making the tests for odor reaction a cage containing a bee was supported horizontally by its apex and the opposite end. The odorous substances used were then held close beneath the cheese-cloth floor, and the behavior of the bee observed through the glass top. Tests were made with oil of peppermint, oil of thyme, oil of wintergreen, honey, honeycomb, pollen, extracted bee stings, flowers of honeysuckle, and leaves and stems of pennyroyal, of spearmint and of scarlet sage.

The "reactions" recorded by McIndoo are the actions of the bee in the cage when the odor comes in contact with it. In some cases, he says, they merely moved the antennæ or stroked them, in other cases they moved away from the source of the odor, and in still others they turned around "as if noticing the odor," jumped quickly toward it, or jumped "as if attacking an enemy."

Workers, queens, and drones showed decided reaction of these sorts to all the odors used, the average reaction time for workers being 3.4 seconds, for queens 4.9 seconds, for drones 2.9 seconds. To most of the odors the bees reacted negatively, turning away from everything but the honey, pollen, honeysuckle, and bee stings. They appeared to search for the first three of these odors, but they quickly moved toward the stings. In control tests made with empty vials a bee might move but "its behavior is quite different from that observed when odors are used."

From these experiments McIndoo concludes "that the olfactory sense of the honeybee is acute and that the sensitiveness to various odors is most highly developed in the drones, and least highly developed in the queens." This conclusion is in accord with observations of other investigators, and especially with those of von Frisch published five years later and based on experiments of an entirely different nature.

*Experiments by von Frisch.*—The experiments of von Frisch (1919) are particularly interesting because they were conducted on bees in their natural freedom about the apiary, and the tests made with extracts of common flowers of the region. Von Frisch, moreover, took advantage of the peculiar trait of bees for collecting honey or pollen from one flower species as long as possible after they have once started on that species. He found that bees could be quite easily "trained" to an odor and that once trained they would go to this odor indefinitely and to no other. This furnished an excellent basis on which to devise experiments on their olfactory sense and their ability to distinguish different odors.

In his experiments von Frisch used small cardboard or earthenware boxes 10 centimeters square and 10 centimeters deep, each with a removable top, and provided with a small round door in the lower part of one side. To begin with, one box was set on a table near the apiary in a position protected from wind and rain, and within it was placed a feeding glass containing sugar-water accessible in a small basin projecting at the bottom. Next, pieces of paper smeared with honey were scattered nearby to attract the bees. After a few bees had found these lures it would not be long until many others were making regular trips from the papers to the hives and back. Then the papers with bees on them were taken to the door of the box and the bees enticed inside by a trail of honey. In this way a steady traffic was soon established between

the box and the hives, while at the same time odorless sugar-water was substituted for the fragrant honey. The last step in the preliminaries consisted of replacing the box with a clean one just like it and likewise provided with sugar-water, but in addition scented with a few drops of flower extract sprinkled on a shelf inside above the door. Thus the bees were trained to associate an odor with the box containing food.

At this stage von Frisch began his tests. The first consisted of placing three empty, odorless boxes on the table beside the scented one, and, after 20 minutes uninterrupted flight by the bees, of changing the position of the boxes so that an empty, odorless box took the place of the scented feeding box. The returning bees were at once disconcerted by the change and flew back and forth before the boxes in all directions. They went past the doors of the empty boxes "as if smelling inside," passed by the unscented boxes one after another, but as soon as they came to the door of the scented one they went quickly within. They appeared to perceive the odor, however, only when within 4 or 5 centimeters of the door. The more boxes used in such a test, says von Frisch, the more interesting the experiment.

So far the behavior of the bees indicated that they found the feeding box by the odor, but to make the evidence more convincing, von Frisch finally replaced all the boxes with clean ones, one of which contained the same odor as before, but none of which contained food. The bees went at once to the scented box and, during a short period, while 123 bees went into the box with the odor, only four went into one of the scentless boxes and none into the other two. Such experiments von Frisch repeated many times and used a large number of different flower extracts—extracts, as before stated, of fresh flowers gathered in the region of his apiary. His records show always the same results and would appear to leave no doubt of the bee's ability to perceive odors clearly, though only at close range.

Further experiments by von Frisch show that bees not only perceive odor but that they distinguish different flower scents with entire certainty. For example, when they have been trained to one odor, such as that of Acacia, they will seek only this odor and, in experiments, could not be attracted by rose odor or lavender odor. Bees trained to oil of orange-peel selected this scent amongst the odors of 43 other ether oils, and were confused by two which are to our sense of similar smell. This suggests

that in nature bees distinguish the different flower species by their odors and are thus enabled to collect nectar or pollen consistently from any particular species as long as it is in bloom. In another set of experiments, however, von Frisch showed that perceptions of both color and form are valuable adjuncts to the olfactory sense of the bees in enabling them to recognize a certain species of flower, or to distinguish between different ones, for it was found that bees trained to odor and color together were attracted from much longer distances than those trained by smell alone. But perceptions of form and color will be discussed in connection with the description of the bee's eyes.

Contrary to what might be expected, von Frisch's experiments indicated that the smell of honey is not a particularly strong odor to the bees, unless the honey is of a strong-smelling variety. A small amount of honey exposed on the grounds of the apiary is sometimes not discovered for several hours, but as soon as one bee finds it the news is spread rapidly, and suddenly the honey is the center of a crowd of bees eager for it. Probably during a period when nectar is scarce, bees make a more intensive search of their neighborhood and thus may appear to discover exposed honey more quickly at some times than at others.

**The Location of the Sense of Smell.**—The problem of determining that bees smell and that they distinguish different odors, however, is a simple one compared with that of identifying surely the organs by which they smell or even the part of the body on which such organs are located. Many investigators have carried out experiments on different insects which have seemed to prove quite conclusively that the sense of smell is located chiefly on the antennæ, and this idea had been pretty generally accepted until McIndoo published the results of experiments on bees (1914) and on beetles (1915) that were at variance with most former ideas.

*Experiments by McIndoo.*—In making his experiments to determine the position of the olfactory organs in bees, McIndoo again confined his subjects in the triangular cages already described, but this time he cut off successive joints of the antennæ and, as before, noted the reaction time of the mutilated bees to the various odors used. Normal workers responded to oil of peppermint, oil of thyme, and oil of wintergreen in an average of 3.4 seconds. But bees with the antennæ shortened reacted more slowly and in proportion to the number of joints missing, those with

seven or eight joints of the flagellum removed did not respond until after 88 or 98 seconds. When all the joints of both antennæ were removed there was no response at all. To contrast the behavior of antennaless bees with normal ones, McIndoo put ten of them into an observation hive with a normal colony and tested them with oil of peppermint held half an inch before their faces, and with smoke blown gently on them. He says that not one of the mutilated bees reacted in the least, although the other bees fled at once from the oil of peppermint and created an uproar in the smoke. He next tried oils of thyme, clove, wintergreen and cedar on 50 others in the same circumstances and with all obtained the same results.

Most investigators have taken such negative evidence of odor perception by bees, or other insects deprived of their antennæ, to mean that the organs of the sense of smell had been removed with the antennæ. But McIndoo contends that bees mutilated by the amputation or extraction of the antennæ are never normal in their actions, that they are, on the other hand, abnormal in so many ways that their lack of response to strong odors may be due to the nervous shock of the operation and not to the loss of the organs of smell. To test this idea he covered the antennæ with glue, succeeding in this with 21 bees without otherwise injuring them. Normal bees had reacted to oils of peppermint, thyme, and wintergreen in 3.4 seconds; bees with the antennæ removed reacted slowly after 88 to 98 seconds, these 21 bees with the antennæ glued reacted on an average in 2.9 seconds.

Such results are striking and suggest at once that the bee's perception of these strong odors from volatile oils is not restricted at least to the antennæ. It is true that the deductions would be more convincing, however, if the tests had been made with milder odors where the question of irritation would be eliminated.

However, McIndoo concludes from his experiments that the antennæ of the bee have little or nothing to do with the sense of smell. He, therefore, looked over the body and other appendages of the insect for sense organs that might be the true odor perceptors, and found the small sense pores (described on page 30) situated on both surfaces of the wing bases, on various parts of the legs, such as the outer and inner surfaces of the trochanters, the upper ends of the femora, the upper ends of the tibiæ and under surfaces of the second and third tarsal joints, also on the sting along the shaft (Fig. 59 F, *Po*) and on the tips and bases of the lancets

(E, *Po*), and finally the two groups of pores situated on the base of the scape of the antenna (Fig. 10 I, *Po*). McIndoo estimated 2,604 of these pores on the drone, 2,268 on the worker, and 1,860 on the queen. Therefore, whatever sense these pores serve, that sense would seem to be most highly developed on the drone and least on the queen.

Next McIndoo made a series of experiments to test the smelling power of bees with the wings removed or with the sense pores on the other parts of the body covered with glue. He found that bees having the wings cut off at the base reacted to oil of peppermint, oil of thyme, and oil of wintergreen in an average of 3 seconds, but that if the wings were pulled off and the entire basal part thus removed the reaction time was increased to 27 seconds—eight times the normal. The same results were obtained by covering the wing bases with glue. With the leg pores glued over, bees reacted in 8 seconds. But, finally, with the wings pulled off and the leg pores glued, the average reaction time was increased to 40 seconds—twelve times slower than the normal.

The removal of the wings, McIndoo says, does not result in any abnormal behavior on the part of bees thus mutilated, since they lived in the cages an average of nearly ten days, which is the usual life of an uninjured bee in confinement. He believes, therefore, that the lengthening of the reaction time in this case is not due to any nervous shock or abnormal condition resulting from the operation of removing the wings or covering the other parts, but to the loss or concealment of most of the olfactory organs. He concludes, then, that the sense pores found on the wing bases, on the legs, on the sting, and on the bases of the antennæ are the true olfactory organs of the bees.

*Experiments by von Frisch.*—These experiments of McIndoo have not been repeated by other workers, but recently von Frisch (1921) has attacked the problem of locating the bee's organs of smell by a different set of experiments. He arrives at conclusions entirely opposed to those of McIndoo, and once more in accord with older ideas on the subject, for he says that, in his observations on bees with the antennæ removed, the insects lost the sense of smell but were not otherwise seriously affected. But again von Frisch experimented on bees at liberty in the apiary, and he used extracts of local flowers, odors presumably much milder than those of the strong-smelling and volatile oils

used by McIndoo. Herein, perhaps, may lie, in part at least, the explanation of the apparent discrepancy between the results of the two sets of experiments.

Using the same methods as in his former experiments, von Frisch trained bees to come to his feeding boxes after sugar-water, but this time he marked a number of them with a spot of color for identification. After the marked bees had made 6 to 12 trips each to the boxes they were given memory tests on odor to be sure they were in proper condition for experimental subjects. Eighteen of them were caught and their antennæ carefully cut off at the base. For catching and holding the bees without other injury during the operation von Frisch used "catching-shears," an instrument shaped like a pair of scissors but with parallel, net-covered, triangular frames at the ends instead of blades. When his 18, now antennaless, bees were liberated they flew about the boxes they had been frequenting, going now into one, now into another, regardless of the presence or absence of the odor. A count of their visits during 5 minutes recorded seven visits to the scented box and 50 visits in all to the three unscented boxes, results very different from that obtained previously with normal bees.

But with McIndoo's statement in mind concerning the abnormal condition of bees with the antennæ removed, von Frisch tested their color sense and their memory for color. For an hour he allowed bees to come for food to a box having its front covered with blue paper, while the fronts of the empty boxes were covered with yellow paper. Then these boxes were replaced with clean ones having the same colors but in different positions and none of them containing food. Seventeen of the visiting bees were now deprived of their antennæ and released. They immediately swarmed about the boxes and in 5 minutes they had made 35 visits to the blue box and none to the others. This experiment, von Frisch claims, shows that the operation of removing the antennæ did not affect the bees' color sense or their memory, and, therefore, leaves no reason to suppose that their sense of smell should be inhibited in case the olfactory organs are on some other part of the body than the antennæ.

Observing that antennaless bees had some difficulty in making their way into the doors of the boxes, the same experiments were repeated by placing small dishes of sugar-water in the centers of squares of paper. Tests for odor sense were made first on gray

paper, and then color tests were made with colored paper, but the results were the same as with the boxes.

Summarizing his experiments, von Frisch says that the results show that bees trained to an odor and then having the antennæ cut off at the root are no longer able to distinguish the training odor from any other odor or from no odor at all, but that bees trained to a color and then suffering loss of the antennæ, still fly to that color and to no other. The absence of odor reaction, then, von Frisch asserts, cannot be attributed to any nervous shock sustained from the operation, but only to the absence of the smell-perceiving organs, and he concludes, therefore, that the antennæ are the seat of the principal olfactory organs of the bee. Occasionally bees without antennæ would make several return trips to the boxes, but generally they never came back from the hive. In the hive, however, the loss of the antennæ depriving the bees of both tactile and olfactory senses would be a serious hindrance to their normal activities.

In the experiments it was found that bees with only eight joints of the flagellum of each antenna cut off were just as insensible to odors as those having the entire antennæ removed, but that if four joints of either flagellum were left intact the bees still gave evidence of perceiving the odors. From this von Frisch concludes that the olfactory organs must be located in the last eight joints of the antennæ, and that if organs of smell are present on other parts of the body their efficiency is so small as to have no effect on the behavior of bees seeking flower odors under conditions of nature. The sense organs most conspicuous on the antennæ and which are limited to the last eight flagellar segments are the so-called *pore plates* (Fig. 10, A, B, G, *SPl*) already described, and these organs von Frisch believes are the principal olfactory organs of the bee.

There appears to be nothing in the experiments of von Frisch, however, that would show that bees with the antennæ removed may not still perceive very strong, penetrating, or perhaps irritating odors such as those McIndoo used in most of his tests, especially if such substances are held very close to a bee enclosed beneath a glass plate. On the other hand, McIndoo's experiments do not prove that antennaless bees can perceive flower odors or any other smells from a distance. Hence it may be that the organs of more delicate odor-perception, which bees need in foraging for nectar and pollen, are located on the antennæ, while

less efficient organs responding only to strong odors at close range are those described by McIndoo on the other appendages of the body.

*Experiments by Minnich.*—Experiments made on the reaction of smell in other insects indicate the same thing. Thus Minnich (1923) finds that the yellow cabbage butterfly protrudes its proboscis in response to odors, and that all normal individuals always respond in this manner after 24 hours or more without food. But, he says, that when the antennæ are covered with vaseline or with a mixture of vaseline and paraffin, or when the antennæ are amputated, the response is decreased 50 to 80 per cent. Twenty-two butterflies of both sexes became 89 per cent responsive when one antenna was removed, and 47 per cent so when both were removed. From his experiments Minnich concludes: "It is thus clear that the elimination of one antenna alone produces a relatively small decrease in response, while the elimination of both antennæ effects a great reduction in the same. Even the elimination of both antennæ, however, fails to abolish the response. Two conclusions may be drawn from these facts: First, the antennæ of Pieris bear important olfactory organs; second, the olfactory organs are not limited to the antennæ." McIndoo (1917) had already described "olfactory pores" in the Lepidoptera similar to those of the bee, situated on the wing bases, the legs and the mouth parts, while on the antennæ he found peg-shaped organs and sense hairs of several varieties. But he says that none of the Lepidoptera have pore plates on the antennæ.

### 4. THE MANDIBLES AND THEIR GLANDS

The mandibles are strong, jaw-like organs in insects that feed on solid substances (Fig. 5, *Md*). Amongst insects that feed entirely on liquids the mandibles in some are modified into piercing blades, and in others are rudimentary or absent. Since the bee feeds on both liquids and solids and uses its jaws also for wax-working tools, it preserves well developed mandibles of the biting type (Fig. 2, *Md*).

**The Structure of the Mandibles.**—Each mandible is a hollow outgrowth of the head containing a prolongation of the head cavity. It is continuous with the head wall by a flexible membrane all around its base, but is more firmly fixed by an anterior and a posterior articulation in this membrane with the chitinous

parts of the head. Both of these mandibular articulations are of the ball-and-socket type, though in the bee the sockets are very shallow ones. The anterior hinge consists of a knob or condyle on the lateral angle of the clypeus (Fig. 6 A, *Clp*) fitting against a socket on the anterior end of the base of the mandible (Fig. 11 A, *j*); the posterior hinge consists of a socket on the lower edge of the postgena (Fig. 6 B, *Pge*) receiving a knob on the posterior edge of the mandibular base. The mandible is

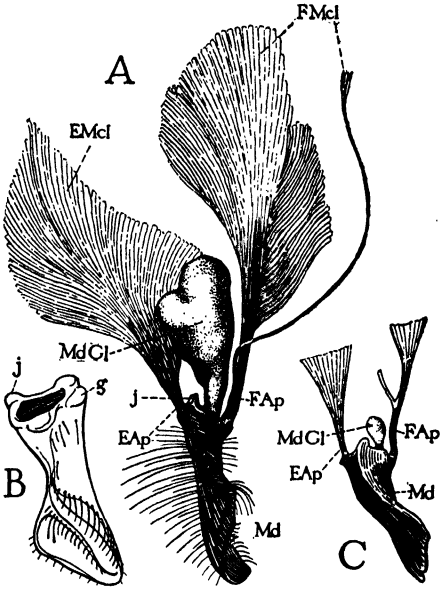



FIG. 11.—Mandibles and mandibular glands of worker and drone. A, anterior view of right mandible of worker, showing extensor and flexor muscles (*EMcl*, *FMcl*) with attachments of their apodemes (*EAp*, *FAp*), and the mandibular gland (*MdGl*). B, inner view of right mandible of worker; *g*, posterior articular surface; *j*, anterior articular surface. C, anterior view of right mandible and mandibular gland of drone, with muscles cut off near bases.

thus able to swing out and in on a lengthwise axis, but, though its principal movement is that of a hinge joint, the articulations are not inflexible and each mandible has considerable play forward and backward, enough to allow the tip of one to slide past that of the other on either the anterior or the posterior surface.

*The Mandibles of the Worker.*—Each mandible of the worker bee (Fig. 11 B) is wide at the base, narrowed through the middle, and expanded again at the end. The terminal enlarged part suggests in shape the bowl of a spoon having the convex face out-

ward and the concave surface inward. The lower edge forms a nearly straight margin sloping from in front downward and backward with the rear angle forming an obtuse point curved slightly inward (A, *Md*). The concave inner face of the "spoon" is traversed by two diagonal ridges and is bordered below by another (B). It is surrounded, except at the point, by a fringe of hairs curved inward from all sides, the upper ones being long, the lower ones short, and the median ridge bears a row of similar hairs curved downward. The outer surface of the mandible is covered with setæ which are very long on the posterior edge where they form a conspicuous brush of stiff bristles. None of the mandibular hairs are branched or plumose in the worker. Sense organs also are situated on the jaws. These organs will be described in the last section of this chapter.

*The Mandibles of the Queen and Drone.*—The mandibles of the queen (Fig. 7 B) are proportionately larger than those of the worker (A), but the mandibles of the drone (C) are smaller, appearing particularly small by comparison with the great size of the drone's head. The jaws of both the queen and the drone are notched and prominently toothed on their cutting edges, the tooth being especially large and sharp on the mandible of the queen (B). This, however, does not mean that either the drone or the queen has developed teeth for any special work of its jaws; the toothed mandible is common to insects generally, as shown in the cricket (Fig. 13 A), the sawfly (Fig. 14 A) and in another species of bee (Fig. 14 F). The mandible of the worker of the honeybee is the most highly evolved one of all of these forms; it is specialized by the *loss* of teeth and by a remodeling in shape to serve new purposes. The incurved points of the mandibles of the worker form an efficient wax-cutting instrument which Lineburg (1924*b*) appropriately names the "wax nippers." The hollowed, ridged inner surfaces of the enlarged ends of the worker mandibles are used for handling pollen as food and for grinding up the wax in comb building. But the same surfaces also fit snugly over the bases of the maxillary lobes when the proboscis is protruded, and enable the mandibles to serve as a support for the proboscis when the bee feeds on liquids. The queen uses her large sharp-toothed jaws for biting her way out of the thick-walled cell in which she is reared, and also for entering the cells of possible rival queens in order to kill them before they emerge. The drone, bred in an ordinary cell with a thin cap,

and fed almost entirely by the workers when fed at all, has little use for his mandibles after liberating himself from the brood cell.

**The Mandibular Muscles.**—Each mandible is moved by two sets of muscles within the head, one pulling on the outer edge of the base, the other on the inner. The outer muscle is, therefore, the *extensor* or opening muscle (Fig. 11 A, *EMcl*), the inner one the *flexor* or closing muscle (*FMcl*). The latter is the stronger of the two since most of the hard work of the mandible falls upon it. Both muscles consist of flat, fan-shaped bunches of fibers diverging from chitinous stalks, the *mandibular apodemes* (*EAp* and *FAp*), which arise from the membrane at the base of the mandible. The distal ends of the fibers are attached to the side walls of the head behind the compound eyes, those of the flexor muscle arising anterior to the others.

**The Mandibular Glands.**—A mandibular gland lies within the head just above each mandible (Fig. 7 A, B, *MdGl*), in the worker having the form of a small bilobed sac (Fig. 11 A, *MdGl*) opening by a narrow neck in the membrane at the inner side of the base of the mandible in front of the attachment of the flexor apodeme (*FAp*). In the queen (Fig. 7 B) the gland is much larger than in the worker. In the drone the true gland is very small (Fig. 11 C, *MdGl*), the large cellular mass exposed above the mandible in a facial dissection being merely a group of fat cells (Fig. 7 C, *FtCls*). The gland consists of an epithelial sac of secreting cells lined with a thin cuticular intima. According to Heselhaus (1922) the cells are penetrated individually by fine canals from the intima.

The glands of the bee's mandibles were first described by Wolff (1875) as olfactory mucous glands, with the idea that their secretion serves to keep moist certain sense organs on the epipharynx or roof of the mouth, Wolff believing that these organs have an olfactory function. Schiemenz (1883) noted that the glands vary in the different forms of the bee according to the size of the mandibles and appear, therefore, to have some function connected with that of the jaws. Arnhart (1906) suggested that the secretion of the glands is mixed with the fresh wax when the latter is worked in the mandibles, and this idea has practically been confirmed by Lineburg (1924*a*) from close observations on workers while engaged in comb building. Lineburg says that when the wax is being manipulated in the jaws "it is clearly seen that some fluid is being added during the process of mastication."

The fluid which appears between the mandibles whenever these organs are used, whether for chewing wax, wood, or the wires of a cage, is either neutral in reaction or very weakly alkaline, while that from the mouth, presumably saliva, is strongly acid. This indicates, at least, a different source for the two liquids, and the most likely source of the former would certainly appear to be the mandibular glands, an idea strengthened by the fact that a channel leads downward on the inner face of each mandible from the outlet of its gland into the deep groove between the two upper ridges of its masticating surface.

Though Heselhaus (1922) states that the secretion of the mandibular glands is acid, and therefore not suitable for a wax softener, the writer has found it impossible to make a test of the gland contents free from the acid body liquids and saliva. The further contention of Heselhaus that the glands are present in Hymenoptera that do not produce wax is not to the point since, as just shown, it is evident that the liquid exudes between the jaws during any use of these organs, and it need not be supposed that it is provided for wax modeling alone.

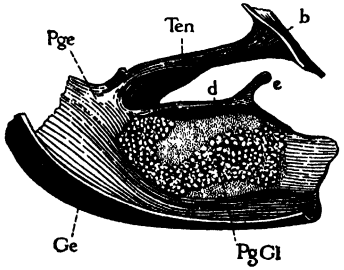



FIG. 12.—Postgenal gland (*PgGl*) of worker, right side, in place against inner wall of postgena (*Pge*). *b*, anterior root of tentorium (*Ten*); *d*, thickened edge of lateral wall of fossa of proboscis; *e*, articular knob of maxillary suspensorium; *Ge*, posterior part of gena.

**The Postgenal Glands.**—A second gland situated in the neighborhood of each mandible of the worker lies against the internal face of the up-turned part of the postgena that forms the side wall of the fossa of the proboscis (Fig. 8 A, *d*). It consists of a flat mass of delicate gland cells (Fig. 12, *PgGl*), each of which opens through a minute canal on the inner surface of the supporting plate. The writer's former error of showing a common duct from these cells has been corrected by Heselhaus (1922). The glands were first described by Bordas (1895) as the "internal mandibular glands," but, since they have no connection with the mandible, Heselhaus would call them the *postgenal glands* on account of their position against the postgenal plates.

### 5. THE PROBOSCIS AND ITS USES

The group of long mouth appendages of the bee projecting downward from the lower part of the head behind the mandibles

constitutes the proboscis (Fig. 2, *Prb*). We should like to call this organ the "tongue," as does the beekeeper who is not hampered by too much scientific learning, but the part in question is not the tongue, nor is it structurally a single organ, though it acts as such. The proboscis of the bee is made up of two sets of parts corresponding with the maxillæ and the labium of other insects, such as the grasshopper (Fig. 5, *Mx* and *Lb*), and it gives us a very interesting example of how an organ or group of organs may be changed in form, without losing the plan of the original structure, in order to be used in a new way for new purposes. Hence, we shall more readily understand the honey-bee's proboscis if we go back to its rudiments in the embryo, and if we examine also the corresponding parts in other insects that indicate the steps by which the bee, with a little remodeling of organs designed first as part of an equipment for eating solid foods, has acquired an organ to enable it to feed on liquids.

**The Origin of the Mouth Parts.**—In the embryo (Fig. 3), as we have seen, the mouth parts arise as simple, paired lobes on the under sides of the last three head segments. The first pair (*Md*) form the mandibles, the next (1*Mx*) the maxillæ, and the third, or second maxillæ (2*Mx*), unite to form the labium of the adult. The mandibles remain as simple undivided lobes that become variously toothed or otherwise modified in form as already described. But the maxillæ become complicated; each develops two small terminal lobes and a long, jointed lateral arm, while its body becomes divided into a basal joint and a distal one. Consequently, in a full-grown insect with simple mouth parts, as for example a cricket (Fig. 13), the maxillæ have the complicated structure of the appendages shown at B, B. Each consists of a basal piece or *cardo* (*Cd*) articulating with the head; of a body or *stipes* (*St*); of two terminal lobes, the inner called the *lacinia* (*Lc*), the outer the *galea* (*Ga*); and of a jointed appendage, the *palpus* (*Plp*) attached to the outer side of the stipes by a subdivision of the latter called the *palpifer* (*Plf*). The second maxillæ of the embryo (Fig. 3, 2*Mx*) move together and unite to form the under lip or *labium*. But the labium develops lobes, appendages, and divisions, which, in the adult (Fig. 13 C), clearly suggest its formation from two united appendages like the maxillæ. Thus the body of the labium shows a basal subdivision called the *submentum* (*Smt*), corresponding with the cardines of the maxillæ; of a *mentum* (*Mt*) corresponding with the stipites; of a termi-

nal part or *ligula* (*Lg*) with four terminal lobes, a *glossa* (*Gls*) and *paraglossa* (*Pgl*) on each side; and of two lateral *palpi* (*Plp*) carried on basal lobes distinguished as the *palpigers* (*Plg*).

**The Evolution of the Honeybee's Proboscis.**—In the cricket a large rounded lobe (Fig. 13, *Hphy*) is attached to the inner face of the ligula, as seen best in side view at D. This is the true tongue of the insect, known as the *hypopharynx*, here secondarily united with the labium. The duct of the salivary glands opens behind

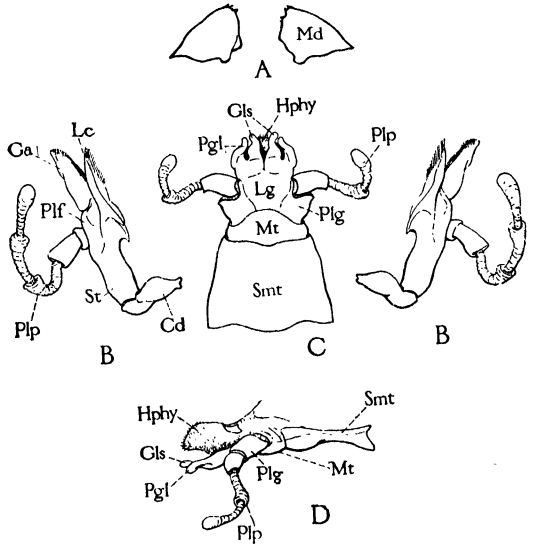



FIG. 13.—Example of typical insect mouth parts, from common black cricket (*Gryllus neglectus*).

A, mandibles. B, B, maxillæ, ventral view. C, labium, ventral view. D, labium and hypopharynx, lateral view.

*Cd*, cardo; *Ga*, galea; *Gls*, glossæ; *Hphy*, hypopharynx; *Lc*, lacinia; *Lg*, ligula; *Md*, mandible; *Mt*, mentum; *Pgl*, paraglossa; *Plf*, palpifer; *Plg*, palpiger; *Plp*, palpus; *Smt*, submentum; *St*, stipes.

the base of the hypopharynx and retains its position even when the hypopharynx is united to the inner face of the labium, or is absent.

The mouth parts of the cricket are typical of those of a great many insects, including most species that feed on solid foods, but they are not well adapted to liquid diets. Consequently, most insects that feed largely or exclusively on liquids have some or all of their mouth parts specially modified for their individual needs. The Hymenoptera, the order including bees and their

relations, feed on both solids and liquids; consequently, they have retained mandibles of the biting type, while the maxillæ and labium have been modified for taking up liquids. The mouth parts of a sawfly (Fig. 14, A, B), one of the least specialized of the Hymenoptera, show the beginning of this modification by the union of the two maxillæ with the labium to form a lapping organ (B). The median parts of this compound structure are easily identified by comparison with the labium of the cricket (Fig. 13 C). An important difference, however, is to be noted in the

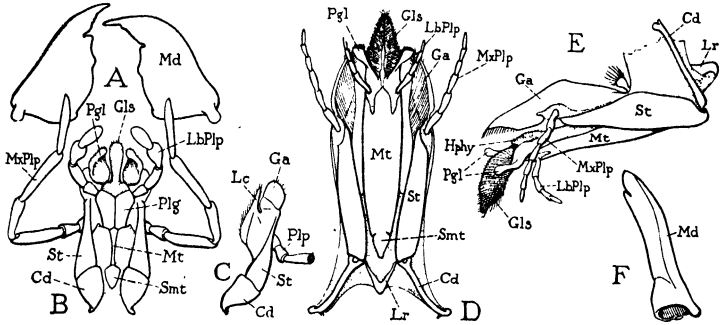



FIG. 14.—Mouth parts of Hymenoptera, showing evolution to the proboscis of the honeybee (Fig. 15).

A, mandibles of current sawfly (*Pteronus ribesii*) with typical notched and toothed edges.

B, lapping organ of sawfly formed of combined labium and maxillæ, the two glossæ of the cricket (Fig. 13 C) here united into a single median tongue or glossa (*Gls*).

C, maxilla of sawfly, separated from labium, distal joints of palpus (*Plp*) removed, showing reduction of the lacinia (*Lc*).

D, proboscis of a solitary bee (*Andrena carlini*) formed of combined labium and maxillæ, the glossa (*Gls*) produced into a short, hairy tongue, the paraglossæ (*Pgl*) reduced, the lacinia of the maxilla (C, *Lc*) entirely gone, the distal ends of the cardines (*Cd*) united by a V-shaped lorum (*Lr*).

E, side view of the same. Compared with G of Fig. 15 shows correspondence of parts in proboscis of honeybee, except that in Andrena there is a rudimentary hypopharynx (*Hphy*).

F, right mandible of *Andrena carlini*.

fusion of the two glossæ into a single, median lobe of the labium in the sawfly (Fig. 14, B, *Gls*) between the paraglossæ (*Pgl*). Also, the palpigers, which in the cricket (Fig. 13 C, *Plg*) are separated by the base of the ligula (*Lg*), are here (Fig. 14 B, *Plg*) contiguous along the median line. The structure of the maxillæ of the sawfly is better seen when one of these appendages is detached from the labium as shown at C, but here again the same parts are present as in a maxilla of the cricket (Fig. 13 B), though it should be

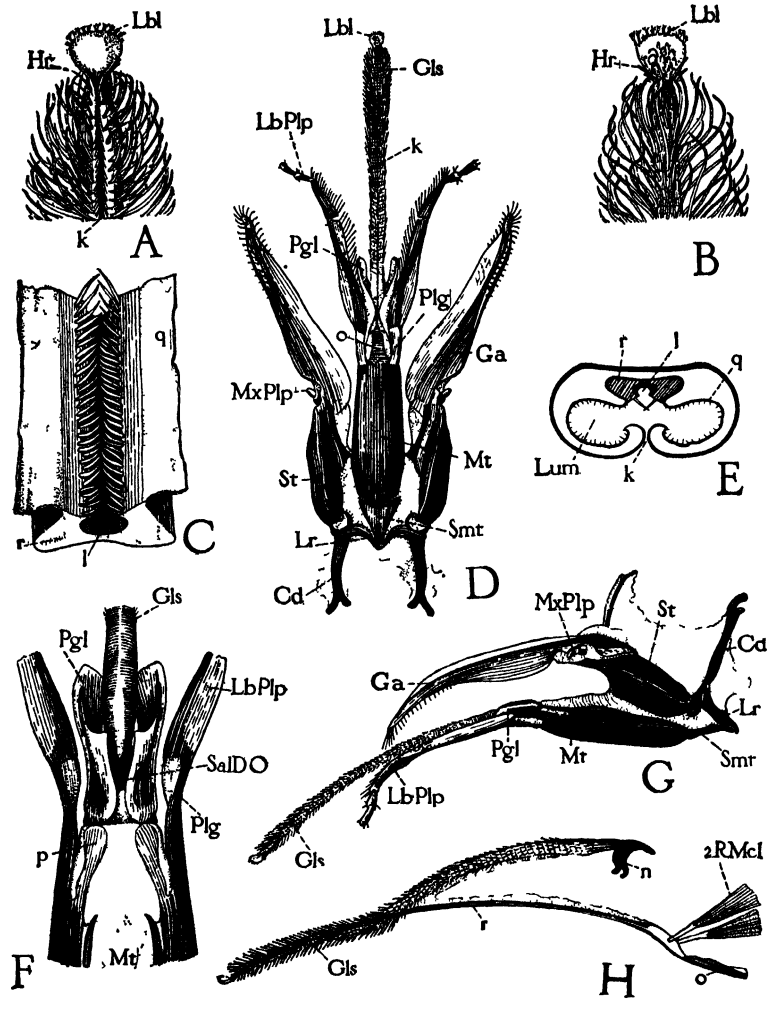



FIG. 15.—The proboscis of the honeybee

A, tip of tongue or glossa, under surface, showing labellum (*Lbl*) with its fringe of branched hairs, the ventral groove of the tongue (*k*), and the guard hairs (*Hr*) at its end.

B, the same, from above.

C, small piece of glossal rod (*r*) with adjoining walls (*q*) of glossal canal (A, *k*) attached, and showing inner channel of the rod (*l*) guarded by rows of hairs

D, the proboscis, ventral view. Compared with D of Fig 14 shows correspondence of parts in proboscis of Andrena, compared with B of Fig 14, and with B, C, B of Fig. 13, shows its origin and evolution from united maxillæ and labium of typical form.

E, cross section of glossa, showing its principal canal (*Lum*) opening through the ventral groove (*k*), and the inner channel (*l*) of the glossal rod (*r*)

noted that the lacinia (*Lc*) is relatively very small and weak in the sawfly.

If next we examine the mouth parts of one of the lower members of the bee family, *Andrena carlini* (Fig. 14, D, E, F) for example, we find the labium and maxillæ (D, E) still united at their bases but prolonged to form a short proboscis suggesting that of the honeybee (Fig. 15, D, G). Yet the parts in the organs of Andrena (Fig. 14 D) are comparable with those of the sawfly (B), though we must note the following differences: The united glossæ form a broad, tongue-like end lobe (D, *Gls*) thickly covered with short hairs. The palpigers of the sawfly (B, *Plg*) are not present as separate sclerites in Andrena (D), being either absent or fused with the mentum (*Mt*)—at least, this is the common interpretation. In the maxilla of Andrena the inner lobe or lacinia, very small in the sawfly (C, *Lc*), is gone entirely, the single large terminal lobe being the galea (*Ga*). One new piece is present; this is a median V-shaped brace, called the *lorum* (*Lr*), between the distal ends of the cardines (*Cd*). The relation of the parts is best seen in side view (E). It may be noted here that a small lobe (*Hphy*) arises from the upper surface of the labium between the bases of the paraglossæ (*Pgl*) in the position of the hypopharynx of the cricket (Fig. 13, D, *Hphy*). The lobe in Andrena is very probably a rudimentary hypopharynx; the opening of the salivary duct is below its apex.

**The Structure of the Proboscis.**—The final step, now, to the proboscis of the honeybee, *Apis*, is an easy one, and its parts (Fig. 15 D and G) may be identified readily by comparing them with those of the proboscis of Andrena (Fig. 14 D and E). In the maxillæ of the honeybee it is to be noted only that the palpi (Fig. 15 D, *MxPlp*) are reduced to little peg-like rudiments, and that the galeæ (*Ga*) form long, flat, tapering blades. In the labium the basal angle of the short, triangular submentum (*Smt*) fits into the angle of the *lorum* (*Lr*); the mentum is a darkly colored, elongate plate (*Mt*) ending in a pale flexible plate (*o*)

F, distal end of mentum (*Mt*), dorsal side, with bases of palpi (*LbPlp*) and glossa (*Gls*), showing opening of salivary duct (*SalDO*) at root of glossa, and paraglossæ (*Pgl*) embracing the base of the latter.

G, lateral view of proboscis, showing parts on left side somewhat separated. Compared with E of Fig. 14 shows correspondence of parts in proboscis of Andrena, except that the honeybee has no hypopharynx (*Hphy*).

H, lateral v_ w of glossa with glossal rod (*r*) torn from its base, showing flexible attachment of rod to small plate (*o*) at end of ventral surface of mentum (D, *o*), and insertion of retractor muscles (*2RMcl*) on base of rod. *n*, basal hooks of glossa.

between the palpigers (*Plg*), which latter support the long, four-jointed palpi (*LbPlp*) of the labium. (According to Macgillivray the plates here marked *Mt* and *o* are the stipulæ fused with the mentum, and the long basal joints of the labial appendages are the palpigers, the palpi proper being three jointed.) The united glossæ (*Gls*) form a long, slender, bushy "tongue" with a flat spoon-like lobe called the labellum (*Lbl*) at its tip; the small paraglossæ (*Pgl*) closely embrace its base. There is no reasonable objection to calling this flexible and very movable median lobe of the labium of the bee the *glossa* or the *tongue*, remembering that it is really the two glossæ fused and that it is not the hypopharynx. The honeybee has no hypopharynx, but the duct of the salivary glands opens on the upper surface of the labium (F, *SalDO*) between the bases of the paraglossæ (*Pgl*) just as in Andrena, which has a small hypopharynx.

Thus we see that, while at first sight there appears to be little in common between the mouth parts of the bee (Fig. 2) and those of the grasshopper (Fig. 5), yet a study of intermediate forms shows that they have almost everything in common. In fact it is surprising that insects in general with all their diversity of feeding habits, have been able to adapt themselves to these habits by only superficial modifications of their fundamental feeding organs.

When the proboscis of the bee is not in use the terminal lobes of the labium and maxillæ are folded back beneath the head. But, when the bee wants to feed on honey or any other liquid, it brings these parts forward and presses the several pieces close together lengthwise in such a way that the maxillary blades roof over the tongue, and the labial palpi fit against its sides beneath the edges of the maxillary lobes. There is thus quickly improvised a tube made of the end lobes of the maxillæ and labium, having the tongue lying along the middle of its floor. The basal parts of the proboscis are now pressed up against the underside of the head, and this brings the hollow of the proboscis tube on a level with the mouth opening. Otherwise there would be, as in Fig. 18, a steep incline or high vertical step from the upper surface of the labium to the mouth (*Mth*). The bases of the maxillary blades now lie between the mandibles, loosely grasped between the hollowed inner faces of the latter, the wide grooves between the mandibular ridges fitting exactly upon the median ribs of the maxillæ above the bases of their palpi.

**The Epipharynx.**—The epipharynx of insects may be described as a dorsal tongue, it being usually a soft lobe situated on the under surface of the labrum above the mouth opening, though it has various forms in different species. In the honeybee the epipharynx (Figs. 17, 18, *Ephy*) is a large, soft, triangular, pad-like structure, with a thin, median lobe depending like a keel from its ventral surface (Fig. 17 B). On each side of the median lobe there is a rounded swelling on the under surface of the rear half of the organ, which is covered by small sense hairs (Fig. 19 A).

The terms "epipharynx" and "hypopharynx" as used in insect anatomy are examples of misapplied nomenclature, for it will be noted that neither of the organs thus named is located in the pharynx, both being outside the true mouth opening.

**How Bees Feed on Liquids.**—A bee feeding on honey plunges the end of its proboscis into the liquid, submerging the tips of the maxillary blades, and spreading the short terminal joints of the labial palpi outward. The long flexible end of the glossa, protruding beyond the other parts, is bent back and applied to the food upside down, while it at once begins a rapid back-and-forth motion. The honey now rapidly goes up through the tube of the proboscis and back into the pharynx. The feeding process is easy to see under a microscope if a bee is given some honey in a small glass tube, and the upward flow of the honey may be made more evident if a little powdered eosin or carmine is first mixed into it. If the honey contains air bubbles these very plainly show its rapid ascent to the mouth. The maxillary lobes remain stationary. Their inner surfaces are concave and smooth. Their bases overlap above the ligula and form here a thoroughly closed passageway leading back toward the mouth. But their rear ends must diverge, and this leaves a triangular space in the roof of the tube that would be open except for the fact that it is plugged by the epipharynx (Fig. 18 *Ephy*).

*The Motion of the Tongue.*—The motion of the tongue or glossa is due in part to a movement of the entire labium, involving a movement of the labial palpi as well as of the tongue. The mentum (Fig. 15 D and G, *Mt*) is hinged loosely upon the submentum (*Smt*), and the latter is set into the socket-like angle of the lorum (*Lr*), while, finally, the arms of the lorum are articulated to the distal ends of the cardines (*Cd*) of the maxillæ. Now, when the labium is pulled back by means of muscles attached to the mentum, the submentum (G, *Smt*) turns in the loral socket

and assumes a position at right angles to the mentum, while the lorum itself swings back on its articulations with the cardines. This freedom of motion is permitted by the loose membrane of the fossa in which both labium and maxillæ are suspended from the head.

The observer, however, cannot fail to note that beside this motion of the entire labium the tongue itself, or glossa (*Gls*), makes a conspicuous movement independent of that of the submentum. It is by far the most active member of the mouth parts during feeding, being constantly thrust out and withdrawn, and otherwise moved about in a way suggestive of its being delicately sensitive. Its tip, which normally extends far beyond the end segments of the labial palpi, can be drawn back entirely within the latter. This contractility at first sight appears to be due to elasticity of the tongue, but a closer examination will show that the entire ligula, that is, the paraglossæ (*Pgl*) as well as the glossa (*Gls*), moves back and forth and that the action is due to the retraction of the ligula into the anterior end of the mentum (*Mt*). The ligula is supported on a membranous cone at the end of the mentum, the walls of which are strengthened by three thin, chitinous plates, two above (F, *p*) and one below (D, *o*). By the contraction of two pairs of muscles situated within the mentum (Fig. 16, 1*RMcl* and 2*RMcl*) and inserted on the base of the ligula, the latter is pulled back into the mentum by the infolding of its own walls. Perhaps the elasticity of the plates in the walls of the cone helps to drive the ligula out again when the muscles relax, but probably its protrusion is largely effected by blood pressure in the mentum produced by constrictor muscles in its dorsal wall (*TMcl*).

But the tongue (*Gls*), finally, possesses also a motile power of its own by which it individually lengthens and shortens. A flexible rod, arising from the median ventral supporting plate of the ligula (Fig. 15 D, *o*), extends through the entire length of the glossa, as shown at H where the rod (*r*) is partly torn from the softer parts of the organ. The base of the rod is turned downward, where it is hinged to the plate of the ligula (*o*), and at the elbow there are inserted parts of two muscles (2*RMcl*) which extend backward through the mentum (Fig. 16). By the contraction of these muscles the rod is bent back at its base; the glossa thereby shortens and becomes bushy just as does a squirrel's tail when the bone is pulled out from its base. The rod

has a transparent and cartilaginous appearance, but it is presumably chitinous, since it is merely a thickening in the roof of a groove along the under side of the glossa, which is to be described presently. The extension of the glossa is probably due to the elasticity of the rod, or perhaps also to blood pressure, but the rod is certainly not in itself contractile as supposed by Cheshire, who looked for evidence of muscular striation in it.

*The Ascent of Liquids to the Mouth.*—By this time our feeding bee has probably had its fill of honey, but another will perform in exactly the same way. The bushy tongue, rapidly sliding out and in past the ends of the stationary maxillary lobes, suggests that it draws the honey into the temporary tube of the proboscis. Perhaps the honey first starts up this tube by capillary attraction, but most likely a strong suction force from the pharynx is soon felt which draws it on into the mouth. The walls of the pharynx are wrapped in sheets of muscle, while other muscles go from its upper or anterior surface to the inner surface of the front wall of the head. The opposing action of these muscles would alternately expand and contract the pharynx, and the latter is, hence, evidently a very efficient sucking bulb.

Worker bees in the hive often eject a large drop of nectar from the mouth upon the rear surface of the proboscis, when the latter is bent backward beneath the head, and then suck it back again into the mouth, both the discharge and the retraction of the drop taking place through the paraglossal channels around the base of the tongue. This action, repeated many times in succession, clearly demonstrates that liquids may go in either direction through the paraglossal channels; but the act is not one of feeding, it probably accomplishes the thorough mixing of the saliva with the nectar.

McIndoo (1916) has given a circumstantial account of how he thinks a bee feeds on liquid food, but his description does not agree with the observations of other writers, though he says (page 41): "It is now generally believed that liquid foods pass up the glossa or tongue by capillary attraction and are then sucked into the mouth." By "passing up the glossa" he means passing up a groove on its under surface, then going up to the dorsal surface of the mentum around the sides of the glossa within the paraglossa, to be finally raised to the mouth opening and sucked into the pharynx "as easily as a person draws into his mouth water held in the palm of his hand." However,

bees do not ordinarily feed in this manner, they have no such fastidious habits, they suck up large quantities of honey at once through the provisional tube of the proboscis and gulp it down, as described above, and as formerly described by the writer (1910), as described also by Wolff (1876) and by Zander (1911). In opposition to McIndoo's metaphor, Zander says that "the bees stick the palpi and maxillary lobes so deep into the liquid that they can suck it up with the tube of the proboscis, just as we on a hot summer's day take an ice-cold drink through a straw." The picture would have been complete if he had described how they grasp the "straw" between the outstretched mandibles. Zander, however, says that when feeding thus, the bees do not move the tongue; those observed by the writer always kept this organ in motion.

**How Bees Feed on Sugar.**—Bees feed on such substances as sugar and bee candy by first dissolving them in saliva spread on with the tongue. They curve the end of the tongue back, apply its upper surface to the food, and move it rapidly back and forth just as they do when feeding on a liquid. In this inverted position of the tongue the recurved spines on the upper surface of the labellum (Fig. 15 B, *Lbl*) apparently rasp the sugar as the saliva flows off the rounded, up-turned under surface of the labellum (A) and is distributed from the fringe of branching hairs.

*Structural Details of the Tongue.*—The minute structure of the glossa or tongue must be studied now before we can understand its particular function during feeding. The tongue is not a solid appendage, nor yet is it a truly tubular one; a compromise is effected by the longitudinal groove (Fig. 15 A and D, *k*) 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, is a part of the dorsal wall of the channel and is, hence, an external structure. The rod is itself grooved along its entire ventral surface (E, *l*) and this groove is converted into an inner tube by two rows of short, stiff hairs which converge from its margins. The lips of the large ventral groove of the glossa are deeply infolded and the walls of the channel are covered with small hairs. The channel ends on the base of the labellum, the small spoon-like lobe at the tip of the tongue (A, *Lbl*). The under surface of the labellum is smooth and convex, its concave surface being dorsal. The edge

is fringed with short, branched hairs curved upward, but the upper surface (B) is provided with strong spines hooked backward.

The glossal rod (Fig. 15 C, *r*) is very flexible and is mostly clear and cartilaginous in appearance, its ventral groove alone (*l*) being lined by a deposit of dark chitin. Its shape is sufficiently shown by the figures (C, E, H). The walls of the outer channel of the tongue consist of a delicate membrane and, with the rod, can be evaginated, probably by blood pressure from within. As Cheshire points out, this permits the channels to be cleaned in case of clogging by pollen or other particles that might lodge in them.

*The Salivary Syringe.*—The duct of the salivary glands of the bee opens on the ligula on the dorsal side of the labium between the bases of the paraglossæ (Fig. 15 F, *SalDO*). When a bee that

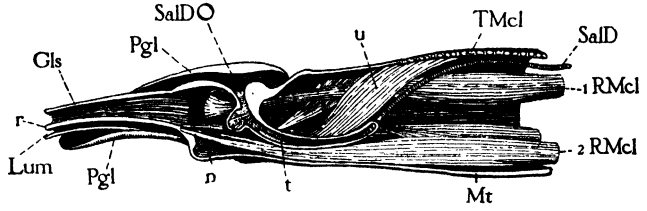



FIG. 16.—Salivary syringe and associated parts of labium.
*Gls*, glossa; *Lum*, ventral canal of glossa; *Mt*, mentum; *n*, hook on base of glossa; *Pgl*, right paraglossa; *r*, glossal rod; 1*RMcl*, 2*RMcl*, retractor muscles of ligula and glossa; *SalD*, salivary duct; *SalDO*, opening of salivary duct on dorsal surface of labium at base of glossal rod; *t*, cavity of salivary syringe; *TMcl*, transverse or constrictor muscles of mentum; *u*, dilator muscle of syringe.

has been fed on sugar alone for some time is given an anæsthetic, a clear liquid, often in large amount, swells the glossal channel and exudes from the end of the tongue. This is apparently saliva, though much of it appears to come from the mouth, probably from the honey stomach (Fig. 66, *Hs*). An examination of the base of the glossa will show very clearly that the liquid enters the groove on the under side of the tongue (Fig. 15 D, *k*) by flowing around the base of the latter through channels beneath the paraglossæ (F, *Pgl*).

The saliva, moreover, is apparently expelled forcibly from the salivary duct by a pump or "salivary syringe" located in the mentum (Fig. 16). The salivary opening on the base of the ligula (*SalDO*) leads into a deep transverse pouch (*t*) with collapsible, cuticular walls, which bends back horizontally in the mentum toward the base of the labium. The salivary duct (*SalD*) turns

downward from the rear part of the mentum to open into the posterior end of the pouch. When the retractor muscles of the ligula (*1RMcl*) pull the latter back into the mentum, the lips of the salivary pouch (*t*) must be closed, while a simultaneous contraction of the muscle (*u*) attached to the roof of the pouch would expand the latter and allow it to fill with saliva from the duct (*SalD*). When, now, these muscles relax, and the ligula is forced out of the mentum by the contraction of the dorsal transverse muscles (*TMcl*), the saliva in the pouch must be discharged on the ligula, but between the overlapping bases of the paraglossæ, and, therefore, driven around the base of the tongue within the paraglossæ, to enter finally the ventral channel of the glossa or the groove of the glossal rod.

Wolff (1876) calls each of the two dorsal longitudinal muscles of the mentum (*1RMcl*) the *retractor linguæ longus*. These are inserted on basal hooks of the glossa (Fig. 15 H and Fig. 16, *n*). The ventral muscle on each side (*2RMcl*) he calls the *retractor linguæ biceps*, because its anterior end divides into two parts, one of which is inserted by a tendinous prolongation on the base of the glossal rod (*r*), and the other upon the base of the ligula. The dilator muscle (Fig. 16, *u*) of the salivary pouch he calls the *protractor linguæ*, because he supposes that 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. But the use of the term "linguæ" in all these names is objectionable, since the lingua of insects is properly the hypopharynx or a part of it. The term "lingua" should not, therefore, be applied to the ligula, which is the section of the labium consisting of the glossa and paraglossa and their common basal part.

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

**Do Bees Take Liquids through the Tongue?**—It has been supposed that when a bee feeds on very small quantities of a thin liquid, such as nectar, the ventral channel of the glossa serves also as a conduit to the mouth. Many writers have given credence to this idea, but none have supported it with direct evidence. McIndoo (1916), however, describes elaborately the bees' method of feeding as if all their liquid foods go up to the mouth through this ventral groove of the glossa by capillary

attraction, assuming that the saliva runs down the narrow groove in the glossal rod at the same time, and that the two streams pass each other in the channels beneath the paraglossæ. He says "this view seems to be the only plausible one" and "Nature could not have devised a better plan." Further on he adds: "The entire process is clear to the writer except where the saliva and liquid food pass around the base of the tongue. It is strange that both liquids can travel in opposite directions along the same route by no force other than capillarity." This is indeed strange, but nature did not devise the plan. The bees will demonstrate just how they feed on honey, and the writer has seen no evidence that food liquids during feeding ever go up the ventral channel

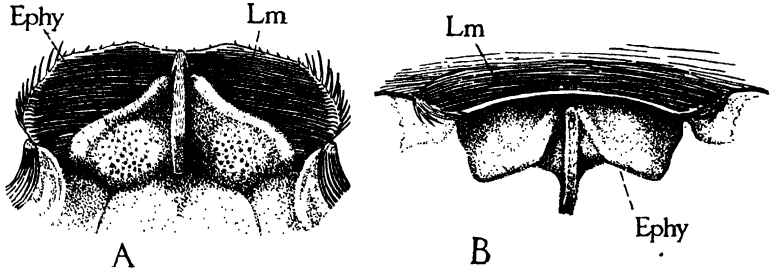



FIG. 17.—Epipharynx (*Ephy*) and labrum (*Lm*) of worker. A, ventral view B, anterior view.

of the glossa. The saliva is copious, probably flows down the groove in the glossal rod, accumulates in the larger channel and is discharged from this over the labellum. No explanations make it seem reasonable that a food liquid could ascend at the same time, and that the two streams could pass in opposite directions within the paraglossæ.

**The Length of the Tongue.**—The idea that the bee takes nectar with the tip of its tongue and through the ventral groove of this organ is purely conjectural and may be only one of the many scientific myths about the ways of the bee, but it has led to much "tongue" measuring with a view of determining from what depth bees can extract nectar from flowers, and, in particular, to decide whether or not the honeybee can get nectar from red clover. According to Zander (1911) the proboscis of German worker bees is about 6 millimeters in length, while, as given by Kulagin, that of Russian bees averages 6.21 millimeters, measured

from submentum to labellum, that of Italians 6.25 millimeters and that of Cyprians 6.5 millimeters. Zander gives the length of the proboscis of the queen as 3.5 millimeters, and that of the drone as 4 mm. As a consequence of this handicap the queen and the drones must be fed by the workers. Even though the groove of the tongue may not be a food conduit, the tongue itself, by its rapid extension and retraction through the tube of the maxillary

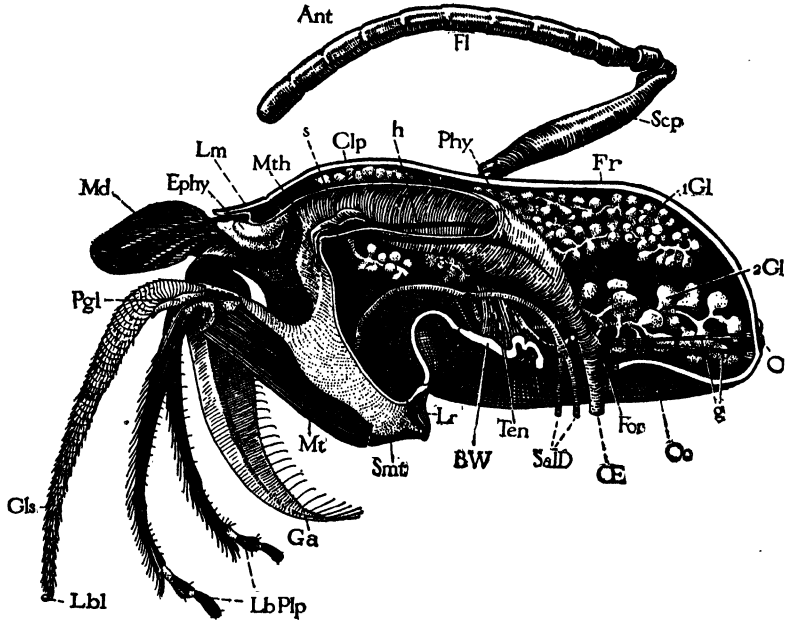



FIG. 18.—Right half of head of worker cut near median plane, with right antenna (*Ant*), right mandible (*Md*), and lobe of right maxilla (*Ga*), but with entire labium and epipharynx (*Ephy*). Internally are shown the pharynx (*Phy*), œsophagus (*Œ*), pharyngeal glands (*1Gl*), postcerebral salivary glands (*2Gl*), and salivary ducts to thorax (*SalD*).

lobes and the labial palpi, very evidently serves to bring honey into the latter, and, therefore, most likely acts in the same manner in the narrow nectar cavities of the flowers. Still, the reach of the tongue may depend on the extent to which the proboscis as a whole can be protruded, in which case the problem of determining from what flowers a bee may collect nectar and from what it may not is one that cannot be a determined merely by measuring the length of any of the organs concerned.

## 6. THE SENSES AND SENSE ORGANS OF THE MOUTH AND THE MOUTH PARTS

Sense organs of several varieties (Fig. 19) are situated on all the mouth appendages, on the epipharynx, and on the pharyngeal plate in the mouth (Fig. 18, *s*). Some of them occur also on the sides and top of the head, on plates of the neck, and on other parts of the body. The sense organs of the epipharynx were described by Wolff (1876), these and the others have been more recently investigated by McIndoo (1916). In studying the functions of the sense organs of the mouth parts, however, the same problem is encountered as in studying the sense organs of the antennæ, namely, that of determining what sense stimuli may be received through each particular kind of sense organ. It is manifestly impossible to isolate the different varieties of organs and to experiment on each one separately. Consequently, ideas of their function are only opinions based on a knowledge of the structure.

**Varieties of Sense Organs in or Near the Mouth.**—The principal varieties of sense organs of the mouth and mouth parts as described and figured by McIndoo (1916) are shown in Fig. 19. It will be seen that all of them, except one (G), are merely sensory hairs of one form or another, and, judging from their similarity of structure, it does not look as if these hairs could receive sense stimuli of very different sorts. On each lateral lobe of the epipharynx (Fig. 17 A, *Ephy*) there is located a group of short, curved hairs with wide, cone-shaped bases. These, shown in section at A of Fig. 19, were first described by Wolff (1876), who thought that they were the olfactory organs of the bee, that the secretion of the mandibular glands was poured over them to absorb odor particles which might then penetrate the thin walls of the hairs and affect the endings of the sense cells within them. McIndoo, however, argues that the walls of the hairs are too thick to be thus penetrated or to receive stimuli of either smell or taste. Organs of another though similar type are shown at B. These consist of short, thick-walled, curved hairs, usually about half sunken into deep sockets of the cuticula. Such organs McIndoo finds particularly abundant on the mandible, but he says they occur also on the pharyngeal plate (Fig. 18, *s*) inside the mouth. Organs of a third variety (C) consist of short hairs similar to those of the last but placed in shallow sockets. Hairs of this sort occur on the mandibles, on the maxillæ and their palpi, on the mentum,

glossa, paraglossæ, palpigers and palpi of the labium, in the mouth cavity, on the antennæ, on the sides and top of the head, and on the cervical plates of the neck (Fig. 23, *Ce*). McIndoo thinks that all the types of sense hairs so far described can have only a tactile function, that is, that they are organs of touch, since their walls are too thick to serve any other purpose. On the middle of the glossa there are long, spine-like, tactile hairs (D), while on the tip of the glossa there are short hairs that have usually been regarded as taste organs, but of which McIndoo says it has never been shown that they have nerve connections.

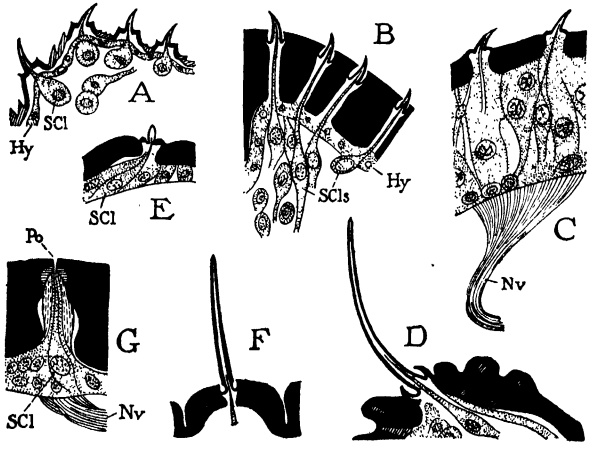



FIG. 19.—Sense organs on the mouth parts of the bee (*from McIndoo*, 1916). A, sense hairs with large chitinous bases on lateral lobes of epipharynx. B, sunken sense hairs on outer surface of base of mandible. C, sense hairs on pharyngeal plate with sublying cellular tissue and sensory nerve (*Nv*). D, long sense hair from middle of glossa. E, short sense peg of maxilla. F, long hair-like peg near tip of maxilla on outer surface. G, sense "pore" organ from mandible.

Hairs of a somewhat different kind from any of the foregoing are found on the maxillæ and on the labial and maxillary palpi, and are similar to those short hairs of the antennæ which have been described as pegs or peg-like hairs (Fig. 10 B, C, *SPg*). Such hairs are blunt; those of the mouth parts are usually short and thin walled (Fig. 19 E), but some of them on the maxilla are long and strongly chitinized (F). The shorter pegs might be regarded as organs of smell, but McIndoo again points out that their walls are too thick for an olfactory sense, and he regards the pegs, both short and long, as but another variety of tactile hairs.

Organs like the "pores" on the base of the antenna (Fig. 10 I) are the only organs of the mouth parts that are not of the hair type. They occur on the mandibles (Fig. 19 G), on the maxillæ, on the palpi and glossa of the labium, in the mouth cavity, on the sides of the head, and on the cervical plates of the neck. These organs have the same structure as those on the legs, the wing bases, and the sting which McIndoo calls the "olfactory pores," the structure of which has already been described in discussing those on the antenna (page 30).

**Do Bees Have a Sense of Taste?**—If bees have a sense of taste we should, of course, expect to find the organs of taste either in the mouth or on the mouth parts, and, at first thought, it seems perfectly reasonable to assume that bees do taste, since they without doubt exhibit a choice in the matter of foods. This last has been made clear by McIndoo (1916) in a series of experiments designed to test the bees' likes and dislikes for different flavors or for substances that should give strong taste reactions. For his experiments McIndoo first prepared some candy by kneading pure powdered sugar with a little honey, a confection of which bees are very fond. Then he mixed into different lots of this candy a little oil of peppermint, quinine, cider vinegar, carbolic acid, and alum, thus obtaining candies of very different flavors. These, and also some chinquapin honey, some honey containing oil of peppermint, some maltose, and some honey containing salt he offered to bees in cages. The results showed a very strong preference on the part of the bees for the pure sugar-honey candy over all the adulterations and the other things given them. None of them liked either the candy or honey flavored with peppermint, 23 per cent ate some of the candy containing quinine, 29 per cent ate some of the candy and vinegar, but only a few bees would touch any of the other items of the menu.

Experimenting next with things that should be repulsive in taste, it was found that bees would not eat candy containing either oil of peppermint or carbolic acid, while some things such as xylol, sulphuric acid, formaldehyde, and lime-sulphur in the candy, though evidently very distasteful, were not totally repelling. Formic acid was less objectionable, while whiskey was least so.

Still another set of experiments indicated that bees distinguish between substances of similar taste. Amongst sweet things they show special preference for cane-sugar candy, maltose, and light-

colored honey; amongst bitter things they much prefer quinine to strychnine; and of sour things they like lemon juice best, though they will take honey containing a few drops of acetic acid, but they totally abjure hydrochloric, sulphuric and nitric acids. When it comes to salts they are rather fastidious, all sodium and potassium salts being distasteful, potassium cyanide entirely repellent, potassium bromide and potassium ferrocyanide endurable, but most bees do not like salt in their candy, if they can get it without.

In summarizing his experiments McIndoo claims the results prove not only that bees are able to distinguish between substances that to us have different tastes, but that they distinguish even between some things, such as quinine and strychnine, which to us have the same taste. As a rule, he finds, bees like things that are agreeable to us, though they will have nothing to do with any food containing peppermint, while, on the other hand, they are rather fond of potassium ferrocyanide in candy, a flavor that we should not appreciate. But McIndoo says that bees like honey best of all things, and that they are able to distinguish very readily between different kinds of honey.

All of these facts, McIndoo points out, would indicate that bees possess a true gustatory sense, *provided that it could be shown that they do not discriminate between the different flavors by an acute sense of smell.* This question, he argues, cannot be settled by experiments, since even with ourselves there is much confusion as to what we taste and what we smell, and the investigator must base his conclusions on the anatomical structure of the sense organs to be found in the mouth or on the mouth appendages.

A detailed study of the sense organs of the mouth and the mouth parts of the honeybee, as given above, McIndoo claims, shows that only the pore organs might serve as organs of taste. Since experiments indicate, however, that the function of these organs on the other parts of the body is an olfactory one, he argues that it is most logical to suppose that those of the mouth parts have the same function. Therefore, he concludes that the honeybee, having no organs of taste, has no sense of taste, and that its apparent reactions to taste stimuli are responses to odors of the substances used in experiments. Some of the substances may be odorless to us and others, distinguished as different by the bees, may be alike to us, but we cannot judge the range or

acuteness of another creature's sense of smell by our own limited olfactory powers.

Most entomologists, probably, will not be convinced by this form of reasoning that insects do not taste, since it places too much reliance on a personal interpretation of the functional possibilities of an observed anatomical structure. It shows, however, that the experimenter who claims a sense of taste for insects must demonstrate it with tests that will clearly avoid a confusion between taste and smell.

## CHAPTER III

## THE THORAX AND ITS APPENDAGES

The second or middle division of the insect's body, counting the head as the first, has long been known as the thorax, a term borrowed from human anatomy, but, since this part of the insect is distinctively that which bears the wings, it is appropriately called the *alitrunk*.

### 1. THE GENERAL STRUCTURE OF AN INSECT'S THORAX

Since both the legs and the wings of insects are attached to the thorax, this region of the body becomes a very important one, and consequently also a highly developed one. The more efficient the appendages of locomotion, the greater the alterations and improvements they require in the machinery for their movement. More complicated motions entail special development of muscles; a specialized musculature involves an enlarging and remodeling of the segments that contain the muscles affected, and special developments of the chitinous walls of these segments to give them proper attachment. In the evolution of any species all such changes must be coordinated, and different insects of the present time show all degrees of specialization of the thorax corresponding with the development of the legs and wings.

If insects had legs only, the thorax would need but a comparatively small amount of reconstruction to accommodate improvements in the acts of running, jumping, climbing or digging; but flying is something entirely different from any of these forms of motion, as man himself has learned, and when insects acquired wings an entire reorganization of the thorax became necessary in order to perfect their use.

**The Principal Parts of a Thoracic Segment.**—Just what may have been the structure of an insect segment in its primitive state is a subject for the theorists to settle, but most any segment of the body, whether it carries appendages or not, has a dorsal and a ventral plate, the two separated on the side by membranous spaces which relieve the segment of the rigidity of a complete

circle. The abdomen of most insects is formed of simple segments of this sort. But the thorax is complicated by the presence of side plates in addition to the back and ventral plates, with the legs attached between the side plates and the ventral plates in all three segments, and the wings between the side plates and the dorsal plates in the second and third segments. A typical thoracic segment, therefore, consists of a dorsal plate, the *tergum*

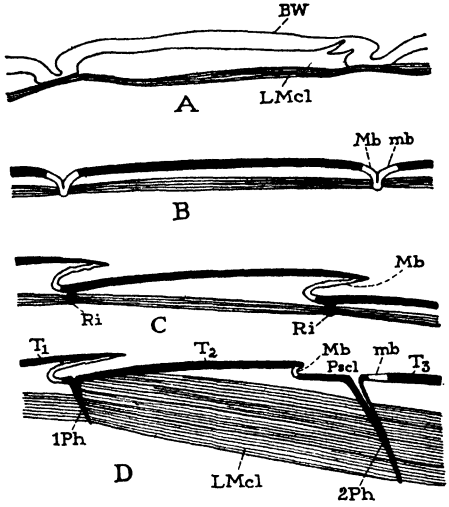



FIG. 20.—Attachment of dorsal segmental muscles and development of phragmas.

A, intersegmental attachment of continuous muscles in embryo of bee (*from Nelson*).

B, muscles of larva cut into segmental lengths by infoldings of intersegmental membranes (*Mb*, *mb*) to which they are attached.

C, attachment of abdominal muscles of adult to ridges (*Ri*, *Ri*) near anterior edges of tergal plates. The ridges apparently produced by chitinization of intersegmental infolds and obliteration of posterior half of original intersegmental membrane (*B. mb*), of which only the anterior half (*Mb*) remains in abdomen of adult.

D, attachment of dorsal thoracic muscles to phragmas. First phragma (*1Ph*) has same relation to adjoining parts as the abdominal ridges (*C*, *Ri*), but the second (*2Ph*), and usually the third, may be free chitinous infolds preserving remnants (*Mb* and *mb*) of original membrane, or they may be united to plate preceding or plate following as in abdomen by obliteration of either membrane remnant. The postscutellum (*Pscl*), when present, is a surface plate developed from anterior lip of phragma.

or *notum*, of a ventral plate, the *sternum*, and of a lateral plate or *pleuron* on each side.

**The Phragmas.**—The tergal plates of the first four body segments are commonly separated, in adult insects, by chitinized

infoldings of the intersegmental membranes known as the *phragmas* (Fig. 21, 1*Ph*, 2*Ph*). The phragmas are developed for the purpose of providing a larger surface for the attachment of the dorsal longitudinal muscles of the thorax. In the embryo, according to Nelson (1915), the longitudinal muscles are attached to the intersegmental grooves of the body wall (Fig. 20 A, *LMcl*). In the larva the grooves form deeper infoldings (B), separating each intersegmental ring into a part before the infold (*Mb*) and a part behind it (*mb*). In the abdomen of the adult bee and most other insects the dorsal muscles are attached to ridges (C, *Ri*) at the anterior edges of the ventral surfaces of the tergal plates. Evidently here the posterior membrane of each intersegmental region (B, *mb*) has been eliminated by the union of the chitinized infold (C, *Ri*) with the tergal plate following it. In the thorax the chitinous fold, or first phragma (D, 1*Ph*), between the prothoracic tergum ($T_1$) and the mesothoracic tergum ($T_2$) is in the same way united with the tergum following it ($T_2$). The second and third phragmas are likewise in some insects fused with the tergal plates behind them, which are the metathoracic tergum and the first abdominal tergum respectively, but more commonly each remains separated by narrow intervening membranes (D, *Mb* and *mb*) from both the tergum in front and the one behind. In this case, however, there is usually developed from the anterior lip of the phragma (2*Ph*) a chitinization of the anterior part of the original intersegmental membrane, which forms a surface plate (*Pscl*) that becomes virtually a part of the preceding segment.

**The Ground Plan of a Wing-bearing Segment.**—Since the prothorax has no wings its structure may be in some respects more primitive than that of the mesothorax or metathorax, but in other ways its composition is obscured by special modifications and by reduction in some of its parts. The wing-bearing segments, on the other hand, are highly developed and their structure is usually taken as typical of a thoracic segment. Moreover, it is necessary to know the basic structure of one of these segments in order to be able to interpret the special modifications of their parts in the various groups of insects. Any conception of the typical generalized structure of these segments, however, is necessarily theoretical, since in all insects they show at least some degree of specialization; but the plan given in Fig. 21 shows the fundamental divisions of the tergum, pleuron, and sternum.

*The Tergum.*—The tergum or notum of each wing-bearing segment of adult insects consists of an *alinotum* (Fig. 21, *AN*), which is the original plate that carries the wings (*W*), and it may include a *postnotum* or *phragmanotum* (PN), consisting of the *phragma* (*2Ph*) and a plate (*Pscl*) developed secondarily from the anterior lip of the phragma. If the phragma, however, fuses with the tergum following it, there is ordinarily no postnotal plate present.

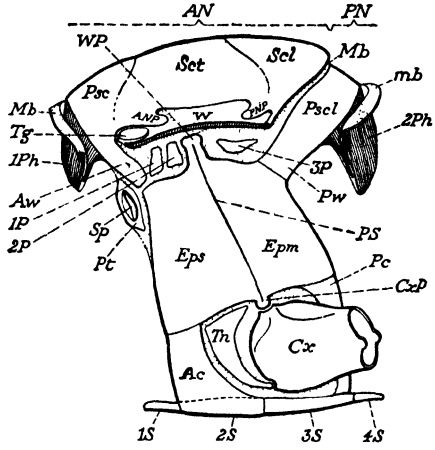



FIG. 21.—Diagram of the parts in a typical adult wing-bearing segment of the thorax, the wing (*W*) cut off at the base and the leg removed beyond the coxa (*Cx*).

*Ac*, antecoxal bridge; *AN*, alinotum; *ANP*, anterior notal wing process; *Aw*, prealar bridge; *Cx*, coxa; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *Mb*, prephragmal remnant of intersegmental membrane; *mb*, postphragmal remnant of intersegmental membrane; *1P*, *2P*, episternal parapteral or basalar plates; *3P*, epimeral parapteron, or subalar plate; *Pc*, postcoxal bridge; *1Ph*, *2Ph*, phragmas (first and second if the segment is mesothoracic); *PN*, postnotum, or phragmanotum; *PNP*, posterior notal wing process; *PS*, pleural suture; *Psc*, prescutum; *Pscl*, postscutellum; *Pt*, peritreme; *Pw*, postalar bridge; *1S–4S*, parts of the sternum; *Scl*, scutellum; *Sct*, scutum; *Sp*, spiracle; *Tg*, tegula; *Tn*, trochantin; *W*, base of wing; *WP*, pleural wing process.

The alinotum is typically divided by more or less distinct transverse sutures into three parts: the *prescutum* (Fig. 21, *Psc*), the *scutum* (*Sct*), and the *scutellum* (*Scl*). The surface plate of the phragmanotum, when present, is commonly known as the *postscutellum* (*Pscl*), since it immediately follows the scutellum. Two lateral lobes of the alinotum, the *anterior notal wing process* (*ANP*) and the *posterior notal wing process* (*PNP*), project into the membranous base of the wing (*W*) to support two of its articular pieces (Fig. 30). An arm of the prescutum (*Aw*)

makes a *prealar bridge* to the pleuron in front of the wing base, corresponding with a *postalar bridge* (*Pw*) from the postscutellum behind the wing base.

*The Pleuron.*—The pleuron of a typical wing-bearing segment has a *pleural wing process* (Fig. 21, *WP*) on its upper edge, which supports the pivotal sclerite of the wing base, and a *pleural coxal process* (*CxP*) on its lower edge, which articulates with the basal segment, or coxa, of the leg. Between these two processes there extends a vertical or slanting *pleural suture* (*PS*), which divides the pleuron into an anterior plate, the *episternum* (*Eps*), and a posterior plate, the *epimeron* (*Epm*). On the inner surface of the pleuron the pleural suture forms a prominent apodeme, the *pleural ridge.*

In the pleural membrane below each wing base there are several small plates, typically two in front of the wing process (1*P*, 2*P*) and one behind it (3*P*). The first have very commonly been called the *paraptera,* and the writer (1909) extended the term to include the whole series. But Crampton (1914) contends that Andouin (1824), who invented the term "paraptere," did not apply it to any of these plates. Crampton, therefore, names the sclerites above the episternum (1*P*, 2*P*) the *basalar plates,* and the epimeral one (3*P*) the *subalar plate.*

*The Thoracic Spiracles.*—The thorax has two breathing orifices or spiracles (*Sp*) on each side, the first situated between the pleura of the first and second segments, the second between the pleura of the second and third segments. But each spiracle belongs to the segment following it, having been moved forward during development. The prothorax, therefore, has no spiracle of its own, though the first often appears to belong to it. A small sclerite containing a spiracle is called a *peritreme* (*Pt*).

*The Sternum.*—In the sternum, a groove often extends crosswise between the leg bases, dividing the sternal region into an anterior plate and a posterior plate, which have usually been distinguished as the true *sternum, eusternum* or *sternannum* (2*S*), and the *sternellum* (3*S*). The front part of the first is sometimes set off by a transverse groove forming a *presternum* (1*S*), while occasionally a *poststernellum* (4*S*) is distinct from the sternellum. The inner surface of the sternum supports an apodemal structure that typically consists of an upright basal piece with two arms spreading upward and laterally, suggestive of a two-pronged fork, and known as the *furca.* But the base of the furca commonly

shows that it arises from paired invaginations of the sternum, which are marked externally as pits, and sometimes it consists of two entirely separate arms. The pits frequently appear to be in the groove between the first and second sternal plates, but in other cases they appear to arise from the second sternal plate itself. Crampton regards the latter case as typical, and he names the furca-bearing sternal plate the *furcisternum*, while he distinguishes the one before it as the *basisternum*. A fourth sternal division he calls the *spinisternum* since it often carries an internal spine when present. Perhaps the different sternal divisions are not homologous in all insects.

*The Pleuro-sternal Parts.*—The basal joint of the leg, the coxa (Fig. 21, *Cx*), is attached between the pleuron and the sternum in a membranous area typically closed in front by an *antecoxal bridge* (*Ac*) and behind by a *postcoxal bridge* (*Pc*). The coxa is usually articulated by its dorsal rim to the pleural coxal process (*CxP*). In some insects it has also a ventral articulation with a small plate, the *trochantin* (*Tn*), which lies in front of it and hinges loosely on the lower edge of the episternum (*Eps*). The coxa of insects with this sort of leg articulation turns on a vertical axis, but not a rigid one on account of the suspension of the trochantin in the articular membrane.

**Modification of the Wing-bearing Segments.**—The insect thorax thus appears to be complicated enough in its simplest, typical form, but when we come to study its variations of development in the different orders of insects, the extent of its modifications becomes bewildering and discouraging even to specialists. Unfortunately, the thorax of the bee is one of those in which the fundamental structure is most obscure, particularly in the pleural region, but by first studying some of the principal modifications in other insects we can understand what has happened to the thoracic pleura of the wing-bearing segments of the bee. At A of Fig. 22 is shown a simple departure from the type (Fig. 21) in the cutting off of a *preëpisternal* plate (*Peps*) from the episternum by a vertical suture. At B both episternum and epimeron are cut into upper and lower parts (*Eps*, *eps* and *Epm*, *epm*) by a longitudinal suture. These divisions are the *anepisternum*, *katepisternum*, *anepimeron*, and *katepimeron* of Crampton (1914). At the same time the trochantin (*Tn*) may fuse with the lower part of the lower episternal plate (*eps*). Again, (C) the suture between the katepisternum (*eps*) and the antecoxal bridge (*Ac*)

may disappear so that these two sclerites fuse into one large plate (*eps*, *Ac*) between the anepisternum and the sternum. In similar fashion the katepimeron (D, *epm*) and the postcoxal bridge (*Pc*) may become fused, while at the same time the sutures limiting the lateral edges of the sternal plates may disappear, resulting in the formation of two plates (*eps*, *Ac*, 2*S* and *epm*, *Pc*, 3*S*) continuous from the upper pleural plates of one side to

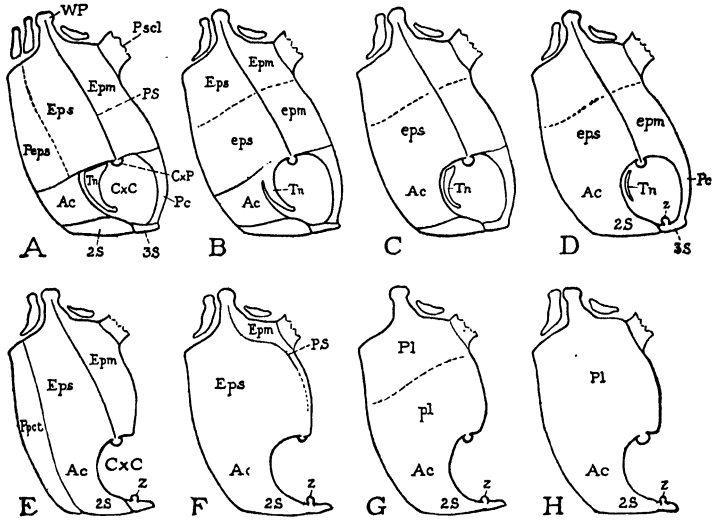



FIG. 22.—A few of the modifications of the pleural and sternal parts in wing-bearing segments, formed mostly by subdivision or fusion of original sclerites. A, a preepisternum (*Peps*) cut off from episternum (*Eps*). B, episternum and epimeron subdivided by horizontal sutures, forming anepisternum (*Eps*), anepimeron (*Epm*), katepisternum (*eps*), and katepimeron (*epm*); suture disappearing between *eps* and *Ac*. C, katepisternum and antecoxal bridge united into one plate (*eps* + *Ac*); trochantin (*Tn*) reduced. D, katepisternum, precoxal bridge, and anterior sternal plate fused into one pleuro-sternal plate (*eps* + *Ac* + 2*S*); trochantin rudimentary; ventral articular knob (*z*) for coxa developed on posterior sternal plate. E, prepectus (*Ppct*) cut off from front of entire pleuro-sternal part of segment. F, pleural suture (*PS*) displaced toward rear edge of pleuron. G, pleural suture gone; pleuron divided into upper pleural plate (*Pl*) and pleuro-sternal plate (*pl* + *Ac* + 2*S*). H, all pleural and sternal sutures obliterated.

those of the other. Along with this specialization by disappearance of sutures, the trochantin (*Tn*) may be reduced (C, D) or entirely lost (E). An articular knob (*z*) then develops on the second sternal plate to articulate with the lower rim of the coxa in place of the lost trochantinal articulation. At E a common condition is shown in which the postcoxal bridge is gone and the coxal cavity (*CxC*) is open behind. The same diagram shows

a cutting off of a *prepectus* (*Ppct*) from the front of the fused episternum, antecoxal bridge, and sternum, a condition found in some Hymenoptera. At F is shown a pleuron in which the pleural suture (*PS*) has moved backward till the epimeron (*Epm*) is almost crowded out, leaving the episternum (*Eps*), precoxal bridge (*Ac*) and sternum (2*S*) fused into one great plate. This diagram represents the mesothorax of the bee (Fig. 25 A), as will be shown presently in the special description of the thorax of the bee. The metathorax of the bee, however, is modified as in the next diagram (*G*) except that it is much narrowed (Fig. 25 B). The pleural suture is here gone entirely, though whether obliterated or crowded completely to the rear edge of the segment it is impossible to say; but the side of the segment is divided into an upper pleural plate (*Pl*) and a lower pleural plate (*pl*), and the latter is continuous through the precoxal bridge (*Ac*) with the sternum (2*S*). At H is shown an extreme case where all the pleural and sternal sclerites are fused into one great pleurosternal plate.

### 2. THE THORAX OF THE BEE

In studying the thorax of the adult bee it must be remembered that in all the higher Hymenoptera this region of the body consists of *four* segments—in addition to the usual three thoracic segments, it includes that which is the first segment of the abdomen in other insects. The proof of this is easily obtained from a study of the pupa, as has been shown by Zander (1910). In the larva of the bee (Fig. 105 A) there is no distinction between thorax and abdomen. During the first part of the pupal period (E, G) the thoracic segments are marked by the presence of the newly everted legs and wings, but even at this stage the first abdominal segment (*I*) shows no particular change. At a later period (H), however, the tergal plate of the first abdominal segment (*I*) is crowded against the contracted third thoracic segment (3); while, finally, in the mature pupa (I), it has become essentially a part of the thorax, and a deep constriction separates it from the second abdominal segment (*II*), which is now the first segment of the new abdomen. The transferred segment is known as the median segment or *propodeum*.

On the other hand, the lateral and ventral parts of the prothorax are dissociated from the anterior end of the thorax and constitute a suspensorium for the front legs (Fig. 23, $Cx_1$), loosely attached

by membrane to the part behind and articulating in front with the back of the head. The rest of the thorax, composed of the pronotum, the mesothorax, the metathorax, and the propodeum, constitutes a solid, compact capsule supporting the wings and the middle and hind legs (Fig. 23), and enclosing the muscles that move them.

**The Prothorax.**—On account of the dissociation of the parts of the prothorax, the tergum and the pleuro-sternum do not appear at first sight to belong to the same segment. They are entirely

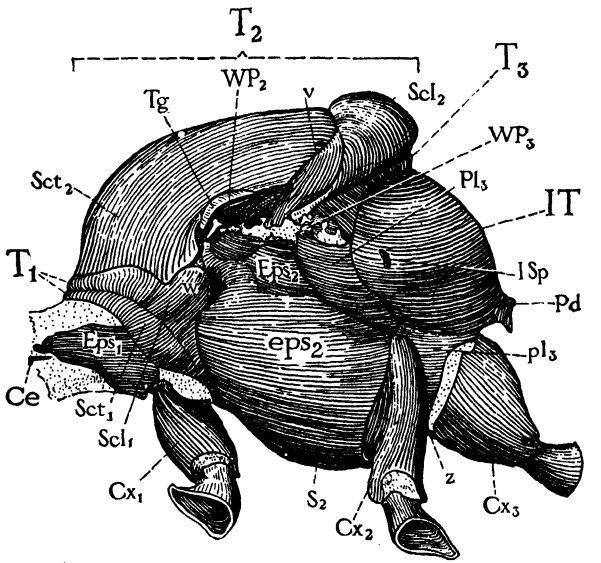



FIG. 23.—Thorax and bases of legs of worker, left side, wings removed, showing subdivisions of prothorax ($T_1$, $Eps_1$), mesothorax ($T_2$, $Eps_2$, $eps_2$, $S_2$), metathorax ($T_3$, $Pl_3$, $pl_3$), and propodeum ($IT$).

separated by a wide infolded membrane and have no points of articulation with each other.

The protergum (Fig. 23, $T_1$) is an integral part of the wing-bearing part of the thorax. It is completely circular in form and sits like a collar upon the anterior end of the mesothorax, to which it is closely attached. It is subdivided by a transverse groove into an anterior and a posterior part, which parts are perhaps the scutum and scutellum (Fig. 23, $Sct_1$, $Scl_1$). The second has a wide, flat lobe ($w$) on each side projecting backward as a protective lobe over the first spiracle, which is in the membrane at the anterior margin of the mesopleuron (Fig. 76).

The pleuron of the prothorax consists of a large triangular lateral plate (Fig. 23, $Eps_1$) supporting the front coxa by its lower posterior angle, and having its anterior end prolonged in the side of the neck to the head where it loosely articulates by a small terminal knob with the occipital region of the latter (Fig. 8 B, $Eps_1$). The lower edge of the plate is reflected on the ventral surface as a wide, rounded mesal extension (Fig. 29) which almost meets the corresponding plate of the opposite side. The lateral plate is traversed by a suture lying close to its posterior edge which extends upward from the articulation of the coxa. This is probably the pleural suture. If so, the small piece behind it, terminating above in a long process buried in a fold of the skin, is the epimeron, and the rest of the pleural plate is the episternum. In some Hymenoptera the prothoracic epimeron is better developed. A small cervical sclerite (*Ce*) lies in the neck membrane just below the anterior end of the episternum.

The prosternum consists of an anterior triangular plate (Fig. 29, $S_1$) lying before the bases of the front coxæ, with its lateral edges underlapped by the ventral parts of the episterna, and of a posterior narrow, parallel-sided part bent upward at an abrupt angle between the bases of the coxæ. The anterior coxæ have no sternal articulations as have the coxæ of the middle and hind legs. The second part of the prosternum bears the furca of the prothorax.

**The Mesothorax.**—The second segment of the thorax constitutes most of the bulk of the middle division of the bee's body. The size of this segment is due apparently to the great development of the mesothoracic wing muscles, which serve as motor organs for both pairs of wings.

The mesotergum (Fig. 23, $T_2$) forms the rounded roof of the thorax. It consists of two parts, the scutum and the scutellum (Figs. 23, 24 A, $T_2$, *Sct*, *Scl*), separated by a distinct transverse suture (*v*) externally, and internally by a strong notal ridge (Fig. 24, B, *VNR*). The latero-anterior areas of the scutellum are partially separated from the median areas by other sutures. Lateral wing processes of the scutum and scutellum (*ANP*, *PNP*) support the articulations of the front wings. When the mesotergum is detached from the rest of the thorax (Fig. 24, A, $T_2$, and C), it is discovered that there is a large posterior internal part of it (*Pscl*) attached laterally to the posterior margins of the scutellum, which does not show on the surface at all. This is the

postscutellum and its phragma (2*Ph*) constituting the postnotum or phragmanotum (*PN*) of a typical segment (Fig. 21). In the bee the postscutellum of the mesothorax is deeply buried in a transverse infolding of the membrane behind the scutellum, but in some of the Siricidæ, one of the lower Hymenopteran families, it forms a plate on the surface of the back as in most insects. In

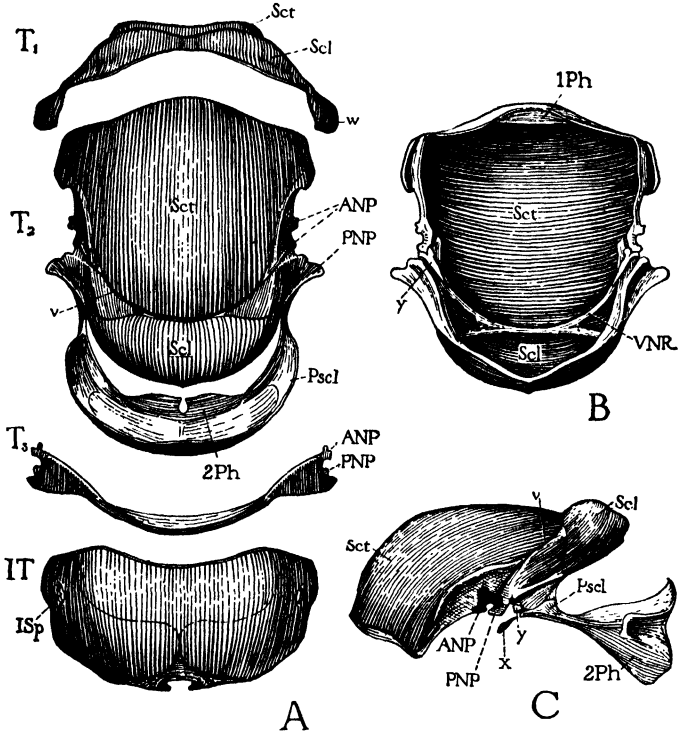



FIG. 24.—Thoracic terga of worker.

A, dorsal view of protergum ($T_1$), mesotergum ($T_2$) with middle phragma (2*Ph*), metatergum ($T_3$), and dorsal plate of propodeum (*IT*). B, ventral view of the alinotum or wing-bearing plate of mesotergum. C, lateral view of mesotergum, showing the alinotum and semidetached postscutellum (*Pscl*) with middle phragma (2*Ph*).

others it is sunken below the surface and mostly concealed between the mesothorax and the metathorax. In higher families it is entirely concealed, and in the bees the median parts are so widely separated from the rear margin of the scutellum that the plate appears to be an internal structure coming to the surface only at its extreme lateral ends.

The pleuron of the mesothorax comprises the large area on the side of the thorax (Fig. 23, *Eps*, *eps*) between the pronotal collar ($T_1$) in front, and the narrow metapleuron ($Pl_3$) and coxa of the middle leg ($Cx_2$) behind. Its upper part is crossed by a diagonal suture that sets off a dorsal sclerite, which was described in "The Anatomy of the Honey Bee" as the "epimeron," on the assumption that the suture just mentioned is the pleural suture. A comparative study of the mesopleura of other species of bees made by S. A. Rohwer, of the U. S. Bureau of Entomology, however, indicates that the posterior half of this suture (Figs. 25 A, 26 A, *l*) is a secondary sutural line, and that the true pleural suture includes only that part of it which curves downward and posteriorly

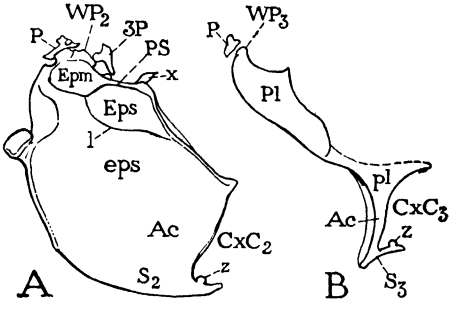



FIG. 25.—Outlines of pleuro-sternal parts of mesothorax (A) and metathorax (B).

In mesothorax pleural suture (*PS*) runs near posterior edge (compare Fig. 22 F), episternum divided by secondary suture (*l*) into upper plate (*Eps*), and into lower plate (*eps*) continuous through antecoxal bridge (*Ac*) with sternum ($S_2$). In metathorax pleural suture lacking, pleuron divided into upper plate (*Pl*), and into lower plate (*pl*) continuous through antecoxal bridge (*Ac*) with sternum ($S_3$). (Compare Fig. 22 G.)

from the wing process. Where this part of the pleural suture meets the secondary suture it bends abruptly upward (Fig. 26 A, *PS*) toward the dorsal edge of the pleuron, and then goes posteriorly around the posterior angle of the latter from which point it can be traced downward as a faint submarginal line to the upper end of the coxal cavity (Fig. 25 A). The epimeron of the mesopleuron, therefore, shows laterally as but a narrow posterior and dorsal marginal strip, except for the part below the wing process where it is expanded into a small oval plate (*Epm*). At the posterior dorsal angle of the pleuron, however, the epimeron is extended mesally as a wide horizontal plate (Fig. 26 B, *Epm*). Here a small sclerite (*x*) articulates between it and the

end of the postscutellum (Fig. 24 C, *Pscl*), probably a detached piece of the latter representing the postalar bridge (Fig. 21, *Pw*).

The rest of the mesopleural area consists of the episternum, but the diagonal suture (*l*) continued downward and posteriorly from the angle in the dorsal part of the pleural suture cuts off a small dorsal or anepisternal plate (*Eps*) from the main body of the sclerite (*eps*).

The wing process of the mesopleuron (Figs. 25 A, 26 A, $WP_2$) is low and broad. A single episternal parapteral plate or basalare (*P*) articulates against its anterior part; and an arm of the suba-

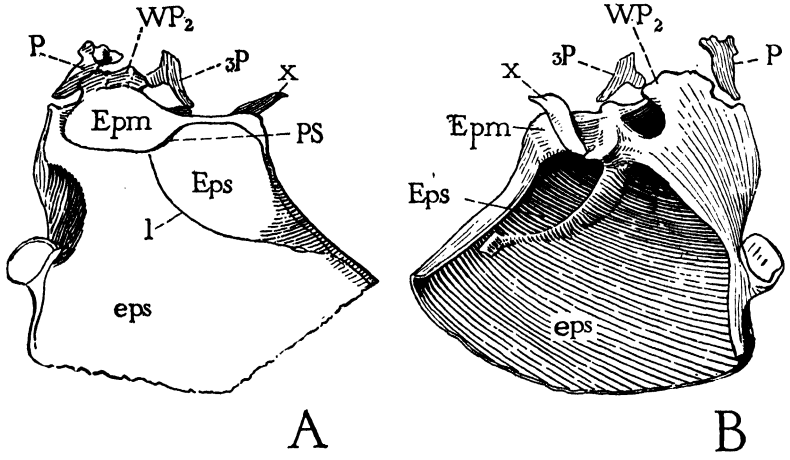



FIG. 26.—Details of upper part of pleuron of mesothorax of worker. A, external view, showing distorted shape of rudimentary epimeron (*Epm*), and subdivision of episternum (*Eps*, *eps*) by secondary suture (*l*). B, internal view of same, showing infolding of dorsal edge of epimeron (*Epm*), and small sclerite (*x*) connecting end of postscutellum with it (see Fig. 24 C, *x*).

lare (3*P*) articulates with its posterior angle. A deep excavation in the upper anterior part of the episternum is covered by the lobe of the pronotum (Fig. 23, *w*) that projects over the first spiracle (Fig. 76). The lower end of the principal episternal plate (*eps*) is not separated from the parts below; it is continuous through the antecoxal bridge (Fig. 25 A, *Ac*) with the sternum ($S_2$).

The mesosternum of the bee can be defined only as the ventral region of the pleuro-sternal area of the mesothorax (Fig. 23, $S_2$). A groove near the front edge of the combined sternal and pleural parts sets off a narrow anterior marginal band (Fig. 27, *a*), which normally is mostly covered by the edge of the protergum. Other-

wise the mesosternum is undivided by sutures, but its midline is marked by a slight ridge which terminates at each end in a small pit. The first pit (Fig. 27, *b*) is just behind the marginal pleuro-sternal band; the second (*c*) is in a wide depression of the posterior part of the sternum that projects between the meso-coxal cavities ($CxC_2$) and carries the knobs ($z_2$) of the sternal articulations of the middle coxæ. The two pits mark the ends of the base of the mesofurca.

**The Metathorax.**—The third segment of the bee's thorax is reduced to a circle of narrow sclerites (Fig. 2, *3*, *3*) crowded between the large mesothorax (*2*, *2*) and the propodeum (*I*). It carries the second pair of wings, but these, as will be explained later, are locked to the first wings by a series of hooks and are moved mostly by the muscles of the mesothorax.

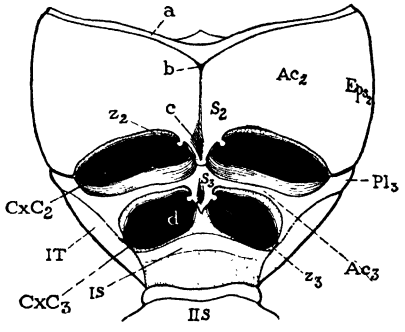



FIG. 27.—Ventral view of mesothorax, metathorax, and propodeum.
*a*, anterior marginal sclerite of pleuro-sternum of mesothorax; *b*, anterior root of mesofurca; *c*, posterior root of mesofurca; *d*, root of metafurca. $z_2$, $z_3$, condyles on sterna for articulation with coxæ.

The metatergum (Fig. 23, $T_3$) is a narrow transverse sclerite, widening on the sides where it carries the anterior and the posterior notal wing processes (Fig. 24 A, $T_3$, *ANP*, *PNP*). It shows none of the ordinary tergal divisions, and there is no postnotal plate or phragma connected with it.

The pleuron of the metathorax slants from the wing base downward and backward to the base of the third leg (Fig. 23, $Pl_3$, $pl_3$). The pleural suture is absent, and consequently there is no division into episternum and epimeron. A transverse suture, however, above the upper end of the middle coxa divides the pleuron into an upper plate ($Pl_3$) and a lower plate ($pl_3$). The lower plate is continuous through the precoxal bridge (Fig. 25 B, *Ac*) with the short metasternum (Figs. 25 B, 27, $S_3$).

The metasternum is a small median plate (Fig. 27, $S_3$) between the bases of the middle and the hind legs, with a posterior triangular tongue projecting between the latter and carrying the sternal articular knobs ($z_3$) of the hind coxæ. It is not defined laterally from the narrower antecoxal bridges. Its midline

presents a deep groove widening posteriorly, which contains a pit that marks the point of invagination of the metafurca.

None of the Hymenoptera have separate trochantinal sclerites (Fig. 21, *Tn*), and since the coxæ of the middle and hind legs are articulated ventrally to knobs of the sternal plates, it might be supposed that the trochantins of their segments have become fused into the sterna. But in other insects, such as flies (Fig. 22 D), the coxæ articulate with the sterna, though remnants of the trochantins are still present as separate sclerites (*Tn*).

**The Endosterna.**—Each thoracic sternum bears a large internal skeletal structure or furca, but since the furcæ of the second and third sterna are united there appear to be but two of them (Fig. 29, $Fu_1$, $Fu_{2+3}$).

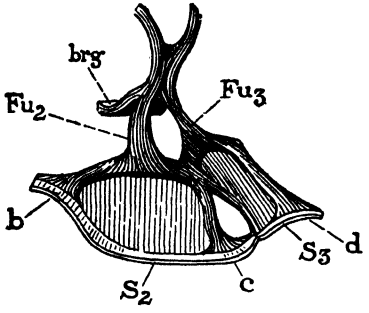



FIG. 28.—Left half of united furcæ of mesosternum and metasternum showing the three roots marked externally by pits (*b*, *c*, *d*, see Fig. 27).

The prosternal furca consists of a large horizontal V-shaped plate (Fig. 29, $Fu_1$) supported on two longitudinal triangular bases that diverge upward from a low median internal ridge of the second part of the sternum. The arms of the furca are wide at their bases where their concave upper surfaces are separated by a median crest. Their outer ends project forward and outward to the pleura of the prothorax where they unite with the pleural ridges. The first thoracic ganglion (Fig. 86, 1*Gng*) lies just before the prothoracic furca and its posterior commissures go through the channel between its basal supports.

The complicated endoskeletal structure formed of the united furcæ of the mesosternum and metasternum lies mostly in the rear part of the mesothorax (Fig. 29, $Fu_{2+3}$). It is supported on two median, vertical plates, one arising from the entire length of the mesosternum (Fig. 28, $S_2$), the other shorter one from the metasternum ($S_3$). The first has two roots corresponding with the two external pits of the mesosternum (Fig. 27, *b*, *c*); the second arises from the single pit of the metasternum. The metasternal plate leans forward and unites above with the mesosternal plate (Fig. 28), leaving an ovate aperture between the bases of the two plates. Above the dorsal fusion each plate forks later-

ally into a right and a left arm, of which the left arms only are shown in Fig. 28 ($Fu_2$, $Fu_3$). The two arms on each side, however, come together and unite a short distance above the basal

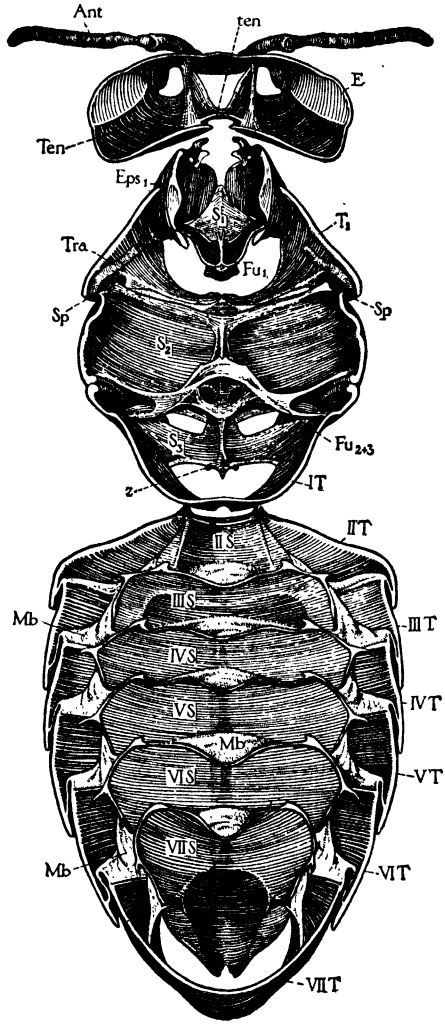



FIG. 29.—Ventral wall of entire body of worker seen from above, snowing endoskeletal parts.

plates, and at their points of union the two pairs on opposite sides are connected by a wide transverse bridge (*brg*). Above the bridge each pair of arms again separates, the two on each side

spreading outward and upward toward the lateral walls of the thorax, where the first unites with the posterior margin of the mesopleuron and the second with that of the metapleuron (Fig. 29). The posterior half of the second thoracic ganglion (Fig. 86, *2Gng*) lies beneath the bridge, and the ventral longitudinal muscles of the thorax are attached to the supports.

In each of the thoracic furcæ there are to be distinguished a dorsal transverse horizontal part extended outward on each side to the pleura, a pair of supporting arms, and a median, longitudinal basal ridge or plate. The two arms are probably to be regarded as the original paired furcal apodemes, and the transverse bridge and the median basal parts as secondary formations. The position of the basal plate on the sternum is, therefore, not significant as to the origin of the furca.

**The Propodeum.**—The propodeum or fourth segment of the thorax being an abdominal segment transferred to the thorax, as already explained, preserves the structure of an abdominal segment in that it consists of only a dorsal and a ventral plate. The dorsal plate or tergum forms the convex upper and lateral posterior part of the thorax (Fig. 23, *IT*) sloping steeply down to the stalk of the abdomen. It contains a spiracle (*ISp*) on each side, a character of all the abdominal terga. The sternum of this segment is a weakly chitinized band (Fig. 27, *IS*) on the posterior ventral surface of the thorax just behind the bases of the third legs and between the lower edges of the propodeal tergum (*IT*).

### 3. THE SPIRACLES OF THE THORAX

There are three pairs of spiracles or breathing holes in the thorax of the bee. The first spiracle on each side is in the membrane between the prothorax and the mesothorax (Fig. 76), the second is in that between the mesothorax and metathorax (Fig. 77), and the third is in the lateral part of the propodeal segment (Fig. 23, *ISp*). The first and second spiracles belong to the segments behind them, being secondarily moved forward, as shown by their origin and development in the embryo. The spiracles of the abdomen of the bee and of most other adult insects are placed in the lateral parts of the tergal plates, as are those of the propodeum, but those of the thorax are on the pleural areas below the level of the wing bases. It is not clear just what significance this may have bearing on the comparative structure of these two regions

of the body, and the problem is complicated by the fact that in adult insects the spiracles of the thorax usually do not have the same structure as those of the abdomen. A detailed description of all the spiracles of the bee is given in Chapter VIII on the Respiratory System (page 194).

### 4. THE WINGS AND THEIR MOTION

The wing of an adult insect consists of a thin *wing membrane* stiffened by *veins* and *cross-veins*, which divide the area of the wing into *cells*, and it is articulated to the wing processes of the thorax by small *axillary sclerites* in its base. The union with the body is flexible and the wing motion is produced by muscles, some of which affect the wing directly, others indirectly by changing the shape of the thorax.

**The Development of the Wings.**—With insects that develop gradually from the young form to the adult form, the wings arise along the edges of the back on the second and third thoracic segments as flat, hollow outgrowths of the body wall, each containing an extension of the body cavity, which is penetrated by branches of the thoracic tracheæ. With insects that change by a sudden metamorphosis from the form of the young to that of the adult, the wings begin their growth either beneath the cuticula of the thorax or in pouches of the hypodermis, and they do not normally appear as external appendages until the last larval skin is shed. In the bee the wings are everted from their pouches during the last larval stage when they may be seen as small pads beneath the larval cuticula of the second and third segments (Fig. 105 C, *W*). During the prepupal stage of the larva the wings enlarge (G), and when the pupa appears (I) they are long flaps overlapping on the sides of the thorax. The wings of the adult are finally completed within the cuticula of the pupal wings, and expand to their mature size and form when released from the latter.

During either form of development, however, the growth of the wings is fundamentally the same. The two surfaces of the pad come together and obliterate the inner cavity except for channels along the lines of the tracheæ. The walls of these channels then become chitinized, the tracheæ shrink, but are not withdrawn, and the intervening parts of the wing surface become very thin. The flat pouch or wing pad thus becomes a membranous wing in which the principal veins are chitinous tubes that originally formed about the tracheæ. Though the veins form

various patterns in the mature wings of different insects, the courses of the primitive tracheæ are much the same in all, and their study often furnishes a means of determining homologies between veins that appear quite different in the adults.

**The Articulation of the Wings.**—Each wing is hinged at its base to the anterior and the posterior wing processes of the notum (Fig. 30, *ANP*, *PNP*), and is supported from below upon the wing process of the pleuron (Fig. 21, *WP*). The basal part of the wing membrane remains soft and flexible, but it contains several articular sclerites or *axillaries* which intervene between

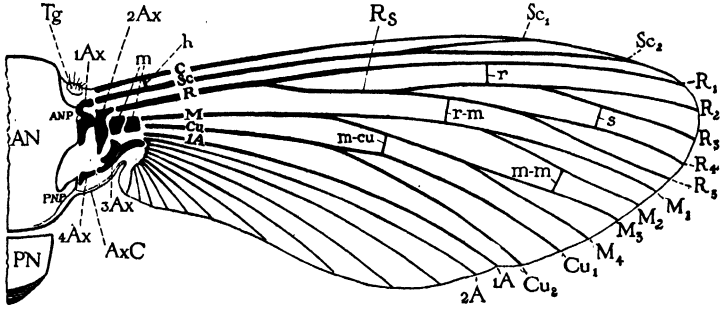



FIG. 30.—Diagram of a generalized insect wing and its articulation to the wing processes (*ANP* and *PNP*) of the alinotal plate (*AN*) of the tergum, with tegula (*Tg*) on anterior edge of wing base, and axillary cord (*AxC*) formed of thickening of posterior edge.

*Axillaries.*—1*Ax*, first axillary (anterior articulating sclerite); 2*Ax*, second axillary (pivotal sclerite); 3*Ax*, third axillary (anal flexor); 4*Ax*, fourth axillary (posterior articulating sclerite); *m*, median plates.

*Wing Veins.*—*C*, costa; *Sc*, subcosta, with two branches ($Sc_1$, $Sc_2$); *R*, radius, with five branches ($R_1$ to $R_5$); *M*, media, with four branches ($M_1$ to $M_4$); *Cu*, cubitus, with two branches ($Cu_1$, $Cu_2$); 1*A*, 2*A*, first and second anals, with others unlettered.

*Cross-veins.*—*h*, humeral; *r*, radial; *r-m*, radio-medial; *s*, sectorial; *m-m*, medial; *m-cu*, medio-cubital.

the proximal ends of the veins and the wing processes of the thorax.

In nearly all insects there are three articulating sclerites in the base of each wing, and in the Hymenoptera and some others there may be four. The *first* (Fig. 30, 1*Ax*) and the *fourth (4Ax) articulate* directly with the anterior and the posterior notal wing process, respectively; the *second (2Ax) is the pivotal* element of the wing base since it articulates below with the wing process of the pleurum; the *third* (3*Ax*) lies in the posterior part of the wing base where it is loosely connected with the fourth,

except where the latter is absent, in which case the third articulates directly with the posterior notal wing process. Usually there are also one or two small *median plates* (*m*) in the wing base having no definite or constant characters. A hairy pad at the anterior root of the wing, often developed as a large scale overlapping the wing base, is the *tegula* (*Tg*). The posterior edge of the basal membrane of the wing is usually thickened, forming the *axillary cord* (*AxC*), which becomes continuous with the posterior edge of the alinotum (*AN*). The phragmanotum (*PN*) never takes any direct part in the support of the wing.

In the honeybee there are four articular sclerites in the front wing (Fig. 31, C), but the fourth is lacking in the hind wing (D). They are all of typical form, though the first in the front wing is so long that it hinges upon both the anterior and the posterior wing processes of the notum.

**The Venation of the Wings.**—A general plan of the arrangement and branches of the veins in a theoretical generalized wing is given in Fig. 30, with the veins and cross-veins named according to the well-known Comstock-Needham system.

The first vein of the wing, which usually forms the anterior margin of the wing in an adult insect, is the *costa* (Fig. 30, *C*). The next 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 into five branches, the first fork remaining single ($R_1$) and the other, the *radial sector* ($R_s$), dividing into four terminal branches ($R_2$ to $R_5$). The next vein is the *media* (*M*) and forms four branches ($M_1$ to $M_4$). The fifth is the *cubitus* (*Cu*), which again is two branched ($Cu_1$ and $Cu_2$). The remaining veins are called the *anals* and are designated individually as the *first anal* (1*A*), the *second anal* (2*A*), 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* (*h*). A second occurs between the first branch of radius and the radial sector. This is the *radial cross-vein* (*r*). The next is between the third and fourth branches of radius and is called the *sectoral cross-vein* (*s*). The fourth is the *radio-medial cross-vein* (*r-m*) between radius and media. The next is the *median cross-vein* (*m-m*) between the second and third branches of media. The sixth is the *medio-cubital cross-vein* (*m-cu*) between media and cubitus.

Most of the veins have well-defined associations at their bases. The first vein or costa (Fig. 30, *C*), though not connected with any of the axillaries, is bound by a tough membrane ventrally to the parapteral plate or plates before the pleural wing process (Fig. 21, 1*P*, 2*P*). The subcosta (Fig. 30, *Sc*) typically

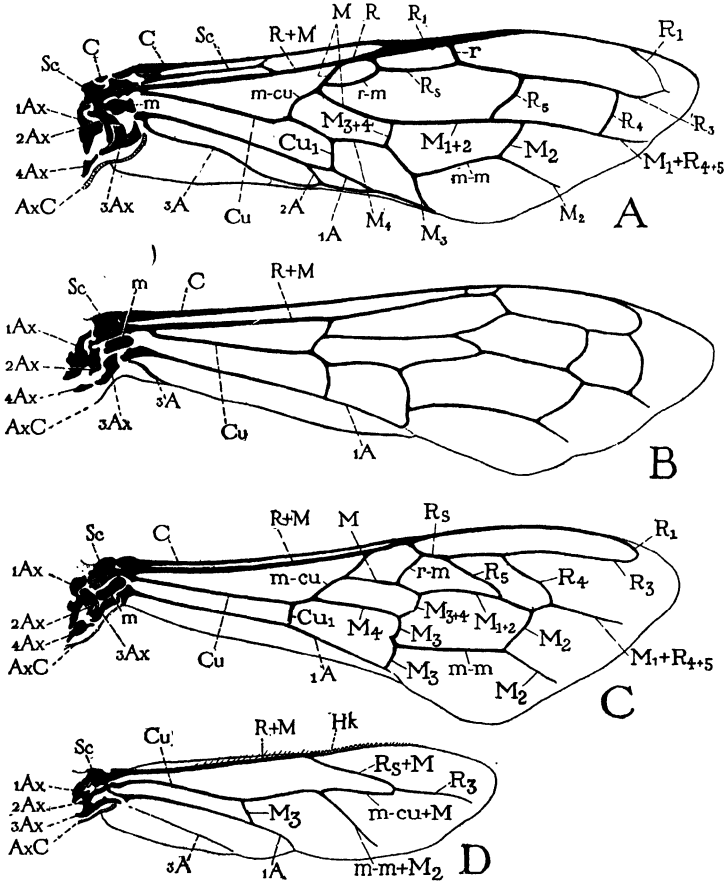



FIG. 31.—Wings of Hymenoptera, with veins and cross-veins named according to the Comstock-Needham system given in Fig. 30.

A, front wing of *Sirex flavicornis*. B, front wing of *Pepsis sp.* C, front wing of honeybee; D, hind wing of honeybee.

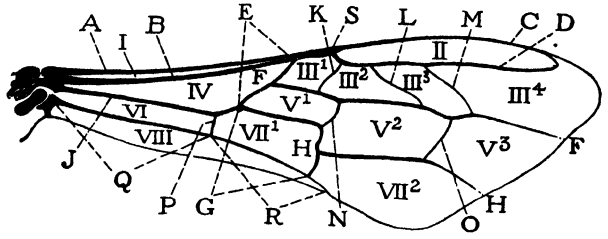
abuts against the end of the curved neck of the first axillary (1*Ax*) The radius is either attached to or touches upon the anterior end of the second axillary (2*Ax*). The media (*M*) and the cubitus (*Cu*) are associated more or less closely with the

median plates (*m*). The first anal (1*A*)' is usually independent from the main group of anal veins, and is often more associated with the base of the cubitus, suggesting that it should be regarded as a second cubitus rather than as the first of the anal series. In the Orthoptera, in which the anal region of the wing is pleated, the first fold occurs between the first so-called anal vein and the second. The other anal veins usually form a definite group, commonly united at their bases, associated with the third axillary (3*Ax*), which, by means of a connected muscle, acts as a lever in the folding of the wing.

A few insects have a generalized wing venation almost identical with that given in the diagram, Fig. 30, but with most of them the arrangement of the wing veins departs from this plan in varying degrees. The wings of the honeybee (Fig. 31 C, D) furnish examples of modifications of wing venation carried to an extreme degree in a way perhaps not yet entirely understood. The Hymenopteran type of venation, however, is more complete in the wings of a sawfly, and Fig. 31 A shows the fore wing of *Sirex flavicornis*, a member of this group, with the veins and cross-veins identified according to the Comstock-Needham system. The subcosta (*Sc*) is here reduced to a small forked vein in the proximal third of the wing, but its base is expanded into a large chitinous piece that forms a prominent shoulder on the anterior root of the wing and articulates with the head of the first axillary (1*Ax*). The radius and media are united into one compound vein (*R* + *M*) in the proximal half of the wing, to which the cubitus (*Cu*) is attached basally. The common shaft of these three veins is connected with the second axillary (2*Ax*). The three anal veins (1*A*, 2*A*, 3*A*) are associated by a common base with the third axillary (3*Ax*). In the distal field of the wing the departure from the typical venation (Fig. 30) is most pronounced, but it appears that the branches of the veins have turned toward the base of the wing and have united with the veins before or behind them.

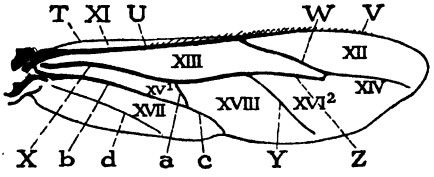
Studying next the fore wing of a higher member of the order, such as *Pepsis*, of the family Pompilidæ, (Fig. 31 B) and then the fore wing (C) and the hind wing (D) of the honeybee, we see examples of increasing specialization in this type of wing venation resulting in a venation so removed from the primitive that the veins can be identified only by a serial comparison with simpler forms.

A consistent application of the system of naming the veins as in the diagram (Fig. 30) applied to the Hymenoptera, however, produces compound terms too inconvenient for use in specific description. Many students of Hymenoptera, therefore, have adopted another nomenclature in which the veins are designated by individual names regardless of homologies with the veins in other orders This system, as given by Rohwer and Gahan (1916), is shown applied to the fore and the hind wing of the honeybee in Fig. 32.




FRONT WING.—*Veins:* *A*, costa; *B*, subcosta; *C*, metacarpus; *D*, radius; *E*, basal; *F-F*, cubitus; *G*, discoideus; H-H, subdiscoideus; *J*, media; *K*, first intercubitus; *L*, second intercubitus; *M*, third intercubitus; *N*, first recurrent; *O*, second recurrent; *P*, nervulus; *Q*, submedius; *R*, brachius; *S*, stigma.

*Cells:* *I*, costal; *II*, radial; *III*, cubital; *IV*, median; $V^1$, $V^2$, $V^3$, first, second, and third discoidal; *VI*, submedian; $VII^1$, $VII^2$, first and second brachial; *VIII*, anal.




HIND WING.—*Veins:* *T*, costella; *U*, subcosteila; *V*, metacarpella; *W*, radiella; *X*, mediella; *Y*, discoidella; *Z*, cubitella; *a*, nervellus; *b*, submediella; *c*, brachiella; *d*, anella.

*Cells:* *XI*, costellan; *XII*, radianellan; *XIII*, mediellan; *XIV*, cubitellan; *XV*, submediellan; $XVI^2$, second discoidellan; *XVII*, anellan; *XVIII*, brachiellan.

FIG. 32.—The wings of the honeybee with veins and cells named according to the nomenclature adopted *by Rohwer and Gahan* (1916).

**The Movement of the Wings.**—The motion of the wing of an insect 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. The muscles that produce the vertical

motion of the wings are much larger than the others and are the largest muscles in the body. They fill the thoracic cavity with a muscle mass which is distinguished by a brownish color from the other muscles, the latter being pale or white by comparison. Furthermore, these muscles are not inserted on the wing bases, but are attached to the walls of the thorax and move the wings by altering the shape of the thorax. They are, therefore, known as the *indirect muscles of the wings.* The other muscles, those that turn the wings forward or backward, are attached to

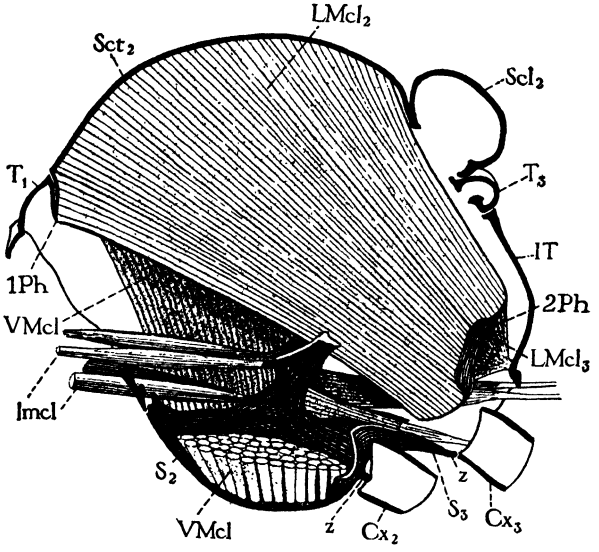



FIG. 33.—Indirect wing muscles and other median thoracic muscles, as seen in vertical, longitudinal section of thorax of drone.

*LMcl*$_2$, longitudinal indirect wing muscles, extending from first phragma (1*Ph*) and mesoscutum (*Sct*$_2$) to middle phragma (2*Ph*); by contraction they elevate back of thorax and depress wings (Fig. 36 B). *VMcl*, vertical indirect wing muscles (cut off near base on left side), extending between tergal and sternal plates of mesothorax; by contraction they depress back of thorax and elevate wings (Fig. 36 A).

sclerites at the bases of the wings themselves and are, hence, called the *direct muscles of the wings.*

*The Indirect Wing Muscles.*—The indirect muscles of flight in the bee may be easily studied by cutting the thorax into lateral halves (Fig. 33). The upper part of the thoracic cavity is then seen to be occupied by a great mass of longitudinal muscle fibers (*LMcl*$_2$) attached in front to the scutellum (*Sct*$_2$) of the mesotergum and to the first phragma (1*Ph*), and behind to the second

phragma (*2Ph*), which, as already explained, is deeply invaginated into the cavity of the thorax. A cross-section (Fig. 35) shows that there are two flat masses of these dorsal longitudinal muscles (*LMcl*), one on each side of the middle plane of the thorax. In each half of the thorax there is another large muscle mass consisting of vertical fibers (Figs. 33, 35, *VMcl*) stretched between the back plate and the sternum. A contraction of these muscles depresses the tergum of the mesothorax and spreads its ends apart, but a contraction of the longitudinal muscles pulls the ends together and elevates the back. Thus an alternate contraction of the two sets of muscles raises and lowers the principal back-plate of the thorax.

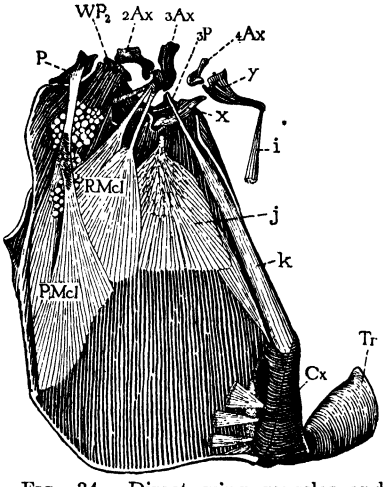



FIG. 34.—Direct wing muscles and other lateral muscles of mesothorax, as seen in internal view of mesopleuron of drone.

*PMcl*, pronator muscle inserted on basalar plate (*P*) before wing process of pleuron (*WP*$_2$). *RMcl*, flexor muscles, inserted on third axillary (*3Ax*).

*i*, muscle of accessory sclerite (*y*) of fourth axillary; *j*, tensor muscle of pleuron; *k*, muscle extending from coxa (*Cx*) to subalar plate (*3P*).

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 (Fig. 36, A) and that an elevation of the dorsum must depress them (B).

*The Direct Wing Muscles.*—The wings besides being moved up and down, can also, as before stated, be extended and flexed, *i.e.*, turned forward and backward in a horizontal plane upon the pleural wing processes. The muscles that accomplish these movements lie against the inner face of the pleuron (Fig. 34), and each wing is provided with a separate set of them. The extensor muscle (*PMcl*) is the most anterior. That of the fore wing arises from the front part of the mesosternum and is inserted by a long tendon upon the first parapteral plate (*P*). But the latter is closely connected with the anterior part of the wing base, so that a contraction of its 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* of the wing. In some insects this muscle is much larger than in the bee. The *flexor muscle* (*RMcl*) consists of three parts arising from the anterior half of the pleurosternum and inserted upon the third axillary (3*Ax*) of the wing base by long tendon-like necks. These muscles are antagonistic to the extensor and by their contraction turn the wing back toward or against the side of the body. The extensor and flexors,

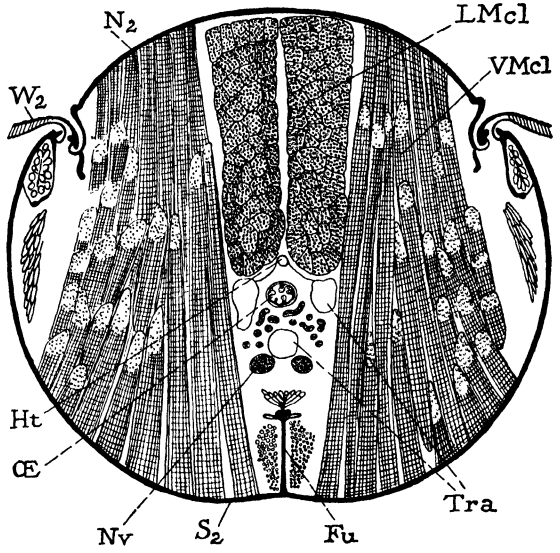



FIG. 35.—Cross-section of mesothorax through bases of wings ($W_2$), showing position of indirect wing muscles.
*LMcl*, longitudinal indirect wing muscles; *VMcl*, vertical indirect wing muscles.

together constituting the direct muscles of the wing, move the wing in the direction of their own pull. The indirect muscles, moving the wings by altering the shape of the thorax, impart a motion opposite to the direction of their contraction. The combined action of all these muscles gives the wings a semirotary or sculling movement as shown in Fig. 37, taken from Stellwaag (1910).

The hind wings have each a set of direct muscles corresponding with those of the fore wings, but there are no indirect wing muscles in the mesothorax. The posterior surface of the middle phragma (Fig. 33, 2*Ph*) is connected with the rear end of the ter-

gal plate of the propodeum (*IT*) by two fan-shaped muscles (*LMcl*$_3$), but since the microscopic structure of the fibers of these muscles is not that characteristic of the wing muscles (see page 137), they are perhaps not the true longitudinal muscles of the metathorax.

*Evolution of Wing Movement.*—In the dragonflies nearly all the wing muscles are inserted directly on the wing bases, but other winged insects move their wings principally by the indirect method. But in the grasshoppers, crickets, stoneflies, and others the two wing-bearing segments are about equal in size, and each is provided with a full equipment of direct and indirect muscles. In the beetles the metathorax is much larger than the mesothorax and the hind wings are developed into the principal organs of

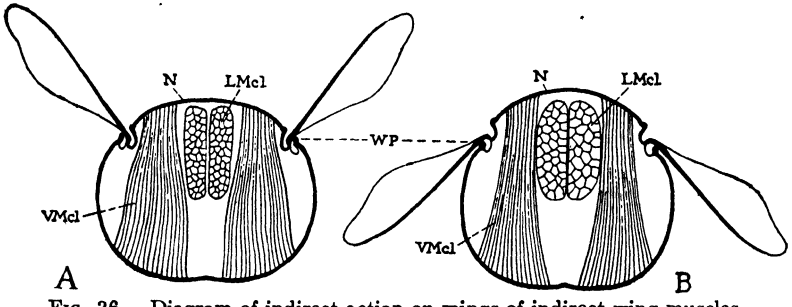



FIG. 36.—Diagram of indirect action on wings of indirect wing muscles. A, cross-section of thorax through pleural wing processes (*WP*), showing wings thrown upward by depression of back plate (*N*) caused by contraction of vertical muscles (*VMcl*). B, the same, but with wings forced down by elevation of back plate (*N*) caused by contraction of longitudinal muscles (*LMcl*).

flight. In most of the moths and in the butterflies, however, the front wings are the larger, and the mesothorax is consequently much more developed than the metathorax, though the latter remains as a distinct and complete segment. But, finally, in the true flies and in the wasps and the bees the metathorax is so greatly reduced and so consolidated with the mesothorax that it is scarcely to be regarded as a separate segment. In the bees the small hind wings are connected with the fore wings by a series of hooklets on their anterior margins (Fig. 31 D, *Hk*) which grasp a posterior marginal thickening of the front wings, and the two pairs thus act practically as one pair. In the flies the hind wings are reduced to knobbed stalks that have no use as organs of flight. Thus insects appear to show that one pair of wings is more efficient for rapid flight than two pairs, and it is clear that

the progressive consolidation of the thoracic segments of the higher insects is correlated with the simplification of the wing action—the bees attaining a unification of both pairs of wings, the flies becoming actually two winged by a reduction of the hind pair.

*Other Muscles Associated with the Wings.*—Besides the muscles described above there are several others associated with the wings, the functions of which are less evident. Most conspicuous of these is a fan-shaped muscle lying against the posterior half of the mesopleurum (Fig. 34, *j*) and inserted by an apical tendon on the outer end of the scutellum. This muscle may be simply an assistant to the large vertical indirect muscles, but Stellwaag (1910) suggests that its purpose is to depress the wing process of the scutellum so that the latter will not interfere with the movement of the first axillary sclerite when the wings are in motion. Another is a long slender coxo-axillary muscle (*k*) attached to the upper end of the coxa (*Cx*) and inserted on the subalar plate (3*P*). A third (*i*) is inserted upon the tip of the accessory sclerite (*y*) of the fourth axillary and is attached to one of the arms of the furca.

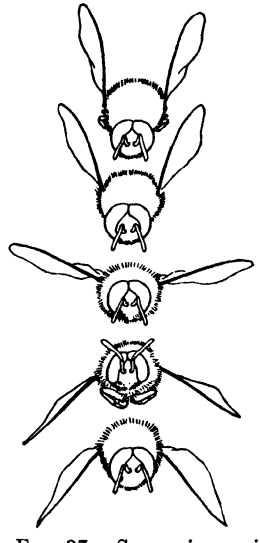


FIG. 37.—Successive positions of the wings of a drone in flight (*from photographs by Stellwaag*, 1910).

## 5. THE LEGS AND THEIR USES

The legs of insects are the ventral appendages of the first three body segments back of the head. They correspond serially with the head appendages which form the antennæ and the mouth parts.

**The Development of the Legs.**—In those insects that grow from egg to adult by direct development, the legs appear on the embryo as three pairs of simple outgrowths (Fig. 3, $L_1$, $L_2$, $L_3$) that develop gradually into the limbs of the adult; but in those insects that have legless larvæ, such as flies and bees, the legs either do not appear at all on the embryo, or their rudiments disappear before hatching. Nelson (1915) says that in the

embryo of the honeybee 60 to 62 hours old "the three pairs of leg rudiments are plainly outlined and constitute low, rounded protuberances" but that "the antennal rudiments and those of the three thoracic legs become reduced to hypodermal thickenings prior to hatching." The larva of the bee, therefore, has no antennæ or legs, and these appendages do not reappear externally until the beginning of the pupal stage, when the buds of the legs and those of the wings become visible through the larval integument some time before the last larval skin is shed (Fig. 105 C, *L*), appearing then as small lobes growing out of pockets in the skin of the pupa, which is still enclosed in the skin of the larva. The buds of the legs and the antennæ, however, had been developing for some time previous from those hypodermal thickenings to which these appendages were reduced in the embryo, and the wings from similar internal thickenings that never before protruded on the surface. All of these appendages made their early growth within closed pockets of the hypodermis (Fig. 108 D), since the bee larva is designed to be antennaless, legless and wingless. But, when the last larval cuticula is loosened preparatory to shedding, the inverted appendage buds turn out of their pockets and expand to a considerable length beneath the larval skin before the last larval molt takes place (Fig. 105 E, G, *L*). When the pupa then casts off the cuticula of the larva and becomes free, the legs and other appendages immediately lengthen and take on forms resembling those of the adult organs (H, I). The appendages of the adult bee are finally formed inside those of the pupa and are at last exposed with the shedding of the pupal skin.

**The Parts of an Insect Leg.**—The leg of an adult insect consists of a definite number of joints or segments (Fig. 38). The basal joint is the coxa (*Cx*). It is articulated above to the coxal process of the pleuron (Fig. 21, *CxP*), and below to either the lower end of the trochantin (*Tn*) or to a knob of the sternum (Fig. 22 D, *z*), except in a few cases where there is no ventral articulation. The next joint is the *trochanter* (*Tr*), a small piece hinged to the coxa in such a manner that it can move in a vertical plane, but usually solidly attached to the next joint, the *femur* (*F*), which is generally the largest part of the leg. The fourth joint, bending downward from the end of the femur, is the *tibia* (*Tb*). Finally comes the *tarsus* (*Tar*) composed typically of five small joints, though the number is frequently less.

The last tarsal joint usually bears a pair of claws movably articulated to its distal end, and generally, between or below the claws, one, two, or three soft adhesive lobes, which are used for clinging to smooth surfaces. Some insects that place the entire tarsus on the support have adhesive pads also on the under surfaces of the tarsal segments. Two lateral terminal lobes arising beneath the claws, as in flies (Fig. 38, *Pv*), are called *pulvilli*. A median lobe is known as an *arolium* or *empodium*, the terms being used indifferently by many writers. Crampton (1923), however, insists that any dorsal median lobe is properly an arolium, and that the name empodium should be restricted to a ventral median lobe. In some insects, as in the bee, the terminal foot structure

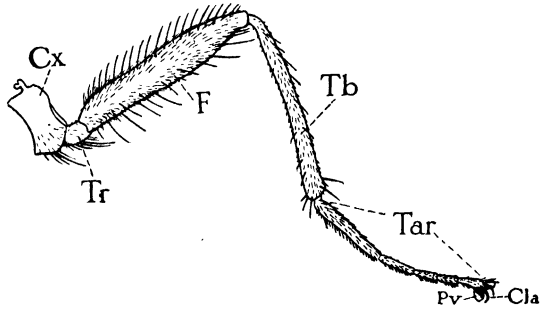



FIG. 38.—Leg of a fly.
*Cla*, claws; *Cx*, coxa; *F*, femur; *Pv*, pulvillus; *Tar*, tarsus; with five joints; *Tb*, tibia; *Tr*, trochanter.

is large and is complicated by having a number of chitinous plates in its walls. It has been regarded by some writers as constituting a sixth tarsal joint and has been designated the "prætarsus" and "claw segment." It is most likely, however, not a true tarsal segment but merely a special development of the end of the fifth joint, and in this sense it may be termed the *articularis* (MacGillivray, 1923).

**The Legs of the Honeybee.**—In the honeybee, and especially in the worker, the legs are highly modified for several purposes beside that of walking. The bee is an artisan of many trades and is provided with tools sufficient for all its needs. Some of its most important tools are parts of its legs. Each leg (Fig. 39 A, D, F), however, preserves all the parts of a typical insect leg (Fig. 38) with a five-jointed tarsus, and most of the special modifications of structure in the legs affect the tarsal joints. The basal

joint or *basitarsus* of the foot (Fig. 39 A, D, E, F, H, 1*Tar*), commonly called the *planta* in bee descriptions, is very large in all the legs as compared with the other tarsal joints, and in the hind leg (E, F, H) has the form of a wide plate flattened in a vertical plane. The next three joints are small and goblet-shaped, each arising by a basal stalk in the cup of the one preceding. In the fore and middle legs these joints are approximately all of equal length, but in the hind leg of the worker the first one is larger and flattened from side to side. The last or fifth tarsal joint in each leg is longer than those between it and the large basitarsus and is of a different form, being narrowed at the base to a slender decurved stalk set into the cup-like cavity in the end of the fourth joint, and enlarged toward its distal end. It carries the terminal foot structures consisting of the claws and the adhesive organ, the details of which in the bee will be described under a separate heading.

*The Fore Legs.*—The legs of the prothorax (Fig. 39 A) are smaller than the others (D, F) and are more freely movable, since the pleuro-sternal parts of the prothorax that support them (Fig. 23, $Eps_1$) are suspended in the walls of the membranous cylinder that constitutes the neck of the bee and are not otherwise attached to the rest of the thorax.

Several structures used by the bee for special purposes occur on the fore legs. The fringe of short, stiff hairs along the anterior edge of the inner surface of the tibia (A, *Tb*) constitutes an *eye brush* used for cleaning the compound eyes. The large first joint of the tarsus (1*Tar*) is covered with long unbranched hairs, forming a cylindrical *pollen brush* used for collecting the pollen grains that become dusted over the fore parts of the body when the bee visits flowers for pollen-gathering purposes. According to Gennerich (1922) this brush is used also for cleaning the mouth parts. At the base of the first tarsal joint there is an instrument used for cleaning the antennæ, and hence known as the *antenna cleaner*. It consists of a semicircular notch (A, C, *h*) in the inner margin of the first tarsal joint, fringed with a comb-like row of bristles, and of a large flat spur (*g*) on the end of the tibia (shown more enlarged in ventral view at B) that projects over the tarsal notch. By extending the front leg, placing the notch of the tarsus against the base of the antenna, flexing the tarsus toward the tibia, and then drawing the antenna backward between the spur and the notch, the bee is able to clean the antenna of pollen or

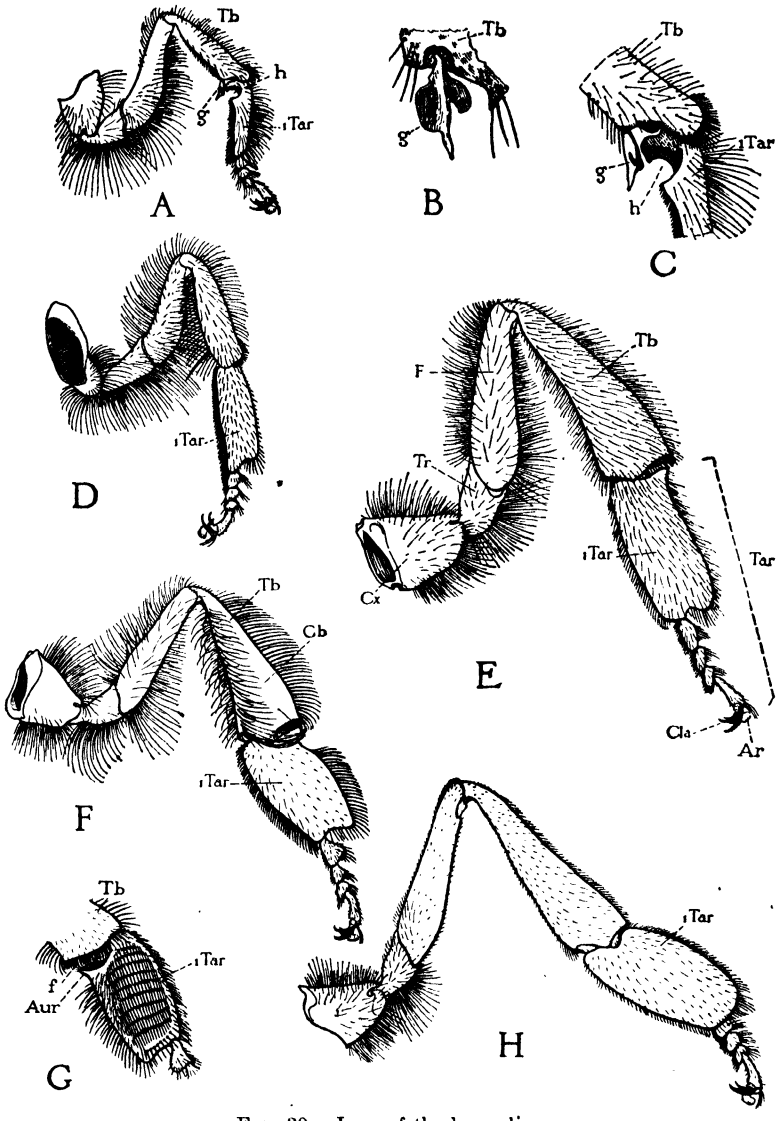



FIG. 39.—Legs of the honeybee.

A, left front leg of worker, anterior surface, showing notch of antenna cleaner (*h*) in base of first tarsal joint (1*Tar*) and spine (*g*) at end of tibia (*Tb*). B, spine of antenna cleaner (*g*) in flat view. C, details of antenna cleaner more enlarged. D, left middle leg of worker, anterior surface. E, left hind leg of queen, outer surface. F, left hind leg of worker, outer surface, showing pollen basket (*Cb*) on outer surface of tibia (*Tb*). G, inner surface of end of tibia (*Tb*) and first tarsal joint (1*Tar*), showing pecten (*f*) on the former, and auricle (*Aur*) and transverse rows of pollen gathering hairs on the latter. H, left hind leg of drone, outer surface.

other matter that may be adhering to it. It is pointed out by Gennerich (1922), however, that the antenna is not actually "grasped" between the spur and the tarsus, since the spur, though flexibly attached, has no muscles connected with it.

*The Middle Legs.*—The legs of the mesothorax are more solidly attached to the thorax than are the prothoracic legs, since their coxæ are inserted between solid plates of the thoracic wall (Fig. 23, $Cx_2$) and are hinged above and below to articular surfaces that permit of only a forward-and-backward movement on a vertical axis. The middle legs (Fig. 39 D) are less specialized than either the fore or the hind legs, but the large basal joint of the tarsus (1*Tar*) is wide and flat and its hairy surface is used for brushing pollen from the body. A prominent spine near the distal end of the inner edge of the tibia serves as a pick for removing the flakes of wax from the wax pockets on the under side of the abdomen.

*The Hind Legs.*—The coxæ of the metathoracic legs are also firmly articulated on a vertical axis to the walls of the thorax (Fig. 23, $Cx_3$), but they have a wider range of motion than those of the mesothoracic legs because their sockets (Fig. 27, $CxC_3$) are bounded posteriorly by the ventral membrane uniting the thorax to the abdomen, which contains only the weakly chitinous sternal plate of the empodeum (*IS*).

The hind legs of the worker are of particular interest because they bear the organs by means of which the bee transports pollen from the flowers to the hive. In all three castes of the bee both the hind tibia (Fig. 39 F, E, H, *Tb*) and the large first segment of the hind tarsus (1*Tar*) are very wide and flat. It has never been noted that the queen or drone make any special use of these parts, but in the worker each forms an important organ concerned with pollen carrying. The outer surface of the hind tibia of the worker (F, *Tb*) is smooth and slightly concave, and is fringed on both edges by long hairs that curve outward, the whole constituting a basket or *corbicula* (*Cb*) in which the pollen is stored for transportation. The inner face of the tibia, except for a narrow space at the lower end, is thickly covered with short hairs directed downward. Each hair has the form shown at I of Fig. 4, being doubly sinuous with the tip flattened and transversely widened. Its surface is longitudinally striated. The special function of these hairs has never been explained. The inner surface of the large basal segment or planta (G, 1*Tar*) of the hind tarsus is

covered with sharp, stiff spines closely arranged in about ten transverse rows. The plantar surfaces are used for brushing pollen from the body, but they are more particularly employed for taking the pollen from the middle tarsi and holding it until it is transferred to the pollen baskets. But the entire process of gathering pollen, transferring it to the pollen baskets, and storing it in the hive will be described in section 6 of this chapter.

**The Terminal Foot Structures.**—The last or fifth joint of each tarsus of the bee carries terminally a pair of large, movable, lateral claws (Fig. 40 A, B, C, *Cla*), and a complicated median organ ending in a soft lobe (*Ar*) turned upward between the claws. All of these parts constitute the *articularis*, according to the nomenclature of MacGillivray (1923), but they have recently been described in great detail for the bee by Arnhart (1923) under the name of "claw segment" (*Krallenglied*). The median part is designated the "adhering apparatus" (*Haftapparat*) by Arnhart. Since its terminal lobe enables the insect to cling to smooth surfaces by means of a sticky exudation, we may call it the *adhesive organ*.

*The Claws.*—The claws (Fig. 40 A, B, C, *Cla*) are hollow appendages flaring outward from their bases and curved downward. Each is bilobed, having a long curved upper point and a smaller under point situated at the base of the other, and each has three long prominent hairs which project downward beneath the points. Two of these hairs arise from the outer surface and one from the inner, the basal hair on the outer side being a particularly long, stiff bristle. The claws of the worker and the queen (Fig. 41 A, B) differ only slightly in details of outline, although the claws of the queen are larger than those of the worker; but the claws of the drone (C) are very strikingly different in shape from those of either female form, having long, straight, slender points and an abrupt bend in the dorsal margin.

The narrow bases of the claws are articulated to small knobs on the angles of a depressed ledge at the end of the dorsal surface of the last tarsal joint (Fig. 40 A, *f*). This articular piece is the *tubercula* of MacGillivray, the *unguifer* of Crampton (1923). MacGillivray describes it as "an associated part of the articularis."

*The Adhesive Organ.*—The organ of the foot by means of which the bee clings to smooth surfaces arises from the end of the fifth tarsal joint between and below the bases of the claws. It consists of a basal stalk and of a soft terminal appendage. The latter

is bilobed (A, *Ar*), but the two lobes are ordinarily bent upward from the end of the stalk and folded together (C). The walls of the stalk and the lobes contain a number of small sclerites. On the dorsal surface of the stalk there is a median plate having the outline of a long-necked flask (A, *a*) with the base against the

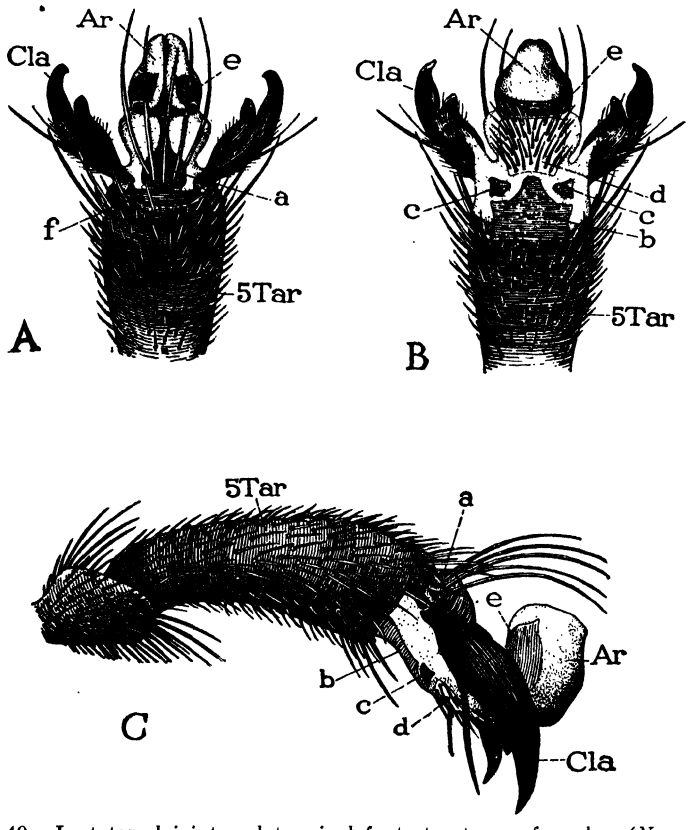



FIG. 40.—Last tarsal joint and terminal foot structures of worker (*Names of parts from MacGillivray*, 1923).

*a*, orbicula; *Ar*, arolium, with lobes bent upward in relaxed position; *b*, calcanea; *c,c*, auxilliæ; *Cla*, claws; *d*, planta; *e*, camera: *f*, tubercula; *5Tar*, fifth joint of tarsus.

tubercula or piece to which the claws are articulated (A, *f*). This sclerite is the "support-plate" (*Stützplatte*) of Arnhart, the *orbicula* of MacGillivray. It may be identified by the five long hairs that spring from its base and curve over the terminal lobes (*Ar*). On the ventral surface of the stalk there is a basal penta-

gonal plate (B, *b*) which may be more or less retracted into the end of the fifth tarsal joint (5*Tar*). This is the "flexor-plate" of Arnhart, the *calcanea* of MacGillivray, the *unguitractor* of Crampton. To its inner surface is attached the tendon of the muscle that retracts both the claws and the adhesive organ. At the distal angles of this plate there are two small sclerites (B, *c*, *c*), one on each side, the *auxilliæ* of MacGillivray. Beyond these is a larger, weakly chitinous, median, quadrate plate (*d*), the "sole" of Arnhart, the *planta* of MacGillivray. This plate is covered by numerous short, stiff, spine-like hairs directed distally and outward.

The terminal bilobed appendage of the adhesive organ is the *arolium* (A, B, C, *Ar*). When not in active use the lobes of the arolium are folded upward and enclose a cavity open dorsally by a narrow cleft between their edges (A). When the claws fail to grasp a smooth support the aroliar lobes are spread out and flattened against the surface, but the mechanism of the foot structures will be fully described under the next heading. The concave dorsal surfaces of the aroliar lobes are covered with short hairs, but their lateral and ventral surfaces are smooth and rounded In the base of the arolium there is a narrow, transverse sclerite (B, *e*) that curves upward in the folded lobes nearly to their dorsal edges (A, C, *e*). This is the "bow" (Bügel) of Arnhart, the *camera* of MacGillivray.

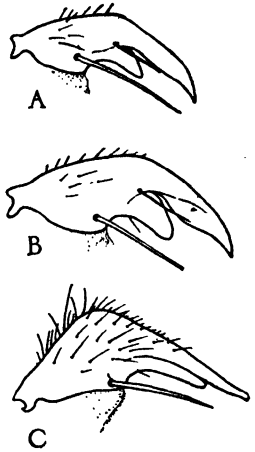



FIG. 41.—Tarsal claws of worker (A), queen (B), and drone (C); outer surface of outer hind claw in each case.

*The Uses of the Foot Structures.*—When the bee walks on ordinary surfaces it uses only its claws for maintaining its foothold, but when it finds itself on a hard, smooth or slippery surface, like that of glass, the claws are of no avail. For such emergencies the adhesive organs are provided; the arolia press down against the surface that the claws strive ineffectually to grasp, their lobes flatten out upon it and cling to it. When the emergency is over, and the claws are able to take hold again, the tension on the arolia is relaxed and their lobes spring back into their original positions. The temporary adhesion by means of

the out-spread arolia is due to a sticky liquid exuded from the *tenent hairs* on the ventral plates (B, *d*) in front of them.

The working of the various parts of the foot by a live bee, and the alternate use of the claws and the arolium, according as the surface to be grasped is rough or smooth, appears to be a very simple matter, but there is no visible external evidence of the means by which the movements are produced. Arnhart (1923), however, in his study of the foot of the bee, shows that the claws are flexed indirectly by the retraction of the flexor plate (Fig. 40 B, *b*), which is moved directly by the tendon of a tibial foot muscle inserted upon it. The relaxation of the claws is due in part to elasticity and in part to the spring of the long hairs projecting downward and backward from their sides.

The flattening of the aroliar lobes, on the other hand, Arnhart claims, is actually brought about, as it appears to be externally, by the forcible injection of a liquid into them. This liquid is a secretion from a thick-walled, glandular sac formed in the end of the tarsal joint by a forward reflection of that part of the hypodermis (*Matrix*) which normally belongs to the distal part of the stalk and to the terminal lobes. These parts, therefore, contain a hollow space continuous with the lumen of the sac, and this entire cavity, which contains the secretion, is thus a space between the cuticula and its hypodermis or probably between two layers of the cuticula, since Arnhart says the gland sac itself has a distinct cuticular lining. Such an arrangement is an unusual anatomical dissociation of tissues normally connected, but a section of a bee's foot examined by the writer appears to confirm Arnhart's description, and Arnhart further says that in the pupa the hypodermis lines all parts of the foot, the retraction being a feature of the adult. The injection of the liquid into the lobes, according to Arnhart, is brought about by the contraction of the same muscle that flexes the claws.

Whenever the nature of the support prevents the claws from taking hold they turn helplessly forward and outward and the tension of the contracting muscle on the flexor plate (B, *b*) is exerted on the plate (*d*) beyond and on the arch (*e*) in the walls of the lobes, resulting in a partial backward rotation and in a retraction of the arch. This also contracts the liquid-filled cavity in the base of the arolium and drives the secretion into the lobes, which consequently expand, while a part of the liquid exudes through the tenent hairs of the planta (*d*) and enables the flat-

tened lobes to adhere to the surface beneath. Arnhart says that a distension of the lobes may be produced artificially by pushing the arch in the base of the lobes forward. When the pressure relaxes the lobes spring back into their resting position by the elasticity of the chitinous arch in their walls. While the natural movements of the foot may be best observed in a bee forced to walk on glass, Arnhart demonstrates that workers must use the arolium for clinging to the smooth surfaces of the petals of certain flowers, and he points out that the organ may be, therefore, of much practical importance to bees in a state of nature.

### 6. THE COLLECTING AND STORING OF POLLEN

Pollen forms an important part of the food of bees, both of the adults and of the larvæ. While it is often called "bee bread" it might better be called the "meat" of the bees, since it is the element of their diet that furnishes them with proteins. The workers, therefore, possess a strong inborn "urge" for collecting and storing pollen, as well as nectar, and have an instinctive knowledge of how to use their equipment for gathering and carrying it.

**Collecting and Carrying Pollen.**—While it has long been a matter of common observation that the workers carry little yellow balls of sticky pollen to the hives in the baskets of their hind legs, it has only recently been ascertained exactly how they load the baskets. Two investigators, Sladen (1911) and Casteel (1912), working independently, have given us substantially the same account, which briefly, is as follows: In their visits to the flowers the bees become dusted all over with pollen, but that which they deliberately seek they scrape off and lick with the tongue, wetting it at the same time perhaps with some saliva but certainly with much regurgitated honey; from which we must infer that the collectors fill their honey stomachs well before setting out on a pollen-gathering trip, although on this point the writers give us no explicit information. The worker's head and foreward parts soon become covered with moistened pollen, which is cleaned off by the pollen brushes of the front legs and in turn scraped off of these and from the middle parts of the body by the brushes of the middle legs. Thus the brushes also become smeared with honey, and finally the body hairs themselves get wet and sticky. Much pollen is now assembled on the inner faces of the broad plantæ of the middle legs. These are next grasped one at a time

between the plantæ of the hindmost legs, and are then drawn forward, transferring their loads each to the inner face of the hind planta of the opposite side. When both the hind plantæ are sufficiently loaded the final act of storing the pollen in the baskets on the outer surfaces of the tibiæ begins.

Before Sladen and Casteel published their observations it had generally been thought that the bees scraped each hind planta over the edge of the opposite tibia and in this simple manner filled the baskets with the pollen adhering to the feet. A dis-

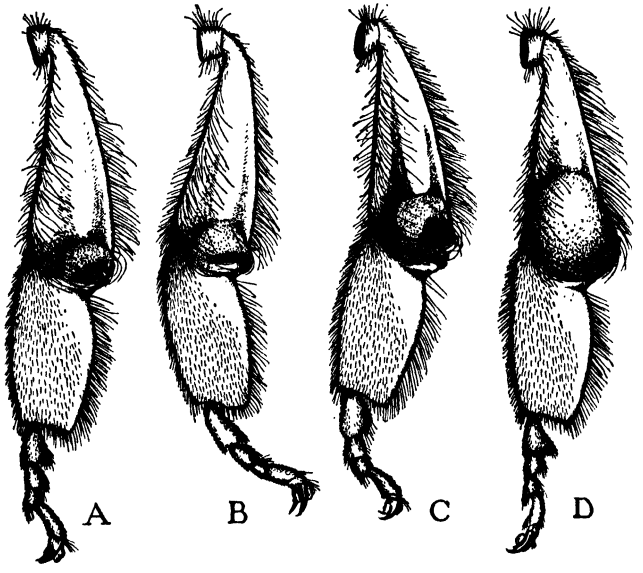



FIG. 42.—Outer surface of hind tibia and tarsus of worker gathering pollen, showing successive stages in growth of pollen mass in pollen basket by additions at lower edge (*from Casteel*, 1912).

concerting circumstance, however, was the fact noted that the pollen accumulates first in a little compact mass at the lower end of the basket and enlarges upward in transverse layers. But the new information shows that the bees proceed quite differently: it very nicely explains the discrepancies of the old theories and shows the true function of another organ previously misunderstood. The upper edge of the hind planta (Fig. 39 G, 1*Tar*) bears a projecting lip or *auricle* (*Aur*) with an end surface sloping upward and outward that fits nicely against the lower end of the

tibia, which is bevelled in the opposite direction. The inner edge of the end of the tibia, moreover, has a comb of stiff spines, the *peecten* (G, *f*) projecting downward. This instrument, formed of the opposing ends of the planta and the tibia, was formerly known as the "wax shears," because it had been imagined that it was used as a pair of pinchers to pick the wax plates out of the wax pockets—an idea which has come to the fate of most ideas about the bee based on human imagination. Sladen and Casteel have each shown that the pecten of one leg scrapes the pollen off the planta of the other, but only a little at a time, and that the two pectenes scrape alternately. The pollen detached naturally falls upon the upper surface of the auricle. The tarsus is now gently bent backward, pressing the auricle against the sloping end surface of the tibia, compressing the pollen and squeezing it outward upon the outer surface of the tibia and into the lower end of the pollen basket, guided by the fringe of hairs on the outer edge of the auricle (Fig. 42 A). Each new mass of pollen forced through the press pushes the last up a little and sticks to its lower edge. Thus simultaneously the entire mass on each side increases upward, growing from the bottom (B, C) by the successive addition of transverse layers, till at last both corbiculæ contain great balls of compact, gummy pollen spreading to their fringes (D).

**The Dance of the Pollen Gatherers.**—Now the pollen-loaded bee flies back to the hive where, according to von Frisch (1923), she goes in amongst the crowd of bees sitting idly on a comb and usually at once performs a special kind of *dance*. This dance is characterized by a sidewise shaking of the abdomen, and von Frisch, therefore, designates it the "tail wagging dance" to distinguish it from the "round dance" of the nectar gatherers. In a typical case the dance proceeds as follows: The dancer first describes a half circle to the right or left on the comb, then goes back in a straight line over the two or three cells traversed to the starting point, from which she describes another half circle in the other direction, and thus completes a circle. Then again she goes back over the diameter to the starting point and once more dances over the first course, thus alternating in half circles first to one side and then to the other. Every time the dancer goes over the diameter of her course she makes the drôle wagging motions of the body. Scarcely has the dance begun when it is to be noted that other bees crowd closely behind the performer,

and when the dance is finished many of the bees that have attended it go out of the hive.

This dance of the pollen gatherers, von Frisch says, is well known to beekeepers and has been many times described in the bee journals, with many interpretations. From his own observations, von Frisch explains the "tail-wagging dance" as announcing to the bees in the hive the existence of a pollen source out-of-doors. The odor of the pollen tells them the kind of flower or flowers furnishing it, and by scouting at large over the surrounding fields they are then able to find it for themselves.

Bees returning to the hive with nectar also, according to von Frisch, announce the fact by a dance, but this dance differs characteristically from the pollen dance, and von Frisch distinguishes it as the "round dance." The performer dances around on the comb in narrow half circles, first in one direction, then in the other, keeping up the dance for a quarter or a half minute, rarely for a whole minute. This dance, as the other, excites the attendant bees to leave the hive, but now they must find the nectar by detecting the odor which the dancer has left from her scent gland in the neighborhood of the food source (see page 117). Von Frisch claims that new bees coming to a dish of sugar-water do not accompany the one that originally discovered it and announced its existence to the bees in the hive.

**Storing Pollen in the Comb.**—When the pollen-laden dancer has ceased her performance, and often she gives several repetitions of it, she seeks a cell in which to deposit her loads. Having selected a suitable one, according to Casteel (1912) she grasps the upper edge of the cell mouth with her front feet, rests the tip of her arched abdomen on the opposite rim, protrudes her hind legs into the cell and, with the middle tarsi, pries loose the pollen balls, which drop to the cell floor. Here they lie usually until some other worker comes up and attends to their proper disposal by packing them securely with the mandibles into the bottom of the cell or into the mass of pollen already present. Probably this bee adds more saliva and more honey to the stored pollen, which changes the latter finally into "bee bread."

**Propolis.**—The workers also carry propolis in the pollen baskets of their hind legs. Propolis consists of resinuous gums that the bees collect from trees, and it is said that they put it directly into the baskets from the feet of the other legs.

### 7. THE SENSE ORGANS OF THE THORAX

Two kinds of sense organs have been described in the legs and wings of the honeybee. Those of one kind are *pore organs* like those of the antennæ and mouth parts, being visible externally only as small pale depressions in the cuticula. The organs of the other kind have no external parts and in their internal structure are of the type of sense organs generally known as *chordotonal organs.*

**The Sense Pores of the Wings and Legs.**—The sense-pore organs in surface view appear to be minute round or oval, dark-rimmed areas on the outer surface of the cuticula, each with a round or elongate light spot in the center. The internal parts are the same as those of the pore organs of the antennæ (Fig. 10 J) described on page 30.

In the honeybee, according to McIndoo (1914), there are 18 groups of these sense pores on the wings and legs of each side. Groups 1 and 2 on each side are situated on the under surface of the base of the front wing; group 3 is on the median plate (Fig. 31 C, *m*) of the dorsal surface of the front wing; group 4 is on the under surface and group 5 on the upper surface of the base of the hind wing; group 6 is on the proximal end of the femur of each leg, groups 7, 8 and 9 are on the outer surfaces of the trochanters; groups 10 and 11 are at the proximal ends of the tibiæ; groups 12, 13, 14 and 15 are on the inner sides of the trochanters; groups 16 and 17 are on the inner surfaces of the proximal ends of the tibiæ; and group 18 is on the ventral surfaces of the second and third tarsal joints. Sense pores of the same sort are found also on the sting in the bee, and similar organs have been described on the legs and wings of other insects by McIndoo and by Erhardt (1916). The sense pores McIndoo claimed are the true olfactory organs of insects, though, as has been shown, there is now pretty conclusive evidence that other organs of the antennæ play a more important part in the perception of odors.

**The Chordotonal Organs.**—The chordotonal organs of the thorax in insects are known to occur in the legs, in the wing bases, and in the rear part of the thoracic cavity. A chordotonal organ, as the term is usually applied, is distinguished by having a well-developed internal hollow rod or *scolopala* enclosing the end of the distal sense-cell fiber. In typical examples, however, a ligament attaches the base of the organ to the body wall. Usually there is no external part, but in the grasshoppers and crickets the

organs occur in connection with membranous tympana of the body wall.

The chordotonal organs of the bee are situated in the tibiæ of all the legs, and have been described by Schön (1911) and by McIndoo (1922). Each consists of a hollow, conical, cellular mass (Fig. 43 A, *SO*) lying in the upper part of the tibia, according to McIndoo, attached at both ends to the hypodermis of the anterior side of the leg. The upper smaller end of the organ

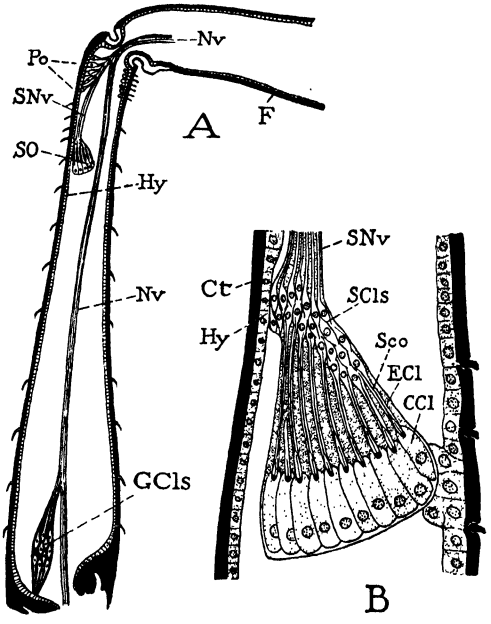



FIG. 43.—Sense organs in the leg of the honeybee (*from McIndoo*, 1922). A, longitudinal section through hind tibia and end of femur of a drone. B, longitudinal section of chordotonal organ, more enlarged. *CCl*, cap cell or distal enveloping cell; *Ct*, cuticula; *ECl*, basal enveloping cell; *F*, femur; *GCls*, "ganglion cells"; *Hy*, hypodermis; *Nv*, nerve; *Po*, sense pores; *Scls*, sense cells; *Sco*, scolopala; *SNv*, sensory nerve of chordotonal organ; *SO*, chordotonal organ.

receives a nerve (*SNv*) which branches from the main leg nerve (*Nv*) just after the latter leaves the femur (*F*), the chordotonal nerve first, however, giving off fibers to the pore organs in the upper part of the tibia (*Po*). In lengthwise sections the organ is fan-shaped (B) and is seen to consist of a number of closely packed sensilla, in each of which there are the same cell elements as in a typical antennal sense organ (Fig. 9 A). The sense cells (Fig. 43 B, *SCls*) form a group in the basal or upper end of the tibial organ; beyond them is a zone of long proximal enveloping

cells (*ECl*); while the distal end of the organ consists of a layer of large, thick cap cells (*CCl*). Each of the enveloping cells contains a long, slender, hollow, rod-like scolopala (*Sco*) with its distal end inserted into the base of a cap cell. The scolopalæ appear to contain axial fibers prolonged from the sense cells; but in this organ there is no evidence that either the enveloping cells or the sense-cell fibers penetrate the cap cells or are attached directly to the cuticula as in the antennal organs.

The chordotonal organs of the legs are the only organs of this sort known in the bee; but Erhardt (1916) describes a chordotonal organ in the base of each wing of a wasp, the distal end of which is attached ventrally.

Another organ of simpler structure occurs in the distal end of each of the tibiæ of the bee, described by McIndoo (1922), "for lack of a more appropriate name," as the *tibial ganglion cells* (Fig. 43 A, *GCls*). This organ is a spindle-shaped mass a little larger than the upper tibial organ. It has a group of cells in the middle which are connected above with fibers from the leg nerve (*Nv*) and which are drawn out below into long processes attached to the hypodermis. As pictured by McIndoo this lower tibial organ resembles the organ of Johnston in the basal joint of the flagellum of the antenna (Fig. 10 H), and both are suggestive of simplified chordotonal organs without scolopalæ.

There is no direct evidence as to the function of the chordotonal organs in any insect, but, as their name implies, they have been regarded as organs for perceiving sound. Where they are attached to membranes free to vibrate, as in the tympanal organs of the front legs of crickets and katydids or of the abdomen of grasshoppers, or where they are held taut in the body cavity by suspensory ligaments, as in many insect larvæ, they might reasonably be supposed to have an auditory function. But where they are attached solidly to the body wall, as in the leg of the bee, they do not suggest the possibilities of vibration necessary in an organ designed to receive sound waves. From an anatomical standpoint, then, it would seem that bees must be deaf. Yet they make sounds other than the buzzing of the wings, such as that known as the "piping" of the queen, and the high-pitched sound emitted by workers even when the wings are removed. Such sounds, probably produced in all cases by the rasping or vibration of small sclerites in the wing bases, may, however, be merely mechanical incidents in no way indicative of the presence of a sense of hearing to perceive them.

## CHAPTER IV

# THE ABDOMEN, ITS GLANDS, AND THE STING

The abdomen is usually a very distinct region of the body of an insect, since it commonly projects from the thorax unsupported except by its attachment to the latter. Its base may be wide and broadly joined to the thorax, though it is usually narrowed at the union, and in the Hymenoptera frequently forms a stalk or peduncle which gives much freedom of motion to the abdomen. The chief function of the abdomen is that of container for the larger viscera, such as the stomach, intestine, and the reproductive organs.

### 1. THE GENERAL STRUCTURE OF THE ABDOMEN

While the abdomen of ordinary insects is of simple external form, its simplicity is apparently due to a suppression of parts it once possessed. This is indicated both by its structure in different insects and by its embryological development.

**The Segments of the Abdomen.**—The abdominal region of adult insects consists usually of 10 segments, though in some Orders it contains eleven. In embryonic stages the abdomen may show as many as 12 segments (Fig. 3), and Nelson (1918) says there is evidence of this number in the embryo of the honeybee, but that the last two segments disappear before hatching. Each segment consists typically of a tergal and a sternal plate, and in some cases there are lateral plates, but it is to be questioned whether the latter are ever to be regarded as homologous with the pleura of the thorax. The terminal segment always carries the posterior opening of the alimentary canal and the orifices of the male and female reproductive organs are usually in the ventral surfaces of the ninth and eighth segments respectively. Several of the posterior segments are commonly modified to serve the purposes of copulation and egg-laying and these segments are frequently retracted into the segments before them, giving to the abdomen the appearance of having fewer segments than it really possesses. Various glands opening

externally, such as the wax glands and scent glands of the bee, are developed in the hypodermis of the abdominal wall.

**The Appendages of the Abdomen.**—Most of the abdominal segments of adult insects are characterized by the lack of appendages, but in an embryonic stage of many species (Fig. 3) each one but the last bears a pair of small ventral protuberances. There lobes form two rows of knobs in line with the appendages of the thorax and the head, which suggests that insects originally had legs along the entire length of the body. All the embryonic abdominal appendages of insects with complete metamorphosis, however, disappear before the larva hatches from the egg, except possibly in caterpillars and other larvæ that have abdominal "feet," which some entomologists believe are developed from the true segmental appendages of the abdomen.

The abdomen of adult insects typically bears near the posterior end in the female an egg-laying instrument or ovipositor; in the male, clasping organs of various sorts; and, in both sexes in the lower Orders, at the end a pair of appendages known as the *cerci*. Any of these parts may be lacking, however, and in many of the Hymenoptera the ovipositor becomes a sting; but, when present, they are in most cases formed from outgrowths of the terminal abdominal segments that appear to represent the primitive abdominal appendages, or parts of them.

*The Gonapophyses.*—The outgrowths that form the ovipositor and homologous claspers of the male are known as *gonapophyses*. The ovipositor is formed from three pairs of gonapophyses, of which one pair arises on the ventral surface of the eighth abdominal segment (Fig. 53 A, 1*G*), while two pairs arise on the ninth segment (2*G*, 3*G*); but it is claimed by some entomologists that the outer pair of the latter (3*G*) really belong to the tenth segment (Fig. 3). Some of the abdominal claspers of male insects appear likewise to be derived from gonapophyses, but others are clearly secondary lobes of the ninth and tenth segments. In insects with complete metamorphosis the growth of the gonapophyses may be suppressed during the embryonic and larval stages. There are, for example, according to Nelson (1915), no abdominal appendages at any stage in the embryo of the honeybee (Fig. 104 L); and there are none present externally on the larva (Fig. 105 A). Yet, at an early propupal period of the worker, small outgrowths appear on the ventral surfaces of the eighth and ninth abdominal segments (Figs. 105 D, 53 A) at the time the

legs and wings become visible on the thorax, one pair on the eighth segment (Fig. 53 A, 1*G*) and two pairs on the ninth (2*G*, 3*G*). All six of them elongate (B) and eventually become the parts of the sting (Fig. 52).

*The Cerci.*—The cerci, which are entirely absent in the honeybee, are best developed in the lower Orders of insects. While theoretically they belong to the eleventh segment, they commonly appear to arise between the ninth and the last segment, because of the suppression of the segments between the ninth and the terminal one of the adult which carries the anus. The apical segment of the adult is customarily enumerated as the tenth (Fig. 53, *X*), except when eleven are distinctly present, though theoretically it may be the twelfth or a remnant of any of the segments back of the ninth.

### 2. THE ABDOMEN OF THE BEE

In the honeybee and most other Hymenoptera, as already explained in Chapter III (page 71), the ten-segmented abdomen of the larva (Fig. 105 A) loses the first segment (*I*) to the thorax during the development of the pupa (G, H, I). As a consequence the abdomen of the adult consists of only nine segments, of which the first (Fig. 2, *II*) is the true second segment. This leads to some confusion in descriptions when the propodeum (*I*) of the thorax is counted as the first segment of the abdomen.

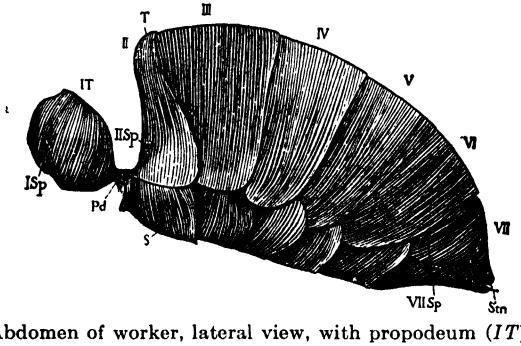



FIG 44.—Abdomen of worker, lateral view, with propodeum (*IT*) or tergum of true first abdominal segment separated from thorax.

**The Abdomen of the Worker.**—In the worker the abdomen (Fig. 2, *Ab*) is broad at the anterior end and abruptly tapered to a point at the posterior end. Its base, however, forms a narrow stalk having a membranous union with the propodeal segment

(*I*) of the thorax, which allows the abdomen a free, independent motion. The abdomen of the worker or the queen has six visible segments, the other three being concealed within the last visible one. Each segment consists of a tergum (Figs. 44, 45, *T*) and of a sternum (*S*), the former reaching far down on the side and overlapping the edge of the sternum. The two plates of the last external segment (*VII*) are separated by a cleft on each side which, when opened, exposes a cavity that lodges the sting and its accessory parts. The abdomen of the male (Fig. 93 D) differs from that of the female in having eight visible segments, though the last two of these are only partially exposed. The differences in the terminal segments of the two sexes will be described later.

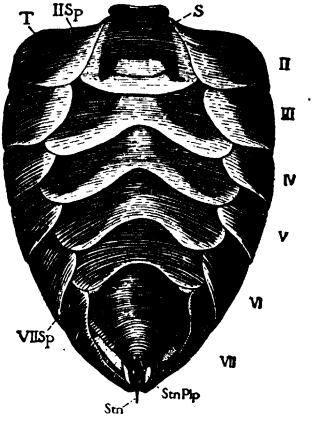



FIG. 45.—Abdomen of worker, without propodeum, ventral view, showing sting (*Stn*) and its palpuslike appendages (*StnPlp*) projecting from sting chamber in last exposed segment (*VII*).

The tergal plates of the abdomen (Fig. 44, *T*) cover both the back and the sides of the segments and each overlaps the one behind by a wide margin. The overlapping edges are connected by large, flexible, intersegmental membranes (Fig. 46 A, *Mb*) each of which forms a wide fold between the terga, which allows the latter much freedom of motion. The under surface of each tergum has a prominent submarginal ridge (*Ri*) to which muscles are attached on the sides of the segment (Fig. 83, *1*).

The ventral abdominal plates of a worker bee are shown from above in Fig. 29 and those of a drone in Fig. 48. Each sternum is widely underlapped by the one next in front, and the intersegmental membrane (Fig. 48, *Mb*) is reflected from the middle of its dorsal surface to the anterior edge of the sternum following. This is more clearly seen on individual plates dissected free from the others (Fig. 49) or in lengthwise sections (Fig. 46 B). Each sternum is thus divided into an anterior region that forms part of the floor of the abdominal cavity, and into a posterior part (Figs. 46 B, 49, *Rd*) that projects as a free flap beneath the segment following. The anterior edge of each sternum is thickened to form a marginal ridge (Fig. 46 B, *Ri*) to which muscles (*Mcl*) are attached and from which there project two small

processes in front and a long arm (Fig. 49, *Ap*) on each side The corresponding sterna of the three forms of the bee differ in size and in shape and in the length of the lateral arms (Fig. 49). In the queen (B) the plates are much longer than in the worker (A), while in the drone (C) they are shorter but their lateral arms are extremely long.

The abdominal spiracles are located on the sides of the first eight tergal plates. The first pair belong to the propodeum (Figs. 23, 44, *ISp*), and in the bee, therefore, constitute the third spiracles of the thoracic region. The next six pairs are small apertures on the sides of the six visible segments of the abdomen (Fig. 44, *Sp-Sp*). The last pair is on the lateral plates of the eighth

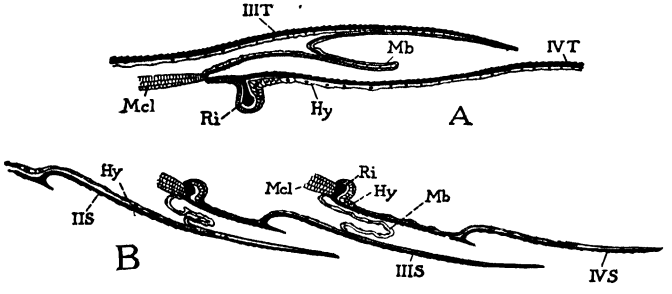



FIG. 46.—Longitudinal sections of abdominal wall, showing union of segmental plates.

A, section through overlapping parts of terga of third and fourth segments (*IIIT*, *IVT*), showing folded intersegmental membrane (*Mb*). B, section through second, third, and fourth sterna (*IIS*, *IIIS*, *IVS*).

tergum concealed within the sting chamber at the end of the body where they form a large aperture on each side (Fig. 56, *Sp*). The structure of all the spiracles will be fully described in the chapter on the respiratory system (page 194).

The last three abdominal segments, which are the eighth, ninth and tenth when the propodeum is counted as the first, are very different in the two sexes on account of their modification in each as parts accessory to the organs of copulation and egg-laying or stinging. In the female these segments are entirely concealed within the seventh and will be described in connection with the sting, but, in the male, parts of both the eighth and ninth segments are visible externally.

**The Abdomen of the Drone.**—The seventh segment of the drone abdomen (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. 93 D, *VIIT* 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 ventro-lateral parts of the ninth segment. It bears on each side two conspicuous lobes—one a small, darkly chitinized, dorsal plate (1*Clsp*) carrying a large bunch of long hairs; the other a large, thin, ventral plate (2*Clsp*). Between these four appendicular lobes is ordinarily a deep cavity which is the invaginated penis (E), but in Fig. 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.

The development of the accessory reproductive parts in the male has been studied by Zander who says (1911) that a pit-like depression appears on the ventral surface of the twelfth segment (the ninth abdominal segment) and that two small lobes grow back from its anterior margin. Each of these lobes then splits into two, which form on each side the upper and lower clasper, while a deep depression growing inward between them forms the inverted penis. In a wasp, according to Zander, the middle pair of lobes unites to form the penis, the duct of which arises as an evagination from its end.

### 3. THE SCENT GLANDS

When worker bees extend the tip of the abdomen, or especially when they bend the tip downward, they often expose a wide pale band on the front part of the last tergal plate, which is ordinarily concealed beneath the overlapping part of the plate in front. A closer examination shows that the pale band is merely a weakly

chitinized area of the tergum, and that its anterior part is abruptly deflected in a sharp fold to form a crosswise canal, limited in front by the intersegmental membrane reflected back to the under surface of the preceding and overlapping tergum. These features are best seen in a section through the contiguous parts of the last two exposed terga of the abdomen (Fig. 47 **A**, *VIT, VIIT*). The floor of the canal (*Can*) is marked in front by a strong, dark, crosswise line formed by the submarginal ridge (*Ri*) beneath, while the crest of the fold (*a*) behind makes another narrower transverse line. The rear margin of the pale band is elevated also in a second small fold (*b*) overhanging the thickly

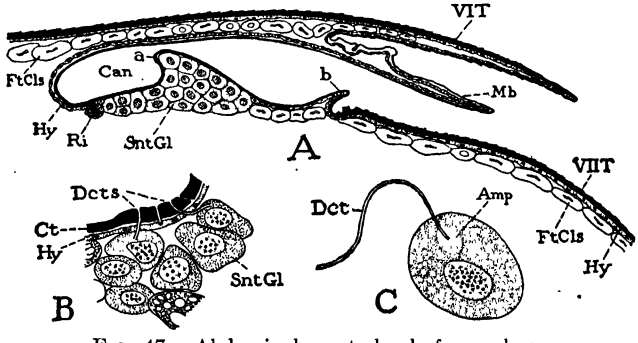



FIG. 47.—Abdominal scent gland of a worker.

A, longitudinal section through overlapping parts of sixth and seventh abdominal terga (*VIT*, *VIIT*), showing transverse canal (*Can*) at anterior edge of latter, and elevated surface between ridges *a* and *b*, with mass of scent gland cells (*SntGl*) beneath.

B, group of scent gland cells (*SntGl*) of newly emerged adult, showing cuticular ducts (*Dcts*) penetrating individual gland cells (*from McIndoo*, 1914).

C, single gland cell greatly enlarged, showing duct (*Dct*) ending in clear ampulla (*Amp*) of cell (*from McIndoo*, 1914).

chitinized part of the tergum behind it. Inside the body, beneath the canal and the crest behind it, is a compact mass of large oval or polygonal cells (*SntGl*) with prominent oval nuclei. These cells are the abdominal scent glands, called also the glands of Nassonoff after their discoverer. Their secretion is discharged through minute ducts (B, *Dcts*) into the canal, where it is said to be visible sometimes as a clear liquid.

The scent glands were first noted by Nassonoff, whose description and crude illustration were published by Zoubareff (1883). Nassonoff suggested that the glands had a perspiratory function, but Zoubareff believed that they excreted a surplus of water absorbed from the newly collected nectar in the honey stomach.

Thus he accounted for the drops of clear liquid that bees often discharge while on the wing before entering the hive. There is no evidence, however, that this liquid comes from any part of the abdomen, and it is most likely an excess of nectar dropped from the mouth.

The structural details of the scent glands, their ducts, and associated parts in the worker bee have been more recently described by McIndoo (1914 *b*) who shows that the gland (Fig. 47 A, *SntGl*) is a group of unicellular gland cells proliferated from the hypodermis of the canal region. Each cell is connected with the cuticula by a delicate, hair-like duct which arises in a clear space or ampulla of a gland cell (C, *Amp*) and opens on the floor of the canal (B, *Dcts*). McIndoo says there are between 500 and 600 of these ducts, which he describes as originating in slender processes of the hypodermal cells that grow inward and connect with the gland cells; but his idea that the tubes are "open" at the inner end within the ampulla of the cell, as shown in his figure (C), is to be questioned. All such intracellular outlets of one-celled glands are probably to be regarded as blind tubular ingrowths of the cuticula, receiving the secretion of the gland cells by osmosis through their delicate walls, just as do the intercellular cuticle-lined ducts of the salivary glands or any other of the larger compound glands of the body.

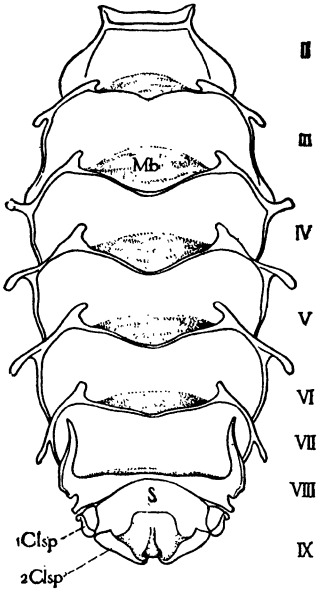



FIG. 48.—Abdominal sterna of drone, dorsal or internal surfaces.

The queen bee also possesses scent glands, according to McIndoo, situated as in the worker and having the same structure except that the cells are about one-third larger. But McIndoo was unable to find corresponding glands in the drone, though this, as he points out, does not mean that the drones may not have scent glands on other parts of the body. Heselhaus (1922) does not describe the scent glands of the honeybee, but he finds on other bees and wasps similar, one-celled, hypodermal glands with intracellular ducts scattered over various regions of the body,

especially on the ventral abdominal plates and on their articular membranes.

The idea that the glands of Nassonoff are scent-producing organs was proposed by Sladen (1901). Noting the peculiar pungent smell that bees give off when they are shaken from a frame of comb before the hive, Sladen identified this odor as the same as that given off from the membrane at the base of

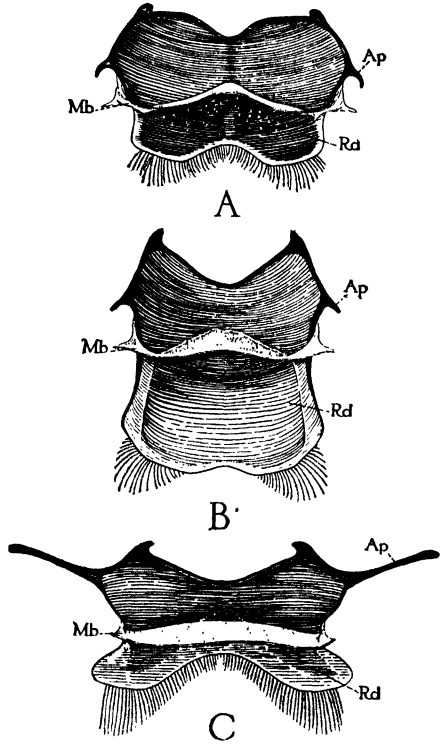



FIG. 49.—Sixth abdominal sternum of worker (A), queen (B), and drone (C), dorsal surface, showing division of each plate by line of attachment of intersegmental membrane (*Mb*) into anterior part forming ventral wall of segment, and into posterior free part (*Rd*) underlapping anterior half of succeeding sternum. (Compare with section, Fig. 46 B.)

the last abdominal tergum, and, therefore, concluded that the gland cells beneath this membrane are the source of the scent of the worker honeybee. At that time the idea was current that bees made a special buzzing sound with the wings when they found the hive entrance, or their queen temporarily lost during swarming, and that this sound, popularly known as the "joyful

hum," served as a signal and guide to the other bees. But Sladen, pointing out that bees were not known to have a sense of hearing, suggested that the sound is merely incidental to a fanning of the wings made to drive the scent away from the body, and that, not the sound, but "the scent produced forms a means of communication between the members of a swarm or colony."

This view concerning the function of the glands of Nassonoff is now generally accepted, and has recently been much elaborated by von Frisch (1923), who includes the abdominal scent as one of the important elements in the "speech" of bees. He observes that a bee gathering nectar from flowers or drinking sugar-water from a dish set out in the apiary flies about the place with the end of the abdomen protruded, and also exposes the outlets of the scent glands while drinking. In this way she marks the position of the food source with her odor, and the other bees, told of its existence by the customary dance of the returning bee in the hive (page 104), are then able to find it for themselves in the field.

### 4. THE WAX GLANDS

The anterior part of each of the last four normal sternal plates in the abdomen of a worker, the part of each underlapped and concealed above the free part of the sternum in front, presents

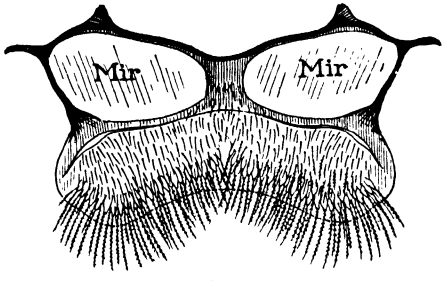



FIG. 50.—Fifth sternum of workers, dorsal surface, showing polished surfaces, the "mirrors" or wax plates (*Mir*), beneath wax glands.

two large, lateral, oval, polished surfaces, often called the *mirrors* (Fig. 50, *Mir*), separated by a narrow, thicker median space. The wax glands of the honeybee are situated over these mirrors and, therefore, on the sterna of segments IV to VII (Fig. 29). The glands are merely thickened parts of the hypodermis (Fig. 51, *WxGl*) over the very thin cuticula (*Ct*) of the mirrors or *wax plates*, as the wax-forming areas are more appropriately named. The wax, probably secreted in liquid form, is extruded through

the wax plates into pockets between the overlapping parts of the sterna, where it hardens into little scales having the form of the plates.

Dreyling (1903) has shown that in young, freshly-emerged workers the hypodermis of the wax plates consists of ordinary cells, but that, as the activities of the bee increase, these cells elongate vertically while clear spaces appear amongst them, and that when their highest development is reached the cells are long slender columns and the interspaces are stored with liquid wax. In old age, most of the wax cells shrink again and in overwintering workers the hypodermis of the wax plates degenerates to a simple sheet of nucleated plasma in which even the cell boundaries are lost. Dreyling says that the wax plates are perforated by extremely fine canals only visible in very thin sections and under the highest power of the microscope, but if

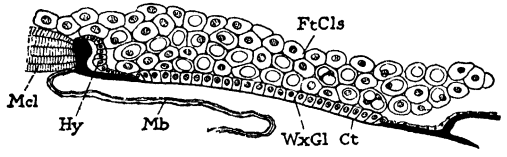



FIG. 51.—A wax gland of young worker. Longitudinal section through wax plate of fifth abdominal sternum (Fig. 50, *Mir*).
*Ct*, thin cuticula of wax plate; *FtCls*, fat cells overlying wax gland, *Hy*, normal hypodermis; *Mb*, intersegmental membrane; *Mcl*, muscle; *WxGl*, wax gland.

such canals are present they are most likely minute invaginated tubes of the cuticula, for, as already pointed out, the cuticula of insects probably nowhere contains actual perforations. Heselhaus (1922) gives a figure of the wax gland of a wild bee (*Osmia bicornis*) in which he shows the outlet canals penetrating the bases of the gland cells. The wax glands of the honeybee are covered by thick layers of fat cells (Fig. 51, *FtC s*) and these were evidently mistaken by Cheshire (1886, Fig. 34) for the wax glands themselves. In the bumblebees the wax glands are developed in the hypodermis on the back of the abdomen.

Wax is ordinarily produced in the hive by the younger bees, or by bees that have not yet passed their prime, which for summer bees is at about 17 days of age and this in general corresponds with Dreyling's statement about the development of the wax glands. But Brünnich (1909) claims that the relation between the age of the bee and the development of the wax glands is not such an exact one as implied by Dreyling. He shows that in

young bees the glands may be small and inactive while in old bees they are sometimes much enlarged, but the number of such cases he cites is not sufficient to weaken the accepted idea that wax is made mostly by those bees that have not yet left the hive to become foragers for nectar and pollen. When comb is needed, a large number of these younger bees feed themselves well on honey and then hang together in vertical sheets or festoons. After about 24 hours they begin to construct comb. During this period their wax glands have been active and wax scales are formed in the wax pockets of the abdominal sterna. The scales are then poked out of the pockets with the spines on the hind tarsi and passed forward beneath the body to the mandibles. By means of these organs the wax scale is ground into a finely granular condition and laid down on the edge of the comb.

### 5. THE STING

The sting of the bee is situated in the sting chamber at the end of the abdomen (Fig. 56), from which it can be quickly protruded when occasion demands. The sting chamber contains also the reduced and modified sclerites of the true eighth, ninth, and tenth abdominal segments; in fact, the chamber is formed by an infolding of these segments into the seventh. A very gentle pull on the tip of the sting suffices to remove it from its place of concealment, but when thus extracted it brings along with it the ninth and tenth segments, most of the eighth, the poison glands, and the terminal part of the alimentary canal. This is due to the fact that the enclosed segments are attached to the surrounding parts by very delicate membranes, for which reason also they tear from the living bee so easily as the latter hurriedly leaves its victim after stinging. The isolated stinging apparatus keeps on automatically pumping, and this perhaps by giving more effective results, compensates for the disability and eventual death of the stinger.

**The Structure of the Sting.**—The sting itself, when extracted from its chamber (Fig. 52, *Stn*), is seen to consist of a straight tapering shaft with its tip directed posteriorly and its base swollen into a bulb-like enlargement. In superficial appearance the shaft appears to be solid, although we shall presently see 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 is shown somewhat diagrammatically in side view by Fig. 52. The base of the sting is connected with the 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 *BGl*) open into the anterior end of the bulb. From the posterior ends of the plates two whitish, finger-like processes (*StnPlp*) project backward. When the sting is retracted these lie at the sides of the shaft (Figs. 55, 56), but in Fig. 52 the sting is shown in a partly protracted position. These appendages are often called the sting "palpi," since they

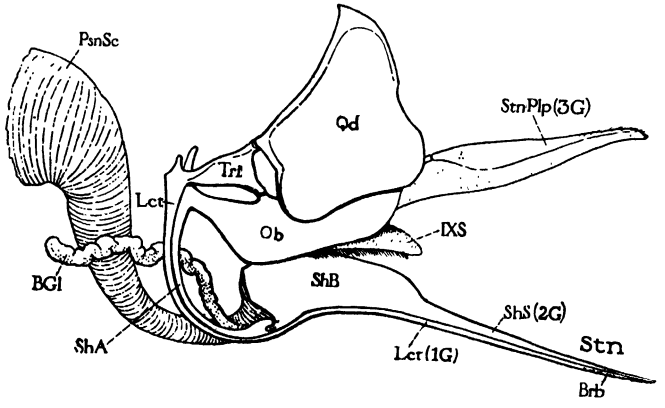



FIG. 52.—Sting and associated parts, left side (semidiagrammatic). Shaft of sting (*Stn*) consist of single dorsal sheath (*ShS*) and two ventral lancets (*Lct*). Sheath swollen at base into bulb (*ShB*) receiving poison from poison sac (*PsnSc*) and alkaline gland (*BG'*). Base of sheath prolonged into curved arm on each side (*ShA*) attached above to oblong plate (*Ob*), which bears palpus-like appendage (*StnPlp*). Base of each lancet (*Lct*) curves upward on basal arm of sheath and is attached above to triangular plate (*Tri*) which articulates with large quadrate plate (*Qd*) partly overlapping oblong plate. Median part of ninth sternum (*IX*) forms membranous fold over base of sting.

appear to be sensitive organs enabling the bee to tell when her abdomen is in contact with the object upon which she desires to use the sting.

A closer examination of the sting shows that it is a more complicated structure than it at first sight appears to be. The shaft, for example, is not a simple, solid, tapering, spear-like rod, but is a hollow organ made of three pieces which surround a central canal. One of these pieces is dorsal (Fig. 52, *ShS*) and is a prolongation of the bulb (*ShB*), while the other two (*Lct*) are ventral and slide lengthwise on track-like ridges of the dorsal piece. Moreover, each basal arm of the sting is double, con-

sisting of a dorsal or posterior piece (*ShA*), which is likewise a prolongation of the bulb, and of 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 as follows: a single, hollow, dorsal piece, known as the *sheath*, consisting of a prominent middle swelling or bulb (*ShB*), of a terminal tapering *shaft* (*ShS*), and of two curved *basal arms* (*ShA*); and two ventral parts consisting of long, slender rods called the *lancets* or *darts* (*Lct*) which slide freely upon tracks on the ventral edges of the sheath and diverge upon continuations of these tracks on the basal arms of the latter (*ShA*). The hollow of the sheath is simply a groove along the entire length of its ventral surface which is expanded in the bulb into a large cavity, but it is closed below by the two lancets and thus converted into a tube, which, as will be explained presently, is the *poison canal* of the sting.

Each arm of the sheath (Fig. 52, *ShA*) is supported at its end farthest from the bulb by an *oblong plate* (*Ob*), which normally overlaps 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-dorsal 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 Fig. 55.

**The Origin and Homologies of the Sting.**—It has already been mentioned that the parts of a sting or an ovipositor originate in six small outgrowths or gonapophyses on the ventral surfaces of the eighth and ninth segments of the abdomen. These are visible in the bee during the last stage of the larva (Fig. 105 D), but they really belong to the pupa developing within the larval skin (E). The first pair (Fig. 53 A, 1*G*) is situated on the eighth sternum immediately behind the opening of the vagina (*VO*); the other two pairs (2*G*, 3*G*) arise from a pocket on the ninth segment. In some insects the six parts remain distinct and form an ovipositor of six pieces or *valvulæ* as in the conehead grass-

hopper (Fig. 54). Here the sheath is formed of two valvulæ (2*Vlv*) closely pressed together, which are derived from the middle gonapophyses of the ninth segment (Fig. 53 B, 2*G*); the dorsal valvulæ (3*Vlv*) are the outer pair of gonapophyses (3*G*) of the

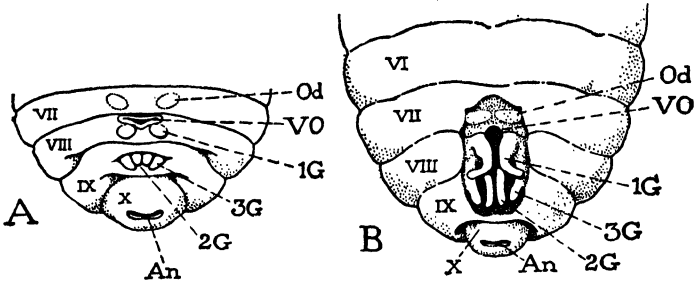



FIG. 53.—Terminal segments of young pupa forming within larval skin, ventral view, showing origin of parts of sting.

A, early stage, showing one pair of gonapophyses (1*G*) on eighth segment just behind opening of vagina (*VO*), and two pairs (2*G*, 3*G*) on ninth segment. B, later stage, showing elongation of gonapophyses; the first pair (1*G*) will form lancets of sting (Fig. 52, *Lct*), second (2*G*) will unit to form sheath (*ShS*), third (3*G*) will form sting palpi (*StnPlp*).

ninth segment; and the ventral pair (1*Vlv*) are the gonapophyses of the eighth segment (1*G*).

If, now, we compare the sting of the worker bee (Fig. 52) with the ovipositor of the conehead grasshopper (Fig. 54) we find a

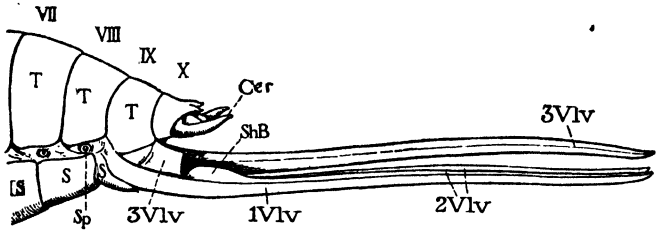



FIG. 54.—Ovipositor of conehead grasshopper (*Conocephalus*), composed of three pairs of valvulæ (*Vlv*).

First valvulæ (1*Vlv*) correspond with lancets of bee's sting (Fig. 52, *Lct*), developed from first gonapophyses (Fig. 53, 1*G*). Second valvulæ (2*Vlv*) correspond with sheath of sting (*ShS*), developed from second gonapophyses (2*G*). Third valvulæ (3*Vlv*, left cut off near base) correspond with palpi of sting (*StnPlp*), developed from third gonapophyses (3*G*).

basic parallelism between all the parts, but with superficial modifications. The lancets of the bee (Fig. 52, *Lct*) are the ventral valvulæ of the grasshopper (Fig. 54, 1*Vlv*), both derived from the gonapophyses of the eighth segment (Fig. 53 A, B, 1*G*);

the sheath of the bee's sting is the united inner valvulæ of the grasshopper's ovipositor (*2Vlv*), or the inner gonapophyses of the ninth segment (*2G*); while the "palpi" of the bee's sting (*StnPlp*) are the dorsal valvulæ in the ovipositor of the grasshopper (*3Vlv*), or the outer gonapophyses of the ninth segment (*3G*).

The sting of the queen is longer than that of the worker and is more solidly attached within the sting chamber. Its shaft is

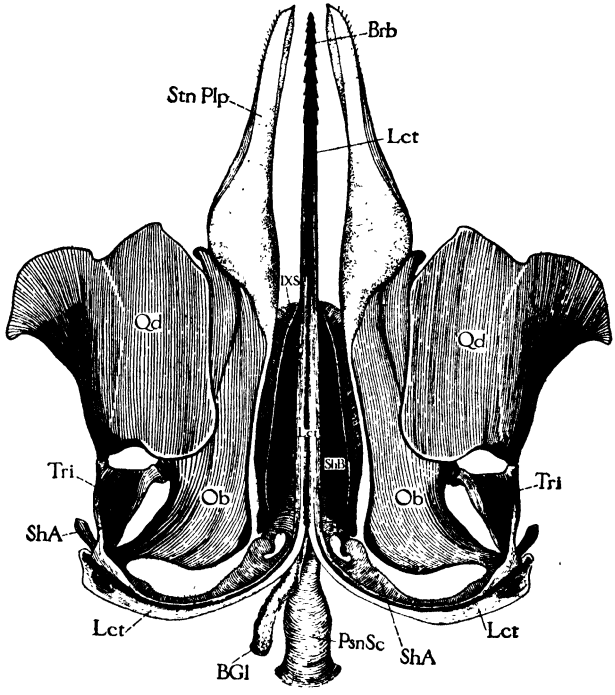



FIG. 55.—Ventral view of sting and associated parts in worker, flattened out. *BGl*, base of alkaline gland; *Brb*, barbs; *IXS*, medium part of ninth abdominal sternum; *Lct*, lancets; *Ob*, oblong plates; *PsnSc*, base of poison sac; *Qd*, quadrate plates; *ShA*, arms of sheath; *ShB*, bulb of sheath; *Tri*, triangular plates.

strongly decurved beyond the bulb. The lancets have fewer and smaller barbs than those of the worker, but the poison glands are well developed (Fig. 94, *AGl* and *BGl*), and the poison sac (*PsnSc*) is very large.

It is only the higher members of the Hymenoptera, such as the wasps and the bees and their close relations, that possess a true sting. The females of the lower members have ovipositors

which closely resemble those of such insects as the longhorn grasshoppers, katydids, crickets, and cicadas, but which, at the same time, are unquestionably the same organ as the sting of the stinging Hymenoptera. Some insects use their ovipositors for making slits or holes in trees or in leaves in which to insert their eggs, or for thrusting their eggs into crevices or into the ground, while the parasitic Hymenoptera use theirs for inserting eggs into the bodies, eggs, or nests of other insects.

An examination of the sting in place within the sting chamber, as shown by Fig. 56, will suggest what the accessory plates

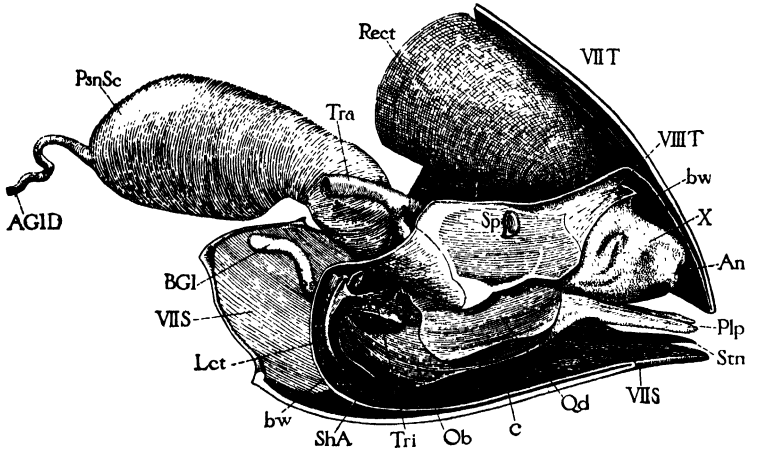



FIG. 56.—Sting of worker in place exposed from left side in sting chamber (*c*) in end of abdomen, showing segmental relationships of parts.

Last exposed segment of abdomen consists of seventh tergum (*VIIT*) and seventh sternum (*VIIS*); next three segments invaginated. Eighth segment comprises eighth tergum (*VIIIT*) with plate containing spiracle (*Sp*) on side, and triangular plate (*Tri*) bearing lancet (*Lct*). Ninth segment comprises quadrate plate (*Qd*), which is probably lateral part of tergum, and oblong plate carrying arm of sheath, and palpus. Tenth segment consists of membranous cone (*X*) with anus (*An*) at end.

represent in other less modified insects. It has already been explained that the last external segment of the female abdomen (Fig. 44, *VII*) is the seventh. Within the dorsal part of the sting chamber is a slight suggestion of the eighth tergum (Fig. 56, *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, in its development, it is a part of the ninth tergum. In many other adult Hymenoptera, moreover, the quadrate plates are undoubtedly tergal, being 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. 52 and 55, *IXS*) must belong to the median part of the ninth sternum.

In the accessory plates of the bee's sting we have an excellent illustration of how the parts of a segment may become modified to meet the requirements of a special function; and in the sting itself, which is merely an ovipositor changed to a defensive weapon by slight alterations, we have 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.

The tenth segment of the worker's abdomen (Fig 56, *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 enclosed in the dorsal part of the sting chamber beneath the seventh tergum.

**The Glands and Poison of the Sting.**—There are three systems of glands associated with the sting. One consists of two sets of gland cells that have been described as *lubricating glands.* The others are the *acid glands* and the *alkaline gland,* which together secrete the liquid that is driven through the canal of the sting, when the bee uses this weapon, and which is injected into the wound, causing the resulting pain and inflammation.

*The Lubricating Glands.*—The lubricating glands lie within the body cavity against the upper edge of the quadrate plate of the sting on each side, where they are easily seen in an extracted sting as small, oblong or ovate whitish masses of cells. Transverse sections through this region show that each cell opens by an individual duct into a pouch of the membrane between the quadrate plate and the spiracle-bearing plate of the eighth tergum. The secretion from the glands is thus poured upon the

outer surface of the quadrate plates and might easily run down upon the arms of the sheath and the bases of the lancets, but its supposed lubricating function is entirely theoretical.

*The Acid Glands.*—The acid glands are connected with the large, conspicuous poison sac (Figs. 52, 55, 56, 94, *PsnSc*), well known to any one at all acquainted with bees, that opens by a narrow neck into the base of the sting. Arising from the anterior end of the sac (Fig. 94) is a narrow tube which soon divides into two branches (*AGlD*). Each branch is a long, much coiled and convoluted tube, ending finally in a small oval enlargement (*AGl*). The terminal bodies are usually regarded as the true

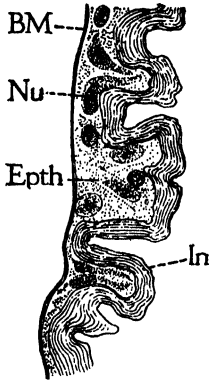



FIG. 57.—Section of wall of poison sac of acid gland of sting.

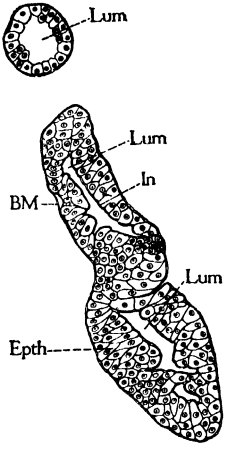



FIG. 58.—Section of alkaline gland of sting.

glands and the tubes (*AGlD*) as their ducts. The epithelium of the latter, however, appears to be a secretory tissue also; if it is not, there is no apparent reason for the great length of the tubes. Furthermore, it does not seem probable that the two little end bodies could produce all the liquid that fills the comparatively enormous sac.

The walls of the poison sac (Fig. 57) are lined by a thick coat of laminated chitin (*In*) 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*), but there are no muscle

fibers of any sort present except a few that are inserted upon the sac from some of the surrounding organs and which apparently act as suspensoria. The liquid contained in the sac has an acid reaction and is said to consist principally of formic acid. Hence, its glands are known as the acid glands (*AGl*) of the sting.

*The Alkaline Gland.*—The alkaline gland is a short and slightly convoluted, opaque whitish tube (Figs. 52, 55, 56, 94, *BGl*) opening directly into the base of the bulb ventral to the opening of the sac. Its walls consist of a thick epithelium of distinct cells (Fig. 58, *Epth*) lined with a thin chitinous intima (*In*) 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 known, therefore, as the *alkaline gland* (*BGl*) of the sting.

*The Poison of the Sting.*—The experiments of Carlet (1890) on the action of the secretions from the acid and alkaline glands of the sting seemed to show that only the mixture of the two liquids has fully effective toxic properties. Experimenting on houseflies and blowflies, Carlet reported that flies stung by a bee died almost instantly; that when artificially innoculated with either secretion alone they did not die for a long time, in spite of the necessary injury from the operation; and that they succumbed much more quickly to consecutive innoculations with the two secretions. Heselhaus (1922), however, claims that Carlet's experiments would require a technique more delicate than could be used on flies, and that his results have not been verified by others. Heselhaus believes that the acid glands alone furnish the poison, and that the secretion of the alkaline gland serves to neutralize the acid that remains in the sting after stinging. He says that the liquid which issues first from the sting of a hornet lightly anæsthethized gives a strong acid reaction with litmus paper, but that after a few seconds no trace of acid properties may be found, the liquid on all parts of the sting being neutral or weakly alkaline. This of course would be of no advantage to the honeybee in cases where the sting remains in the victim. Heselhaus suggests further that since the alkaline secretion has a high fat content it may serve also as a lubricant for the sliding parts of the sting that cannot be affected by the secretion from any other gland.

**How the Bee Stings.**—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 liquid 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 Fig. 94 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

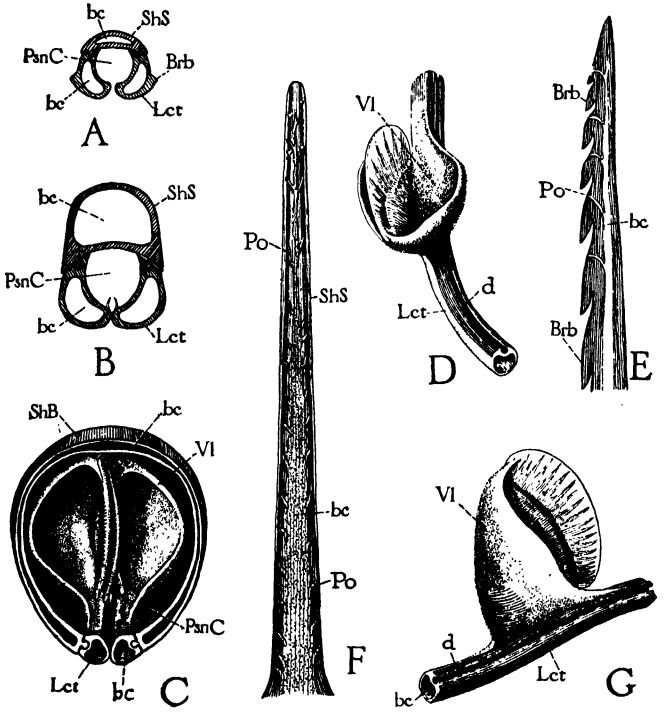



FIG. 59.—Details of sting of worker.

A, cross-section through shaft of sting near tip, showing lancets (*Lct*) attached by tongue-and-groove articulations to sheath (*ShS*), poison canal (*PsnC*) between sheath and lancets, and prolongation of body cavity (*bc*) in each. B, section of same near base. C, section through bulb of sting, showing enlarged poison canal (*PsnC*) containing the two valves (*Vl*) of lancets. D, part of left lancet carrying valve (*Vl*), dorsal view, showing groove (*d*) of lancet. E, tip of lancet much enlarged, showing barbs (*Brb*) and sense pores (*Po*). F, dorsal surface of shaft of sting, showing sense pores (*Po*). G, lateral view of valve of left lancet.

process of stinging that the triangular plates (Figs. 52, 55, *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 corresponding 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 at A, B, and C of Fig. 59. 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 contain prolongations of the body cavity (*bc*). Between them, however, is enclosed another cavity through which the poison flows. This is the *poison canal* (*PsnC*). In the bulb (C) the body cavity of the sheath (*ShB*) is reduced to a narrow cleft (*bc*) by the great size of the invaginated poison canal (*PsnC*).

It will here 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 function 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 pouch-like lobes, having their concavities directed posteriorly, attached to the upper edges of the lancets (Fig. 59 D, G, *Vl*) on the anterior ends of the parts of the latter that slide within the lower edges of the bulb chamber. The two lobes lie side by side within the bulb (C, *Vl*) 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 liquid-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 work alternately, the lobes being of such a size as to be effective either when acting together or separately. A cross-section through the sting a short distance from its tip shows that the lancets are here separated by a narrow cleft (Fig. 59 A), while elsewhere (B, C) their inner edges are contiguous. This cleft forms the exit for the poison from the poison canal.

Some of the earlier writers believed that the poison left the sting not only from between the lancets but also from certain pores along their sides (Fig. 59 E, *Po*). Similar pores, however, are present on the shaft of the sheath (F), and it will be noted that they communicate with the internal or body cavity of the parts and not with the poison canal. McIndoo (1914) has shown that these pores contain the endings of sense organs which are the same as those on other parts of the body for which his experiments indicate an olfactory function.

## CHAPTER V

# THE MUSCLES

After studying the cuticular skeleton of an insect and the mechanisms of its movable parts, it becomes of interest to know something of the organs that produce its motions. These organs are the *muscles.*

The more important sets of muscles in the adult bee are described in connection with the parts with which they are associated. According to their origin the muscles belong to two groups, those of the body wall and those of the stomach wall; but in insects there is no structural difference between these two sets. The muscles of insects are formed in the embryo from the cell layer known as the mesoderm (Fig. 104 K, *Meso*), which splits into two sheets, one applying itself to the body wall, the other to the wall of the stomach, and from these two divisions of the mesoderm arise the two groups of muscles. The muscles that originate in the embryo of the bee are designed for the use of the worm-like larva and could not serve the purposes of the adult bee. In the pupal stage most of the larval muscles are, therefore, broken down by a rapid dissolution, while new muscles are built up according to the needs of the adult. The new muscles however, arise also from mesodermic tissue, as reported by most investigators, and thus the original plan is preserved amid the temporary confusion of reconstruction.

### 1. THE GENERAL STRUCTURE OF INSECT MUSCLES

A muscle is a piece of animal tissue endowed when alive with a high degree of the property of *contractility.* Its fundamental, anatomical element is a *fiber.* In vertebrate muscles the fibers are grouped into bundles or fasciculi which are surrounded and bound together by connective tissue forming a sheath over the entire muscle, called the *epimysium.* The muscles of most insects usually have no enclosing sheath, their fibers being separate and associated only by the proximity of their attachments, or loosely held together by fine tracheal tubes that branch

over them and interlace amongst them, as seen in the cross-section of part of a leg muscle of a bee shown at A of Fig. 61.

A muscle fiber has many of the constituent parts of an ordinary body cell, being composed of a protoplasmic substance, the *sarcoplasm*, and surrounded by a delicate membranous wall, the *sarcolemma*, but it contains many nuclei. The fibers originate in long, spindle-shaped cells called *myoblasts*, and some writers have claimed that each myoblast forms a fiber, its original single nucleus dividing many times without a corresponding division of the cell itself. Others, however, assert that a number of myoblasts unite to form each fiber. The recent investigations of Jordan (1920*a*) indicate that fibers are produced by both methods; in the wing muscles of a wasp, he says, the myoblasts unite end to end while their nuclei multiply by repeated direct division. The nuclei of insect muscles are often so large and stand out so prominently at the surface that they give the fiber a very irregular, warty contour, while, on the other hand, they may be small and buried in the substance of the fiber, in some cases forming rows through its axis. But the distinctive feature of a muscle fiber is the presence within it of contractile *fibrils*. The exact origin of the fibrils is not known, but one or more of them appear in the myoblast at a very early stage as a lengthwise strand of protoplasmic substance close to the nucleus The fibrils multiply either by a splitting of the original fibrils or by the formation of new ones. Eventually they fill most of the body of the fiber, being evenly distributed through it, or grouped in flat plates or lamellæ radiating irregularly from the central axis. The tissue of all insect muscles, so far as known, and that of the ordinary voluntary muscles of vertebrates is characterized in appearance by alternating light and dark cross-lines, the so-called *striations*.

Many muscles of insects contain large, dark-staining bodies in the sarcoplasm between the fibrils. These bodies are known as the *sarcosomes*.

The muscle fibers of insects, however, are otherwise not all alike. In most of them the fibrils are very minute threads having no visible organization; in others the fibrils are comparatively thick strands with a very definite structure. The muscles of the young or larval stages of all insects, and most of the muscles of adult insects are composed of fibers of the first type; the muscles of the wings of adult insects, and certain other muscles in some species are formed of fibers of the second type. Muscles of the

first kind, moreover, are characteristic of the whole class of the Arthropoda, which includes the crabs, lobsters, spiders, centipedes, and other forms, as well as the insects. Such muscles, therefore, are evidently the primitive type in this group of animals, while those of the other kind are to be regarded as a more evolved type. The first may be conveniently distinguished in insects as the *larval type* of muscles; the second as the *wing type.* Some writers refer to the first as the "leg" type, but this term is clearly too restrictive. In adult insects, however, the larval type of muscles shows various modifications, and in the Hymenoptera the ordinary muscles of the adult are so different from the muscles of the larva that they will be described separately.

### 2. THE LARVAL MUSCLES

A piece of muscle fiber of a bee larva is shown at A of Fig. 60. The fiber is surrounded by a distinct outer sheath or sarcolemma (*Sarl*), within which is first a layer of clear sarcoplasm (*Sar*)

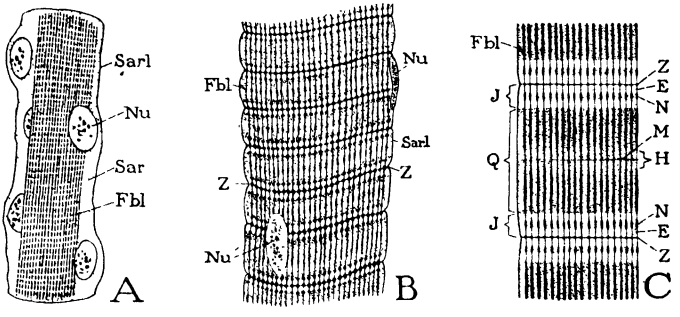



FIG. 60.—Structure of insect muscle.

A, surface view of muscle fiber of honeybee larva, showing outer sarcolemma (*Sarl*), superficial sarcoplasm (*Sar*) containing nuclei (*Nu*), and inner core of fibrillated tissue (*Fbl*).

B, fiber of leg muscle of adult May-beetle, showing muscle segments separated by telophragmata (*ZZ*).

C, diagram of muscle structure. *E*, end disc; *Fbl*, fibrilla or sarcostyle; *H*, median disc; *J*, light disc; *M*, mesophragma; *N*, accessory disc; *Q*, dark disc; *Z*, telophragma.

containing large oval nuclei (*Nu*) bulging at the surface, and then an inner darker core composed of many fine longitudinal fibrils (*Fbl*) crossed by alternating light and dark bands.

The muscles of a larval bee are so small, however, that they do not serve well for the study of muscles of this type. Further details will be more easily seen in the abdominal or leg muscles of an adult May beetle, especially if stained with hematoxylin

or with methylene blue. In the beetle muscle (Fig. 60, B) the superficial sarcoplasm is less abundant and the nuclei (*Nu*) are not so numerous, but the structure of the internal part is more distinct than in the muscle of the bee larva. The light and dark cross-bands are wider, and each of the former appears to be cut through the middle by a distinct dark line having a beaded appearance (*Z*). These lines are the edges, or the optical diameters, of transverse partitions through the fiber, either membranes or nets, attached all around to the sarcolemma (*Sarl*), which divide the tubular fiber into a series of muscle segments. The very distinct longitudinal fibrils (*Fbl*) pass through the partitions and are attached to them, the points of union giving a knotted or beaded appearance to the partitions when seen from the side.

Such a confusing variety of names has been given to the finer parts of the muscle fiber by different writers that we cannot here include a synonomy of the many terms that have been applied to the same or supposedly corresponding parts, nor a review of the various ideas that have led up to our present interpretation of muscle structure. Therefore, only the recent more standardized nomenclature and symbols, as defined by Jordan (1920, 1923), will be used in the following descriptions. The cross-partitions of the fiber are the *telophragmata* (Fig. 60 C, *Z*), the segments are the *sarcomeres,* the fibrils are the *fibrillæ* or *sarcostyles* (*Fbl*). The dark cross-bands are formed by a median *dark disc* (*Q*) in each sarcomere; the light bands are formed by the two terminal *light discs* (*J*) of adjacent sarcomeres separated by the intervening telophragma (*Z*). Besides these characters there are others that show less distinctly. The sarcomere is usually crossed through the middle by a very delicate median partition, the *mesophragma* (*M*), which bisects a pale area, the *median disc* (*H*), in the middle of the dark disc. Finally, each light disc (*J*) is often cut crosswise by a narrow, dark *accessory disc* (*N*), which sets off a light *end disc* (*E*) next the telophragma. How the fiber assumes a different appearance in contraction will be shown in the last section of this chapter.

All the dark cross-bands of the fibers in fixed and stained muscles of this type appear to be due to a thickening of the fibrillæ at certain levels repeated regularly in each sarcomere. Van Gehuchten (1886) believed these thickenings to be the artificial results of the coagulation of albuminoids in the sarco-

plasm and their precipitation about enlarged parts of the fibrillæ, or longitudinal "trabeculæ," as he called the latter. The fibrillæ thus clothed with condensed and stained material he termed "batonets." Various other writers have held the same or a modified view of the cause of the banded appearance of the fiber. But Jordan (1920), while he admits that the darker appearance and deeper staining reaction of the dark disc may be due in part at least to the segregation of substances in the sarcoplasm, claims that "the striping of the striated muscle fiber results from the segregation of darker and lighter (chromatic and acromatic) substances in alternating dark and light discs." The light and dark discs or "striations" of relaxed muscle tissue have long been known as the isotropic and anisotropic substances, respectively, on account of their opposite effects on polarized light, the first obscuring the rays, the second transmitting them. Jordan, however, says that in the muscle of a wasp "the deeper staining disc is not coextensive with, nor the result of the presence and stratified distribution of, specific anisotropic materials." Furthermore, he says, "that anisotropy and the deep-staining character of the dark disc are two essentially distinct phenomena seems proved by the fact that the sarcostyle of the wasp's wing muscle is only very feebly anisotropic, while the dark disc stains quite as intensively as that of the fibers, like those of insect leg muscle, where the anisotropy is relatively intense and most sharply segregated."

### 3. THE ORDINARY MUSCLES OF THE ADULT BEE

During the change from the larva to the adult the bee acquires an entirely new set of muscles, muscles adapted in their arrangement and attachments to the mechanisms of the adult. The fibers of the scanty larval musculature break up at the beginning of the pupal stage and are dissolved in the blood, the substances of their composition being used as food by the newly forming tissues of the adult. The new muscles are formed probably in much the same way as the embryonic muscles of the larva were formed, originating as myoblasts from the mesodermal tissue at certain places on the body wall, but since different writers still disagree on the details we cannot yet make any positive statement on this point.

The new muscles of the adult, as already explained, are of two different kinds, one comprising only the indirect muscles of the

wings, the other all the rest of the muscles. We are here concerned only with the latter, and these in the bee differ very conspicuously in structure from the discarded muscles of the larva. The fibers (Fig. 61 B) are thicker, those of the thorax and legs being mostly about 15 microns in width, though they vary from 10 to 25 microns. Their segments or sarcomeres are proportionately larger, and in superficial appearance are more like those of the adult beetle fiber (Fig. 60 B). Each is distinctly fibrillated and crossed by wide light and dark bands, the former cut by the beaded lines of the telophragmata (Fig. 61 B, *Z*), the latter showing in places faint indications of mesophragmata. Accessory discs are not distinct in specimens examined by the writer. In

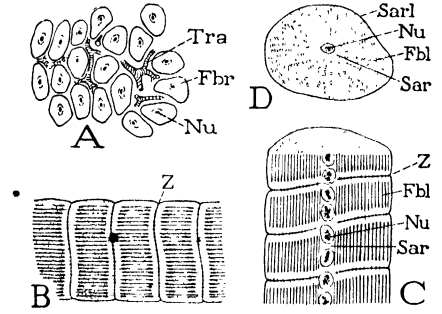



FIG. 61.—Structure of ordinary muscles of adult honeybee.
A, cross-section of part of leg muscle showing fibers (*Fbr*) interwoven by tracheæ (*Tra*) but otherwise unconnected. B, surface view of leg muscle fiber. C, longitudinal section of leg muscle fiber, showing central core of sarcoplasm (*Sar*) containing nuclei (*Nu*). D, cross-section of same muscle showing arrangement of sarcostyles or fibrillæ (*Fbl*) in radial lamellæ.

the adult beetle fiber (Fig. 60 B) the nuclei (*Nu*) are situated as in the larval fiber (A) in a layer of sarcoplasm just beneath the sarcolemma; the nuclei of the adult bee muscles are arranged in a row (Fig. 61 C, D, *Nu*) through an axial core of sarcoplasm (*Sar*) extending the entire length of the fiber. In these muscles there is but a thin layer of superficial sarcoplasm, and the surface of the fiber is smooth and even except for constrictions of the sarcolemma at the attachments of the telophragmata (*Z*), but such constrictions are probably artificial results of the swelling of the sarcoplasm or the contraction of the sarcomeres in specimens placed in water or treated with chemical reagents.

In surface view, the adult muscle fibers (Fig. 61 B) appear to be traversed by minute fibrillæ like those of the larva, too small to

show any internal structure, and the fiber has the same appearance in longitudinal section (C), but in transverse section (D) the fibrillæ (*Fbl*) are seen to be arranged in flat bundles or lamellæ radiating outward from the central core of sarcoplasm (*Sar*), many of them splitting into two or more leaves at the outer ends. The two views do not entirely harmonize for the fibrils appear to be closely packed in the lamellæ. Some writers have regarded the lamellæ themselves as being flat fibrillæ or masses of fibrillar substance not split up into separate fibrils.

Muscles of this type are characteristic not only of the adult bee but of the adults of all the higher Hymenoptera, probably of the entire order, and of the flies of the Order Diptera as well. According to Keilich (1918) the muscles of a larval sawfly (*Cimbex*) are likewise of this sort, having lamellated fibrils and axial nuclei, while the muscles of an adult water beetle (*Dytiscus*) are similar, having several rows of internal nuclei in connecting bands of sarcoplasm. Also, the muscles of other arthropods besides insects may have the lamellar arrangement of the fibrillæ, some with the nuclei in the axis of the fiber, others with the nuclei at the surface. While this type of muscle, then, appears to be a specialized one in the higher Hymenoptera, it is clear that it has been developed independently in various groups.

Sarcosomes have not generally been noted in the body and leg muscles of insects, but Jordan (1920) says they occur in the leg muscles of a wasp and show plainly in both the dark and the light discs of specimens fixed in Flemming's fluid. Since, however, they are here dissolved by alcohol, he believes that in these muscles they consist largely of fatty materials (lipoids).

### 4. THE INDIRECT WING MUSCLES

The great muscles of the wings that occupy so much of the space in the thorax are characterized in appearance by the thickness of their fibers in most insects and by a brownish color which contrasts strongly with the whiteness of the other muscles. In structure they are distinguished from the ordinary body muscles by the large size and individuality of their fibrils. When a fiber of one of these muscles is dissected in a drop of water or glycerine it breaks up readily into a multitude of fine threads, which, though not over 3 microns in thickness, are very coarse elements as compared with the delicate fibrillar strands often barely visible in the other muscles. Yet, since these fibrils of

the wing muscles are not further divisible, they are generally regarded as the true fibrillæ or sarcostyles.

In the honeybee and other members of the higher families of the Hymenoptera, the indirect wing muscles occur only in the mesothorax, those of the metathorax having been lost apparently as a part of the scheme for unifying the motion of the wings. The vertical pair of these muscles (Fig. 33, *VMcl*) lies in the lateral parts of the mesothorax, each muscle being attached above to the tergum and below to the ventral parts of this segment. The longitudinal pair consists of two laterally compressed bundles

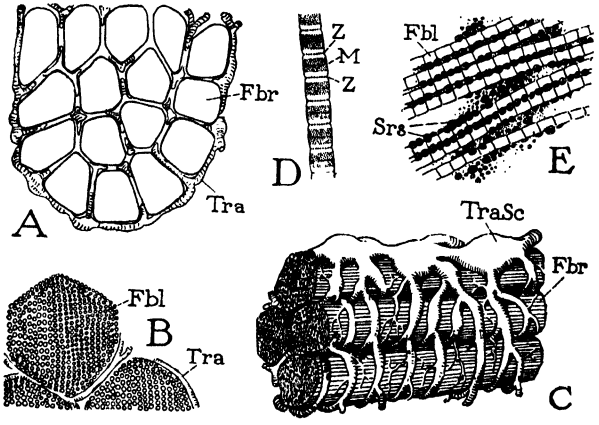



FIG. 62.—Structure of indirect wing muscles of honeybee.
A, cross-section of lower part of a dorsal muscle, showing enormous fibers (*Fbr*) interlaced by tracheæ (*Tra*). B, cross-section of fibers of wing muscle, showing ends of large sarcostyles (*Fbl*). C, group of wing muscle fibers, showing air sacs and tracheæ. D, sarcostyle of wing muscle. E, group of sarcostyles of wing muscle (*Fbl*) artificially separated, showing darkly-stained sarcosomes (*Srs*) between them.

of fibers lying dorsally between the verticals and extending through the mesothorax, metathorax and propodeum, being attached in front to the mesonotum and first phragma ($Sct_2$, 1*Ph*) and behind to the deeply invaginated second phragma (2*Ph*). Their action as elevators and depressors of the wings has already been described (page 87).

The fibers of the wing muscles are of enormous size, being from 90 to 160 microns in diameter in the bee. They are packed close in each muscle, their polygonal forms in cross-section (Fig. 62 A, *Fbr*) fitting neatly together but still separated by spaces which admit the numerous tracheal branches that penetrate

between them. Sections of the fibers show that each consists of an evenly arranged mass of sarcostyles (B, *Fbl*) held in a clear matrix of sarcoplasm. There is no distinct sarcolemma about the wing-muscle fibers in the bee, however, the outermost sarcostyles being at the surfaces of the fibers, and the writer also has not been able to identify nuclei in these muscles, though the nucleated walls of tracheal tubes (B, *Tra*) adhering closely to a fiber often give a deceptive appearance in sections of both a sarcolemma and superficial muscle nuclei. In most other insects the nuclei are very distinct and numerous in the wing muscles and a sarcolemma has been noted in some species. The nuclei usually lie in a thin, superficial layer of sarcoplasm, though they may be buried in the body of the fiber, or occur in both positions in the same species. Janet (1907) describes and figures the nuclei in the wing muscles of ants as situated at the surface and also in the deeper parts of the fiber among the fibrillæ, and Jordan (1920) says that most of the nuclei in the wing muscles of the wasp are in the body of the fibers. In the wing muscles of a dragonfly, according to Keilich (1918) the sarcostyles are arranged in definite lamellæ radiating outward from a central core of sarcoplasm containing the nuclei, a structure very suggestive of the body muscles of adult Hymenoptera. Keilich finds a distinct sarcolemma about the wing-muscle fibers of certain Orthoptera but says it cannot be distinguished in many other insects, including the honeybee. Jordan says the wing-muscle fibers of the wasp have a delicate sarcolemma. The wing-muscle fibers, however, always have such a compact appearance and such even surfaces as to suggest that there must be in all cases some sort of a retaining wall about them.

The sarcostyles of the wing muscles have a very definite structure and one, in many ways, strikingly similar to that of a fiber itself. Each is a cylindrical thread (Fig. 62 D) about 3 microns in thickness extending through the entire length of the fiber, and very clearly consisting of an internal plasma and a delicate outer wall, the *sarcostylic membrane* of Jordan. It is crossed by alternating light and dark bands, and the former are bisected by distinct telophragmata (*Z*), cutting the tubular sarcostyle into a series of sarcomeres, while through the middle of each segment there is a very faint, dark line, presumably the edge of a mesophragma (*M*). The surface membrane is usually constricted at the attachments of the telophragmata, but, as in the case of the fibers of the other muscles, this is probably

an artificially produced condition. Some investigators have observed a faint, longitudinal striation within the substance of the sarcostyles, which they have interpreted as a still finer fibrillation (metafibrils), but others contend that such lines are merely the result of fixing and staining reagents.

The light and dark discs of the sarcostyles are so evenly aligned that they give the appearance of transverse striation on the fiber as a whole, and the telophragmata so closely coincide in neighboring sarcostyles that they form distinct, dark, wavy lines across the entire fiber. Janet (1907) suggested that there must be some invisible continuation of the telophragmata bridging the interfibrillar spaces, an opinion which Jordan (1920) has further substantiated from observations on twisted pieces of fibers in which the telophragmata act as if they are actually continuous from one sarcostyle to the next. A study of the sarcosomes shows that they appear to be held within the limits of the sarcomeres between interfibrillar membranes in some species but not in others, and this suggests that the telophragmata may be ruptured or lacking in some cases between the sarcostyles. If so, we have here also an explanation of why the sarcostyles are so much more easily separated in some muscles than in others. There is no evidence of interfibrillar connections between the mesophragmata of any muscles.

The high degree of development of the sarcostyles in the wing muscles appears to be related to their power of very rapid contraction. The worker bee is said to make 190 vertical strokes of the wings in one second, and the housefly 330. In the grasshopper, whose wing motions are slow, the fibers of the wing muscles differ but little from those of the ordinary body muscles. On the other hand, the muscles that vibrate the singing discs on the abdomen of the cicada have a structure identical with that of the wing muscles of swift-flying insects, showing that this type of fiber is not necessarily limited to the wing muscles.

Another feature characteristic of the indirect wing muscles is the large number of sarcosomes regularly present in the sarcoplasm between the sarcostyles. In fresh specimens the sarcosomes have a faint brownish tint and they perhaps account for the distinctive brown color of the wing muscles. In stained specimens they become very dark The sarcosomes of the wing muscles of the bee (Fig. 62 E, *Srs*) are large oval bodies normally forming continuous rows between the sarcostyles (*Fbl*), though in

dissected specimens they may break up into masses of irregular grains of various sizes, many of which still adhere to the edges of the sarcostyles; but they have no regular arrangement with relation to the sarcomeres, indicating that the telophragmata of the wing muscles in the bee do not stretch unbroken between the sarcostyles. The sarcosomes of the bee are apparently of an albuminoid nature principally, but nothing definite is known of their function. Some writers have suggested that they are masses of reserve food material in the muscle, but their regular shapes and constant size do not argue in favor of such a theory. Jordan (1920), in discussing the sarcosomes of the wing muscles of the wasp, says that the evidence "seems to indicate that the sarcosomes are not transient nutritive reservoirs, but are formed during the early stages of muscle histogenesis, to remain throughout the life of the individual." On the other hand, he finds a great variability in size and staining reaction among the sarcosomes in the wing muscles of a mantis, and concludes that in this insect they undergo physical and chemical changes which would indicate that they are here of a transient character, as are the sarcosomes in the leg muscles of the wasp, while their dissolving in alcohol suggests that their contents are principally of a fatty nature. But the wing-muscle sarcosomes of the wasp, he says, are almost as well preserved in alcohol as in other fixing reagents, and therefore must consist of some other substance in addition to fats.

A third distinguishing character of the wing muscles is the great number of tracheal branches that ramify over their surfaces and penetrate between their fibers. This abundant tracheation of the wing muscles is evidently a response to the great demand for oxygen which their activity as movers of the wings must produce. In the bee (Fig. 62 A, C) the surface of each wing muscle is sheathed in a layer of branching air tubes and small, irregular sacs (*Tra, TraSc*) from which numerous parallel tracheæ arise and proceed directly into the body of the muscle, crossing the fibers at right angles, and giving off many fine branches which ramify over the surfaces of the fibers but do not enter them. Some writers claim that in some insects the wing-muscle tracheæ penetrate the sarcolemma of the fibers and end amongst the sarcostyles, but probably they mistook for fibers closely bound bundles of small fibers, such as occur in flies. This provision for rapid oxidation in the wing muscles is common to all insects

that vibrate the wings rapidly in flight and cannot, therefore, be attributed in the honeybee to the habit of warming the hive in winter by the activity of the wing muscles.

Most of the tracheæ that branch upon the wing muscles come from the great trunks of the prothoracic spiracles (Figs. 80, 81, *Tra*), the trunks that are principally infested by mites in bees afflicted with Isle of Wight disease. This has suggested that the principal symptom of the disease, the loss of the power of flight, results from the partial asphyxiation of the wing muscles through the clogging of the tracheæ by the mites; and a pathological condition of the wing muscles in diseased bees has been described by White (1921) as affecting both the sarcostyles and the sarcosomes. He claims, furthermore, that similar symptoms accompanied by an atrophy of the thoracic muscles may be induced artificially by a closing of one of the first spiracles; closing both kills the bee too quickly to produce pathological effects in the muscles. On the other hand, bees may have the tracheæ crowded with mites and still show no abnormal conditions of the wing muscles.

### 5. THE ATTACHMENT OF THE MUSCLES

In order to be effective as motor organs the muscles of the body wall must be firmly attached to the parts they are to move. When the fibers are first formed they have no intimate connection with any part of the body wall and are in all cases separated from the cuticular parts by the intervening layer of hypodermis. Yet, when they are mature they are fastened to the cuticula by a system of tendenous strands passing through the hypodermis (Fig. 63, A, B, E, *Tfbl*). The manner by which this union is established has created a problem on which there is still some difference of opinion.

According to Henneguy (1906), Janet (1907), Riley (1908), and most other investigators, the tendon strands are formed as chitinizations of the substance of the hypodermal cells themselves, being cuticular filaments that become secondarily attached at their inner ends to the ends of the muscle fibrillæ, while their outer ends are anchored into the soft inner layer of the cuticula. Jordan (1919), however, claims that "the fibrils among the hypodermal cells and within the chitin are actually muscle fibrils which have lost their cross-striated condition." Downey (1912) says that in the crayfish the muscle fibrils become attached

to the tendon fibrils by being dovetailed or spliced into the latter, and Riley believes that the connection is made in the same way in insects. Maziarski called the tendon fibrils in Crustacea the "tonomitomes," Henneguy named them the *tonofibrillæ* in insects, and Janet refers to them as *filaments de resistance.*

The area of the tonofibrillæ at the end of a muscle in stained specimens (Fig. 63 B, *Tfbl*) makes a distinct clear band between the inner edge of the cuticula (*Ct*) and the striated part of the muscle (*Mcl*). In the muscles of the bee the tonofibrillæ are in most places arranged in groups corresponding with bundles of

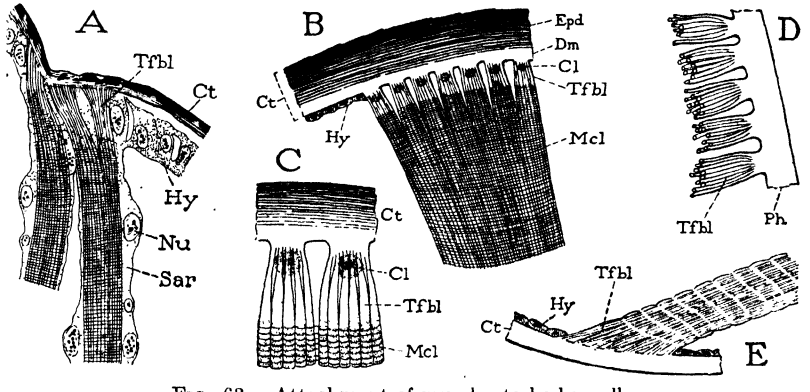



FIG. 63.—Attachment of muscles to body wall.

A, section of muscles and body wall of larva of bee, showing muscles attached to cuticula by tonofibrillæ (*Tfbl*). B, attachment of wing muscles of adult bee to thoracic tergum, showing separation of sarcostyles into groups at end of muscle. C, two fibril groups of wing muscle, showing continuity of sarcostyles and tonofibrillæ, and remnant of hypodermal cell (*Cl*) amongst the latter. D, groups of tonofibrillæ of wing muscle attached to phragma (*Ph*). E, attachment of a leg muscle, showing bundles of tonofibrillæ.

*Cl*, remnant of hypodermal cell amongst tonofibrillæ; *Ct*, cuticula; *Dm*, dermis; *Epd*, epidermis; *Hy*, hypodermis; *Mcl*, muscle; *Nu*, nucleus; *Ph*, phragma; *Sar*, sarcoplasm; *Tfbl*, tonofibrillæ.

the muscle fibrillæ (B, E), which latter are plainly separated at the ends of the fibers, though soon lost as individual fascicles in the body of the fiber. The grouping of the tonofibrillæ is particularly noticeable at the ends of the indirect wing muscles (B), where also the bundles of fibrillæ are correspondingly distinct. In places where the muscles are broken away from their attachments, the grouping of the tonofibrillæ is very clearly seen (D), each bundle arising from a narrowed base which is continuous with the support, the latter being, in the example given, the second thoracic phragma (*Ph*). There are about 12 tonofibrillæ in

each group, and from 15 to 20 groups may be counted in a section at the end of a single fiber of the wing muscles.

The normal hypodermis (B, E, *Hy*) ends against the outermost tonofibrillæ of each fiber, but each bundle of tonofibrillæ, in the case of the wing muscles, contains a nucleated cell remnant (B, C, *Cl*). These cells are conspicuous in stained sections of the wing muscles and make the grouping of the tonofibrillæ all the more evident. Cell remnants were not observed among the tonofibrillæ of the other muscles, either in the larva (A) or in the adult (E). Where they occur, however, the cells in the centers of the tonofibrillar bundles suggest that the fibrils of each group had their origin from a single hypodermal cell, if they are products of the hypodermis, or that they penetrated between the cells to attach to the cuticula, if they are prolongations of the muscle fibrils. In some muscles tonofibrillæ are not evident, and in such cases each fibrillar bundle of the fiber appears to be attached to the cuticula by one intervening hypodermal cell with a large nucleus. In sections of larval muscles the outer ends of the tonofibrillæ may be seen actually penetrating the inner dermal layer of the cuticula (A, *Cl*), but evidence of this mode of attachment was not observed in the adult. In the larva the outer sarcoplasm of the muscles (A, *Sar*) appears to be directly continuous with the hypodermis (*Hy*), and this has furnished ground for the idea that the muscles of insects are of ectodermal origin; but all embryologists agree that they arise in the embryo from the mesoderm.

As already explained (page 8) the muscles of insects are in many places attached to internal ridges or arms which are clearly simple infoldings of the body wall. But in some cases they are inserted on the ends of what appear to be long, slender tendons, often with a cup-like expansion at the end to receive the end of the muscle. Such "tendons," however, are also in their origin only tubular ingrowths of the cuticula and hypodermis, as has been beautifully illustrated by Janet (1907).

### 6. THE CONTRACTION OF MUSCLES

The movements of insects are nearly all made by the alternate pulling in opposite directions of opposing sets of muscles, as already seen in the study of the mandibles and the motion of the wings. Some movements, however, are produced by muscles in one direction only, and in the other by the flexibility of the

part to which the muscles are attached. Also, some of the movements of soft parts or of soft-bodied larvæ are due to blood pressure, but the pressure of the blood in one part of the body results from the contraction of muscles in some other part.

The method by which muscle tissue contracts is still not entirely understood, though it is a subject on which much has been written. Van Gehuchten (1886) believed that the fibrillæ or sarcostyles (trabeculæ) of insect muscles are the parts that actually shorten in contraction, and that the rest of the tissue only changes shape accordingly, the sarcolemma being curved outward between the attachments of the telophragmata. Jordan (1920), however, shows that this beaded appearance so commonly

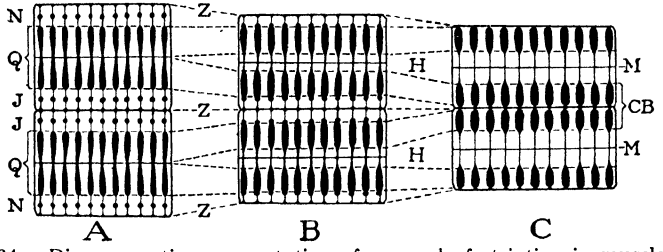



FIG. 64.—Diagrammatic representation of reversal of striation in muscle fiber during functional contraction (*as explained by Jordan*, 1923).

A, two segments or sarcomeres of normal relaxed fiber (lettering as on Fig. 60 C). B, mid-phase of contraction, *Q*-discs separating and moving toward opposite telophragmata (*Z*), widening light median discs (*H*). C, complete contraction, with *Q*-discs from adjoining sarcomeres moved against telophragmata, obliterating light *J*-discs and contained *N*-discs, and forming the new dark contraction band (*CB*).

seen in specimens of muscle fibers and fibrillæ results only from an artificial contraction or swelling of the muscle tissue by water or fixing reagents.

In fresh specimens of insect muscles there may be seen, besides the normal relaxed fibers, contracted fibers of two sorts, one kind having the usual striation, the other with the striation reversed, that is, with the dark bands enclosing the telophragmata and the light bands crossing the middle of the sarcomeres. The contracted fibers of the second sort are shown by Jordan to be fibers in normal or functional contraction, which, he says, is always accompanied by a *reversal* of striation. The change from the condition of the resting or relaxed fiber to that of a contracted fiber is illustrated diagrammatically in Fig. 64. At the beginning of contraction the dark substance of the dark disc (A, *Q*) separates

at the middle, revealing a light median disc (B, *H*) cut by the mesophragma (*M*). The two halves of the dark disc then move toward the opposite ends of the sarcomere, widening the median disc, and crowding against the accessory discs (*N*) and finally against the telophragmata (*Z*), where the two that have thus come together from neighboring sarcomeres form a new dark disc, the *contraction disc* (*CB*). At the end of contraction, therefore, the fiber has the appearance shown at C. The conspicuous light bands present at this stage are in the middle of the sarcomeres and are the widened median discs (*H*) crossed by the mesophragmata (*M*), while the dark bands occupy the region on both sides of the telophragmata, since they are the contraction discs (*CB*) formed by the approximated halves of the original *Q*-discs, which have temporarily obliterated the intervening light *J*-discs of the resting muscle and have obscured the accessory discs (*N*). The effect of the muscle tissue on polarized light, however, is not altered by the change in contraction, and Jordan (1920) claims that anisotropy and the deep-staining character of the dark discs are two essentially distinct phenomena. He says: "Reversal of striation concerns the deeply staining substance of the dark disc, not at all the phenomenon of anisotropy. The contraction band is a genuine new structure, not an optical illusion." The shape of the fiber in contraction changes by the shortening and consequent widening of the sarcomeres.

The wing muscles in contraction undergo the same reversal of striation as the other muscles, the change taking place within the substance of the sarcostyles themselves. The sarcosomes become crowded, especially in muscles where the telophragmata bridge the spaces between the sarcostyles, and their long axes are in some cases reversed from a longitudinal to a transverse direction.

## CHAPTER VI

## THE ALIMENTARY CANAL AND ITS GLANDS

Living things contain nothing in their physical substance that does not occur in their physical environment. Therefore, all primary foodstuffs or aliments of life must come from the earth or air. Protoplasm, the living substance of plants and animals, however, consists of chemical compounds vastly more complex in composition than that of the ordinary chemicals of inanimate nature, and most living organisms cannot use these simpler things as food. Hence, some intermediary agency must bridge the chemical gap between the non-living and the living, and the agent which accomplishes this in nature is chlorophyll, the green substance in the leaves of plants. Chlorophyll, using the energy of the sun radiated out as sunlight, synthesizes food from the simple chemicals taken by the plant out of the earth and the air. This elaborated food is then used directly by the protoplasm of the plant tissues, and indirectly by the protoplasm of animals that feed on plants or that eat other animals that have fed on plants. The adult honeybee is a strict vegetarian, its natural food being the nectar and pollen of flowers, but the larvæ are fed on gland secretions of the workers, which is animal material derived from plant material.

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

An animal in nature exists without taking thought of its physical condition. Yet, it is always subject to destructive forces, for not only are many things in its environment adverse to its welfare, but its very activities entail a constant wear and tear on its parts. In this respect it may be likened to a machine. But an animal differs from a machine in that it makes its own normal repairs for a pretty definite length of time. By a continual renewal of worn-out tissues it counteracts depreciation until its power of self-repair is exhausted. Then it weakens and

dies. Living, therefore, means constant rebuilding of tissues, and rebuilding involves the use of new material, *i.e.*, food.

**Organs Concerned with Nutrition.**—It is no exaggeration, then, to say that eating is the most important thing an animal does, or 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 subservient to or dependent upon that which furnishes food to the tissue 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 through the air, and to kill, tear and chew it when obtained. The blood is the servant of the stomach since one of its functions is to carry the products of digestion to the body cells. The heart and diaphragms in insects supply the motorpower of the blood. The respiratory function is accessory to that of digestion inasmuch as it furnishes the oxygen which unites with the waste products from active cells and renders them capable of being removed from the blood. The removal is accomplished partly by the respiratory system itself, partly by special excretory organs. Thus we see that the sense organs and the muscles are the agents that, by cooperation, obtain 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; and the respiratory and excretory organs are the refuse gatherers that remove waste products. The agency that controls the activities of all these organs is the nervous system; it regulates the others in the performance of their duties and coordinates their actions so that they will all work together. The nervous system makes a unified organism out of what would otherwise be simply a complex mass of variously specialized cells; but it too must be fed.

**Length of Life.**—The length of time during which an animal may repair its waste is not entirely a matter of strength or vitality; a living period is granted to each species according to the time it requires for the accomplishment of its most important function, which is that of reproduction. The length of life of most species of insects is pretty definitely fixed; some live but a few weeks, others live all summer, still others go through the cycle of an entire year, while a few live for several or for many years. Most

insects die shortly after reproduction is completed. Individuals may live longer or shorter within the life-time limit of the species according to external conditions, their activities, or their vitality, and in general their lives are prolonged by inactivity as if they have a definite amount of vital force to expend which may be used rapidly or conserved. Worker bees in summer live only about six weeks, those that pass the winter must live for several months, the queens may live four years or longer.

**Separation of Nutritive and Reproductive Functions.**—The reproductive function alone contributes nothing to the individual; in fact, the production of the germ cells, and the nourishing of the embryo and the young create a demand upon the parent organs for material which is to be separated from the individual producing it. But, biologically, each generation is to be considered as a continuation of the one before. Life is a series of forms in which the parts concerned with nourishment are periodically renewed. With most animals the reproductive function and the feeding or vegetative function are carried along together after the period of attaining maturity. With the higher insects, however, the two functions are largely separated into two stages of the living period of the individual, the creature doing most of its feeding during a larval stage, and maturing its reproductive elements during an adult or imaginal stage which derives much of the nourishment for its rapid development from the surplus stored by the larva. But with the social insects in which the adults again feed the larva and make provision for their protection, the adults themselves require an abundance of food. This has resulted in another complication arising from a division of labor amongst the adults; the latter have become differentiated into feeding individuals, and into reproductive individuals. Thus, in the honeybee, the production of the reproductive elements is left to the queens and the drones, while the feeding of the entire colony and all the other labors of the hive devolve upon the workers. Amongst ants this specialization is carried to a still greater degree and there may be several forms of workers, each adapted to special kinds of service, and there may be even two kinds of queens.

**Metabolism.**—The living elements of the body are the cells. A cell is a very highly organized mass of protoplasm, the structure of which is more fully described in the first part of Chapter XII (page 265). The cells are segregated into groups called

tissues and organs, each group serving some particular purpose, or specialized for doing some particular thing—muscle cells contract, fat cells store up food reserves, gland cells secrete, and so on. But this devotion to a specialty does not mean that each cell does not perform also those vital processes necessary for its remaining alive and in proper form to do its particular work. The complex chemical components of its body substance, or *protoplasm*, are constantly being reduced to simpler compounds which are expelled from it, while new protoplasm is built up from the supply of food material brought to it by the blood directly or indirectly from the stomach. This double process of destruction and reconstruction is known as *metabolism*, while the two phases, the breaking-down process and the building-up process are known respectively as *katabolism* and *anabolism*.

**Digestion.**—There is one thing that the specialized body cells cannot do, they cannot build up their tissues from the raw food materials that the animal obtains in nature. The work of changing natural foodstuffs into substances that the cells can *assimilate* is the special function of the cells of the stomach and certain glands, and the process of changing the food from one form to the other is that known as *digestion*. The change is a chemical one brought about by substances of the class known as *enzymes*, which are contained in the digestive liquids. The digestive powers of different animals vary according to the nature of their food, but are dependent in all cases on the particular enzymes present in their digestive secretions. The special digestive powers of the honeybee will be discussed in the last section of this chapter (page 173).

**Absorption and Assimilation.**—The products of digestion must have two qualities: They must be soluble in the animal liquids, and they must be capable of passing through moist animal tissues. The digested food is first dissolved in the liquids of the alimentary canal, then it is *absorbed* through the walls of the canal and, in insects, thus passed directly into the blood, since insects have no intervening lymphatic system, next it is carried by the blood to the various cells of the body, and finally it passes through the cell walls into the cells themselves. Here it is *assimilated* or reconstructed by the anabolic processes of the cells into protoplasmic substances similar to the original food materials, substances which cannot escape through the cell membranes until the process of katabolism again breaks them

down into simpler, soluble compounds that may diffuse back into the blood.

**Excretion.**—The waste products of the cell metabolism consist of substances composed principally of carbon, hydrogen, oxygen and nitrogen. These are converted by the inhaled oxygen, activated again by enzymes, into still simpler substances such as carbon dioxide, water, and various nitrogenous compounds. The first, being a gas, diffuses from the blood into the air in the tracheal tubes, and so reaches the exterior through the spiracles. Much of the water in the form of vapor is given off in the same way. The nitrogenous compounds and probably some of the water are separated from the blood in insects by the excretory glands known as the Malpighian tubules, which convey their products back into the alimentary canal, whence they are discharged with the residue of undigested food.

## 2. THE ALIMENTARY CANAL

The alimentary canal of the adult insect is a tube extending through the body from the mouth to the anus. It is differentiated into various parts, some distinguished merely by differences of diameter or shape and others by differences of structure. In Hymenopteran larvæ that live parasitically in the bodies of other insects or in cells containing their food, the rear end of the stomach is temporarily closed, and the waste products of digestion are not discharged until the larva is full grown and has ceased feeding.

**Development of the Alimentary Canal and Its Parts.**—Students acquainted with general embryology know that the very young single-walled embryo of most animals suffers a caving-in of one side until it becomes an open, two-layered sac called a *gastrula*. The inner layer or *endoderm* in such cases becomes the alimentary canal. With insects, however, no such thing happens, at least not in a way that can be very well identified with this typical method of endoderm formation. A mass of cells grows inward at each end of the ventral surface of the embryo (Fig. 104 I, *AMR*, *PMR*), and the two masses expand about the yolk as two irregular cups with their rims turned toward each other (J). Finally the rims come together and unite, and the yolk thus becomes enclosed in a capsule which is to be the stomach or *ventriculus*, called by embryologists the midintestine or *mesenteron* (Fig. 65, A, *Ment*). At the same time a tubular ingrowth

forms at each end of the body. The front one is called the fore-intestine or *stomodeum* (Figs. 104 J, 65 A, *Stom*) and the rear one the hind-intestine or *proctodeum* (*Proc*). Each one abuts against the corresponding wall of the mesenteron or its rudiment

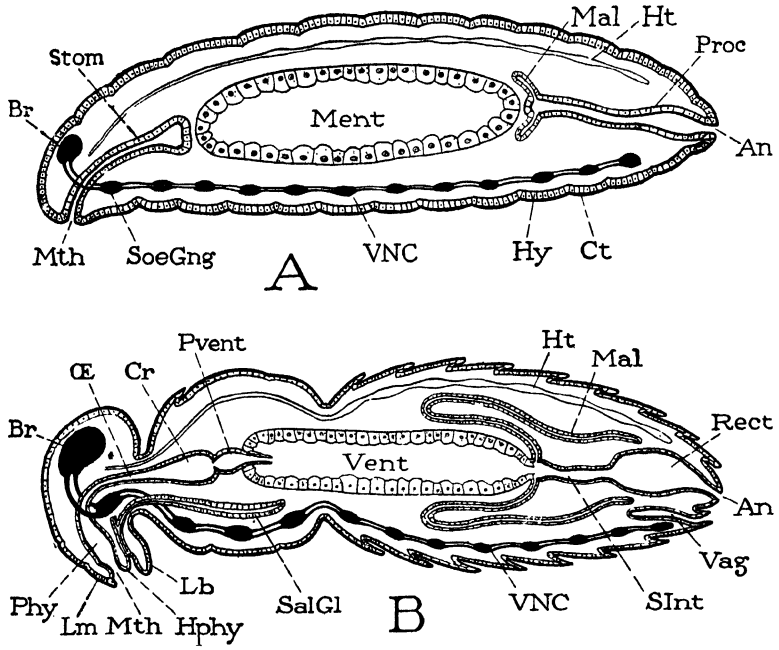



FIG. 65.—Formation of the alimentary canal and differentiation of its parts.

A, diagrammatic lengthwise section of insect in embryonic stage, showing alimentary canal forming of original embryonic stomach or mesenteron (*Ment*) and anterior and posterior ingrowth of ectoderm, the stomodeum (*Stom*) in front, the proctodeum (*Proc*) behind.

B, corresponding section of mature insect, showing union of stomodeum and proctodeum with mesenteron. The stomodeum has differentiated into pharynx (*Phy*), œsophagus (*Œ*), crop (*Cr*), and proventriculus (*Pvent*); the proctodeum into rectum (*Rect*), and small intestine (*SInt*), with Malpighian tubules (*Mal*) arising from anterior end; the mesenteron has become the ventriculus (*Vent*) of adult.

*An*, anus; *Br*, brain; *Cr*, crop; *Ct*, cuticula; *Hphy*, hypopharynx; *Ht*, heart; *Hy*, hypodermis; *Lb*, labium; *Lm*, labrum; *Mal*, Malpighian tubules; *Ment*, mesenteron; *Mth*, mouth; *Œ*, œsophagus; *Proc*, proctodeum; *Pvent*, proventriculus; *Rect*, rectum; *SalGl*, salivary gland; *SInt*, small intestine; *SœGng*, subœsophageal ganglion; *Stom*, stomodeum; *Vag*, vagina; *Vent*, ventriculus; *VNC*, ventral nerve cord.

and finally opens into it, thus establishing an alimentary canal of three parts, open at each end of the body (Fig. 65 B). The stomodeum becomes differentiated into the *pharynx* (*Phy*), the

*œsophagus* (*Œ*), the *crop* (*Cr*), and usually a *proventriculus* (*Pvent*); the midintestine or mesenteron becomes the stomach or *ventriculus* (*Vent*); the proctodeum forms the *small intestine* (*SInt*) and the large intestine or *rectum* (*Rect*). From the anterior end of the intestine a number of slender tubes grow out into the body cavity, usually four or six of them, though the number may vary from two to many (A, *Mal*). These are the *Malpighian tubules* of the adult (B), excretory organs comparable in function with the nephridia of worms and the kidneys of vertebrates. Since the stomodeum and proctodeum are ingrowths of the ectoderm, all parts derived from them, including the Malpighian tubules, are lined with a cuticula continuous with that of the body wall.

**The Pharynx.**—The pharynx of the adult bee (Figs. 8 B, 18, 66, *Phy*) lies in the anterior part of the head close behind the clypeus, extending from the mouth dorsally to above the level of the bases of the antennæ where it turns posterior and contracts to the much narrower œsophagus (*Œ*). Its walls are invested in a sheet of muscle fibers, and other muscles are stretched between it and the facial wall of the head. By the alternate contraction of these two sets of muscles the pharynx is evidently expanded and contracted, and in this way is undoubtedly able to perform a sucking action by which liquid foods are drawn up into it from the proboscis. On the floor of the pharynx just within the mouth there is a wide chitinous *pharyngeal plate* (Fig. 18, *s*). The anterior end of the plate is narrowed and prolonged into two points which bend down over the lower lip of the mouth. The posterior angles of the plate are prolonged into two long arms (*h*) which extend backward and curve upward in the lateral walls of the pharynx. Just before the junctions of the arms with the plate there are two chitinous pockets, one on each side, extending downward and posteriorly from the plate (Fig. 71 D, *i*) and opening on its dorsal surface. These pockets receive the ducts of two large *pharyngeal glands* (*lGl*) lying within the head, which are the brood food glands of the bee and will be discussed in the next section of this chapter. The pharyngeal plate of the drone (Fig. 71 E) is shorter than that of the worker and usually lacks the receptacles for the pharyngeal glands, which are entirely absent in the drone. Heselhaus (1922) records one case in which he found the receptacles present, however, in a drone. The glands are present in the queen but are very small and rudi-

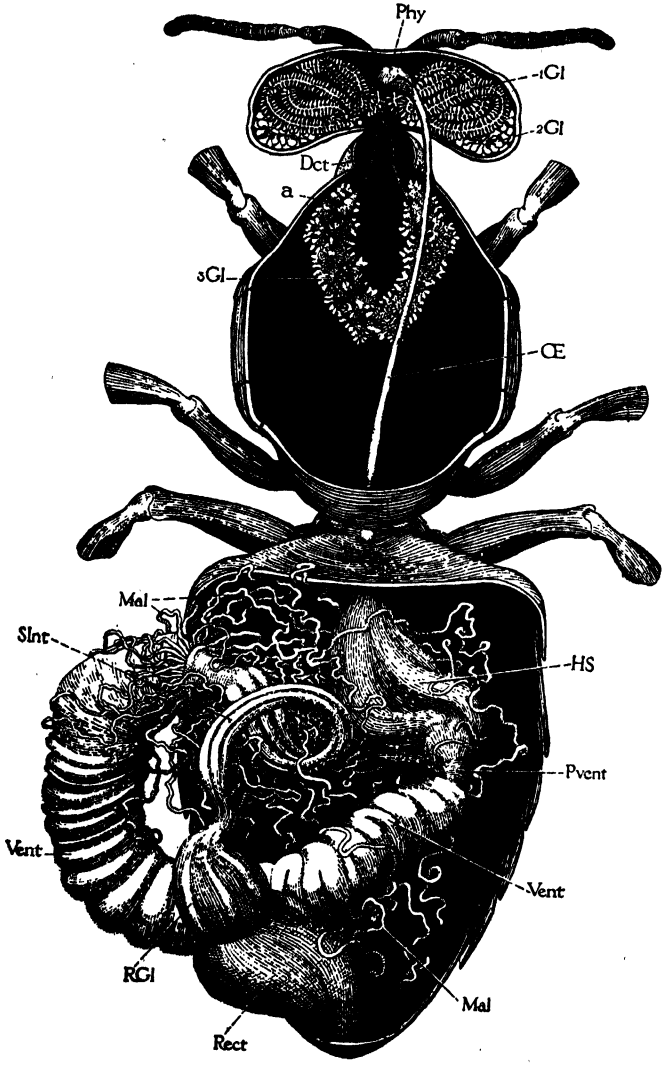



FIG. 66.—Alimentary canal and associated glands of worker, seen from above, ventriculus pulled to left.

*a*, reservoir of salivary gland; *Dct*, duct of salivary gland; 1*Gl*, pharyngeal glands; 2*Gl*, postcerebral glands; 3*Gl*, thoracic salivary glands; *HS*, honey stomach; *Mal*, Malpighian tubules; *Œ*, œsophagus; *Phy*, pharynx; *Pvent*, proventriculus; *Rect*, rectum; *RGl*, rectal gland; *SInt*, small intestine; *Vent*, ventriculus.

mentary. Definite groups of fat cells lying against the under side of the pharyngeal plate (D, E, *FtCls*) have been mistaken for glands. A large mass of sense cells lies below the posterior angles of the plate in both sexes (*Scls*) which bear short, curved hairs projecting into the pharynx (Fig. 19 C).

**The Œsophagus.**—The œsophagus is a simple, narrow tube (Fig. 66, *Œ*) which goes posteriorly from the pharynx through the thorax and into the abdomen where it enlarges into the sac-like crop or honey stomach (*HS*). Its epithelium in adult bees is rudimentary, consisting of a thin, nucleated, protoplasmic layer against the outer surface of the thick, folded intima (Fig. 68, *In*). On the outside, however, there are two well-developed muscle layers, an outer one of transverse or circular fibers (*TMcl*) and an inner one of longitudinal fibers (*LMcl*).

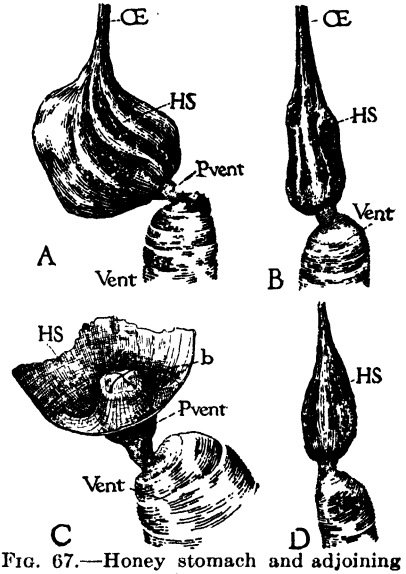



FIG. 67.—Honey stomach and adjoining parts of alimentary canal.

A, honey stomach (*HS*) of worker. B, same of queen. C, honey stomach of worker with walls mostly removed exposing "stomach mouth" (*b*), or opening to ventriculus (*Vent*) through proventriculus (*Pvent*), closed by four strong lobes (see Fig. 68, *b*). D, honey stomach of drone.

**The Honey Stomach.**—The honey stomach (Figs. 66, 67, *HS*), as the crop of the bee is called, is simply an enlargement of the posterior end of the œsophagus within the anterior part of the abdomen, and the histological elements of its walls (Fig. 68, *HS*) are continuations of those of the œsophagus (*Œ*). The honey stomach is largest in the worker (Fig. 67 A), but it is present as a slenderer sac in both the queen (B) and the drone (D). Its principal function in the bee is to hold the nectar which the worker carries back to the hive from the flowers, or the honey with which it supplies itself on certain occasions such as swarming. When empty it collapses to a small flabby pouch; when filled it is a great balloon-shaped bag with thin, tense walls. The anterior end of the proventriculus, the following part of the alimentary canal (Fig. 67 C, *Pvent*), is invaginated into the rear

wall of the honey stomach, and, if the latter be slit open, a thick, cylindrical elevation will be seen projecting into its cavity from its posterior end with the x-shaped mouth of the proventriculus on its summit (Fig. 67 C, *b*).

**The Proventriculus.**—The proventriculus is the last division of the alimentary canal derived from the stomodeum (Fig. 65, *Pvent*). In the adult bee it forms a neck-like stalk (Figs. 66, 67, *Pvent*) between the honey stomach (*HS*) and the true stomach or ventriculus (*Vent*), with its anterior end deeply sunken, as just noted, in the posterior end of the honey stomach. The four, thick, triangular lips of its mouth (Fig. 67 C, *b*) mark the ends of four internal longitudinal ridges or folds of its walls. It has often been supposed that the proventricular mouth enables the worker to pick out pollen grains from the nectar in the honey stomach and pass them on into the stomach, leaving the nectar to be carried to the hive and stored in a cell of the comb. But the worker does not eat pollen while she is engaged in collecting nectar, and if pollen is found in the honey stomach along with honey, it is only such as was contained in the honey when taken from the cell. By cutting open the honey stomach in a freshly killed bee the proventricular mouth may be seen still in action. The four lips, each armed with slender recurved spines, spasmodically open wide with a quivering motion and then roll together tightly and sink into the mouth. This, of course, suggests their picking imaginary pollen grains out of nectar, but the action is probably merely the ordinary process by means of which the proventriculus passes to the ventriculus any kind of food in the honey stomach. Nearly all insects have some such proventricular apparatus which simply takes the food from the crop as it is needed by the stomach. In some insects chitinous teeth, ridges, or plates on the walls of the proventriculus form a straining apparatus to prevent coarse, indigestible parts of the food from entering the stomach, while in some it may serve as a grinding apparatus comparable to a bird's gizzard. Trappman (1923), however, says that the proventriculus of the bee does not crush or break the pollen grains, and that its special function in bees is to prevent the food in the honey stomach that is designed for storage in the hive from going into the stomach, and likewise to prevent it from being contaminated by material from the stomach.

A longitudinal section through the proventriculus of a queen is shown in Fig. 68. The proventriculus of the queen does not

differ from that of a worker, but the honey stomach (*HS*) is slenderer and more symmetrical. The two muscle layers of the œsophagus (*LMcl* and *TMcl*) are continued over the walls of the honey stomach (*HS*), but the circular, outer fibers cease at the rear end of this organ, while the longitudinal fibers proceed posteriorly over the exposed part of the proventriculus (*Pvent*) and on to the ventriculus as an external layer (*LMcl*). A new set of *internal* circular fibers begins on the proventricular walls, where they form thick masses (*TMcl*), and extend back over the entire length of the ventriculus (*Vent*) beneath the longitudinal fibers. Hence the muscle layers on the œsophagus and honey stomach are in reverse order from those of the ventriculus. A large bundle of lengthwise muscles lies in each of the four folds of the proventricular wall, which, by contracting, pull the lips inward. The opening of the lips is probably accomplished by the constrictive action of the circular muscles. The epithelium of the proventriculus (*Epth*) is lined by a thick, smooth, cuticular intima (*In*), and the lips of the mouth (*b*) are provided with bristles pointing inward and backward into the mouth.

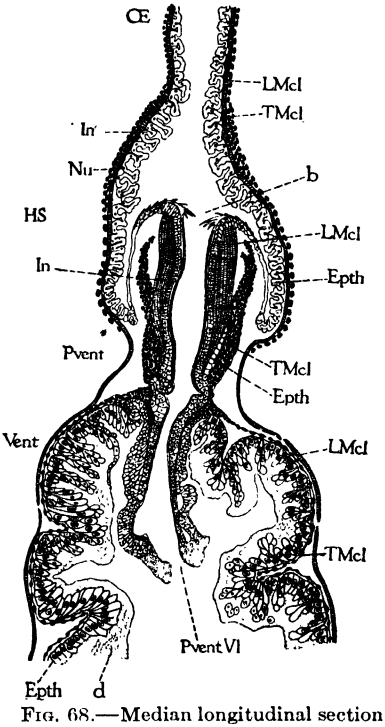



FIG. 68.—Median longitudinal section through base of œsophagus (*Œ*), honey stomach (*HS*), proventriculus (*Pvent*), and ventriculus (*Vent*), of queen.

The opening of the proventriculus into the ventriculus is guarded by a long, tubular fold, the *proventricular valve* (Fig. 68, *PventVl*). The inner layer of the fold is a prolongation of the wall of the proventriculus, since it has a cuticular lining, but the outer layer appears to be reflected from the ventricular wall. The true orifice between these two parts of the alimentary canal, therefore, is at the extreme end of the fold. The proventricular valve would appear to constitute an effective check against the

escape of any food from the ventriculus back into the honey stomach; it looks like one of those traps that permit an animal to enter by a tapering funnel but which prevent its exit when once in. Yet Schönfeld (1886) has elaborately described experiments in which, by gently tapping the honey stomach and the ventriculus at the same time, he induced the ventriculus to discharge its contents through the proventriculus into the honey stomach and even into the rear end of the œsophagus. The writer, however, by similar experiments could never get any such results. The conspicuous movement of the proventr cular mouth is always a swallowing motion, and its down-pointing bristles suggest that it is not designed for reverse action. All former arguments in favor of regurgitation by the ventriculus, however, were put forth to defend the theory, now practically discarded, that the larval brood food is a product of the ventriculus and not of the pharyngeal glands.

**The Ventriculus.**—The ventriculus or stomach (Fig. 66, *Vent*) is the largest part of the alimentary canal of the bee. It consists of a wide cylindrical tube bent into a U-shaped loop. Its surface is wrinkled by numerous transverse constrictions which give it a segmented appearance, but its shape is more constant than that of the other parts of the alimentary canal, since its size and diameter do not vary so much according to its contents. When examined in dissections under alcohol the ventriculus has an opaque white appearance, but in the natural condition, or as seen in a freshly killed bee, it is of a brownish color with lighter rings corresponding with the constrictions. The latter form internal folds where the walls are thicker than elsewhere, and the dark color between the folds is due to the brown contents of the ventriculus showing through the thinner parts of its walls.

*Structure of the Ventricular Wall.*—Sections of the ventriculus (Fig. 69 A) show that it consists of an internal cellular layer or epithelium (*Epth*), limited by a basement membrane (*BM*), and surrounded by layers of very slender striated muscle fibers. The outermost muscle layer consists of longitudinal fibers (*LMcl*). Within this layer is another of transverse fibers (*TMcl*), and these two layers are the only ones commonly reported on the stomach wall of insects; but White (1918) describes in the adult honeybee a third layer of very fine longitudinal striated fibers lying within the transverse fibers and next the basement membrane. The writer has not been able to discover this layer in any sections examined.

*The Ventricular Epithelium.*—The epithelial layer of the ventriculus consists of numerous cells of various sizes irregularly arranged

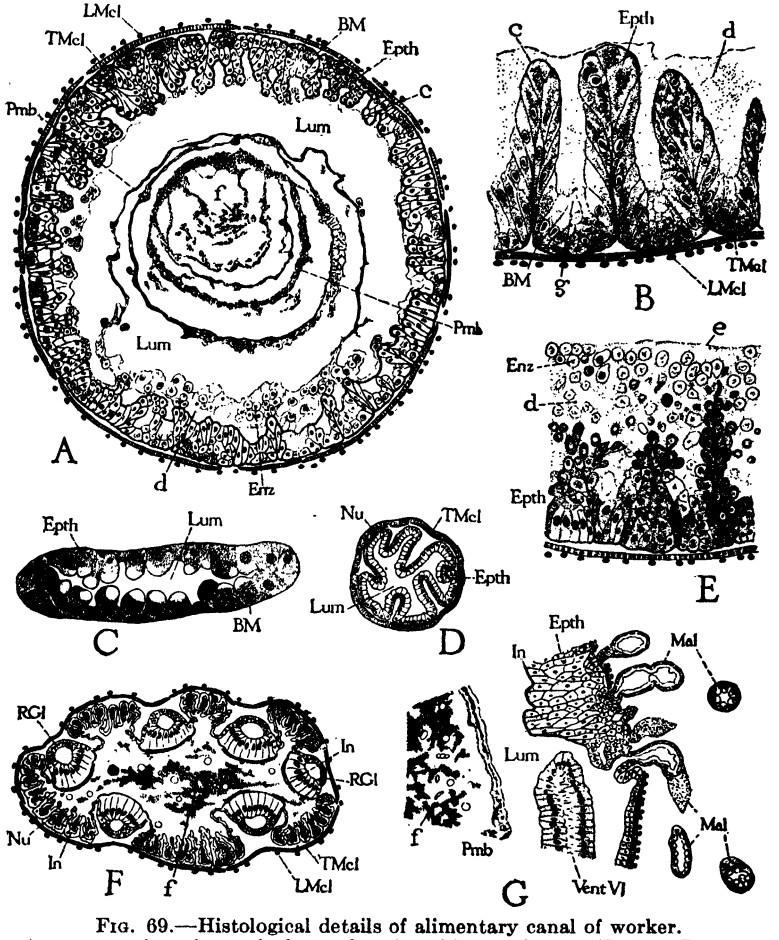



FIG. 69.—Histological details of alimentary canal of worker.

A, cross-section of ventriculus and peritrophic membranes (*Pmb*). B, section of ventricular wall with epithelial cells in resting condition. C, section of Malpighian tubule. D, cross-section of small intestine. E, section of ventricular wall with epithelial cells proliferating small digestive cells. F, cross-section of rectum through rectal glands (*RGl*). G, slightly oblique cross-section through posterior end of ventriculus and anterior end of intestine, showing openings of Malpighian tubules (*Mal*) into the latter.

*c*, thickened inner border of ventricular epithelium; *d*, gelatinous mass covering inner surface of ventricular epithelium; *e*, inner edge of gelatinous mass; *f*, food remains; *g*, cells at bottom of cups of ventricular epithelium.

(Fig. 69 A, *Epth*). The inner walls of the cells next to the lumen are thick and in sections form a distinct dark line giving the

appearance of an intima of some sort (A, B, *c*). The outermost cells rest on the basement membrane (*BM*). The entire epithelium is thrown into numerous transverse folds extending irregularly into the lumen, but if any part of it be stretched out flat it assumes a screen-like appearance, and it is then to be seen that its inner surface is full of little pits. Sections show that these pits result from circular invaginated folds of the epithelium and basement membrane (Fig. 69 B), forming irregular internal epithelial cups with small cells at their bottoms and larger cells on their lips. Figure 69 B is a more symmetrical example of this structure than is ordinarily seen, but it apparently represents a normal resting stage of the epithelium. The cups are filled by a clear, granular substance (*d*) that looks as if it might be a gelatinous mass in life, which also covers the outer ends of the folds, its outer margin sometimes following the contour of the cups, but usually being more or less continuous over the irregularities of the cellular folds.

*Methods of Secretion in the Ventriculus.*—A more common condition of the epithelium is that shown at E of Fig. 69. Here the cells on the lips of the cups appear to be very actively dividing and proliferating a large number of small cells (*Enz*) which are given off into the covering mass. These are not mere pieces of cells constricted off from the bodies of the cells, although this process occurs also, as will presently be shown, but they are actual small cells with distinct nuclei. These liberated cells are most probably charged with digestive enzymes, for those in the containing matrix appear to be in all stages of degeneration and dissolution.

At some places a different form of activity may be noted in the epithelial cells; instead of proliferating small nucleated cells, their inner ends grow out as long necks containing clear spaces, evidently filled with liquid in life, and the ends of the necks then swell and become constricted off as free globules. This is the ordinary form of secretion and discharge of digestive fluids in the ventriculus of insects, described for the bees by Trappmann and illustrated in Fig. 5 of his paper (1923). Hertig (1923) distinguishes two kinds of digestive cell bodies given off thus, one consisting of rounded granules, the other of elongate, stalked, non-nucleate bodies. Both Trappmann and Hertig mention also the separation of entire epithelial cells from the basement membrane and their discharge into the lumen of the ventriculus,

though neither of them note the proliferation of small nucleate cells described in the last paragraph. The several processes of secretion may occur in neighboring parts of the epithelium, but usually one or the other predominates.

*Inclusions of the Ventricular Cells.*—The cells of the ventricular epithelium contain a great many minute colorless granules, often crowded in the cytoplasm, and uniformly distributed in all the cells of the ventriculus. These granules have been described by Koehler (1920), who claims that tests show them to be chiefly crystals of a calcium salt, and she is inclined to regard them as merely useless calcium matter unavoidably taken in with the food, and discharged thus through the walls of the ventriculus. The insect having little inorganic material in its skeleton has small need for calcium. Many living organisms also occur in the cells of the ventricular epithelium, including the one known as *Nosema apis*, which has been regarded as the cause of one form of "paralysis" in bees.

*The Striated Band of the Ventricular Epithelium.*—The deeper part of the granular layer covering the inner surface of the ventricular epithelium shows in sections, especially where the mass is thin, a faint striation of lighter and darker lines perpendicular to the surface. Hertig (1923) says that in the adult bee the layer is formed "for the most part of many fine hairs." To the writer, however, the striation appears to be due to the presence of more darkly stained lines in a clear matrix, for in many places the mass has a continuous denser inner border that forms a distinct marginal line (Fig. 69 E, *e*) and may show no evidence of striation. The inner surface of the ventricular epithelium of insects in general is usually covered by a similar layer, the *striated band.* It is evidently derived from the epithelial cells, but there has been much difference of opinion as to the nature of its striations. In the larva of the bee the structure of the mass is more typical than in the adult, forming here a very definite layer of even thickness, 7 to 10 microns in depth, continuous over all the inner surface of the ventriculus. In sections it is distinctly striated, but it does not appear to be primarily an aggregation of separate filaments. It contains numerous elongate vacuoles of various sizes perpendicular to the surface, many of which are wide open at the surface; the "striations," in fact, appear to be due to the presence of great numbers of slender vacuoles in the substance of the mass, apparently

accumulations of a clear digestive secretion which enlarge until they break through the surface film into the lumen of the ventriculus. Thus at places the edge of the mass has a frayed-out appearance in sections.

*The Peritrophic Membrane.*—In the ventriculus of the adult bee the substance of the granular layer, or striated band, becomes filled, as already described, with the protoplasmic bodies given off from the epithelial cells (Fig. 69 E), and in this way becomes impregnated with the digestive enzymes. Its inner border usually forms in sections a distinct, darkly stained, granular line (*e*), the "border membrane" of Trappmann (1923). In many places it can be seen that the entire mass separates from the epithelial cells, and that the latter cover themselves with another similar exudation of granular matter. This process, furthermore, is, clearly, repeated indefinitely. The layers of cast-off substance then shrink, either by a condensation or by a dissolving of their outer parts, until only the denser inner borders remain, and these finally form film-like cylinders about the food mass (A, *f*) in the middle of the ventriculus. These investitures of the food are known as the *peritrophic membranes* (*Pmb*). In places the membranes enclose between them remnants of the granular mass containing degenerating digestive cell bodies, and the outermost one is often seen in sections (A) still attached in part to the surface of the epithelium. Trappmann (1923) describes the formation of the peritrophic membranes of the bee in essentially this same manner, though he believes that the films represent only the "border membranes" of the striated layer, apparently not noting that the layer may increase in thickness to a deep granular mass in which all appearance of striations is lost. The old idea that the peritrophic membrane of insects is a backward prolongation of the chitinous intima of the proventriculus has been discredited in all recent investigations on its origin.

*The Ventricular Valve.*—The epithelium at the posterior end of the ventriculus forms a short double-layered fold or *ventricular valve* projecting into the anterior end of the intestine in the same way that the proventricular valve projects into the anterior end of the ventriculus.

**The Small Intestine.**—The small intestine is a narrow tube (**Fig. 66,** *SInt*) connecting the rectum (*Rect*) with the ventriculus (*Vent*) after making a loop upon itself. Its anterior end is somewhat widened and carries the circle of Malpighian tubules

(*Mal*). Its inner walls are thrown into six longitudinal folds (Fig. 69 D) that project into the lumen. The epithelium (*Epth*) consists of a single layer of regular cells with a distinct cuticular intima on its inner face. On the outside there is a thick layer of circular muscle fibers (*TMcl*), but this part of the alimentary canal has no longitudinal muscles.

**The Malpighian Tubules.**—The Malpighian tubules are numerous in the bee (Fig. 66, *Mal*), there being perhaps a hundred of them—long, whitish, convoluted thread-like tubes, wrapped and coiled about one another and about the viscera of the abdominal cavity, all opening separately into the anterior end of the intestine behind the base of the ventricular valve (Fig. 69 G, *VentVl*). (The section from which G was drawn being somewhat oblique, only a part of the valve is seen in this figure.) The walls of the tubules consist of a single layer of epithelial cells with a thin, internal cuticular intima. The inner ends of many of the cells usually contain clear spaces and bulge more or less into the lumen (Fig. 69 C), but the writer has never seen specimens showing the ends of the cells constricted off in the manner of the secreting ventricular cells, as described by Trappman (1923). This form of excretion is not usual in glandular organs derived from the ectoderm. Trappmann also says that the tubes are emptied by the contraction of muscle fibrillæ on their outer surfaces, but muscle fibers have not been generally noted on the Malpighian tubules of insects and the writer cannot find any on those of the bee.

The Malpighian tubules are unquestionably the excretory organs of insects corresponding in function with the kidneys of vertebrates. Small crystals of nitrogenous and other substances are commonly found in them, the most usual being urates, calcium oxalate, leucin, phosphates, and calcium carbonate. During metamorphosis in some insects dense masses of crystallized substances often accumulate in the tubules and in the intestine, and are voided from the anus as soon as the adult insect emerges. The excretory products of the bee have not been analysed, but probably the feces ejected in the spring by wintering bees are full of excreta from the Malpighian tubules.

While the Malpighian tubules normally arise in the embryo of insects as outgrowths from the anterior end of the intestine (Fig. 65 A, *Mal*), those of the honeybee larva, as shown by Nelson (1917), are not connected with the intestine and are closed at their basal ends. The connection of the tubules is established

with the intestine, according to Nelson, at the time of the union of the ventriculus with the intestine, and the accumulated products of both are then discharged at the same time through the intestine.

**The Rectum.**—The rectum or large intestine (Fig. 66, *Rect*) is a large, thin-walled sac lying in the rear part of the abdominal cavity. Its anterior end narrows abruptly where it becomes continuous with the small intestine (*SInt*), and its posterior part

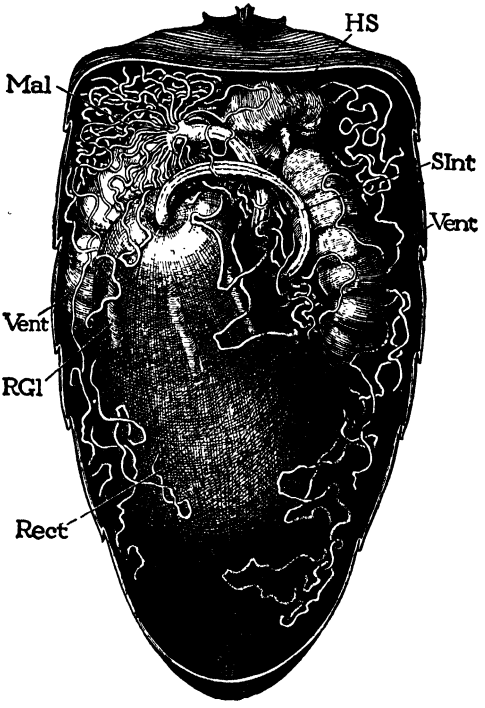



FIG. 70.—Interior of abdomen of an over-wintered worker before first flight in spring, showing rectum (*Rect*) enormously distended with undischarged feces.

contracts to a slender tube which opens at the anus (Fig. 53, *An*) in the rudimentary tenth abdominal segment (*X*). The epithelium of the rectum in an adult bee is very much reduced, constituting merely a thin, nucleated protoplasmic layer against the outer surface of the transparent cuticular intima (Fig. 69 F, *In*). Outside of the basement membrane there is a layer of transverse muscle fibers (*TMcl*) that form a close sheet all over the rectum, and external to this an outer layer of smaller scattered

longitudinal fibers (*LMcl*). The musculature of the rectum thus resembles that of the ventriculus (A) in the arrangement of the fibers. The epithelium and intima are ordinarily very much wrinkled and thrown into numerous longitudinal folds. This gives the rectal sac a great distensibility and allows it to hold an immense accumulation of material. Bees never eject their feces in the hive, and during prolonged cold periods in winter they are forced to retain so much intestinal matter that the rectum swells to an enormous bag occupying all available space in the abdomen (Fig. 70).

*The Rectal Glands.*—Near the anterior end of the rectum there are six, longitudinal, regularly spaced thickenings in its walls, the so-called *rectal glands* (Fig. 66, *RGl*). When the rectum is distended the glands bulge on the outer surface as six opaque ridges, but when it is empty they sink into the walls and protrude into the lumen (Fig. 69 F, *RGl*). Each gland is a hollow, cylindrical tube with a very thick inner wall and a thinner outer wall. The outer wall is composed of two irregular layers of small cells, but the inner wall consists of a single layer of long pyramidal cells with nuclei near their apices. The rectal walls between the glands are thin and folded and appear to be more directly continuous with the outer walls of the glands than with the inner. The latter are strongly convex on their inner surfaces, which are covered by thick smooth intima, continuous with that of the rest of the rectal walls but particularly chitinized on the edges of the glands, which form prominent shoulders on each side. The lumen of each gland is a closed internal cavity lined with cuticular intima, having no communication with either the body cavity or the lumen of the rectum.

Nothing definite is known of the function of the rectal glands. Trappmann (1923) has described a secretory activity in their cells and a discharge of products into the rectum. He says that substances are formed in both the inner and outer epithelial layers of the glands, which can be distinguished by staining reactions as elaborated products of the cells. Those produced in the cells of the outer wall are discharged into the lumen of the gland, where they are reabsorbed by the cells of the inner wall. The inner cells now contain both their own products and the products of the outer cells and finally all of these substances are discharged by osmosis through the inner surfaces of the glands into the cavity of the rectum. The structure of the organs

would seem to meet the requirements of a mere secretory function very awkwardly, and suggests that they must serve some other purpose. They are well provided with tracheæ; branches from trunks on their exterior surfaces go through the outer epithelium, traverse the lumen, and break up into finer branches that penetrate between the cells of the inner wall. Pavlovsky and Zarin (1922) believe that the rectal glands are the seat of energetic oxidizing processes, and that they are the source of a seasonal production of catalase.

### 3. THE ALIMENTARY GLANDS

Various glands are associated with the alimentary canal of insects either by anatomical continuity or by function. Most adult insects have a pair of *salivary glands* opening near the mouth, the Hymenoptera have a pair of *pharyngeal glands* opening into the pharynx, many insects have glandular pouches or tubes connected with the stomach, they nearly all have the excretory glands of the intestine called the Malpighian tubules and the so-called rectal glands, and some have other glands associated with the rectal orifice. Of these several gland systems, the honeybee has only the salivary glands, the pharyngeal glands, the Malpighian tubules, and the rectal glands. The last two have already been described in the preceding section.

**The Salivary Glands.**—The salivary glands of insects do not open into the true mouth but on the external ventral surface of the head near the mouth or on one of the mouth appendages. Typically the orifice is between the base of the hypopharynx and the labium (Fig. 65 B), but it may be on either one of these appendages or at the tip of a labium-hypopharynx when these two parts are consolidated. The glands are developed as two ingrowths of the body wall of the head which unite at their outer ends to form a common median terminal duct and outlet. Nelson (1915) says that these glands of the honeybee larva appear as two small pits in the head wall of the embryo just behind the bases of the newly formed second maxillæ. The pits elongate inward while their orifices approach on the ventral wall of the head and unite. The fully formed glands of the larva consist of two long, slender tubes lying in the lower part of the body cavity and opening by a common duct in the head, with its orifice on the end of the mentum. In the bee larva, and in many other larvæ, including the caterpillars, these glands are silk

glands rather than salivary glands, since they produce the thread with which the larva spins its cocoon.

The corresponding glands of the adult honeybee are much more complex in structure than those of the larva, consisting of two pairs of many-branched glands, two of which are located in the head (Fig. 66, *2Gl*) and two in the thorax (*3Gl*). Their common duct (Fig. 16, *SalD*) ends in a deep tubular invagination (*t*) of the upper surface of the labium which opens between the two paraglossæ (Figs. 15 F, 16, *SalDO*). For this reason apparently Heselhaus (1922) calls this gland system of the bee the "labial glands," but the term could not be extended to the homologous glands of other insects commonly known as the "salivary glands" since they do not usually open on the labium. In the bee the two divisions of this gland system have been designated the *head salivary glands* and the *thoracic salivary glands*, but since their secretions appear to be different they may be distinguished by the terms *postcerebral glands* and *thoracic glands* used by Bordas and Heselhaus. The outlet of the common duct is involved in the "salivary syringe" (Fig. 16) of the labium, from which the duct (*SalD*) extends upward through the base of the labium into the head (Fig. 18) where a branch is given off on each side to the postcerebral glands (Figs. 18, 66, 71 C, *2Gl*), while the main trunk turns backward below the cross-bar of the tentorium and goes through the foramen magnum where it divides into two branches (Fig. 18, *SalD*) that end in the pair of thoracic glands (Fig. 66, *3Gl*).

*The Postcerebral Glands.*—The postcerebral glands (Figs. 18, 66, *2Gl*) lie against the posterior walls of the cranium. In the worker each consists of a loosely arranged mass of pear-shaped follicular bodies or acini (Fig. 71 F) the individual ducts of which unite irregularly with one another and eventually form the single duct on each side that joins the common salivary duct just before the bases of the mesocephalic pillars of the tentorium (Fig. 18, *Ten*). In the drone these glands consist of delicate masses of very small follicles (Fig. 71, B) flattened against the rear walls of the head (C). Heselhaus (1922) says the secretion of these glands in the worker is of a very fatty nature and he suggests that it may be mixed with the wax when the latter is manipulated in comb building. These glands in the drone, he believes, are functionless since their lobules are rudimentary and most of their cells degenerated to fat.

A cellular mass lying against the face of the drone on each side of the clypeus (Fig. 7 C, *FtCls*) appears to be a detachment of the postcerebral gland and was formerly so described by the writer, but closer inspection shows that it is merely a group of fat cells. Similarly a mass of cells above the ocelli in the queen (B, *FtCls*) and the drone (C) was described by Bordas (1895) as "postocellar glands" with ducts opening into the anterior end of the œsophagus. Other investigators, however, have not found the "ducts," and Heselhaus reports that the supposed glands are but masses of fat cells.

*The Thoracic Glands.*—The thoracic glands of the adult bee lie in the lower part of the anterior half of the thorax between the ventral ends of the vertical wing muscles (Fig. 66, 3*Gl*). The two are widely separated anteriorly but their posterior ends are contiguous. Each consists of a mass of small many-branched, glandular tubules opening into several collecting ductules which empty into a sac-like reservoir at the anterior end of the gland (*a*). A duct (*Dct*) runs forward from the reservoir and unites with the corresponding duct from the opposite side just behind the head to form the common median salivary duct, which receives the two ducts of the postcerebral glands in the head and finally ends in the "salivary syringe" which opens on the anterior surface of the labium as already described. The thoracic glands of the adult are developed during metamorphosis from the silk glands of the larva. Schiemenz (1883) says they are formed inside the outer coverings of the anterior parts of the larval glands. The postcerebral glands, he says, are developed as outgrowths from the common duct of the thoracic glands.

The histology of the thoracic glands shows nothing peculiar to them. The tubules consist of a single layer of simple epithelial cells enclosing a narrow lumen lined with a thin, cuticular intima. The secretion accumulates in the inner ends of the cells and is discharged by osmosis through the intima into the lumen. Schiemenz claims that the product of these glands is alkaline or neutral in reaction, but Heselhaus says that the liquid discharged on the tongue of the bee is certainly acid. Its physiological effect on the food of the bee is not known; it is used copiously in dissolving solid foods such as sugar, as has already been described (page 54). The thoracic glands are well developed in all bees and in wasps, and Heselhaus believes that their secretions are largely used by many species for building material, as

cement by those species that construct nests of bits of sand or of sawdust, and as glue in the preparation of paper from wood pulp by the wasps. It is not clear, though, how the secretion of the thoracic glands and the postcerebral glands can be used for different purposes when they must both be discharged from the same duct.

**The Pharyngeal Glands.**—The pharyngeal glands, or brood food glands of the worker bees, lie in the head, where they are

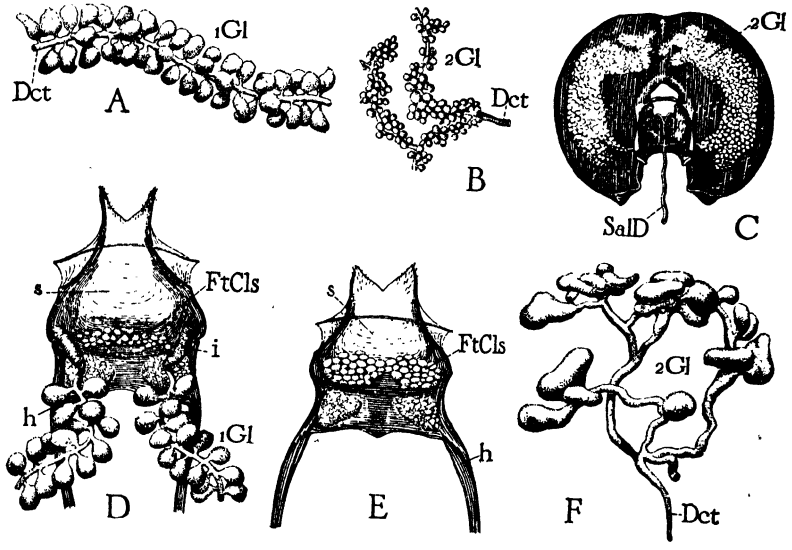



FIG. 71.—Pharyngeal and postcerebral glands of head, with associated structures. A, part of pharyngeal gland of worker. B, part of postcerebral gland of drone. C, postcerebral gland of drone in normal position against posterior wall of head, showing union of ducts with common salivary duct (*SalD*). D, pharyngeal plate (*s*) of worker, ventral view, showing receptacula (*i*) for ducts of pharyngeal glands (1*Gl*). E, pharygeal plate of drone. F, part of postcerebral gland of worker.

closely packed about the brain in the upper and the anterior parts of the head cavity (Figs. 7, 18, 66, 1*Gl*). Each consists of a long string of small ovate, cellular bodies attached by short necks to all sides of a duct (Fig. 71 A). The ducts from the two glands open into the floor of the pharynx through the pharyngeal plate (Fig. 71 D, *s*), each ending in one of the chitinous tubular pockets (*i*) near the lateral edge of the plate. In the queen the pharyngeal glands are small and rudimentary and they are absent in the drone of the honeybee (Fig. 71 E). A small mass of cells

lying against the under surface of the pharyngeal plate in both worker and drone (D, E, *FtCls*) were formerly described as "ventral pharyngeal glands" and as "sublingual glands," but they are merely definite groups of fat cells.

The lobules of the pharyngeal glands are solid cellular bodies in which each cell is individually connected with the main duct by a fine chitinous tubule, the group of tubules arising in the neck of the lobe. The tubules are difficult to trace in sections but they may be demonstrated very clearly by treating a part of the gland with weak caustic, which dissolves the protoplasmic part of the cells and exposes the bunch of ductlets. Each lobule of the gland, therefore, is to be regarded as a group of one-celled glands arising from a common duct, though each gland cell group is surrounded by a thin membranous tunic. In the bumblebees each secretory cell with its ductule forms an independent appendage on the main duct.

It is now generally conceded that the pharyngeal glands are the organs which form the brood food or "royal jelly" given to the larvæ in the comb cells by the workers, though some writers have claimed that this substance is "regurgitated chyle" from the stomach. In "The Anatomy of the Honey Bee" the writer gave a long review of the evidence on both sides of this question, but, since recent opinion is unanimous in favor of the glands, the discussion need not be repeated here. The fact that the glands are so highly developed in the worker, at best rudimentary in the queen, and entirely absent in the drone shows that in the honeybee they must be connected in some way with the special functions of the worker. The comparative studies of Schiemenz (1883) and Cheshire (1886) have shown that the development of the pharyngeal glands in different species of bees bears a pretty close relation to their degree of social organization; but it is only in the honeybees apparently that the glands are known to serve as elaborators of brood food. Though Heselhaus (1922) says that the glands in the bumblebee queen are used chiefly in the preparation of larval food, Sladen (1912) describes the food of the bumblebee larva as consisting of pollen and honey. It would therefore appear that the pharyngeal glands have been developed as brood-food glands in the honeybees by a secondary specialization of glands originally serving some other purpose. In the bumblebees and the solitary bees the glands are well developed in both sexes and their secretion, as Heselhaus points

out, must be used principally by the individual, perhaps only to moisten the food, or possibly to add digestive enzymes to it. Also, in such species, though glandular matter is not visible in the provender of the larva, which apparently consists only of nectar and pollen, it cannot be stated that the female may not inject into it small amounts of enzyme-containing secretion from the pharyngeal glands. The glands are said to be large in the wasps (Vespidæ) which feed their larvæ bits of insects masticated in the jaws, not regurgitated material or food predigested in the mouth or stomach. But it is not known, as Heselhaus again states, whether or not the female wasps add anything from the pharyngeal glands to the larval food.

**The Brood Food.**—The food given to the young honeybee larva in the comb cell is a gummy paste of a milky white color when fresh, through when removed from the cell it soon acquires a darker tone with a yellowish tint. Under the microscope it appears to be a homogeneous, very minutely granular substance. It is strongly acid and very acrid and pungent to the taste. This food is placed in the larval cell at about the time the egg hatches. Most observers have stated that it is put into the cell just after the young larva leaves the egg, but Bertholf (1923) asserts that the egg does not hatch until it is surrounded by the larval food. The queen larva is fed this gland food or royal jelly exclusively during the whole of its lifetime; the worker and drone larvæ, however, have pollen and honey added to their diet during the third day, and thereafter are fed largely on these substances. The difference in the food of queen and worker larvæ, both produced from fertilized eggs, therefore would appear to account for their different development, which idea, furthermore, seems fully established by the fact that it is common practice with beekeepers to rear queens from worker larvæ placed in queen cells under conditions where there can be no chance for the attendant bees to substitute a queen larva. This proves at least that there are not two different kinds of female eggs; yet it is hard to believe that mere feeding can produce two forms with so many anatomical differences, which differences, moreover, adapt each form very specifically to its special duties in the community. The worker is the more specialized form of the two female castes in most respects, but the characters of both queen and worker are fixed and hereditary through the queen, and all together they represent the full complement of structural

features and instincts belonging to the female sex, which, in the bee, are portioned out to the female castes according to the division of labor between them. Most likely, then, the truth of the case is that a dual potentiality resides in every female egg and young larva, and that the development of the latter is guided one way or the other according to the stimulus of the food. Still, however, there is a discordant element in the fact that, with solitary bees, honey and pollen alone bring all the female larvæ to the full development of all their primary and secondary sex characters, while the development of the former with the honeybee depends on a pure diet of royal jelly, which must be regarded as a secondarily specialized food. In the ants, where there is a still greater subdivision into castes, the development of the various forms is not known to be dependent on food. It is clear that this whole subject needs a thorough investigation.

**The Feeding and Growth of the Larvæ.**—The relation between feeding and the rate of growth of worker larvæ of the honeybee has recently been studied by Nelson and Sturtevant (1924). They find that each larva at hatching is given an amount of food equal almost to 40 times its own weight. During the first two days of its life the average larva increases in weight from .10 milligram at hatching to 4.687 milligrams, an addition of about 46 times its weight at hatching. It therefore needs but little extra food during this period. By the end of the third day, however, it has added about 245 times its weight at hatching, but from now on, though it grows rapidly, it increases at a much slower proportional rate each day, until it attains its maximum weight of about 158 milligrams at the time its cell is closed. After the second day, according to Nelson and Sturtevant (not after the third day as formerly held), the worker larva is given undigested pollen grains and honey, and for the rest of its life is fed chiefly on these substances; but during this period it is fed only such amounts as it can consume at once and is, therefore, fed many times and with increasing frequency as it grows older. Such feeding is called *progressive feeding* to distinguish it from the *mass feeding* of the young larva and of the larvæ of solitary bees. When the cap is being put on its cell, usually at about four and one-half days after hatching, the larva is given its last rations, and from now on until it emerges from the cell as a full-fledged bee it must subsist on the reserve food materials it has stored in its body, chiefly in the cells of its fat tissue, as will be explained later.

The feeding of the brood is done mostly by young workers, those up to a month in age that have not yet taken up the work of gathering nectar and pollen in the field. These feeding bees are known as *nurses*. Some interesting observations on their activities have been made by Lineburg (1924*a*) in correlating the number of visits they make to the cells with the growth of the larva as described by Nelson and Sturtevant. Lineburg finds that the nurses make an average of about 1,300 visits a day to each brood cell from the time the queen lays an egg in it until the larva reaches maturity, or over 10,000 visits during the entire period of seven or eight days. This figure, moreover, does not include records of numerous calls of "inspection," mere brief peeps into the cell by a nurse to see that all is right within; a call recorded as a "feeding visit" lasts from two seconds to three or four minutes. The number of visits are comparatively few and short on the first and second day, especially on the second, since the larva is supplied with such a large amount of food at the start; but after the beginning of the third day the visits rapidly increase both in number and in length. The total time given by the nurses to a single larva, Lineburg finds, is 6.57 per cent of the lifetime of the larva, but the demands of the larva so increase as it grows older that, on the fifth day, the nurses actually spend 19.68 per cent of this day in its cell, approximately four and three-fourth hours, involving no less than 2,855 visits.

### 4. DIGESTION IN THE HONEYBEE

Digestion is a matter of chemistry. Nervous stimuli are necessary to incite the digestive glands and the muscles of the alimentary canal to action, but they have nothing to do with what goes on in the stomach. Digestion, with complex animals, as has already been explained, consists in a changing of the food materials into forms that can be dissolved in the body liquids and absorbed by the body membranes and tissues. Each kind of animal has the power of digesting those particular things in its food that it needs for its nourishment; other things pass through its alimentary canal as unused residue. The digestive powers of different animals differ very much and may be quite unlike even in closely related species. Digestion depends in general on the presence in the alimentary tract of chemical substances known as *enzymes*, and the digestive individuality of any species therefore depends on what enzymes it possesses. In most cases the diges-

tive enzymes are contained in the liquids discharged into the alimentary canal from the gland cells of its walls or from the special glands opening into it, though in some cases they are apparently formed by microscopic organisms living in the alimentary canal. An enzyme is a substance which has the power in some unknown way of producing a specific chemical change in some other substance. Only minute quantities of the enzyme are necessary to accomplish the change, and the enzyme itself is not perceptibly used up in the process. The digestive changes caused by enzymes on food materials are of the sort known chemically as hydrolysis.

The digestive powers of any particular animal may be studied, then, in two ways: The investigator may attempt by chemical analyses to find out what enzymes occur in the alimentary tract, or he may proceed by feeding the animal chemically pure substances and noting the results.

**Classes of Food Materials.**—The bulk of all food materials of animals belongs to three classes of chemical compounds: The *proteins*, the *carbohydrates*, and the *fats*. Proteins, which are composed of carbon, hydrogen, oxygen, and nitrogen, form the more permanent substance of animal and plant protoplasmic tissues; carbohydrates and fats, which consist of the same elements except nitrogen, form the less stable parts of the tissues. Besides these substances animals need small quantities of inorganic salts, and vitamines. Most foods contain all of these constituents but in varying proportions.

**Digestion of Proteins.**—The principal source of protein in the bee's diet is pollen, since honey contains but an inconsequential amount of proteid matter. Pollen is used by the adult bees and, as we have seen, is fed by the nurses to the worker and drone larvæ after they are two days of age. Pollen, or its derivatives stored in the body, however, is an essential element in the food of all bees in the hive, both young and adult at all times, since the workers are able to produce the glandular proteid food only from the pollen which they themselves have eaten. The pollen grains are surrounded by a tough impervious coating of cellulose, a carbohydrate indigestible by bees, and consequently the pollen shell must be punctured or broken by the mandibles of the bee before the rich interior of the grain can be affected by the digestive enzymes. According to Petersen (1912) enzymes that digest proteins are abundant in the alimentary canal of the bee

and are furnished mostly by the ventriculus, though he thinks some are contained in the secretion of the salivary glands. He says that tests indicate the presence of tyrosin in the ventriculus of the bee, and Pavlovsky and Zarin (1923) report pepsin, trypsin and chymosin, all being known digestive enzymes of proteids.

**Digestion of Carbohydrates.**—While, then, the proteids obtained from pollen are an essential element in the bee's diet, the bee is famous for its liking for sugar carbohydrates. Carbohydrates furnish the energy necessary for physiological reactions, and without them bees could not long maintain their normal activities. Bees obtain carbohydrates from nectar, from honeydew, from honey, and from the sugar fed to them by the beekeeper. Nature, however, offers a superabundance of carbohydrates and not all of them eaten by any particular animal are made use of by it. Hence, a knowledge of an animal's real food cannot be had by merely observing what it eats, it must be determined what elements of its natural food materials are made available to its tissues. There are three classes of carbohydrates differing in the complexity of their molecules, and only those of the class having the simplest construction can be absorbed and utilized. The others, if they are used at all, must be hydrolyzed, *i.e.*, digested. Three common carbohydrates can be absorbed by most species without hydrolysis; these are dextrose (glucose or grape sugar), levulose (fructose or fruit sugar), and galactose. The honeybee, however, cannot utilize galactose. The carbohydrates of the more complicated kinds must be reduced to one of the simple sugars by the digestive enzymes.

The digestion of carbohydrates by the honeybee has recently been studied by Phillips (1924). In a series of feeding experiments he gave bees chemically pure sugars and starches and noted the length of time they lived on each particular substance beyond the average time at which others died when given nothing but water under conditions otherwise the same. Without food bees die very quickly, their average existence when starved being only a little over one day. By his experiments Phillips found that bees easily utilize dextrose and levulose, the two common sugars in nature that do not require hydrolysis for absorption. They as readily, however, digest cane sugar and they can also use maltose, two sugars of the second class that must be changed, the first being hydrolyzed by invertase into dextrose (grape sugar) and levulose (fruit sugar), and the second

by maltase into dextrose. Of the rarer sugars in nature it was found that bees can use trehalose and melezitose. But the bees in the experiments starved as quickly on lactose or milk sugar and raffinose as when no food was supplied. Other substances found to be entirely unavailable in a pure state are dextrins, starches, inulins, glycogen, and various other highly complex carbohydrates. Honeydew and glucose were found to be harmful to the bees only in proportion as they contained dextrin and other indigestible carbohydrates.

Analyses of the alimentary canal of the honeybee for enzymes made by Pavlovsky and Zarin (1922) suggest in general the same limited digestive powers for carbohydrates as that determined experimentally by Phillips, except that there is a discrepancy with regard to starches. Phillips found that bees died on soluble starches as quickly as if they were given nothing at all, and that when fed on honey and starch the starch remained in the alimentary tract unaltered, as could be demonstrated by staining with iodine. Yet Petersen had claimed that small amounts of starch could be digested by bees, and Pavlovsky and Zarin report the presence of amylase (diastase), the starch digesting enzyme, as present in the bee's alimentary canal. Phillips points out, however, that a probable error in the experiments by these investigators lies in the fact that pollen, which contains starch, likewise contains the enzyme for its digestion, and that the muscles of the stomach wall, containing glycogen, most probably contain also the hydrolyzing enzyme of glycogen, which is identical with amylase, the hydrolyzing enzyme of starch. Hence tests made on either the contents of the stomach or on the stomach tissue might show the presence of amylase without proving it to be a digestive enzyme of the alimentary tract. According to this, then, if bees can utilize starch in small quantity, they do so by means of the diastase in the pollen they eat—on starch alone they quickly starve.

**Digestion of Fats.**—The fats are apparently but little used by bees. Though pollen is rich in oil, much oily material accumulates with the other refuse in the intestine, as shown by Petersen, though Pavlovsky and Zarin report that lipase, the fat-splitting enzyme, is present in the ventriculus of the worker and the drone. Yet fat is formed within the body of the larva in large quantity by the cells of the fat tissue and is consumed internally during metamorphosis, as will be described in Chapter IX.

**Absorption in the Alimentary Canal.**—Beyond these few elementary facts there is still little known of the details of the digestive processes of the bee, or of the absorption of the digested food by the various parts of the alimentary canal. According to Steudel (1913) in the wasp and bumblebee absorption takes place principally from the ventriculus, where there are not two kinds of epithelial cells, the same cells that secrete digestive liquids during their active stages, absorbing the products of digestion during their resting stages.

The liquid in the ventriculus is usually of a brownish color and of a slimy nature, and the contents of all parts of the alimentary canal have been said to be alkaline during digestive activity, and either neutral or weakly alkaline at other times. Pollen apparently does not stay long in the ventriculus, though a considerable amount of it often collects in the posterior end; but a great mass of pollen grains accumulates in the rectum. Since the pollen of the ventriculus does not show much evidence of digestion and is contained in the peritrophic membranes, while that of the rectum consists mostly of empty pollen shells, it appears that albuminoid absorption takes place largely in the intestine. The adult worker bees that remain alive and active all winter to maintain the warmth of the colony feed themselves on the honey stored in the hive, and since bees do not void their excrement in the hive the rectum becomes enormously distended with the accumulated wastes (Fig. 70, *Rect*). When, on warm days, the bees fly out, they at once eject this matter, which is of a yellowish orange color and of a semiliquid or pasty consistency. In addition to the alimentary refuse it probably contains also a large amount of nitrogenous excreta from the Malpighian tubules.

# CHAPTER VII

## THE CIRCULATORY SYSTEM

If a freshly killed bee is lightly pricked in any of the soft membranes between the segments, a small drop of a clear brownish liquid oozes out. This is its *blood.* Since the blood of most animals is kept in motion by special organs, these organs and the blood are known as the *circulatory system.*

### 1. THE BLOOD AND ITS FUNCTIONS

A complex animal could not exist if its body were made up entirely of solid organs and fixed tissues, any more than a city might be inhabitable if built of masses of houses continuous in all directions. In each there must be space given over to open highways of communication where a circulating medium or vehicles can distribute the necessities of life from receiving stations to consumers. In the animal the liquid blood, flowing through tubes or through spaces between the organs, plays the rôle of distributor, carrying the nutritive and energy-forming substances from the alimentary canal and respiratory organs to the cells of the various tissues where they are consumed, but the blood acts also as ash collector by taking the waste products of combustion from the tissues and carrying them to the special organs of excretion.

**The Function of the Blood.**—The food taken into the stomach is changed by the digestive processes into substances that can be absorbed through the walls of the alimentary canal and dissolved in the blood. The gases of respiration may also simply dissolve in the body liquid in lower animals, but vertebrates have red corpuscles in their blood which contain a substance called hemoglobin that has a great capacity for taking up oxygen or carbon dioxide. The hemoglobin, therefore, acts as a special carrier for the respiratory gases and enables the blood to carry much more of them than could be simply dissolved in its liquid part or plasma. Few insects or other invertebrate animals have hemoglobin in their blood, but, as will be shown in Chapter VIII on respiration, the blood of many invertebrates, perhaps including

insects, contains other substances which may also be carriers of oxygen and carbon dioxide.

**The Structure of the Blood.**—The blood of insects is not contained in special blood vessels; it simply fills the spaces in the body cavity not occupied by the various organs, and thus directly bathes the surfaces of all the tissues. The blood consists of a liquid, the *blood plasma* or *hemolymph*, and of cellular bodies, the *blood corpuscles* or *leucocytes*, floating in it. According to Nelson (1915), the leucocytes are produced in the embryo from the median ventral part of the mesoderm. In the bee larva, he says, the leucocytes are always to be seen in process of division, and probably keep up their numbers entirely by this means. Anglas (1901) thinks that some of those of the adult bee are formed in the pupa from the cells of the dorsal diaphragm. The leucocytes act as scavengers, and they are probably always ready to consume broken-down tissues and disease germs. They were formerly regarded by some investigators as the active agents in the breaking down of the larval tissues during metamorphosis, but this idea is now for the most part discarded. The activity of the leucocytes during metamorphosis is of the same sort as at any other time, but may increase in degree when there is most work for them to do. During metamorphosis they have commonly been known as *phagocytes*, and their function of engulfing particles of disintegrating tissues is called *phagocytosis*. But recent studies show that the leucocytes are not as active in any way in the metamorphosis of many species as they were formerly supposed to be.

**The Blood of the Honeybee.**—The blood of the adult honeybee is a pale, brownish liquid containing a few granular leucocytes (Fig. 85, I). The blood of the larva is a clear liquid, constituting, according to Bishop (1923*a*), from 25 to 30 per cent of the entire weight of the larva. It is slightly heavier than water, its specific gravity being 1.045. The plasma is rich in proteins, but contains, Bishop asserts, no specific oxygen carrier comparable with the hemoglobin of vertebrate blood; and its oxygen-carrying capacity "is within a reasonable error the amount that could be physically dissolved." In reaction the larval blood is more acid normally then the blood of mammals, and has, Bishop states, "a fair buffer value," which is to say that it possesses considerable power of absorbing alkaline or acid substances without materially changing its own condition.

## 2. THE HEART AND THE DIAPHRAGMS

Though there are no special blood vessels such as veins and arteries in insects, there may be very definite spaces amongst

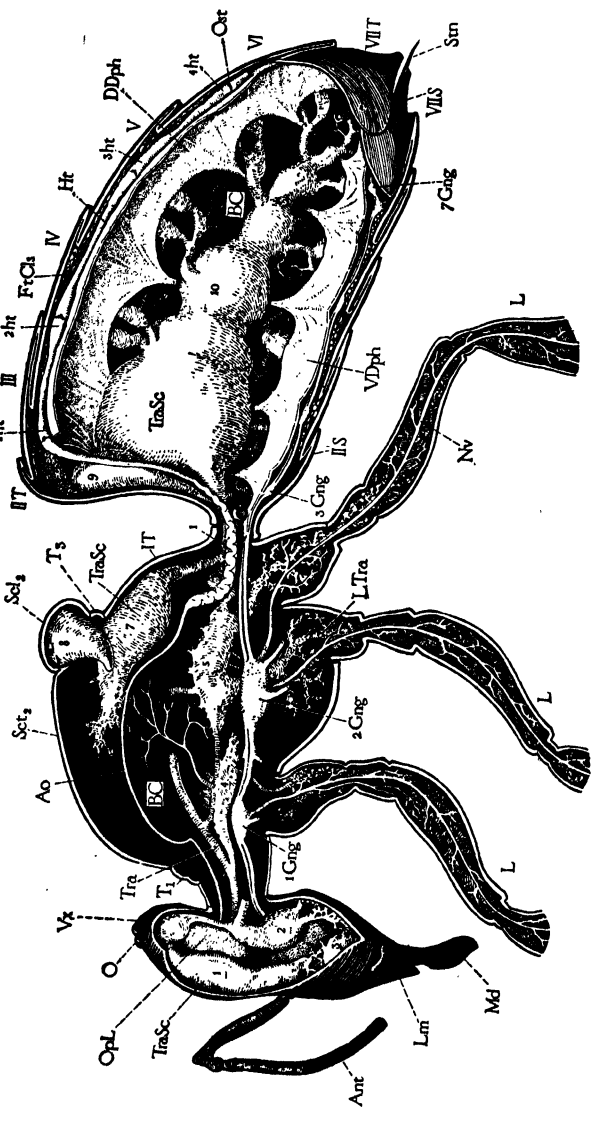



FIG. 72.—Longitudinal section of entire body of worker, with muscles and alimentary canal removed, showing disposition of air sacs (*TraSc, 1–10*), position of heart (*Ht*) and aorta (*Ao*), dorsal diaphragm (*DDph*), ventral diaphragm (*VDph*), and ventral nerve cord (*1Gng–7Gng*).

the viscera through which the blood flows. Special dorsal and ventral channels or *blood sinuses* are usually partially shut off

from the rest of the body cavity by transverse sheets of membranous or muscle tissue known as the *dorsal* and *ventral diaphragms*. When the diaphragms contain muscle fibers they are rhythmically contractile and play an important part in maintaining and directing the general circulation of the blood. In the dorsal sinus, however, there is a median tube extending through most of the length of the body, which is independently contractile, and which is usually regarded as the chief blood-propelling organ of the insect. This organ is the *heart* or *dorsal vessel*. Its posterior part, or the heart proper, is chambered and has paired openings, the *ostia*, along its sides to permit the entrance of the blood; its anterior part is a simple, slender tube, the *aorta*, opening at its anterior end into the front part of the thorax or into the head. The dorsal sinus, containing the heart, is sometimes known as the *pericardial sinus*, and the dorsal diaphragm beneath it as the *pericardial septum*. Two cellular masses lying in the dorsal sinus, one along each side of the heart, are composed of cells distinguished from those of the diaphragm as the *paracardial cells*.

**Development of the Circulatory Organs.**—The heart and the dorsal diaphragm are formed in the embryo from the mesoderm layers which grow upward in each side of the body to form also the fat and the muscles (see page 294). The upper margins of these layers become thickened as they bend inward beneath the back, and enlarge vertically while their inner, opposing faces become hollowed lengthwise. Approaching from right and left their edges soon touch and unite, and the cellular masses thus come to be the walls of a tube enclosing a narrow, median channel. This is to be the heart. The lateral wings of mesodermic tissue flaring outward from each side of the tube form the dorsal diaphragm and the paracardial cells, while the space above becomes the pericardial sinus. Further development adds the final touches which convert these simple rudiments into functional working organs. The cellular walls of the heart are transformed into muscle by the development of contractile strands within them; perforations appear in each side of the heart which allow the blood to enter from the dorsal sinus; the outer edges of the diaphragm become attached to the body wall at the front of each segment. When the young larva is hatched its circulatory apparatus is ready to begin its duties, though Nelson says there are no muscles in the dorsal diaphragm of the young bee larva.

In the larva of the bee (Nelson 1924) the dorsal vessel extends from the ninth abdominal segment into the head where it ends between the brain and the œsophagus. The slit-like openings, or ostia, are present in each body segment from the second to the eleventh. The slender anterior part in the first segment and the head is the aorta, which is tubular in form but open along its under surface in the larva as well as at its anterior end. The heart muscles surround the tube crosswise as a double row of every delicate semicircular fibers.

**The Heart.**—An easy way to study the circulatory organs of the adult bee is to cut the abdomen lengthwise with a pair of scissors into an upper and a lower half, then submerging the halves in a dish of water and removing the adhering parts of the alimentary canal. The inner surface of the dorsal piece will be covered by the delicate dorsal diaphragm, through which the median heart may be seen; while the thicker ventral diaphragm is stretched across the ventral piece, usually folded at the overlapping edges of the sterna.

The dorsal vessel of the adult bee extends from the posterior part of the sixth segment of the abdomen forward into the head (Fig. 72, *Ht*). It has thus been shortened by the length of three segments since the larval stage, when it reached back into the ninth abdominal segment. Besides this decrease in length other changes have taken place. The part in the abdomen is now very wide and club-shaped, increasing in width to the posterior end. Toward the middle of the third, fourth, fifth, and sixth segments the diameter enlarges somewhat, resulting in the formation of a series of four segmental chambers (Fig. 72, 1*ht*-4*ht*), the sides of which are perforated by the slit-like ostia (*Ost*). But these four chambers and corresponding four pairs of ostia are all there are in the adult bee, though in the larva there were three more pairs of ostia in the next three segments preceding, besides the posterior three pairs lost with the shortening of the tube from behind. In the second segment of the abdomen the heart becomes a simple tube and turns downward to the peduncle where, as it passes into the propodeum, it bends into a series of serpentine convolutions enclosed in a delicate transparent sheath (Fig. 72, *i*). Then, straightening out again as the slender aorta (*Ao*), it arches upward and forward between the dorsal longitudinal thoracic muscles, and finally goes through the neck into the head where it ends openly beneath the brain.

The chambered part of the heart is a thick-walled tube composed entirely of fine, transverse, striated muscle fibers arranged

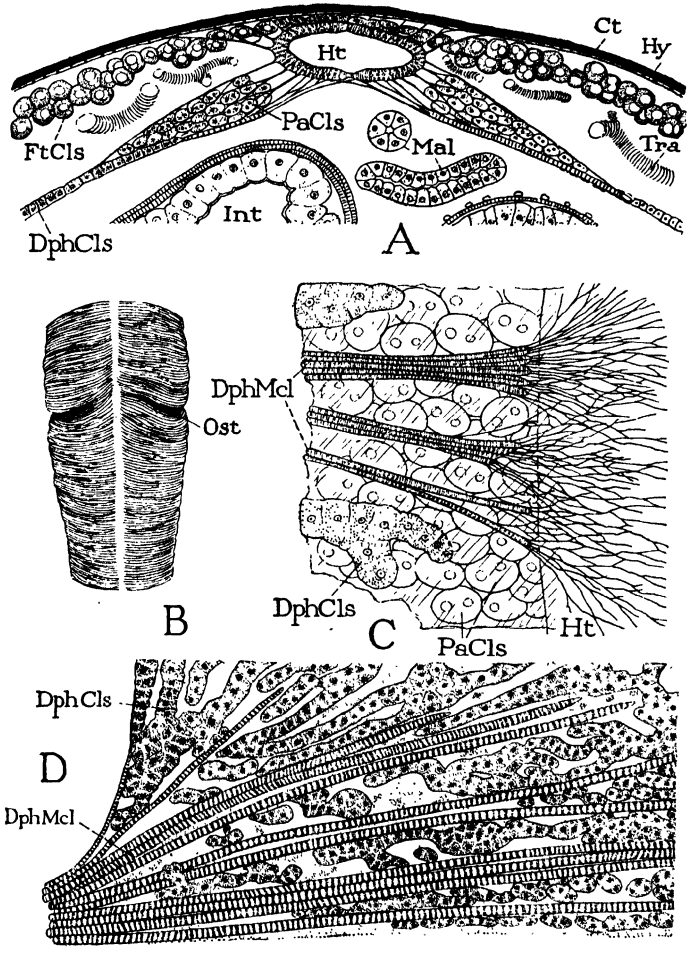



FIG. 73.—Details of heart and dorsal diaphragm.
A, cross-section through dorsal part of abdomen, showing heart (*Ht*) suspended from dorsal body wall, diaphragm attached to heart walls below, fat cells (*FtCls*), paracardial cells (*PaCls*), and tracheæ (*Tra*) in dorsal sinus. B, middle part of a heart chamber showing pair of lateral slit-like ostia (*Ost*). C, diaphragm muscles (*DphMcl*) ending in tendinous branching fibrils on under surface of heart (*Ht*), diaphragm cells (*DphCls*), and paracardial cells (*PaCls*) seen through diaphragm. D, piece of dorsal diaphragm, showing diaphragm muscle fibers (*DphMcl*) and strands of diaphragm cells (*DphCls*).

in semicircular or completely circular bundles (Fig. 73 B). The muscular structure is well shown in cross-sections (A, *Ht*).

Both the outer and the inner walls of the tube are lined by sarcolemma, there being no endothelium or cellular lining of any sort. But in longitudinal sections the heart looks like an epithelial tube composed of thick, nucleated cells bulging irregularly into the lumen, since the nuclei lie in axial rows and the striations do not appear in this view. The muscular structure is continued through the anterior tubular part as far as the convoluted section, but here becomes extremely faint and gives way to flat, nucleated cells. The walls of the aorta are very thin and show no structural elements.

The anterior three heart chambers give evidence of origin from paired rudiments in the retention of a pale dorsal and ventral seam (Fig. 73 B) where the muscles are separated by constrictions dividing them into lateral halves (A, *Ht*), but in the last chamber the muscles are continuous around the whole circumference of the tube. Nelson (1915) describes very faint contractile fibers traversing the cells of the heart in the bee larva. It is remarkable that the heart of the adult bee should be so strongly muscular in contrast. According to Anglas (1901), the muscle tissue of the heart of a wasp larva is only a very weak differentiation of the inner faces of the original heart cells, but even this he says disappears in the adult with the development of the muscles of the diaphragm. He further states, however, that he could find no trace at any time of muscularity in the heart of either the larva or the pupa of the bee.

The heart is suspended from the dorsal body wall and held firmly in place by many fine, branching threads that go upward and outward from the sarcolemma of its dorsal half (Fig. 73 A). Similar fibers bind its lower half to the dorsal diaphragm and to its muscles, as will be presently described. Nelson (1924) states that the heart of the larva is clothed externally by a loose network of minute, branched, connective tissue cells, many of which unite with the hypoderm and adjacent fat cells and serve to anchor the heart in position. Apparently, then, the thread-like fibers of the adult are of cellular origin though they have lost all trace of cell structure and appear to be processes of the sarcolemma.

Both the heart and the dorsal diaphragm pulsate forward. The blood comes into the dorsal sinus by way of the lateral openings above the edges of the diaphragm and then enters the heart through the ostia. The latter are somewhat obliquely vertical

slits in the heart walls, one on each side near the middle of each dilation or chamber of the heart. The lips of the ostia are produced into the lumen of the heart as long flaps extending inward and forward. The pressure against them from within during systole serves to close them and to prevent the exit of the blood, while the contraction of the heart brings the opposing flaps of each pair together and they thus probably serve also as valves counteracting the backward flow of the blood. There are no special valves between the heart chambers as formerly stated.

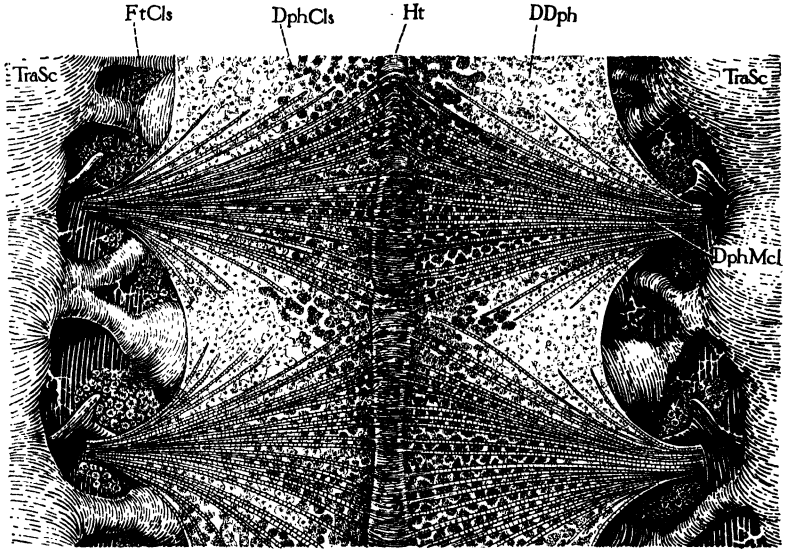



FIG. 74.—Piece of dorsal diaphragm and associated organs, from a drone, seen from below.

*DphCls*, diaphragm cells; *DDph*, dorsal diaphragm; *DphMcl*, diaphragm muscle fibers in fan-shaped bunches attached near anterior margins of tergal plates; *FtCls*, pericardial fat cells; *Ht*, heart seen through transparent diaphragm; *TraSc*, lateral tracheal air sacs.

**The Dorsal Diaphragm and Dorsal Sinus.**—The dorsal diaphragm (Fig. 72, *DDph*) stretches across the upper part of the abdominal cavity from within the sixth segment, not counting the propodeum, to the front part of the second (*III*) where it ends in a free transverse margin. Its lateral edges are drawn out into points which are attached to the tergal plates of the second to the sixth segments, inclusive at the bases of the prongs on their anterior margins (Figs. 74, 75), and the free borders between the attachments form deep semicircular notches. The

dorsal sinus over the diaphragm thus communicates with the general abdominal cavity by a series of wide, flat openings above the margins of the diaphragm. The sinus contains the median, tubular heart (Figs. 72, 75, *Ht*), the sacculated, pericardial tracheal branches (Fig. 75, *HtTraSc*), a mass of paracardial cells (Fig. 73 A, *PaCls*) on each side of the heart, and a thick padding of opaque pericardial fat cells against the dorsal body wall (Figs. 72, 73 A, 74, *FtCls*).

By removing a piece of the dorsal diaphragm and the heart, staining, and mounting in glycerine, the various tissues composing the diaphragm and associated with it may be easily seen. The diaphragm itself consists of a flat layer of muscle and cellular tissues united by extremely delicate intervening membrane. Perhaps in an earlier stage the membrane consists of a dorsal and a ventral layer, since Nelson (1924) says there are two membranes in the diaphragm of the larva of the bee, and Anglas (1901) records the presence of two in the wasp. In sections of the diaphragm of an adult bee, however, the membranous areas show as single, delicate strands attached to the edges of the cells or muscles and bridging the spaces between them.

The diaphragm cells are loosely scattered toward the edges of the diaphragm, but for the most part they form everywhere between the bundles of muscle fibers, irregular groups and long branching and reuniting bands in which cell boundaries are often indistinct (Figs. 73 D, 74, *DphCls*). In sections (Fig. 73 A) the rows of these cells are seen to have a very definite upper and lower border as if enclosed between two membranes, but the intervening spaces, as just noted, are bridged by a single membrane attached along the edges of the cells.

The muscles of the diaphragm consist of fan-shaped groups of fibers radiating toward the heart from the five points of attachment to the body wall on each side (Fig. 74, *DphMcl*). The fibers have a robust appearance, though they are flat and very slender, being from 10 to 20 microns in width. Most of the larger ones are branched. In their very distinct cross-striation and lengthwise fibrillation the dorsal diaphragm muscle fibers resemble those of the other adult body muscles, but apparently they do not have axial nuclei. Here and there superficial nuclei may be seen in an outer layer of sarcoplasm. A few of the anterior and posterior fibers in each fan end in the diaphragm (Fig. 93 D), but most of them reach the edge of the heart. Here

they expand and divide into two or several small branches and these then break up into great brushes of fine branching threads, which either are inserted on the under surface of the heart, or join beneath it in an intricate network with threads from the opposite side (Fig. 73 C). The writer formerly (1910) made the erroneous statement that the fibers of the diaphragm muscles are mostly continuous beneath the heart from one side to the other. The plainly striated part of the fibers ends abruptly where the final branching begins. The terminal tendons may be of the nature of tonofibrillæ (though, if so, tonofibrillæ are not necessarily of hypodermal origin), but where they are inserted directly on the walls of the heart (A, *Ht*) they are clearly seen to be continuous with the outer sheath of its muscular wall. The other similar strands that come to the sides of the heart from among the paracardial cells (*PaCls*) are attached to it in the same manner. It would seem most probable that all these strands should be of the same nature, and, as above pointed out, those at least that serve as suspensoria of the heart have been shown by Nelson to arise from connective tissue cells.

It is thus seen that the dorsal diaphragm and particularly its muscle fibers are intimately connected with the ventral half of the heart, and that the heart is suspended from the dorsal wall of the abdomen by tendinous threads attached to its dorsal half. The whole structure, then, suggests that the muscle fibers of the dorsal diaphragm, often called the "wing muscles of the heart," may act as dilators of the tube. Yet the heart will continue its rhythmic pulsations after the diaphragm and its muscles are torn from their attachments, showing that it is independently capable of both systole and diastole. The chief function of the diaphragm muscles is to produce the vibrations of the diaphragm itself, which, pulsating from behind forward, pumps the blood up into the dorsal sinus where it comes in contact with the heart. In the young larva of the honeybee, Nelson (1915) says, the dorsal diaphragm consists of an extremely thin membrane in which no muscle fibers are visible.

**The Paracardial Cells.**—The paracardial cells form masses along the sides of the heart. In dissections of fresh material they appear to be loose aggregations of cells, but in sections (Fig. 73 A, *PaCls*) it is seen that they are covered by a delicate membrane. The membrane is attached mesially to the heart, and appears to arise laterally from the dorsal surface of the dia-

phragm. The cells are interlaced also by branching strands from the heart which are lost amongst the cells, but which apparently arise likewise from the diaphragm. The paracardial cells are oval in shape (C) and most of them are clearly binucleate. Nelson (1915) distinguishes two kinds of cells in the diaphragm of the bee embryo, flat, diaphragm cells proper, and larger paracardial cells. In "The Anatomy of the Honey Bee" (1910) the paracardial cells were designated the "pericardial" cells. The paracardial cells are quite distinct from the pericardial fat cells (Figs. 73 A, 74, *FtCls*), which form a layer across the dorsal part of the pericardial sinus above the heart and against the hypodermis of the body wall.

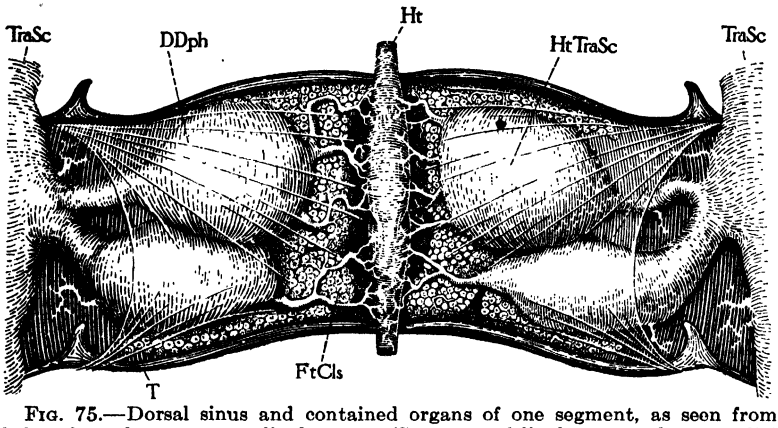



FIG. 75.—Dorsal sinus and contained organs of one segment, as seen from below through transparent diaphragm. (Structure of diaphragm, and paracardial cells not shown.)

*DDph*, dorsal diaphragm; *FtCls*, pericardial fat cells; *Ht*, heart; *HtTraSc*, pericardial tracheal air sacs; *T*, tergal plate; *TraSc*, lateral tracheal air sacs.

**The Ventral Diaphragm.**—The ventral diaphragm is a sheet of thin tissue, transparent when fresh, stretched across the ventral part of the abdominal cavity from the front edge of the peduncle back to the base of the sting. Its lateral margins are drawn out into points (Fig. 72, *VDph*) which are attached to the anterior edges of the sternal plates, the free parts between the attachments forming a series of deep scallops. When the abdomen is contracted the diaphragm is thrown into wide transverse folds, and, in specimens freshly killed with an anæsthetic, it may often be seen still pulsating with strong, wave-like motions running *backward*. When the specimen is treated with alcohol, or a piece of the diaphragm is stained, the latter becomes opaque, and a

microscopic examination shows that it is really a sheet of muscle fibers. The fibers radiate from the lateral attachments, but they cover the entire surface and are closely packed even along the free parts of the edges. They are a little more slender than the fibers of the dorsal diaphragm, measuring from 3 to 8 microns in width, and are like the other body muscles in that they have the nuclei in axial rows. The ventral diaphragm contains no cellular elements, other than the muscles, and appears to have no supporting membrane.

**The Ventral Sinus.**—The ventral sinus, or space beneath the ventral diaphragm, communicates with the general abdominal cavity by the lateral openings along the scalloped borders of the diaphragm between the points of attachment (Fig. 72). The abdominal nerve cord (*3Gng-7Gng*) lies in the upper part of the sinus. On the floor is a layer of fat cells, and the ventral commissures of the tracheal system with their sac-like swellings traverse the sinus from one side to the other through the lateral openings and lie between the nerve cord and the fat cells. All these parts may be seen very clearly through the diaphragm itself in its natural, transparent condition.

### 3. THE CIRCULATION OF THE BLOOD IN THE BEE

The circulation of the body liquid and the course it follows through the abdomen may be demonstrated easily by the following method, since the heart and the diaphragms continue to pulsate for some time after the other body muscles are paralysed by an anæsthetic or the body dismembered. Pin an asphyxiated bee to a block of cork or paraffin and remove the top of the abdomen by making a horizontal incision all around it with a pair of small scissors. 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 such as carmalum in a water solution. Almost immediately the color will appear in the ventral sinus of the abdomen where it is forced backward by the wave-like vibrations of the ventral diaphragm. From the sinus it goes upward from the lateral openings through well-defined spaces between the air sacs and the alimentary canal and particularly up wide channels against the lateral walls of each segment. It will be noted in this experiment that the blood enters the abdomen from the thorax by way of the ventral sinus

only, and that it has very definite courses through the abdominal cavity.

The dorsal circulation cannot be observed in this same specimen because the back is removed. Therefore, take another bee and fasten it in the same manner, but now make simply a shallow median slit through the body wall of the back so as to expose the dorsal sinus and the heart from above. 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 with the blood, but in sufficient amount to give white blotting paper a distinct tint. In a short time, however, the heart becomes filled with the stained blood and appears as a colored tubular band along the median line. The blood, therefore, driven up the lateral and visceral channels of the abdomen from the ventral sinus by means of the rearward contractions of the ventral diaphragm, is drawn into the dorsal sinus through the openings along its sides by the contractions of the dorsal diaphragm, which expand the sinus. Within the sinus it is driven ahead, along the sides of the heart, by the forward pulsations of the diaphragm, and soon it enters the heart itself by way of the lateral ostia to be pumped anteriorly through the aorta and finally out into the cavity of the head. From the head it makes its way backward again through the thorax and once more enters the ventral sinus of the abdomen. Thus the blood has a definite and rapid circulation through the larger spaces of the body cavity. But it also bathes all the tissues of the body and penetrates all the appendages, though it perhaps does not move actively in all parts or flow through the appendages. In many places the interchange of nutrient substances and waste products in solution is probably accomplished largely by diffusion.

# CHAPTER VIII

## THE RESPIRATORY SYSTEM

When a bee comes in from the field and alights at the entrance of the hive its abdomen is rapidly expanding and contracting, suggestive that the insect is very much out of breath after its recent exertions. This is a very simple act of replenishing its supply of oxygen and of getting rid of its surplus gases, but it requires a complicated internal mechanism and involves complex chemical reactions which are as yet but little understood in insects.

### 1. THE GENERAL PHYSIOLOGY OF RESPIRATION

The existence of almost every living thing, whether animal or plant, depends on a constant supply of air. Air consists principally of a definite mixture of two elemental gases, oxygen about one-fifth, and nitrogen about four-fifths, and contains a varying amount of a third gas, carbon dioxide. Animals require only the oxygen from the air. This oxygen does not permanently become a part of the protoplasm of the animal, so far as known; it is employed temporarily for the purpose of uniting with certain substances in the tissues to form unstable compounds which, when broken down, result in the formation of carbon dioxide, water, urates and other nitrogen-containing compounds, with the production of heat. The carbon dioxide gas and some of the water, in the form of vapor, are exhaled by insects through the respiratory organs, the urates are discharged either in solution in water or in the form of small crystals mostly through the Malpighian tubules, the heat is radiated.

In general, the more active an animal is, the more oxygen it consumes and the more carbon dioxide it gives off. Its breathing system is developed in proportion to its needs. Most insects lead very active lives, except during their dormant periods, and they are correspondingly provided with well-developed organs for respiration.

**Body Heat and Hive Temperature of Bees.**—Insects have no direct means of controlling the radiation of heat from their

bodies; consequently, in general they possess no measurable warmth above that of the surrounding air. Most of them are hot or cold according to the weather, and their activities depend on the heat they get from without, though the degree of heat necessary for their activities varies with different species. Bees in active motion, however, are said to have a temperature slightly above that of the air about them, but they liberate a large amount of heat generated by the action of their muscles. During winter, bees in the hive supplied with plenty of honey, or sugar in other forms, are able to create a sufficiency of heat, principally by rapid movement of the wings, to maintain through the coldest weather an air temperature of from 57 to 94° F. in the protected center of the cluster. This accumulated heat in turn warms the bees and not only prevents them from dying of cold but keeps them in proper condition for continuing their heat-forming activities.

**Types of Respiratory Organs.**—Different kinds of animals receive air into their bodies in various ways. Those that live in water and breathe beneath the surface use the air that is naturally dissolved in the water, some of them absorbing it directly through the skin of the body, though most of them are provided with thin-walled gills. A few aquatic insects have external gills in the form of delicate pouches or hollow filaments containing blood, through the walls of which it is supposed that gases of the water and of the blood are exchanged directly. But nearly all insects, whether they live on land or in the water, have a respiratory system consisting of internal, branching air tubes, opening at the spiracles and penetrating to all parts of the body. The lungs of vertebrates consist of somewhat similar branching air tubes opening to the exterior, but the tubes are contained in sacs occupying only a small part of the body cavity, and the blood must be brought to them to receive oxygen and to give off its carbon dioxide. The breathing tubes of insects are called *tracheæ* and all together constitute the *tracheal system.*

**Respiration in Insects.**—Inhalation and exhalation with insects are effected either by means of respiratory movements of parts of the body, or simply by the diffusion of gases from the surrounding air into the tracheæ through the open spiracles, and from the tracheæ in the opposite direction. But the transfer of gases between the end tubules of the tracheæ and the interior of the body is probably due to that physical property of gases

which causes them to go through moist membranes in the direction of the least amount of gas of each kind. Those gases that are present in the tracheal air in greater amount than in the blood pass into the latter through the delicate end tubules of the tracheæ; those present in greater amount in the blood pass out into the tracheal tubules. Thus oxygen normally goes into the blood, and carbon dioxide comes out of it.

**Oxygen Carriers of the Blood.**—The amount of gas that can dissolve in the blood liquid or *plasma* is in any case very small, but active animals need a large amount of oxygen and must discharge a corresponding amount of carbon dioxide. The blood of vertebrates possesses a special oxygen and carbon dioxide carrier called hemoglobin, a substance contained in the red blood corpuscles. Hemoglobin has the property of seizing and holding large amounts of these two gases wherever there is an abundance of either, but each gas as quickly escapes from it wherever there is a scarcity of its kind. For this reason hemoglobin is a very effective transporter of oxygen to the tissues and of carbon dioxide from them, being always in eager pursuit of one or the other, according to whichever it lacks, but never able to hold either where there is a relative scarcity of the one with which it happens to be principally charged.

Only a very few insects have hemoglobin in their blood or in special cells of the body. For this reason it was formerly supposed that the blood of insects did not carry oxygen or carbon dioxide, and that the exchange of these gases took place directly between the cells of the various tissues and the fine end tubules of the tracheæ (Fig. 82 C, D). In "The Anatomy of the Honey Bee" (1910) it was pointed out that a direct exchange of gases between the tracheoles and the tissues would seem physiologically inadequate, yet no oxygen-carrying substance had been found at that time in the blood of insects. It has been known for some years, however, that the blood of many other invertebrates, including crabs, crayfish and lobsters, contains an oxygen and carbon dioxide carrier in the form of *hemocyanin* which is dissolved in the plasma. Hemoglobin is an iron compound; hemocyanin has copper as its characteristic element. Recently it has been shown by Muttkowski (1921) that analyses of the blood of many different kinds of insects always give a constant amount of copper, and an amount nearly equal to that in the blood of the crayfish. From this Muttkowski concludes that

hemocyanin is present also in the blood plasma of insects and that it serves as the carrier of oxygen and carbon dioxide. The widely branching system of air tubes in the insect, then, probably relieves the blood of much of the work of distributing oxygen and of carrying off carbon dioxide, but, though the tracheæ end in very fine, thin-walled tubules lying against the outer surfaces of the tissue cells, we need not believe that the gases are exchanged only by passing through the walls of these tubules directly into the cells and from the cells directly into the tubules. The blood of insects must play some intermediate rôle in respiration, though not such a leading part as it does in vertebrates.

## 2. THE SPIRACLES

The breathing apertures or *spiracles* of the bee have already been mentioned in connection with the external structure of the thorax and the abdomen. In the worker and queen there are seven spiracles visible externally on each side of the body (Fig. 2, *Sp-Sp*), and three others that are hidden by overlapping parts of the body wall, making ten pairs in all. The first three pairs are located on the thorax, the other seven on the abdomen, but, as already explained (page 112), the third thoracic spiracles belong to the propodeum and are therefore the true first abdominal spiracles.

**The First Thoracic Spiracles.**—The first spiracle on either side of the thorax of the bee lies a short distance below the front of

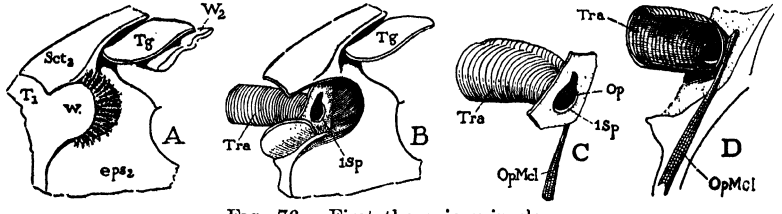



FIG. 76.—First thoracic spiracle.

A, showing position of left spiracle in cavity beneath lobe (*w*) of posterior edge of protergum ($T_1$). B, protergal lobe removed exposing spiracle (1*Sp*) in membranous anterior wall of cavity, and showing large tracheal trunk (*Tra*) attached. C, same spiracle, more enlarged, with most of surrounding parts removed, showing closing operculum (*Op*) and opercular muscle (*OPMcl*). D, corresponding spiracle on right seen from within trachea, showing insertion of opercular muscle on arm of operculum.

the base of the first wing, but it is completely concealed beneath the flap-like lobe (Fig. 23, *w*) projecting back from the rear margin of the protergum ($T_1$). The edge of this flap is provided

with a thick brush of branched hairs (Fig. 76 A), but when the flap is lifted or removed (B) there is exposed beneath it a deep pocket with a part of the intersegmental membrane forming its front wall, and it is in this membrane that the first spiracle (1*Sp*) is located. The spiracle is irregularly oval in shape, its longest diameter being vertical and about .14 of a millimeter in length. It is mostly closed, however, by an oval plate or operculum (C, *Op*) attached along the upper half of the spiracle rim. The great tracheal trunk (*Tra*) opening through this spiracle goes forward from it and rapidly widens to its greatest diameter of about a quarter of a millimeter. At D an inner view of the corresponding spiracle on the right side is seen from within the trachea. A small arm projects upward from the upper, inner angle of the operculum to which is attached the upper end of a long, slender muscle (*OpMcl*). This muscle serves to close the aperture of the spiracle, for it is evident that its contraction must pull the operculum down against the lower rim of the spiracle. It appears, however, that the door cannot be very widely opened and that the entrance is never more than a crescentic slit (C, 1*Sp*) beneath the lower edge of the operculum. But, when the operculum is closed, there is nothing to hold it firm, and for this reason, apparently, the mites that cause Isle of Wight disease in bees (Fig. 82*a*), are able to get into the tracheæ through this spiracle.

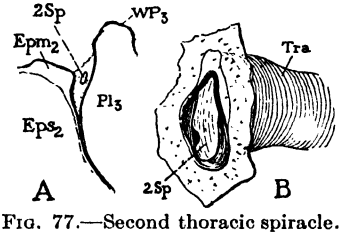



FIG. 77.—Second thoracic spiracle. A, showing position of spiracle on left side in membrane between upper ends of mesepimeron (*Epm*$_2$) and metapleuron (*Pl*$_3$). B, same spiracle, more enlarged.

**The Second Thoracic Spiracles.**—The second spiracle on each side of the thorax is in the membrane of the deep fold beween the upper ends of the mesepimeron and the metapleuron (Fig. 77 A, 2*Sp*). It is very minute and is apparently a simple aperture with a delicate chitinous rim, but without any closing device. It is entirely too small to admit the Isle of Wight disease mite. This spiracle, on account of its obscure position and small size, has long been a puzzle to bee students trying to find it. A description and figure of it were first published by Walker (1913). The spiracle is difficult to find in old bees, but in young bees it shows plainly, and Fig. 77 B was drawn from a worker not yet emerged from the comb cell.

**The Propodeal Spiracles.**—The spiracles of the propodeum (Fig. 23, *ISp*) are the largest of all the spiracles in the bee. Each is plainly exposed on the side of the propodeum (*IT*) and presents to the exterior a long oval aperture .23 millimeters in length and .06 in greatest width. It is surrounded by solid, raised lips that slant toward the opening (Fig. 78 A), and it is closed by a valve that projects forward from within the rear lip and underlaps the front lip. At B of Fig. 78 the spiracle of the left side is shown with the outer lips cut off. The closing valve (*Vl*) is thus clearly exposed and is seen to consist of a membranous central part bounded by a hard chitinous rim (*a*). It is also to be noted that the front edge of the spiracle has a wide inner lip that underlaps the edge of the valve. This lip is seen better at C

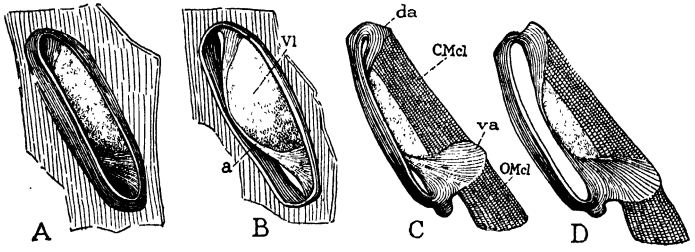



FIG. 78.—Third thoracic spiracle (spiracle of propodeum).
A, left spiracle, outer view, closed. B, same spiracle, with outer lips of aperture removed, exposing the closing valve (*Vl*) with chitinous edge (*a*). C, inner view of right spiracle, closed by contraction of closing muscle (*CMcl*) stretched between dorsal and ventral arms of valve (*da*, *va*). D, same spiracle, opened by contraction of opening muscle (*OMcl*) inserted on ventral arm of valve.

which gives an inner view of the right spiracle. The closed valve thus fits into a deep groove between the outer and inner lips, where its edge is held securely as is that of a sliding door received into a groove on the door post. The closing mechanism of this third spiracle is quite different from that of the first spiracle. The ends of the chitinous rim of the valve form two large knobs (C, *da* and *va*), between which is stretched a wide muscle (*CMcl*). The contraction of this muscle springs the valve forward and can evidently press its free edge tightly into the groove between the spiracle lips. Another muscle (*OMcl*) is inserted on the lower edge of the ventral knob (*va*) and is attached by its other end to the wall of the thorax below. This muscle appears to be for the purpose of opening the valve, for, by contracting, it would flatten the arch of the latter and open the spiracle aperture as shown at D. Though the propodeal spiracles

are large enough to admit two full-grown Isle of Wight disease mites abreast, no mites have ever been found in the tracheæ leading from them, and apparently for the reason that the edge of the closed valve is securely locked in the manner above described.

**The Abdominal Spiracles.**—The spiracles of the abdomen are located on the sides of the tergal plates of the first seven segments. Since the spiracles of the propodeum are the true first abdominal spiracles, the others belong to segments *II* to *VIII*, but the last pair is not visible externally unless artificially exposed (Fig. 56, *Sp*). The external openings of the abdominal spiracles are narrow slits about .06 millimeters in length, except those of the

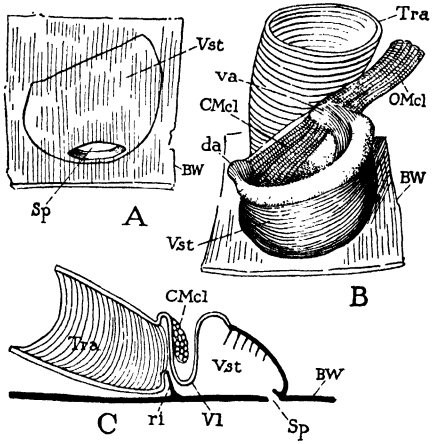



FIG. 79.—Details of an abdominal spiracle.
A, outer view, showing external opening (*Sp*) and outline of vestibule (*Vst*). B, inner view of spiracle and connected trachea (*Tra*), showing wall of vestibule (*Vst*), dorsal and ventral arms (*da*, *va*) of semicircular valve, with closing muscle (*CMcl*) stretched between them, and opening muscle (*OMcl*) inserted on ventral arm. C, vertical section of spiracle, showing aperture (*Sp*) in body wall (*BW*), vestibule (*Vst*), valve (*Vl*), closing muscle (*CMcl*), and trachea (*Tra*).

last pair which are larger. Each opens into a pocket or vestibule of the body wall, the outline of which (Fig. 79 A, *Vst*) is visible through the latter (*BW*). The inner wall of the vestibule is covered with hairs (C) showing that it is merely a secondary invagination of the external body wall. With the exception of this entrance chamber, the spiracles of segments *II* to *VIII* of the abdomen have the same essential construction as those of the propodeum, or segment *I*. Each is closed by a valve (C, *Vl*) which projects like a trapdoor in front of the opening from the vestibule (*Vst*) to the trachea (*Tra*), its free edge resting against

a high ridge (*ri*) of the body wall to which the outer lip of the trachea is attached. The fold of the valve contains a muscle (*CMcl*) stretched between its knob-like chitinous ends (B, *da* and *va*), and the contraction of this muscle closes the tracheal entrance in the same way that the orifice of the propodeal spiracle is closed. The valve is opened by a long, slender muscle (*OMcl*) inserted on its ventral knob (*va*) and attached to the lateral apodemal arm of the sternal plate of the same segment (Fig. 83, *OMcl*). In most insects there is also a dorsal closing muscle attached to the dorsal knob of the valve (*da*), but the bee does not possess this muscle.

### 3. THE TRACHEAL SYSTEM

The tracheal system of insects consists generally of two main longitudinal trunks, one in each side of the body, extending along the lines of the spiracles, connected with the latter by short tubes and with each other by segmental transverse ventral commissures. In each segment, branches are given off to the body wall and to the internal organs, which branch minutely upon all the tissues. In the thorax specially large tubes are given off from the main trunks 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. In some orders of insects there is another pair of longitudinal trunks situated in the dorsal part of the body. These are connected by vertical commissures with the lateral trunks and with each other by transverse dorsal commissures. Aquatic insects that do not have blood gills either have tracheal gills which absorb the oxygen that is dissolved in the water, or they come to the surface for air.

**The Tracheæ and Air Sacs of the Bee.**—The entire body of the honeybee is abundantly supplied with tracheal tubes and especially with air sacs. The general tracheation of the thorax, however, is very difficult to study on account of the soft and flabby texture of the tracheæ, which makes the latter almost invisible when empty of air. But there are two large strong tubes against the lateral walls of the prothorax (Fig. 72, 80, 81, *Tra*) which arise at the first spiracles (1*Sp*) and go forward through the neck into the head. In the thorax each gives off a large internal trunk that runs posteriorly and subdivides into branches that go to the first legs, to the large wing muscles of the mesothorax,

and to the ventral thoracic air sac (*5*). The two trunks that enter the head form there a number of head air sacs, one on each

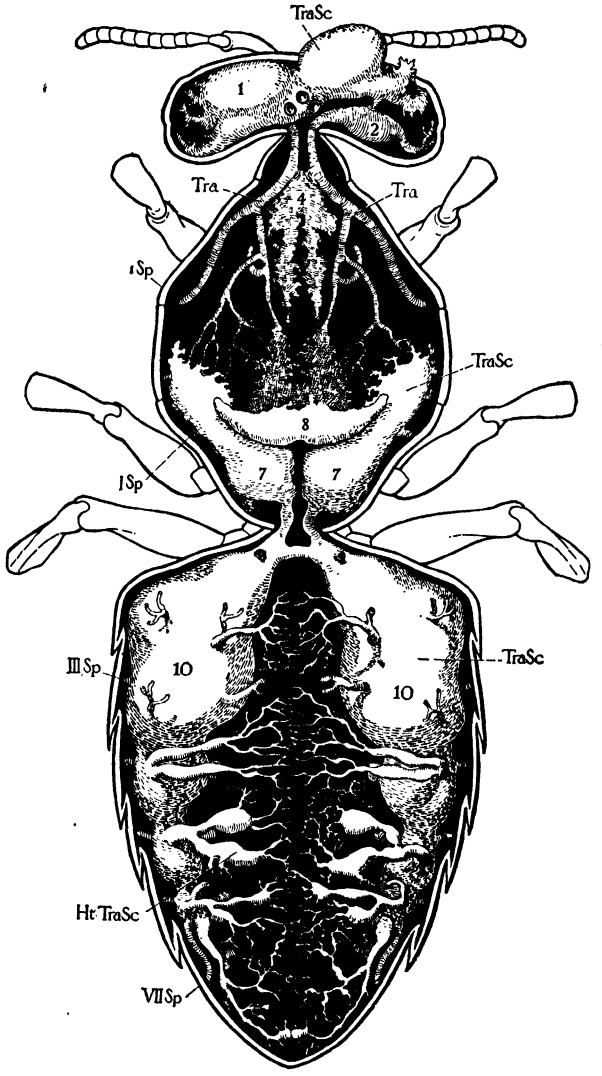



FIG. 80.—General tracheal system of worker, showing dorsal and lateral parts from above; one pair of abdominal sacs (Fig. 72, *9*) removed, and ventral commissures of abdomen not shown (Fig. 81).

side (Figs. 72, 80, *2*) lying against the base of the compound eye and about the optic lobe, another (Fig. 72, *3*) being situated above

the base of the mandible, and a third large median one (Fig. 81, *1*) lying against the upper part of the face and covering the top of the brain. In the rear part of the thorax there is dorsally a large

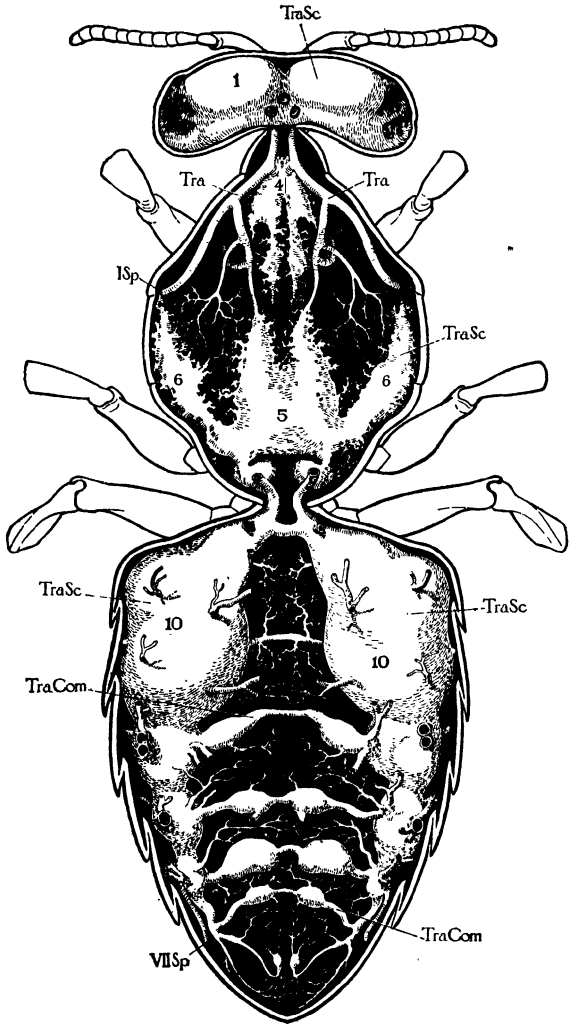



FIG. 81.—General tracheal system of worker, showing lateral and ventral parts as seen from above after removal of dorsal tracheæ and air sacs of thorax and abdomen.

air sac in each side of the propodeal segment (Figs. 72, 80, *7*) connected with the propodeal spiracle (Fig. 80, 1*Sp*) of the same

side by a short trachea. Above these sacs there is a narrow, median, transverse sac (*8*) occupying the cavity of the turgid mesoscutellum (Fig. 72, $Scl_2$). In the ventral part of the thorax there is a large median sac (Figs. 72, 81, *5*) which gives off two lateral sacs (Fig. 81, *6*), and also trunks to the middle and hind legs. The various thoracic tracheæ and air sacs finally unite in two large tubes in the peduncle which go posteriorly into the abdomen.

In the abdomen the two tracheal trunks from the thorax expand into two enormous air sacs (Figs. 72, 80, 81, *TraSc 10*). Each of these sacs is largest in the anterior part of the abdomen, somewhat constricted in each segment, tapers posteriorly, and ends in tracheal branches to the terminal segments. The sacs are connected with the seven spiracles of the abdomen by spiracle tracheæ, all of which are very short except the last two on each side; and they are united with each other by six transverse ventral commissures (Fig. 81, *TraCom*), four of which are themselves distended into small air sacs. Dorsally (Fig. 80) the lateral sacs give off large segmental trunks, which branch upon the body wall and the internal organs; those of segments *III* to *VI* divide into two sacculated branches (Fig. 72) which enter the pericardial sinus to supply the heart and surrounding tissues with tracheæ (Fig. 75, *HtTraSc*).

**The Structure of Tracheæ.**—Under the microscope a trachea appears to be merely a thin-walled branching tube with numerous crosswise lines winding spirally around its wall (Fig. 82 A); but its actual structure is more complicated than this. The fundamental part of the tube is a very thin layer of flat epithelial cells (B, *Epth*). The cells are covered on their outer surfaces by a delicate basement membrane (*BM*), and on their inner surfaces by a thicker, pale yellowish or brownish chitinous intima (*In*). At each of the spiracles the tracheal layers become identical with those of the body wall, the epithelium and basement membrane of the trachea being continuous with the hypodermis and its basement membrane, and the intima with the cuticula covering the external surface of the body. The tracheæ, in fact, are mere ingrowths of the body wall and originate in the embryo as pits in the latter, which, deepening, branching, and uniting within the body, come to form the complicated system of air tubes and air sacs of the adult insect (see page 291).

The spiral lines of the tracheal walls, called *tænidia* (Fig. 82 B, *Tæ*) are thread-like thickenings of the intima projecting as fine ridges into the lumen of the tube. They wind around the latter from right to left, followed inward from the spiracles, and most of them end after making from one to several revolutions. The end of a broken trachea usually unravels in a narrow ribbon of several parallel tænidia. The tænidial thickenings of the intima give a rigidity to the tracheal walls that keeps the tubes open and allows free circulation of the contained gases. The air sacs, which may be regarded as enlarged parts of the tracheæ,

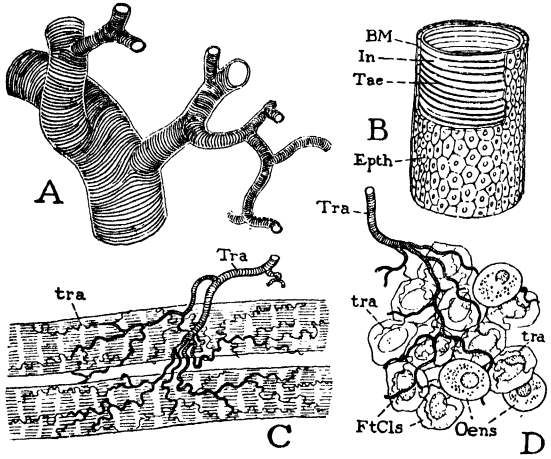



FIG. 82.—Structure and terminal branches of tracheæ.
A, piece of trachea, showing ribbed appearance and branching. B, structure of tracheal tube, showing epithelium (*Epth*) of flat cells, outer covering of basement membrane (*BM*), and inner cuticular lining with spiral thickenings or tænidia (*Tæ*). C, tracheal branches ending in tracheoles (*tra*) on muscle fibers. D, tracheation of piece of fat body, showing tracheoles on fat cells (*FtCls*), but not on œnocytes (*Oens*).

have, however, no tænidia in their walls; they collapse at once when punctured and become almost invisible when empty of air. Their walls are roughened in most places by numerous corrugations or irregular thickenings of the intima, but similar thickenings occur also in the walls of the tracheæ between the tænidial ridges.

Most of the tracheæ in the body of the bee are more like air sacs in their structure than like normal tracheæ, since most of them lack well-developed tænidia. They are consequently very distensible and when filled with air show as a multitude of silvery, opaque vessels, but when empty they collapse and their delicate

walls are very difficult to follow in dissections. The smaller branches are so numerous in the thorax and the legs that they appear to form everywhere a network of glistening air cavities amongst the muscle fibers and other tissues. It is only the large trunks from the first spiracles (Figs. 80, 81, *Tra*) and their branches in the thorax and the head and some of the abdominal trunks that have the ordinary tracheal character and appearance.

**The Tracheoles.**—The inner ends of the smallest tracheal branches end in minute tubules called *tracheoles* (Fig. 82 D, *tra*). The tracheoles differ from normal tracheæ in lacking the spiral tænidia and in being unbranched. They issue often in bunches

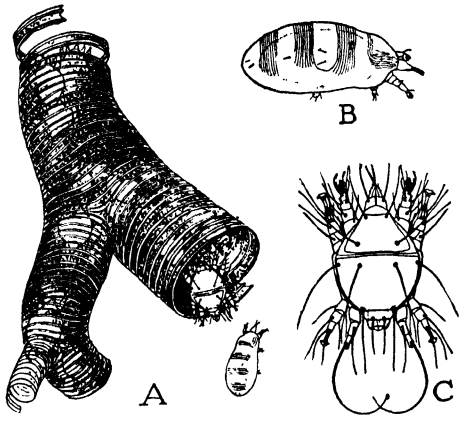



FIG. 82 A.—Isle of Wight disease mites and infested trachea.
A, piece of prothoracic trachea containing mites. B, immature mite. C, adult mite.

from the ends of the terminal tracheæ and run in winding, serpentine courses over the surfaces of all the internal organs, penetrating between muscle fibers (C) and amongst the cells of other tissues (D), but probably never entering the fibers or cells themselves. The tracheoles are closed at their free ends and it is by diffusion through their delicate walls that the respiratory gases are exchanged between the air and the blood as already explained.

**The Function of the Air Sacs.**—The body of the bee, on account of its numerous large and small air sacs, is probably more abundantly aerated than is that of any other insect. The reason for the air sacs of insects is a subject concerning which there has been considerable difference of opinion. In general, insects that are active fliers have more or larger air sacs than those that spend

most of their time on the ground or fly but little. For this reason some entomologists believe that the air sacs give a buoyancy to flying insects by lessening their weight without a corresponding decrease in size, just as a bag, inflated with air, is more buoyant in air than is the same bag filled with water or crumpled into a small mass. On the other hand, others believe that the air sacs are storage chambers for air to be used while the insect is on the wing, arguing that breathing would be difficult during rapid flight. A bee, however, though it "holds its breath" when forcibly submerged in water and keeps its air sacs distended with air, shows immediate signs of distress and becomes rigid and apparently suffocated in a very few minutes. It will revive after a long submergence, but it has been dormant in the meantime. This would indicate that the air held in the air sacs cannot long serve the respiratory needs, and that the active bee must have a constant renewal of air through its spiracles.

### 4. THE BREATHING MOTIONS AND MUSCLES

Most of the smaller insects do not make any respiratory movements, that is, they do not inhale or exhale by expansion and contraction of a part of the body. With them gases are exchanged through the spiracles and tracheæ by passive diffusion, as has been demonstrated by Krogh (1920). But many of the Orthoptera and Hymenoptera at times keep up a pulsating motion of the abdomen very suggestive of respiration. Such breathing movements of the grasshoppers and katydids consist of a strong elevation and depression of the ventral wall of the abdomen.

**The Respiratory Movements of the Bee.**—With the honeybee the respiratory motion is principally a rapid lengthening and shortening of the abdomen, accompanied by only a slight vertical expansion and contraction. The respiratory movements of a worker bee are most pronounced just after any special activity, but when the bee is resting quietly the movements usually cease to be perceptible. The expansion and contraction of the abdomen is made possible by the thin, infolded membranes that unite the overlapping edges of the segments and their dorsal and ventral plates, allowing the segments to be drawn out or pulled together like the parts of a telescope, and the tergum and sternum of each to be more separated or brought closer together. These movements are produced by the muscles of the abdomen, which are therefore often called the "respiratory" muscles, though they are

simply the ordinary abdominal muscles that produce any of the ordinary motions of the abdomen of any insect as well as the respiratory movements of those that "breathe."

**The Respiratory Muscles.**—The abdominal muscles of the bee are stretched between the edges of the plates of the body wall. The general plan of their arrangement is the same in each segment and is shown on the left half of two consecutive segments by Fig. 83. The plates on the left side of this figure (*IIIT* and *IVT*) are the left halves of the back or tergal plates of the third and fourth segments, seen from the inside. Those overlapping internally

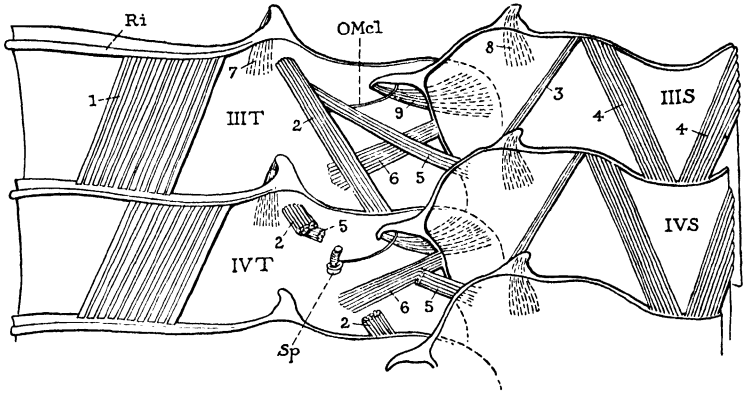



FIG. 83.—Abdominal muscles of respiration in left side of two consecutive segments.

*IIIS*, *IVS*, median parts and left halves of third and fourth abdominal sterna, dorsal surface; *IIIT*, *IVT*, left halves of corresponding terga; *1*, dorsal intertergal retractor muscle; *2*, lateral intertergal retractor; *3*, lateral intersternal retractor; *4*, median intersternal retractor; *5*, inner tergo-sternal retractor; *6*, outer tergo-sternal retractor; *7*, intertergal extensor; *8*, intersternal extensor; *9*, tergo-sternal extensor; *OMcl*, opener muscle of spiracle; *Ri*, submarginal ridge of tergum; *Sp*, spiracle.

on the right (*IIIS* and *IVS*) are the corresponding lower or sternal plates cut off a little to the right of the middle. There are nine sets of muscles in each segment indicated by the numbers *1* to *9*. First there is a wide band of oblique muscles (*1*) on each side of the back part of the tergal plate, extending forward and outward from the front margin of one to a ridge near the front margin of the plate overlapping in front. Next there is a slenderer band of oblique tergal muscles (*2*) toward the edge of the lateral part of each back plate, sloping in the opposite direction from the first set, going from the front edge of one plate to near the front edge of the preceding plate. The contraction of these

two muscles pulls the rear tergal plate forward beneath the other. The lower or sternal plates (*IIIS* and *IVS*) are brought together likewise by two sets of oblique muscles (*3* and *4*) going from the front margin of one to the front margin of the plate in front, and converging to form an inverted V on each half of each plate. These four sets of muscles produce the lengthwise contraction of the abdomen.

On each side of each abdominal segment there are two oblique muscles (Fig. 83, *5* and *6*) that cross each other and extend from the upper part of the side of each back plate (*T*) to the overlapped edge of the ventral plate (*S*). The contraction of these sets of muscles pulls the two plates of each segment together and

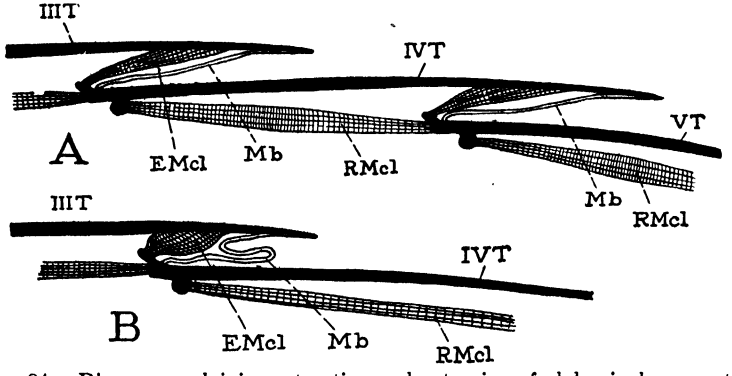



FIG. 84.—Diagram explaining retraction and extension of abdominal segments. A, abdominal terga retracted by contraction of intertergal retractor muscles (*RMcl*), intersegmental membranes (*Mb*) extended. B, abdominal terga extended by contraction of intertergal extensor muscles (*EMcl*), intersegmental membrane (*Mb*) folded.

hence decreases the vertical diameter of the abdomen. The six sets of muscles thus far described are *retractor muscles* and therefore the ones that produce the expiratory movement in breathing.

The expansion of the abdomen, the inspiratory movement of respiration, is produced by three extensor muscles (*7*, *8*, *9*) in each half of each segment. The first of these (*7*) is inserted on the small apodemal arm projecting from the front margin of the back plate (*T*) and goes rearward, in the fold between the segments, to the rear part of the overlapping plate in front. The second (*8*) is similarly attached between the overlapping edges of the ventral plates (*S*). The contraction of this set of muscles (*7* and *8*) separates the plates to which they are attached and lengthens the abdomen. The third extensor muscle (*9*) on each

side is attached above to the end of the long lateral apodemal arm of the sternum (*S*) and goes downward to the overlapping edge of the corresponding tergum (*T*). Its contraction separates these two plates and increases the vertical diameter of the abdomen.

The mechanism of the shortening and lengthening of the abdomen is shown more clearly by the diagrammatic longitudinal section through the back plates given in Fig. 84. The consecutive terga (*IIIT*, *IVT*, *VT*) are seen to be connected by infolded intersegmental membranes (*Mb*). At A the retractor muscles (*RMcl*) are contracted and the plates thereby pulled together as far as the membrane will allow. At B the extensor muscles (*EMcl*) are contracted with the result that the plates (*IIIT* and *IVT*) are pushed apart and the connecting membrane (*Mb*) thrown into a fold. By the alternate action of these two sets of muscles in all the segments at once the abdomen is shortened and lengthened, while, with the simultaneous action of the vertical and oblique muscles along the sides of the segments (Fig. 83, *5*, *6*, *9*), there results a general contraction or expansion of the abdomen in both lengthwise and vertical directions.

The abdominal muscles of the bee were long ago described by Carlet (1884). But Carlet did not mention the extensor muscles of the back plates (Fig. 83, *7*), and he stated that the external oblique muscles of the sides (*6*) were attached to the front margins of the back plates following, an error already noted and corrected by Betts (1922).

## CHAPTER IX

## THE FAT BODY AND THE ŒNOCYTES

The spaces amongst the larger organs in the body cavity of most insects are largely filled with masses of a soft cellular tissue which usually spreads out also in flat sheets against the body walls. The entire mass of this tissue has long been known as the *fat body* because its cells contain globules of an oily liquid that can be demonstrated to be of a fatty nature. The cells, however, perform other important functions besides that of forming and holding fat. In the larval stage of some insects they store up glycogen which is consumed during metamorphosis, and in the pupal stage they elaborate proteid substances which are discharged into the blood to be used as food for the growing adult. Berlese, therefore, called these cells *trophocytes*, a name more suggestive of their various functions than that of "fat cells." But the term "fat body" is still generally retained, though we must now recognize that the fat tissue is an important organ of various activities in the physiology of the insect. In the Hymenoptera some of its cells contain small crystals of urates and are distinguished as the *excretory cells*. In this Order also certain cells known as the *œnocytes* are imbedded amongst the fat cells and appear to be an integral part of the fat body, though they are said to have an entirely separate origin.

**Embryonic Origin of Fat Cells and Œnocytes.**—The fat cells are formed in the embryo from the lateral plates of the mesoderm (page 294). In most insects all the fat tissue is produced from the outer or somatic mesodermal layers, but in the bee and other Hymenoptera, according to Nelson (1915), only that part of the fat body which lies in the pericardial cavity is derived from the somatic layers, the rest being formed from the inner or visceral layers. The excretory cells of the fat body in the bee are probably only specialized fat cells. The œnocytes, however, are derived from the ectoderm and are but secondarily associated with the fat cells in the Hymenoptera. Nelson (1915) says: "The œnocytes are produced by immigration of cells from

localized areas of the lateral ectoderm. There are eight pairs of these situated on the first eight abdominal segments, in line with the openings of the tracheal invaginations." In most other insects the œnocytes commonly remain at all stages in segmental groups along the sides of the abdomen.

**Fat Cells and Œnocytes of Young Larva.**—In the larva of the honeybee the fat body forms a loose mass of lobes and branching strands occupying most of the space in the body cavity between the alimentary canal and the body wall. The white color of the larva is due to the density and whiteness of the fat tissue pressed against the transparent skin. In a very young larva the fat cells, as described by Nelson (1924), are fewer in number than in later stages and differ but little from the cells of the embryonic mesoderm from which they are derived. But at the end of two days the cells have multiplied and have so increased in size that the fat body now has nearly attained its final relative bulk.

At this stage the larval fat body consists of many small, closely pressed, polygonal fat cells (Fig. 85 A, *FtCls*) with the large œnocyte cells (*Oen*), each the size of five or six fat cells, crowded amongst them. The fat cells contain small liquid globules of various sizes in their cytoplasm which become black when treated with osmic acid, or a dark brownish red when stained with Soudan III, either test showing that they are drops of fatty oil. The cells, then, are already performing their function of producing and storing fat.

**Fat Cells and Œnocytes of Old Larva.**—In the half-grown or full-grown larva the lobes and branches of the fat body have such definite shapes and such regular contours that their component cells appear to be retained in an enveloping sheath, though no such membrane can be distinguished. In fresh specimens the boundaries of the cells are difficult to see, but staining brings out the cell walls and shows also that the finely granular cytoplasm in many or most of the cells is vacuolated with pale yellowish oil globules. The nuclei are regularly oval in those cells that contain little fat, but in the others they are distorted into various shapes apparently by the oil globules pressing on them from all sides. Treatment with Soudan III turns these globules red, when they become the most conspicuous elements in the cell (Fig. 85 B, *FtCl*). Now, however, certain large cells of a natural yellowish color stand out in strong contrast to the others by their

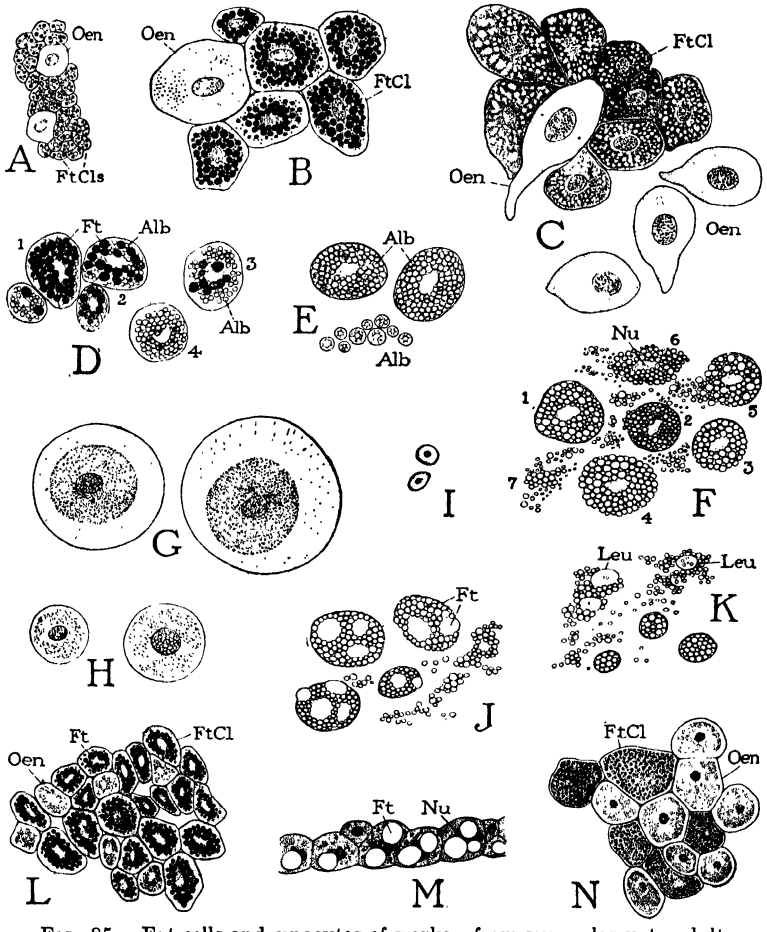



FIG. 85.—Fat cells and œnocytes of worker, from young larva to adult.

A, piece of fat body of very young larva stained with Soudan III; œnocytes (*Oen*) uncolored, fat cells (*FtCls*) with small globules of fat.

B, fat body of old larva; fat cells filled with oily globules.

C, fat cells and œnocytes of old larva, stained with Gram's iodine solution, showing presence of glycogen in cytoplasm of fat cells.

D, fat cells of early propupal stage, showing accumulation of albuminoid bodies (*Alb*) in cytoplasm.

E, fat cells of young pupa (after shedding of larval skin) filled with albuminoid bodies (*Alb*).

F, fat cells of later pupal period, showing cells in all stages of disintegration; *5*, *6*, *7*, liberating contents into blood.

G, œnocytes of young pupa, now floating free in blood.

H, œnocytes of later pupal period.

I leucocytes.

J, fat cells of pupa nearly mature, in which albuminoid granules have disappeared and tissue of cells is reduced to masses of oil globules.

K, remains of larval fat cells persisting in young imago.

entire lack of fatty inclusions. These are the œnocytes (*Oen*). Also there are other smaller cells that contain no fat but which have a varying number of small, spherical, crystalline granules in their cytoplasm. These are the excretory cells. The inclusions are always of the same shape and have the form characteristic of leucin crystals.

Both fat cells and œnocytes in the mature larva (B, C) have increased enormously in size since the earlier stages (A). They are all pressed closely together in compact masses and their shapes are mostly polygonal. The œnocytes, however, have not increased in the same proportion as the fat cells and some of them are now smaller than the largest fat cells. Many have the same forms as the fat cells (B) but others, especially those near the edges of the fat masses, are oval, and pointed at one end (C), while a few have long necks thrust out between the fat cells.

**Storage of Fat in the Fat Body.**—The oil globules in the fat cells (B) are usually largest and most densely packed near the nucleus, leaving a zone of clear protoplasm at the periphery of the cell. When pieces of the fat body that have been stained with Soudan III are crushed and treated with ether, the exuding oil droplets can be seen under the microscope first to decrease in size and then suddenly to explode and disappear. The staining tests with osmic acid and Soudan III and the solubility test with ether leave no doubt that the oily globules in the fat cells are fats that have been produced in increasing amount within the cells during the growth of the larva. Nearly all investigators now agree on this point, though a few have disputed it. Moreover, the analyses of Straus (1911) on the composition of the honeybee larva show that the worker larva accumulates a large quantity of fat in its body during its growth, the amount increasing from .04 milligram on the second day to 6 milligrams at the end of the larval stage, a fat content which is more than 17 per cent of the dry weight (34.6 milligrams) of the body of the mature larva. In the drone larva, according to Straus, fat does not appear until the third day and then continues to increase

L, fat body of foraging worker in spring, stained with Soudan III; œnocytes small and numerous, fat cells filled with oil globules but containing no albuminoid bodies or glycogen.

M, section of dorsal fat body of young adult worker, showing large vacuoles of fatty oil (*Ft*).

N, fat body of over-wintering bee in early April; œnocytes compact and densely granular.

till the end of the sixth day, or for a short period after the capping of the cell.

**Storage of Glycogen in the Fat Body.**—A second important function of the fat cells of the bee larva is the storage of glycogen, a function which most investigators have overlooked. If a mature larva is cut open and placed in iodine solution, the exposed fat tissue at once turns dark, blackish to the naked eye, and after prolonged washing in alcohol the fat cells alone retain a rich, reddish-brown color (Fig. 85 C). This is the usual microchemical test for the presence of glycogen. Larvæ of successively younger stages show less and less iodine coloration of the fat cells. The iodine stain shows in the cytoplasm, the fat globules remaining as clear spaces (C) in the position of the dark globules of specimens stained with osmic acid or Soudan III (B). The analyses of bee larvæ made by Straus (1911) give results for glycogen which confirm the evidence from staining reactions. Straus shows that there is a rapid accumulation of glycogen in the body of the worker larva from the second day, when the glycogen content is only .08 milligram, to the sixth day, when glycogen has increased to 11.5 milligrams, or over 33 per cent of the dry weight of the body. In the drone larva glycogen does not appear until the beginning of the fourth day, after which it increases in amount to the end of the sixth day, and then shows a decrease on the seventh day, when the drone brood cell is capped.

The usual sources of glycogen in the bodies of animals are the carbohydrates of their food. Straus shows that the accumulation of glycogen in the worker larva is small until the beginning of the third day, after which it rapidly increases to the end of the fourth day, and then continues at a lesser rate until the peak is reached at the beginning of pupation. Both fat and glycogen are rapidly consumed during the pupal period. Glycogen never reappears in any appreciable amount in the bee, but the fat cells again accumulate much fat in the adult stage. According to Straus no other free-living animal is known to store up such a large amount of glycogen as does the honeybee larva. The subject of glycogen storage in insects in general has been but little investigated, but some other species are known to accumulate it during the larval period. Bataillon and Couvreur (1892) have shown that glycogen is present in the silkworm, and state that the amount is doubled after the spinning of the cocoon, reaching its maximum just after the beginning of pupation.

In its glycogen-storing capacity the fat body of the insect larva, in those species that store glycogen, may be likened to the liver of vertebrate animals.

**Fat Cells and Œnocytes of Prepupal Larva.**—The next period in the history of the fat tissue is that of the final stage of the larva when the latter is sealed in the brood cell of the comb. The larva has now eaten the last remnants of its food and has enclosed itself in a parchment-like cocoon of material spun from the silk glands. Already the intestine (Fig. 65 B, *Int*) has united with the stomach (*Vent*) and the latter has been emptied of its accumulated contents. Most of the fat cells are now detached from one another and float free in the blood, as do also the liberated œnocytes. The fat cells, released from the pressure of the mass, become more regular in shape and assume oval, elliptical, or spherical forms. Their cytoplasm is still filled with oily globules, but it begins to show also other smaller granular inclusions which are not colored by fat stains or by iodine.

**Fat Cells of Propupa.**—During the first stage of the pupa, when the insect may be designated a *propupa*, but when it is still contained in the larval skin (Fig. 105 E), the fat cells are all floating free in the blood, which to the naked eye now appears to be a thick, granular, creamy liquid that fills the body cavity. Some of the fat cells are still exactly like those of the last larval, prepupal, stage. In such, the cytoplasm is crammed with large and small oil globules which stain intensely with Soudan III, but amongst these globules are many of the small, clear granules that remain entirely uncolored (Fig. 85 D, *Alb*). Others have only a few oil globules which are mostly stained less darkly (D, *2*, *3*, *4*), but in these the colorless granules are most numerous or at least most conspicuous, and some cells are filled entirely with them. If the cells are crushed the granules scatter in the surrounding liquid or adhere in small masses but they do not float about so freely as the liberated oil droplets.

**Storage of Albuminoids in the Fat Body.**—Berlese (1902) first explained the nature of these non-fatty inclusions that appear in the fat cells at the beginning of pupation. Since they color readily in eosin and other such stains, he regarded them as accumulations of albuminoids elaborated in the fat cells to be later given out into the blood as food for the newly forming imaginal tissues and organs. That this is the true nature and general history of these bodies is now confirmed and well estab-

lished for many insects by subsequent investigators. The proteid composition of the grains may be convincingly shown by the common test with Millon's fluid as follows: Put a large drop of the pupa blood heavily charged with floating fat cells on a microscope slide; add a drop or two of Millon's solution and gently heat the slide over an alcohol flame. Almost immediately a strong, pink color appears in the mixture. Examination under the microscope will show that the oil globules are unaffected, that the cytoplasm of the cells has a slightly pinkish tint, but that the enclosed granular bodies have become decidedly red in color. The same test applied to the fat tissue of a half-grown larva gives only the general tinting of the cell protoplasm, the color being deepest in the denser cytoplasm about the nucleus and in the protoplasm of the nucleus itself. No albuminoid inclusions are differentiated at this stage.

**Fat Cells and Œnocytes of Pupa.**—During the early part of the true pupal period, just after the larval skin is shed (Fig. 105 I) but before the eyes have begun to darken, many of the fat cells become completely filled with the albuminoid granules (Fig. 85 E). Others again contain oil droplets of various sizes which appear to be the beginning of a second accumulation of fat in the cytoplasm. All of the fat cells at this stage are very fragile and are easily ruptured by the pressure of a cover glass, their contained globules and granules spreading through the surrounding liquid; and even in a drop of fresh blood, taken directly from a pupa and examined without a cover glass, the plasma is seen to be full of free albuminoid bodies and droplets of oil. In such specimens, though many of the fat cells are intact (F, *1*) others lack a part (*2*, *3*, *5*) or all of the cell wall (*4*). Some of the latter (*3*, *4*) preserve the original cell outlines, but others (*2*, *6*) have their contents streaming from the ruptures. Still others (*6*) appear to be cells in a state of natural dissolution, being formless masses of grains and oil globules held in a thin matrix of cytoplasm surrounding a nucleus. Finally, there are everywhere in the blood large and small masses or loose aggregations of granules and oil droplets (*7*), apparently the remnants of fat cells in the last stages of disintegration.

The œnocytes (Fig. 85 G) at this stage are enormous spherical cells floating free in the blood, each consisting of a dense granular, central body containing the oval nucleus, and of a wide, peripheral zone of perfectly clear substance.

By the time the pupa has reached the age when the eyes have turned brown, the blood is still charged with the larval fat cells and their disintegrating fragments. But now the majority of the entire cells have ragged outlines, while the blood plasma is filled with oil droplets and albuminoid granules, some of the latter adhering in small masses but most of them floating free. The progress of disintegration of the larval fat cells has clearly advanced since the earlier pupal stage when the eyes of the pupa were yet pale. It is now to be noted also that the oil droplets have become more numerous and that the albuminoid granules have decreased in numbers.

The œnocytes (H) have become much smaller than in the last stage (G) and have lost their wide, clear, marginal zones. Their nuclei are coarsely granular as in the larval stages, but their cytoplasm also is now densely granular except for a narrow, clearer layer just within the cell wall.

The next step in the maturing of the pupa is marked externally by the brownish tint which begins to color the thorax. At this period the fat cells in the blood have greatly decreased in numbers, and most of those that remain are in various stages of disintegration. The few that are still intact in the fresh blood are so delicate that they will not support the weight of a cover glass without breaking and dispersing their contents. They are now filled almost entirely with oil globules, though in some a few albuminoid granules are still present. The free bodies in the blood, however, are nearly all oil droplets as is shown by staining with Soudan III.

The œnocytes are still more reduced in size, but are numerous, mostly of oval forms, and have a solid opaque appearance.

The final phase of the development of the pupa is indicated by a strong brown coloring of the thorax and a tinting of the abdomen. The fat cells in the blood are now less abundant than ever before, and still fewer of them retain their membranes. The albuminoid granules are entirely absent, evidently they have been dissolved in the blood to be consumed by the growing tissues. Staining with Soudan III, however, shows large quantities of fat present, both as free oil droplets of various sizes and as globules in the persisting cells and cytoplasmic masses. At the end of this period, just before the shedding of the pupal skin, the remaining larval fat cells in the pupal blood are little more than masses of fat globules. Their nuclei are of indefinite outline, the walls having disappeared, and their cytoplasmic parts are filled with

small droplets and distended with large vacuoles of oily liquid, some of the latter bulging at the surface (J). So fragile are the cells at this stage that they cannot be studied under a cover glass, and a drop of Soudan III on fresh material breaks the cells up immediately and scatters their contents. But since all the liberated globules are strongly colored by the stain, it is evident that little is left of the fat cells at this stage but these fatty oil droplets, which have already begun to merge into large globules that will soon burst the remnants of the cell wall and terminate the existence of the larval fat cells.

**Fat Cells and Œnocytes of Newly Formed Imago.**—The young worker imago that has shed the pupal skin, but which is not yet liberated from the brood cell of the comb, has an ample amount of blood in its abdomen; but the plasma is a thin, clear liquid much different in appearance from the creamy fluid that filled the body cavity during the pupal stage. Yet it still contains a few larval fat cells and free droplets of oil. But the cells are all very small (K) and are nothing but masses of oily globules retained in a delicate membrane. Some are distorted with large vacuoles as at the end of the pupal stage. Leucocytes (K, *Leu*) are sometimes to be seen in the masses of free oil droplets, and some of them appear to contain a few globules. Other than this the writer observed no indication of phagocytosis (see page 179) in connection with the destruction of the larval fat cells, and even here the evidence is too uncertain to be of any value. The blood of the fully matured adult is a clear, brownish liquid containing the leucocytes but no detritus or any other matter except that normally dissolved in it.

An occasional small œnocyte is to be seen floating in the blood of the new imago, but the imaginal fat body is now already formed, and, as in the larva, most of the adult œnocytes are imbedded amongst its cells.

**General Discussion of Functions of the Fat Body.**—The foregoing series of observations clearly suggests that the majority of the fat cells of the bee larva gradually disintegrate in the later pupal stages and liberate their contents directly into the blood plasma, where they are dissolved to furnish nourishment for the growing tissues of the imago. The last of the free cells persist into the early part of the adult stage, but here they are soon lost.

This sketch of the history of the fat cells of the bee during metamorphosis, based on the writer's personal study, is in every way parallel with the history of the fat tissue of the apple maggot (Snodgrass, 1924), and both are in entire accord with recent work by Bishop (1922, 1923) on the fat cells of the bee. But there is less uniformity in the conclusions of earlier writers, and it seems certain that some of their opinions must now be discarded. The most important papers on the fat tissue of the honeybee and other Hymenoptera are those of Koschevnikov (1900), Terre (1900), Anglas (1901), Berlese (1902), Pérez (1903), Koehler (1921), and Bishop (1922, 1923). But studies made on other insects have contributed much to our general knowledge of the physiology of the fat cells. Especially important is Berlese's paper (1901) on the adipose tissue of the blowfly, in which he first showed that the fat cells act as elaborators of proteid or albuminoid bodies during the first stages of metamorphosis. The presence of the albuminoid granules in the fat cells, however, was perhaps first noted by Van Rees (1889) who gave a detailed account of what he took to be the destruction of the fat cells of the blowfly by phagocytes. But Berlese discredits his interpretations and suggests that what Van Rees thought were phagocytes in the cells are the albuminoid bodies in process of elaboration. Koschevnikov, Terre, Anglas, and Berlese all agree that phagocytes do not attack the fat tissue during metamorphosis. Koschevnikov (1900) described the proteid granules in the fat cells of the bee, though he did not recognize their nature. He noted also the dissolution of the cell membranes and the scattering of the cell contents in the blood as described also by Terre (1900) and by Anglas (1901). Berlese (1902), however, denied that the fat cells of the bee disintegrate by the loss of their membrane, claiming that the materials elaborated in the cells enter the blood by osmosis, while the cells themselves persist to form the fat tissue of the adult. Only in the higher Diptera, he insists, are the larval fat cells destroyed. Pérez (1903) in describing the fat tissues of the ant, likewise discredits the idea that their cells normally disintegrate. He believes that the appearance of a natural dissolution is due to the reagents used in histological work or to rough handling, that most of the fat cells are destroyed by phagocytes, and that the others persist to form the fat body of the adult after their contents have been dissolved out by osmosis. Recent investigations, however,

leave little doubt that the disintegration of the cells is a natural process.

All investigators now agree that the fat body of the insects with complete metamorphosis, at the end of the larval stage, is a veritable storehouse of food materials held in reserve for the reconstructive processes and the formation of the imago. The substances known to be contained in the fat cells prior to metamorphosis are fat, glycogen and albuminoids. It will next be of interest to follow more closely the history of these several substances.

*Analyses of Bee Larvæ.*—The analyses made by Straus (1911) show that at the end of the active life of the larva, that is, when the larva is sealed in the brood cell by the worker bees, its body contains over 50 per cent, by dry weight, of reserve materials. Though the external change to the pupa does not take place for several days after the capping of the brood cell, the processes of histolysis begin at once, and, therefore, the entire period of 12 days spent by the worker in the closed cell may be regarded as one physiological stage, that of the metamorphosis. By further analyses Straus shows that both the fat and the glycogen contents decrease rapidly from the sixth day to the end of the pupal stage, when but little of either remains. The larva attains its maximum weight of 175.6 milligrams on the first day after the closing of its cell, but on the second day a decrease begins which continues throughout the transformation period to a minimum of 117 milligrams just before the emergence of the adult, after which the weight increases again to 120 milligrams. The glycogen content shows a steady decline from the peak, 9 milligrams, on the sixth to almost nothing on the tenth day, followed by a slight fluctuation ending with .60 milligram at the time of the emergence of the adult. Fat likewise shows a decline from 6 milligrams on the sixth day to .20 milligram on the tenth day, with an increase to 1.90 milligrams at the end of the twelfth day. Tests of the fat cells with iodine also indicate a rapid decrease of glycogen throughout the transformation period, the amount present at the end being too small to be detected by staining methods. Tests for fat, however, with Soudan III, as has already been shown, indicate a great increase in the oily contents of the fat cells toward the end of the pupal period; but the disappearance of such a large number of the cells themselves and the relatively small size of the fat body of the adult bee probably

account for the diminution of the total fat content as obtained by Straus in his analyses of the entire body.

*Fat in the Fat Body.*—The utilization of fat by the tissues of vertebrate animals depends on the presence of a fat-splitting enzyme, or lipase, and physiologists tell us that the conversion of glycogen into glucose in the vertebrate depends on the presence of the pancreatic secretion. What takes the place of these agents in insects we do not know, but suspicion falls at once on the œnocytes as the most likely source of enzymes for the fat cell products on account of the close association of the two sets of cells. The œnocytes have been regarded as ductless glands and as excretory organs, but with little evidence to support either view. The only chemical analyses of their composition were made by Glaser (1912) on those of the leopard moth caterpillar. But Glaser reports negative results in tests for lipase, thus disposing of the idea that the œnocytes furnish the fat-splitting enzymes, but he says the œnocytes react positively to tests for oxidase. From this he concludes that the œnocytes supply the oxidizing enzymes in insects, which leaves us still in ignorance of the source of the enzymes that render the stored fat and glycogen available for consumption.

*Glycogen in the Fat Body.*—Glycogen in the animal body is merely a storage form of carbohydrates and its source in the bee larva is undoubtedly the honey sugars, mostly dextrose and levulose, of the larval diet. Sturtevant (1924) shows by chemical analysis that sugar disappears entirely in the pupa of the bee two days after the capping of the cell, presumably being all converted by this time into glycogen. Some writers have attempted to connect the formation of glycogen with the disappearance of the fat, but there seems to be no evidence to support this idea. Before glycogen can be used by the animal tissues it must be reconverted into glucose, and there is evidence that this change takes place in insects. Bataillon and Couvreur (1892) and Bataillon (1893) show that in the silkworm the amount of glycogen reaches its maximum on the first day following pupation, after which it decreases and disappears at the end of the pupal period. Sugar, on the other hand, increases during metamorphosis and reaches its maximum three or four days before the emergence of the adult. This, then, suggests that glucose is formed at the expense of the glycogen, at least in the silkworm.

*Albuminoids in the Fat Body.*—The activity of the fat cells in the larvæ of higher insects as elaborators of albuminoid substances, first described in the blowfly and other insects by Berlese (1901, 1902), has been amply substantiated since by the work of many other writers. Berlese believed that the albuminoid bodies were formed in the cytoplasm of the fat cells by enzymes given out from the nuclei acting on substances absorbed into the cytoplasm from the nutritive materials in the blood. Nakahara (1917), however, described small bodies as given off by the nuclei of the fat cells in the larva of the cabbage butterfly, and believed that these bodies became the albuminoid granules found in the cytoplasm. Bishop (1922, 1923) and others have since demonstrated the presence of granules in the nuclei of the fat cells of the bee which pass out into the cytoplasm, where each becomes the basis of an albuminoid globule. According to Bishop the identity of the granules in the nucleus with those in the cytoplasm is best shown by staining with Heidenhain's hematoxylin mordanted with iron-alum. At first the granules stain intensely black, but as they increase in size the centers become clear and finally the entire globule looses its affinity for this stain. In later stages, on the other hand, the bodies take ordinary cytoplasmic dyes, indicating that their composition has changed during their development from nuclear to cytoplasmic substances. Other nuclear stains affect the granules less strongly and show that an abrupt change takes place in them as they cross the nuclear border and come in contact with the cytoplasm.

The nature of these nuclear extrusions is not definitely known, but Bishop suggests three possible explanations: they may be nuclear waste, bodies carrying enzymes, or particles of elaborated nutriment. To the second he gives most weight. He says that the behavior of the nuclear substance suggests "that it is an agent rather than a reacting substratum," and that "though the bulk of the albuminoid globules is derived from cytoplasmic material, these bodies are formed only under the influence of nuclear granules, one to each globule." Finally, he says: "The nuclear extrusions, then, may carry an enzyme for modifying the cytoplasm, which is only activated when it comes in contact with the cytoplasm, or they may contain an activator of cytoplasmic enzymes already present, which in turn occasions the modification of the material in their vicinity." The nuclear granules, according to Bishop, enter the cytoplasm during the early part of meta-

morphosis, at which time, he says, the nuclear membranes of the fat cells of the bee larva disappear. This he would explain by assuming "that the nuclear membrane may be only a phase border between two colloid complexes of different consistency; that the nucleus and cytoplasm approximate a common consistency due to altered physiological activities accompanying metamorphosis, allowing the nuclear granules to disperse freely throughout the cell." Later the nuclear membranes are reformed. The final release of the albuminoid globules by the dissolution of the fat cell walls and the disintegration of the cells themselves, and their disappearance by dissolving in the blood has already been described.

**The Fat Body of the Adult.**—The origin of the fat body of the adult is a subject on which there has been considerable difference of opinion. The writer has not studied the formative stages of the new adipose tissue of the bee, but its structure in the mature pupa would suggest that it consists of loose masses of persisting larval cells that have spread out in thin layers against the body wall of the abdomen. At this stage the cells are delicate and fragile like those floating free in the blood, and they do not adhere to one another in definite sheets as they do later in the adult. Anglas (1901) and Pérez (1903) likewise describe the adult fat body in wasps and ants as formed from larval fat cells that are not destroyed. Berlese (1902) claimed that all the larval fat cells go over into the fat tissue of the adult in the bee, since he did not believe the disintegration of any of the larval cells to be a normal process. Koschevnikov (1900) described the new tissue as formed from the nuclei of the larval fat cells which become surrounded by masses of the granules liberated from the disintegrating cells. He probably saw fragments of these cells themselves, or examined the imaginal fat cells at a stage when they were too fragile to withstand the disruptive action of fixing reagents.

In the newly formed worker bee, not yet escaped from the brood cell of the comb, the fat cells are already densely filled with fatty oil globules staining intensely in Soudan III. The droplets are readily extracted and dissolved in ether. The fat body of the mature worker consists mostly of thin layers of cells spread against the body wall of the abdomen, especially in the dorsal and ventral blood sinuses. The dorsal sheet forms a protective padding between the heart and the body wall of the back, and

thicker masses on each side of the heart (Figs. 72, 73 A, *FtCls*). This part of the fat tissue is often distinguished as the *pericardial fat body*. The ventral sheet of fat tissue is particularly developed over the wax glands. A less well-defined band lies along each side of the abdomen. As in the larva, the fat body of the adult consists of fat cells proper and of excretory cells, and includes the œnocytes (Fig. 85 L, *Oen*). All the cells are much smaller than those of the mature larva (B, C), and the œnocytes are now (L) smaller than the fat cells and in some specimens more numerous, especially in the ventral tissue. But the two sets of cells are sharply differentiated in Soudan III, the fat cells being strongly stained on account of their abundant fat contents, while the œnocytes retain the bright yellow color characteristic of them when seen by transmitted light under the microscope.

The physiology of the fat tissue of the adult bee and the changes that the fat cells undergo during the life of the adult have been less studied than the corresponding phases in the larva. According to the analyses of Straus (1911) the amount of fat in the adult bee increases slightly during its life from 1.10 milligrams to 1.80 milligrams, while glycogen continues to decrease from 1.50 milligrams to .90 milligram. The relatively small amount of fat in a young imago, however, as compared with that in the larva, is due to the small size of the adult fat body and not to any lack of fat in its cells. The fat becomes so abundant in the adult tissue of young summer bees that the cells become swollen with large globules which press against the nucleus from all sides and distort it into grotesque shapes, sometimes almost dividing it between them (Fig. 85 M).

Koehler (1921), in a paper on the changes of the fat cells during the life of the adult bee, says that the fat cells of wintering bees in January contain a large amount of albuminoid material in the form of large granules, but that by spring the albuminoids have been mostly used up, being present in only a small percentage of the bees. During the summer, she says, the fat cells contain no albuminoids, the latter appear at the end of September in old bees that have ceased to act as nurses for the brood. The inference from this, as she points out, is that albuminoids are elaborated into the brood food as fast as they are produced in the nursing bees, but that after this they begin to accumulate in the fat cells as food reserves for winter. The fat cells of bees examined in January by the writer contain but a very small amount of fat,

as tests with Soudan III easily show, but they are densely filled with small granules of varying sizes having the appearance and staining properties of the albuminoid granules of the late larval and early pupal fat cells. This, therefore, seems to confirm Koehler's statements. In the spring the fat cells of a worker that has spent the winter in the hive are filled with dark masses of granules (Fig. 85 N). At this time both the œnocytes and the fat cells have increased in size as compared with those of a young worker (L). The œnocytes have become very compact in appearance, having well-defined polygonal or elliptical outlines and being densely filled with coarse granules except for a distinct peripheral zone of clear cytoplasm. The fat cells appear to be more plastic, having less regular outlines moulded about the solid, symmetrical œnocytes, thus reversing the relation in the larva (C).

## CHAPTER X

## THE NERVOUS SYSTEM AND THE EYES

The study of the bee thus far has shown that an insect is far from being a creature of simple construction. Its body is a complex system of organs each designed for performing some particular act or function. An organ, however, though composed of living cells, is incapable of doing anything of itself—it is inert until stimulated into action; the muscles would not contract, the glands would not secrete, and the animal would cease to live were it not for a vital force that incites the tissue of each cell into its own special form of activity. This force is generated in certain cells of the body set apart for this purpose, and from them it is given out to the other cells. The tissues concerned in the production and distribution of this force constitute the *nervous system.* But the nerve force is not limited to nerve cells: it is merely a combination of those properties of irritability and conductivity possessed by all living matter, which are particularly developed in the nerve cells and hence conspicuously characteristic of them. The nerve force itself, finally, is inert until it is made active or changed in some way by influences acting upon it, just as the electricity in a telephone or telegraph wire produces no effect on the receiver until it is influenced by the transmitter.

### 1. THE GENERAL FUNCTIONS OF THE NERVOUS SYSTEM

Since all the things an animal does, consciously or unconsciously, depend upon the nervous system, the functions of the nervous system are coextensive with the activities of the animal, but all animal activities may be grouped under a few general headings.

**Nervous Stimuli.**—The evidence of life in living matter is its reaction to other forces or *stimuli.* The stimuli that set the nerve force of a complex animal into action come either from outside the body or from within it. External influences are received by the sense organs which transform the outer physical forces or the chemical effects of external substances into active nerve energy.

This energy then is transmitted through the nerves or by some change in the nerves to the receiving stations of the central nervous system. Internal influences come from chemical changes

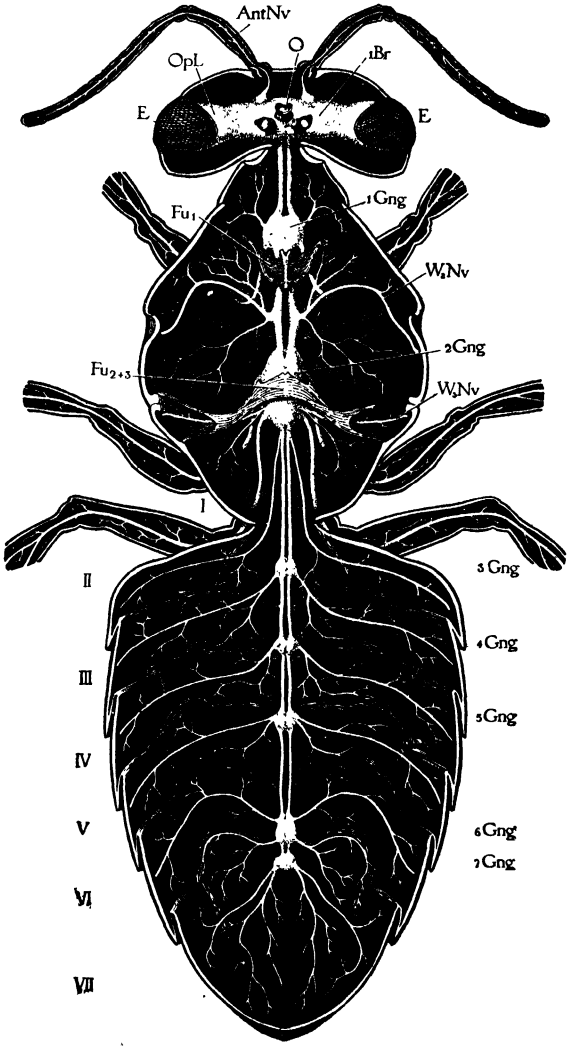



FIG. 86.—Nervous system of worker, dorsal view.

or chemical substances that are formed within the body. But, wherever or however the nervous force is activated, on reaching the central cells it induces in them an activity which goes outward

by way of other nerves to muscles or to glands which stimulates or inhibits the special functions of their cells.

**Coordination of Nervous Activities.**—In order that an animal may remain "alive," however, it is necessary not only that all its organs should be induced to perform their individual rôles, but that they should all work together and accomplish definite results. The muscles, for example, must perform harmonious movements to produce walking, flying, breathing, or swallowing; the heart beats must be in proper rhythm; the glands must secrete their products at the right time and in needed amounts. Hence, the functions both of stimulation and of *coordination* devolve upon the nervous centers.

**Vegetative Functions.**—Under this head we may include those functions of the nerve centers that are concerned merely with keeping the animal alive, the regulation of those processes that go on unconsciously with us, including secretion, excretion, digestion, respiration, the beating of the heart, the storage of surplus food materials.

**Tropisms.**—The visible phenomena of life, however, consist of those activities of the animal which are made in response to external stimuli. Such responses may be conscious or unconscious, and performed either mechanically or by an act of the will. Some entomologists claim that insects occasionally give evidence of a lowly developed power of reasoning, and that they may perform voluntary acts, but these are still matters of dispute. We do not really know that insects possess even consciousness, that they are in any degree aware of their own existence, and we do not know, therefore, that they have conscious sense perceptions. We do know, however, from their responses, that they are affected by external forces—by light, heat, odor, pressure, sound, and perhaps taste—acting upon the specially sensitized innervated cells of the sense organs.

Simple muscular reactions to external stimuli are known as reflex actions, but responses that involve coordinated series of actions that accomplish definite results are called *tropisms*. The specific, innate habit that an insect may have of going toward the light or of going away from it, of going upward on a vertical surface, of burrowing into the ground, of seeking warmth, of going toward certain odors and away from others are all examples of tropisms. Tropisms are named after the stimulus that activates them and are positive or negative according as the

animal goes toward the stimulus or away from it. An insect that goes toward the light is said to be endowed with positive phototropism, one that avoids light is said to possess negative phototropism. Reaction to heat is known as thermotropism, reaction to odor and taste as chemotropism, reaction to moisture as hydrotropism. The tropism of an animal is supposed to be a property of its organization comparable with that of plants which causes movements in them in response to external influences. A tropic action in an animal assumes that the animal does the thing unconsciously and inevitably under a definite set of conditions; when the conditions are changed the tropism may be altered, or some other tropism may have ascendancy, and the responses of the animal will change. The possession of a specific tropism translates the stimulus received from without into coordinated motor stimuli to the muscles, which causes the animal to perform the act that constitutes its specific reaction to the particular external stimulus.

**Instinct.**—If we are forced to admit that we have no positive proof of consciousness or intelligence in insects, we have, for that reason, all the more evidence of a wonderfully high degree of nervous coordination in the working of their tropisms. This coordination between impressions and responses, fixed and inherited, is what we call *instinct*. Much interesting literature on the bee owes its readableness to the author's endowment of his subjects with human emotions and some intelligence, or his making it appear that they do things from a blind sense of obligation. The bee of literature, in this respect, often is quite a different creature from the bee of science, but the possibility of the parallelism proclaims the existence of a fundamental principle, which is, that the conditions of life—especially community life—impose on living beings, no matter how widely separated, certain demands, and that these demands may be met in one of two ways—either by instinct or by intelligence. Insects have specialized on instinct; they do, therefore, by instinct many things that we, under the same circumstances, should do by reason. Since the substance of all life is the same, it should not be held impossible that insects may have a feeble consciousness or that they may have an occasional spark of intelligence, sufficient at least to enable them to retain an impression of associated objects or events, or even to perform acts that require some degree of reason.

## 2. THE STRUCTURE OF THE NERVOUS SYSTEM

The nervous system of an insect differs in the arrangement of its parts and in its anatomical details from that of a vertebrate animal, yet each is composed of a central trunk and peripheral branches, and, in the final analysis, both consist of the same elements, nerve cells and nerve fibers, having the same general relationships to one another and to the internal and external organs of the body. The principal difference is one of position, the main trunk of the insect being ventral, that of the vertebrate dorsal.

**Nerve Tissue.**—The nerve tissue consists of cells and binding membranes. Nerve cells are called *neurons*, or *neurocytes*, and differ from most other cells in being branched. A long branch is a *nerve fiber*, and a nerve trunk is merely a bundle of minute prolongations of the cell bodies. All nerves, therefore, originate in cell bodies, which are usually called simply the nerve cells. Each nerve is invested in a thin sheath called the *neurilemma*. Those nerves that convey impulses inward to the nerve cells are called *afferent* nerves; those that carry them outward from the nerve cells are called *efferent* nerves. Sensory nerves belong to the first class, motor nerves to the second. Groups of nerve cells are called *ganglia*. Most of the cells occur in masses together with connecting bundles of fibers, which constitute the *central nervous system*. These masses of cells and fibers also are known as ganglia. The nerves branching to all parts of the body constitute the *peripheral nervous system*.

**The Origin of Nerve Tissue.**—Though all parts of the nervous system of the adult lie within the body, *the nerve tissue is of ectodermal origin*. It first appears in the embryo of an insect as two external folds along the ventral side of the body, the *neural ridges* (Fig. 104 K) with a median *neural groove* (*NlG*) between them. The inner cells of the ridges separate and become the original nerve cells or *neuroblasts* (*NBl*), the outer cells remaining as the hypodermis of this region. The rows of neuroblasts then become differentiated into two chains of ganglion cell groups alternating with fiber commissures, there being thus originally two separate ganglia lying side by side in each body segment. Each pair of ganglia, however, soon becomes connected by fiber tissue derived from the cells of the inner surface of the neural groove, and thus the paired ganglia are united at an early stage into the single segmental ganglionic masses of the adult. Yet,

in its structure each adult ganglion retains evidence of its double origin in that it consists of two lateral cellular swellings connected transversely by a double commissure of internal fibers forming two cross-bars between the strands of longitudinal fibers continued forward and backward as the longitudinal commissures.

**The General Plan of the Central Nervous System.**—The central nerve trunk of an insect lies free in the ventral part of the body cavity, where it extends along the midline from the head posteriorly a varying distance, but not beyond the eighth abdominal segment in adult insects. It consists (Fig. 65 A, *VNC*) of a series of small nerve masses or ganglia connected by pairs of nerve trunks known as the *longitudinal commissures.* Typically there is a ganglion in each of the first 11 segments of the body and two in the head. One of the latter above the œsophagus is the *brain* (*Br*), the other below it is the *subœsophageal ganglion* (*SœGng*). The body ganglia, however, usually do not present this simple typical arrangement since they commonly unite in various combinations in different species of insects, which reduces the apparent number, as for example in the bee where there are only seven separate ganglia back of the head (Fig. 86, 1*Gng*-7*Gng*). But the multiple nature of a compound ganglion is usually apparent in its structure and in the number of nerve trunks that are given off from it.

The two nerve masses of the head, the brain and the subœsophageal ganglion (Fig. 65, *Br* and *SœGng*), are compound ganglia in all adult insects. The head of an insect, as has already been described (page 11), is formed by the consolidation of the first six primitive embryonic segments (Fig. 3), each of which had its double nerve ganglion. The ingrowth of the body wall that eventually forms the anterior part of the alimentary canal, the stomodeum (Fig. 65 A, *Stom*), penetrates between the commissures that connect the third and fourth pairs of head ganglia. As the segments of the head region unite to form the cranium, the three pairs of ganglia in front of the stomodeum combine to form the brain, and the three behind it fuse to form the subœsophageal ganglion. The two composite-head ganglia of the adult, therefore, remain connected by the pair of nerve cords embracing the œsophagus, which are known as the *circumœsophageal commissures.* The brain throughout life shows its triple origin in its form and structure for there are usually to be distinguished three more or less well-defined parts. The first is known as the

*protocerebrum*, the second as the *deutocerebrum*, and the third as the *tritocerebrum*. Each subdivision gives off nerves to the head appendages that originally belonged to its particular segment. The three divisions of the subœsophageal ganglion are usually less evident in the external form of the mass, but they are revealed in the internal structure and are proclaimed by the three pairs of nerves given off from this ganglion to the mouth appendages.

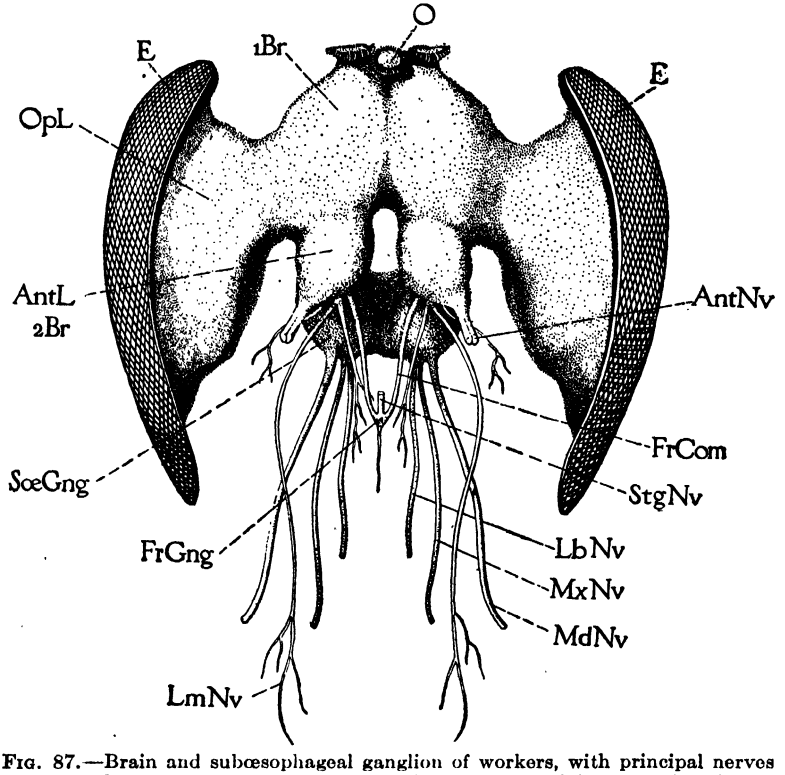



FIG. 87.—Brain and subœsophageal ganglion of workers, with principal nerves from each part, and corneæ of compound eyes on optic lobes, anterior view.

**The Brain.**—The brain of the honeybee (Fig. 87) is in most respects very highly developed, but its third division, the tritocerebrum, is so reduced that it does not appear as a separate external part. The bulk of the bee's brain, therefore, consists of the two protocerebral lobes (*1Br*) and the two deutocerebral lobes (*2Br*). The first support the ocelli or simple eyes (*O*) above and carry the great *optic lobes* (*OpL*) of the compound eyes (*E*) on the sides. The deutocerebrum consists of the two prom-

inent *antennal lobes* (*AntL*), sometimes called the olfactory lobes, which give off the large sensory *antennal nerves* (*AntNv*) and two smaller nerves that go to the muscles that move the antennæ. The tritocerebral region is marked externally only by the bases of the nerves on each side that normally belong to it, which in the bee's brain issue from beneath the deutocerebral lobes. These nerves are the *labral nerves* (*LmNv*) and the *frontal commissures* (*FrCom*). The latter unite in a small nerve mass known as the *frontal ganglion* (*FrGng*) from which a median trunk, the *stomatogastric nerve* (*StgNv*, cut off near its origin in the figure), goes posteriorly beneath the brain on the dorsal wall of the pharynx. Just where the pharynx contracts into the tubular œsophagus the stomatogastric nerve gives off two short branches that end in small *pharyngeal ganglia* which are connected by slender nerves with the brain. The rest of the main trunk then breaks up into branches that go posteriorly on the œsophagus.

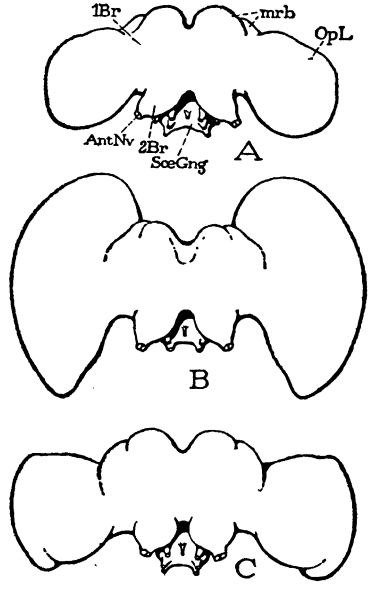



FIG. 88.—Brain and optic lobes of queen (A), drone (B), and worker (C), showing relative size of parts in each (*from Jonescu*, 1909).

*AntNv*, base of antennal nerve; 1*Br*, protocerebral lobe; 2*Br*, deutocerebral or antennal lobe; *mrb*, surface swellings over internal mushroom body (Fig. 89, *MrB*); *OpL*, optic lobe; *SœGng*, subœsophageal ganglion.

*External Structure of the Brain.* The external shape and the size of the brain differ considerably in the three forms of the bee, as has been shown by Jonescu (1909). The brain of the drone (Fig. 88 B) as a whole is much larger than that of either the queen (A) or the worker (C), but most of its greater bulk is due to the large size of the drone's head and to the great development of the optic lobes in the drone. The true brain itself, the part consisting of the protocerebrum (A, 1*Br*), is relatively smallest in the drone (B) and actually largest in the worker (C).

The optic lobes of the brain (Figs. 87, 88, 89, *OpL*), as already pointed out, are by far the largest in the drone (Fig. 88 B), being

much smaller in the worker (C), and still smaller in the queen (A), in each form corresponding in size with the size of the compound eye. The structure, however, is the same in all three forms. The ocelli and the part of the brain from which the ocellar nerves arise are alike and equally developed in queen, worker, and drone.

The second principal division of the brain, the deutocerebrum (Figs. 87, 88 A, *2Br*), consists principally of the prominent antennal or olfactory lobes, and of the roots of the large sensory nerves of the antennæ (*AntNv*) and those of the smaller motor nerves that go to the antennal muscles. The volume of the antennal lobes is about the same in the worker and the drone, but is considerably less in the queen. In the inner structure of the lobes, however, Jonescu states, there is a distinct difference between the drone and the worker in that the lobes of the drone are less complicated and the root branches of their nerves fewer.

*General Internal Structure of the Brain.*—The internal structure of the bee's brain presents features of much interest. It has been particularly studied by Kenyon (1896) and by Jonescu (1909). A section of the brain (Fig. 89) shows that it is composed of an outer cellular layer (the light parts in the figure) and of an internal fibrillar tissue (the darker parts in the figure). The latter forms a number of differentiated masses of which Jonescu distinguishes seven as parts of the protocerebrum. These are the *protocerebral lobes* (Fig. 89, *PrL*), the *mushroom bodies* (*MrB*), the *central bodies*, the *nuclei of the cerebral bodies*, the *intercerebral bridge*, the *roots of the ocellar nerves*, and the *optic lobes* (*OpL*). One pair of these parts, those which have unfortunately been named on account of their shape the "mushroom bodies" (*MrB*), are of particular interest because they appear to be the principal centers of what may be called the "mental" activities of the insect. We must qualify the use of the term "mental" in this connection, however, by understanding that it is used to refer to those brain functions of the insect which take the place of true mental activities, namely, instincts and reflexive actions depending on impressions received from the sense organs. Insect psychology is a subject as yet little investigated scientifically and it is not certain that even the most highly endowed insects can be accredited with voluntary actions or reason.

*The Mushroom Bodies.*—The two mushroom bodies (Fig. 89, *MrB*) lie in the upper part of the brain with their roots buried in

the protocerebral lobes (*PrL*). Their positions are marked externally by two swellings on the dorsal surface of the brain (Fig. 88 A, *mrb*) between the optic lobes (*OpL*), and in front of the ocelli. Each body (Fig. 89, *MrB*) consists of a mushroom-shaped mass of fibrillar tissue having two cup-like depressions in its upper expanded end, and its stalk, which is correspondingly double, sunken into the protocerebral lobe (*PrL*) of the same side. The cups are filled with masses of ganglionic brain cells that produce the elevations just noted on the surface of the brain. Kenyon says that the ganglion cells of the cups of the mushroom bodies are different from the other ganglion cells of the brain and suggest those elements, called *Purkinje cells*, characteristic of the gray matter of the brain of higher vertebrates. All investigators

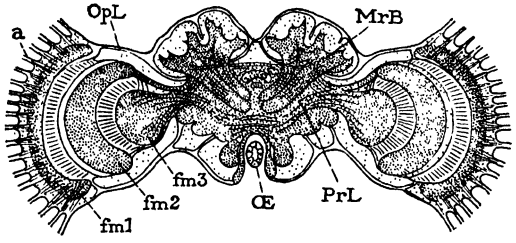



FIG. 89.—Vertical cross-section of brain of worker (*from Jonescu*, 1909). Dark parts represent fibrillar masses, outer light parts cellular tissue. *a*, fringe of subretinal nerve ends; *fm*1, *fm*2, *fm*3, outer, middle, and inner fibrillar masses of optic lobe; *MrB*, mushroom body; *Œ*, œsophagus; *OpL*, optic lobe; *PrL*, protocerebral lobe.

have noted the large number of nerve tracts both sensory and motor that center in the mushroom bodies from all parts of the brain, from the compound eyes, the ocelli, and the antennæ, and also from the subœsophageal ganglion and the ventral nerve cord. For this reason the bodies are regarded as the seat of the "mind" of the bee, or, as Kenyon puts it, they "are the elements that control or produce actions that are distinguished by the term intelligent." Jonescu says the mushroom bodies must be the place in the central nervous system of the insect where the various sense impressions are recorded and where actions are coordinated, and the place also where associations once acquired are retained—in which sense they may be regarded as organs of intelligence. The mushroom bodies are larger in the worker than in either the queen or the drone and are relatively smallest in the drone; a condition, as Jonescu points out, to be

expected if they are the centers of instinct and memory and of associated actions.

**Correlation of Instinct and Brain Development**—A direct correlation may be traced, as Jonescu has interestingly brought out in his discussion, between the structural differences in the brains of the worker, queen and drone on the one hand, and the special instincts, faculties and activities of the three forms of the bee on the other. The great size of the eye of the drone, for example, is unquestionably of much importance to the drone during the mating flight when he must follow on the wing the rapidly flying queen. In general, however, the eye is an organ of more varied use in the worker since the worker has a multitude of duties to perform that demand a clear and discriminating vision and a good memory, but such faculties may depend rather on brain development than on mere eyesight. The small development of the eyes and the optic lobes in the queen is clearly to be correlated with her life of retirement within the hive where she is constantly attended by the workers. With regard to the antennal lobes and the antennal senses the same relations may be traced between the development of the lobes and the use or importance of the senses that center in them. The mass of these lobes, as already stated, consists principally of the roots of the sensory antennal nerves, and, though the lobes are of about equal size in the worker and the drone, the antennal nerve roots are more highly developed in the worker. We have seen in Chapter II that the antennæ of both sexes are covered with sense organs of various sorts, some of them more numerous in the drone than in the worker. Here again, perhaps the drone has special need for some one sense at some particular time in his life; but the worker in general must have far more precise and discriminating antennal senses, especially if flower odors are perceived and distinguished largely by means of them, and the greater complexity of the antennal nerve roots in the worker brain would seem to attest that the worker does have a keener receptive faculty for senses centering here than has the drone, notwithstanding his greater number of antennal sense organs.

Of the three forms of the honeybee, then, the worker unquestionably has the best brain and the greatest "mental" endowment; and, furthermore, the bee belongs to the most "intellectual" group of insects, the Hymenoptera, for all investigations show that the brain is more highly evolved in this order than in any

other. Accepting the mushroom bodies as the center of all brain activities, and their size relative to that of the rest of the brain as indicative of brain development, Alten (1910) and Armbruster (1919) have made comparative studies based on measurements of different parts of the brains of numerous species of Hymenoptera, by which they arrange the species in series according to the increase in proportional size of the mushroom bodies, and, therefore, supposedly according to mental capacity. Alten took four measurements from transverse vertical sections of the brain (such as Fig. 89) as follows: (*a*) the greatest width across the two mushroom bodies; (*b*) the greatest width of the two protocerebral lobes; (*c*) the greatest width between the outer edges of the two middle bodies of the optic lobes; and (*h*) the greatest height of the mushroom bodies. Then, dividing *a* by *b*, *a* by *c*, *h* by *b*, and *h* by *c*, he obtained four indices that would show the relative increase in the size of the mushroom bodies as they exceed in width and height the two less variable dimensions. On this basis the Tenthredinidæ or sawflies are found to be at the bottom of the series, and the social bees and wasps at the top. Alten's paper is replete with illustrations made from sections of the brains of the various species studied, and contains an interesting discussion of the relationships of the various Hymenopteran families as brought out by these comparative brain studies. The subject is one of interest, however, rather to the student of Hymenoptera in general than to a specialist on bees.

Armbruster (1919) devised a more precise means of making brain comparisons for various species of bees and wasps by adding Alten's four indices and dividing the sum by four, obtaining thus a single figure which he calls the *brain index*. This, he says, "is nothing more than the numerically expressed relationship between the two actual dimensions of the mushroom bodies and a constant in the same brain, therefore, a numerical expression for the relative development of the 'sphere of intelligence' between brain and brain, and thus also of the degree of psychic development of one species above another."

Calculating by this method from Alten's brain measurements, Armbruster obtains brain indices for numerous species of bees and wasps which he tabulates in a graded series. By Armbruster's test the most "intellectual" insects are amongst the bumblebees, the brain index of the queen of *Bombus* (*Bremus*) *agrorum*

being 3.138, and that of the worker of *B. terrestris* being 3.153, the maximum known for any insect. The queen of a wasp, *Vespa vulgaris*, comes third with an index of 3.074, while the worker of *Bombus agrorum* is fourth with an index of 3.019. The indices of all other species studied fall below 3; that of the worker of the honeybee is 2.572, that of the queen 2.526, and that of the drone 2.455. Lowest in the list is the male of a solitary bee, *Andrena carbonaria*, with an index of 2.034. It is disappointing to find that our *Apis mellifera* does not stand at the head of the class. The social species in general have better developed brains than solitary species. Males usually have less brain power than females. With the wasps and bumblebees the queens excel the workers, but with the honeybee the worker has the best brain. The comparatively low indices for the worker and queen of the honeybee is perhaps due to the complete division of labor between these two forms in this species; with wasps and bumblebees the queen must at times be able to perform the ordinary functions of both queen and worker. Armbruster points out that there is much variation in brain development amongst different species in the same genus, and also that brain indices are not indices of relationship amongst genera.

**The Subœsophageal Ganglion.**—The circumœsophageal commissures are so short in the bee that the subœsophageal ganglion (Fig. 87, *SœGng*) appears to be attached directly to the tritocerebral region of the brain. The lower ganglion is a wide, flattened mass of nerve tissue from which issue the three pairs of large nerves to the mouth parts, the *mandibular nerve* (*MdNv*), the *maxillary nerve* (*MxNv*), and the *labial nerve* (*LbNv*). Some writers regard the two head ganglia as together constituting the "brain," but the two nerve masses are usually distinguished as in the above description. From the posterior end of the subœsophageal ganglion a pair of long thick commissures extend backward through the neck to the first ganglion of the thorax (Fig. 86, 1*Gng*).

**The Ventral Nerve Trunk.**—The ventral nerve trunk of the thorax and abdomen in the bee consists of only seven ganglia and their uniting commissures (Figs. 72, 86, 1*Gng*-7*Gng*). The first ganglion (1*Gng*) is in the prothorax where it is situated above the sternal plate in front of the prosternal furca (Fig. 86, $Fu_1$). Its principal nerves go into the first pair of legs. The second

ganglion is a very large nerve mass (*2Gng*) lying before the bases of the middle legs and beneath the arch of the combined furcæ, or the endosternum, of the mesothorax and metathorax ($Fu_{2+3}$). This ganglion is clearly a compound ganglion because the nerves from it go to the bases of both pairs of wings, to the middle and hind legs, to the muscles of the mesothorax, metathorax, propodeum and first segment of the abdomen behind the peduncle. It is, therefore, unquestionably composed of the ganglia properly belonging to all four of these segments. The first and second free ganglia of the abdomen (*3Gng*, *4Gng*) lie in the true second and third segments, but since the nerve branches from these ganglia go to the segments behind them in each case, the ganglia themselves undoubtedly belong to these segments, that is, to segments *III* and *IV*. The next three ganglia (*5Gng*, *6Gng*, *7Gng*) lie in the segments they innervate (*V*, *VI*, *VII*) and hence belong to the fifth, sixth and seventh segments of the abdomen. The seventh ganglion, however, supplies also all the segments back of it with nerves and is, therefore, evidently a composite ganglion formed by the union of the ganglia properly belonging to the seventh, eighth, ninth, and tenth segments.

According to Nelson (1918) there are 11 separate ganglia in the abdomen of the embryo of the honeybee at a certain stage, corresponding with 11 abdominal segments, but at a later stage the ninth, tenth and eleventh ganglia unite. When the larva hatches there is a separate ganglion in each of the body segments from the first to the twelfth inclusive, the last being the compound ganglion just mentioned. During the growth of the larva, however, the terminal ganglion unites with the eleventh and the mature larva has a chain of only 11 separate ganglia, 3 in the thorax and 8 in the abdomen. This is the typical arrangement of ganglia both in larval and adult insects. During the pupal stage of the bee the ganglia further condense to form the system of seven adult body ganglia above described.

With insects, all muscle coordination is not delegated to the brain; the head may be cut off and the decapitated body may still be able to walk in an awkward fashion. The body of a bee may be greatly mutilated but it will still remain "alive" if the nervous system is left intact. The segments may be severed from one another and yet each will be able to move its appendages so long as its nerve center is not destroyed. This shows that the body ganglia are independent centers of stimulation in insects,

but full coordination results only when all the parts are together and intact.

### 3. THE SIMPLE AND THE COMPOUND EYES

With insects, even the senses apparently do not all center in the brain, for the sense organs of the mouth and mouth parts are innervated from the subœsophageal ganglion, and there are sense organs on the legs, on the bases of the wings, and on various other parts of the body whose nerves go to body ganglia. Only the antennal nerves and the nerves from the simple and compound eyes go directly to the brain. The sense organs of the antennæ and the mouth parts have been described in Chapter II, and those of the hind legs in Chapter III. The two sets of eyes, the three ocelli (Figs. 6 A, 87, *O*) and the two compound eyes (*E*), are so intimately associated with the brain that they may be described more conveniently in connection with the nervous system. The essential element, however, in any insect sense organ is a modified hypodermal cell sensitized by union with a nerve, and, anatomically, such organs should be considered as a part of the body wall.

**The Ocelli.**—The three ocelli of the bee are situated at the front of the top of the head (Figs. 6 A, 87, *O*). One is anterior and median, the other two lie close behind it and just to either side of the midline. All are connected with the brain by nerves that enter the protocerebral lobes posterior to the mushroom bodies. The ocelli of bees are organs of the adult only and are formed during the pupal stage.

The structure and development of the ocelli of the bee have been studied by Redikorzew (1900), and the following is a résumé of his description. The ocelli originate in the very young pupa, before the latter has yet shed the larval skin, as mere thickenings of the hypodermis at points where the cells, still in a single layer, have already become connected with the ends of nerves (Fig. 90 A). As development proceeds the hypodermal thickening rapidly increases in size, pushing inward, and the cells become differentiated into outer and inner layers (B, *VB* and *Ret*), with a loose group of unspecialized *interstitial cells* (*a*) at the bottom of the mass which form a packing amongst the branches of the nerve (*Nv*) and between the innermost ends of the other cells. The entire ocellar structure at this stage is invested in a cellular membrane (*Mb*). The outer of the two organized cell strata

(*VB*) becomes a transparent layer over the deeper cells in the finished ocellus, called the *vitreous body*. The inner stratum (*Ret*) consists of cells directly connected with the ends of the nerve fibers, and hence this layer becomes the true receptive part of the mature eye corresponding with the retina of a vertebrate

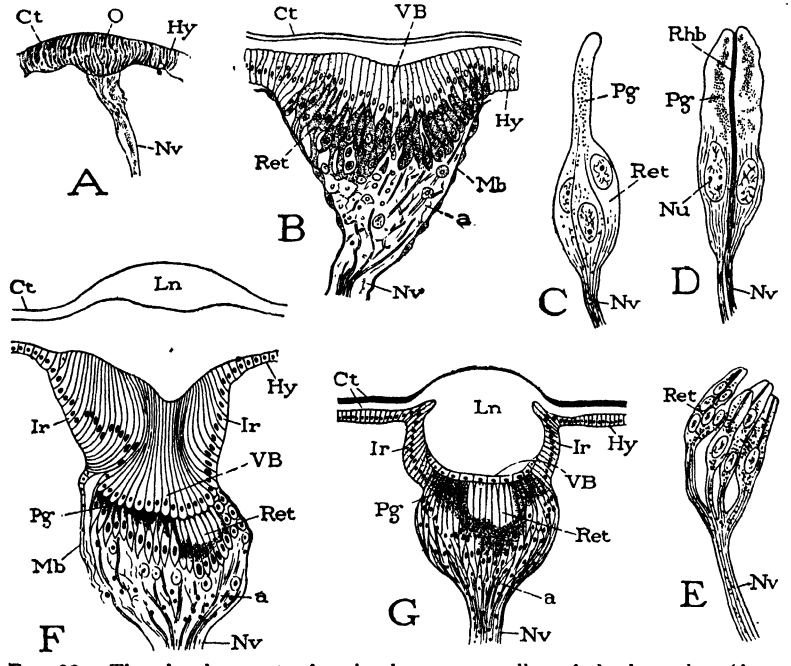



FIG. 90.—The development of a simple eye or ocellus of the honeybee (*from Redikorzew*, 1900).

A, longitudinal section of median ocellus of very young pupa, consisting of thickening of hypodermis (*Hy*) with nerve (*Nv*) attached.

B, section of lateral ocellus at later stage; cells differentiated into outer layer (*VB*) and inner layer (*Ret*), with mass of interstitial cells (*a*) at base.

C, single group of retinula cells of young pupa; rhabdom not yet formed, small amount of pigment (*Pg*) present.

D, retinula of two cells at later stage, with rhabdom (*Rhb*).

E, four retinula cell groups connected with one nerve.

F, transverse section of left lateral ocellus of old pupa; cuticula thickened to form lens (*Ln*), vitreous body (*VB*) and retina (*Ret*) well differentiated, hypodermis around vitreous body thickened to form iris (*Ir*).

G, longitudinal section of median ocellus of adult; lens (*Ln*) greatly thickened, surrounded by iris (*Ir*); vitreous body (*VB*) reduced to flat layer of cells separating lens from retina (*Ret*).

eye. In the ocellus the retina cells remain attached lengthwise in groups of twos and threes or sometimes in larger numbers on the ends of the nerve branches (C, D, E), and these groups of

retina cells are called the *retinulæ*. The opposing surfaces of the cells in each retinula secrete a transparent substance of some sort which forms in the axis between the cells a single, slender optic rod called the *rhabdom* (D, *Rhb*). Rhabdoms are characteristic of all fully formed insect eyes whether simple or compound.

During the stages of development following that shown at B the parts of the ocellus become better defined and the structure as a whole takes on its characteristic form. The cuticula over the outer surface of the ocellus (A, B, *Ct*) thickens to form a *lens* (F, G, *Ln*). (The lens normally rests on the outer cellular layer, but in the figure at F it is shown detached as it usually appears in specimens prepared for study.) The cells of the vitreous body (F, *VB*) elongate and grow inward. The hypodermal cells immediately surrounding them become very long and form a thick ring, called the *iris* (*Ir*). Finally the parts attain their mature form and the ocellus has the structure shown at G. The lens (*Ln*) is now very thick and biconvex, though much more convex on the inner surface than on the outer. The vitreous body, on the other hand, is greatly reduced in size and forms only a thin layer of flat transparent cells (*VB*) between the lens and the retinulæ (*Ret*). The iris (*Ir*) surrounds the inner part of the lens, the crystalline body, and the outer ends of the retinulæ cells. The ends of its outermost cells also fill a circular constriction of the lens, which, in the cross section (G), appears as two lateral folds projecting into the body of the lens. The retinulæ (*Ret*), the interstitial cells (*a*), and the nerve fibers form a large compact mass with the main nerve trunk (*Nv*) entering its base. The retinulæ cells contain a dark pigment (*Pg*), and their rhabdoms are perpendicular to the inner face of the vitreous body.

The ocelli are probably poor organs of vision, being very short-sighted and capable of distinguishing only between different intensities of light or between light and darkness. The dark pigment of the retinulæ (C, D, F, G, *Pg*) has been shown to collect in the basal parts of the cells in animals kept in the dark, but to assemble in their outer ends under the influence of light. It appears, therefore, to play some important part in the function of the ocelli. Pigment is present usually in even the most primitive of eyes in lower animals.

**The Compound Eyes.**—The great compound eyes of insects are quite different in structure from the ocelli, but they likewise are formed from the elements of the body wall—the cuticula,

the hypodermis, and the basement membrane, with nerve fibers attached to certain of the hypodermal cells. These eyes are called "compound" because they are made up of a great many separate eye elements, each complete in itself and having its own nerve fiber. The outer surface or *cornea* (Fig. 86, E, Fig. 91, *Cor*) consists of as many separate little lenses as there are parts

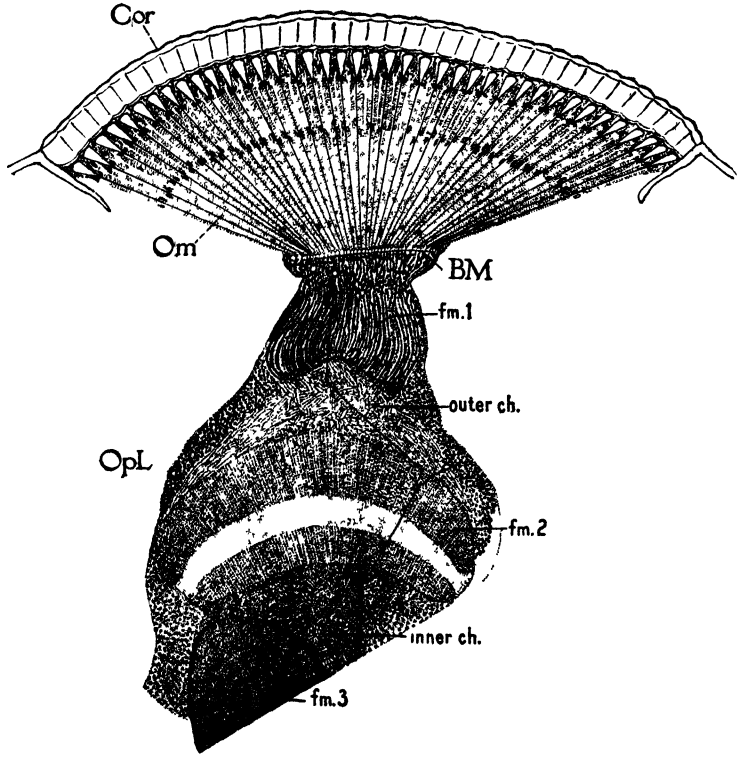



FIG. 91.—Horizontal section of compound eye and optic lobe of worker (*from Phillips*, 1905).

*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.

in the body of the eye, each one belonging to an individual eye element, which is known as an *ommatidium* (Fig. 91, *Om*).

The surface of a compound eye presents a honeycomb appearance under the microscope since the lenses are usually six sided and are separated by narrow spaces forming hexagonal *facets*. The number of facets varies greatly in different insects, but

usually there are several thousand of them, and the number for some species has been estimated as high as 30,000. The compound eyes of the bee are covered by long, straight, unbranched hairs or setæ set on the rims of the facets. The eyes appear particularly hairy in young bees since many of the hairs become brushed off in old bees. The ommatidia (Fig. 91, *Om*) are long and slender, and they all converge inwardly to the outer end of the optic lobe of the brain (*OpL*) from which they are separated by the basement membrane (*BM*), each being a group of modified hypodermal cells.

The compound eye of the honeybee has been studied by Phillips (1905) and the following description, together with Figs. 91 and 92, are taken from his paper: The ommatidia in a cross-section of an eye (Fig. 91) diverge like the ribs of a fan from the end of the optic lobe (*OpL*) to the cornea (*Cor*). Each one (Fig. 92 A) has the form of a long, slender tube tapering inwardly and separated from its neighbors by an outer sheathing of pigment cells (*o-p. c.*) containing a dark coloring matter. At the outer end of each ommatidium is one of the divisions of the cornea which constitutes the individual *crystalline lens* (*CL*) for the ommatidium. Beneath the lens is a *crystalline cone* (*CC*) having its apex directed inwardly. In line with the middle of the lens and cone is a long *crystalline rod* or *rhabdom* (*Rhb*) which extends through the axis of the ommatidium. (For the sake of distinction the transparent rhabdom is represented in black in A of Fig. 92.) Surrounding the rhabdom is a cylinder of eight or nine long *retinulæ cells* (*ret*), each with a conspicuous nucleus (*ret.n*) above its middle. The inner ends of the retinulæ cells rest upon the basement membrane (*BM*), and each group is here connected with a nerve fiber (*Nv*) that penetrates the membrane from the optic lobe (Fig. 91, *OpL*). The arrangement of the retinulæ cells about the rhabdom in each ommatidium is shown in cross-sections at F and G of Fig. 92. The inverted apex of the crystalline cone (*CC*) is surrounded by the *corneal pigment cells* (A, B, *c-p. c.*), while the outer pigment cells (*o-p. c.*) invest the entire structure beneath the lens, including the base of the cone, the corneal pigment cells, and the retinulæ cells. The latter thus isolate the inner elements of the ommatidium from those of surrounding ommatidia, and their pigment makes of each eye element a dark chamber comparable with the blackened interior of a camera box.

According to Phillips (1905) the ommatidia of the compound eye of the bee originate from the ectoderm as groups of hypodermal cells which become arranged in the form of spindles

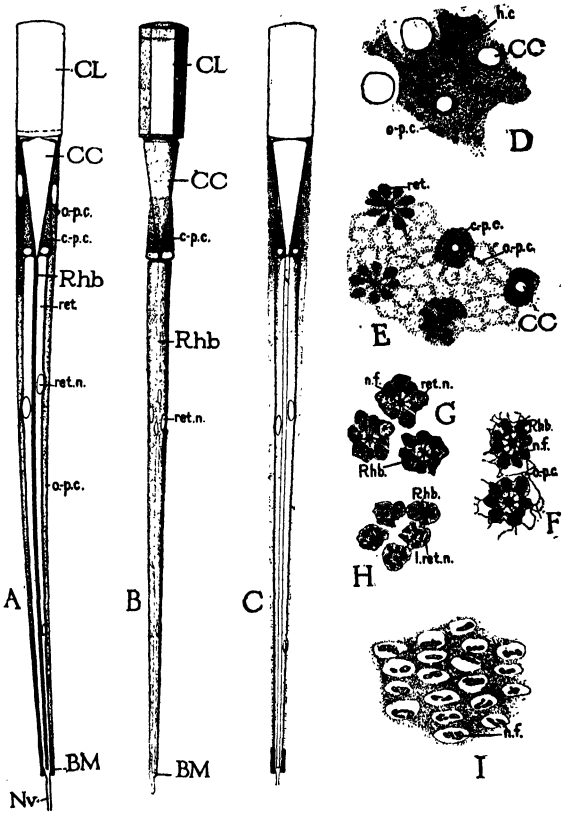



FIG. 92.—Histological details of compound eye of worker (*from Phillips*, 1905). A, an ommatidium with surrounding pigment cells. B, the same without pigment cells. C, longitudinal section of an ommatidium. D, cross-section of eye through outer ends of crystalline cones. E, cross-section through outer ends of retinulæ. F, cross-section of retinulæ through outer ends of rhabdoms. G, cross-section of retinulæ in region of distal nuclei. H, cross-section of retinulæ in region of proximal nuclei. I, cross-section through basement membrane of eye, showing perforation by nerve fibers.

*BM*, basement membrane; *CC*, crystalline cone; *CL*, crystalline lens; *c.-p.c.*, corneal pigment cell; *h.c.*, *hair cell; l.ret.n.*, proximal retinular nucleus; *n.f.*, nerve fiber; *Nv*, nerve; *o.-p.c.*, outer pigment cell; *ret.*, retinular cell; *ret.n.*, distal retinular nucleus; *Rhb*, rhabdom.

surrounded by smaller cells. The spindle cells develop into the retinulæ, and the surrounding cells differentiate into the pigment

cells and cells that are to compose the cone. The retinulæ cells sink below the cone cells, and the latter, by a transformation of their protoplasm into a transparent substance, form the crystalline cone of the mature ommatidium. The adjoining surfaces of the retinulæ cells are transformed into the rhabdom. From this it is evident that the development of the elements of a compound eye is in many respects comparable with the development of the parts of an ocellus, the principal differences being that the groups of retinulæ cells are not isolated or separated by pigment cells in the ocellus, and that the lens and the crystalline body in the ocellus do not break up into separate elements for each retinula group. The ocellus is imperfectly compound in its retina, but simple in its other parts. The larvæ of bees and other members of the true Hymenoptera do not have eyes of any sort, but in the sawflies, which are more primitive Hymenoptera, the larvæ have a single large ocellus on each side of the head, which, Redikorzew says, has the retinulæ cells grouped in fours and each set surrounded by true pigment cells. If, then, the single lens over this eye is replaced, when the last larval skin is shed, by a faceted cornea with an individual lens over each retinula group, it is easy to see how the compound eye of the adult might have developed from a larval eye of this sort in the Hymenoptera. The ocelli of caterpillars, which form two groups on the sides of the head, are, however, according to Redikorzew, each the equivalent of one ommatidium, and a simple multiplication of their number would produce a compound eye. The median ocelli of insects are, therefore, to be regarded as structures distinct from the lateral ocelli of larvæ, the latter perhaps being larval prototypes of the compound eyes of the adult.

The optic lobes of the brain (Figs. 87, 89, 91, *OpL*) consist principally of the nerve fibers of the compound eyes. In each lobe the fibers form three dense fibrillar masses, distinguished as the *outer*, *middle* and *inner fibrillar bodies* (Figs. 89, 91 *fm*1, *fm*2, *fm*3). Between each two of these masses the fibers separate and cross one another in a horizontal plane (Fig. 91), forming the *outer chiasma* (*outer ch.*) and the *inner chiasma* (*inner ch.*). The crossing of the fibers does not show in vertical sections (Fig. 89). Jonescu (1909) says that in the outer chiasma all the fibers go from the outer body to the middle body, but that from the middle body a number of the fibers go direct to the proto-

cerebral lobes. The fibers from the inner body go into the brain in two large bundles. The optic lobes belong to the protocerebrum or brain division of the first primitive head segment (Fig. 3), but there is no evidence that the eyes in any way represent appendages of this segment.

**Insect Vision with Compound Eyes.**—There has always been much discussion as to how insects see with the compound eyes, but the most probable explanation is that each ommatidium registers the vertical rays of light that strike upon its lens and pass through the apex of the crystalline cone, the oblique rays being absorbed by the pigment cells. Each ommatidium, therefore, may be said to "see" only that part of the object or field of vision directly ahead of it, while the entire image will be made up of as many units as there are facets in the cornea of the eye. This explanation of insect vision with the compound eyes is known as the theory of "mosaic" vision, first proposed by Johannes Müller (1826). Modern opinion is divided mostly on the question as to whether the units of the image are small sections of the field or merely points of light.

In general, insects appear to be very short sighted and it is probable that most of them are not able to see distinctly as we do at any range. The compound eye would appear to be an organ particularly well adapted for perceiving motion, and there is no doubt that insects become aware of moving objects very quickly. On the other hand, bees and wasps must get a very good impression of the form of stationary objects, since it is now well established that their supposed "sense of direction" and "homing instinct" are mostly matters of good perception and memory of landmarks. There is likewise much evidence that bees perceive and distinguish most of the colors that we see, and that bees and other insects see the ultraviolet rays as a color quite different from any of those in the part of the spectrum visible to us. Many flowers reflect these ultraviolet rays and this fact must be taken into account in any studies on the relationships between insects and flowers. The entire subject of insect vision, however, is one too large to review here; the student may find the more recent ideas on how insects see, on the perception of form and color by bees, and on the importance of ultraviolet in insect and flower studies given in the works of Exner (1891), Lovell (1909, 1910), Hess (1913), von Frisch (1914), Eltringham (1919), Minnich

(1919), and Lutz (1924). It is truly discouraging, however, that we must still be so ignorant about the perceptive powers of insects, considering the amount of experimenting that has been done on the subject. If we could only *be* insects for a short time we should know a great deal more about them than we probably ever shall know otherwise.

## CHAPTER XI

## THE REPRODUCTIVE SYSTEM

The reproductive system comprises those organs that house the cells which are to produce the individuals of the next generation, and also the tubular passageways that serve for the extrusion of these cells to the exterior, the various internal accessory glands or receptacles, and the external organs of copulation and egg-laying. Some of these parts are formed from the mesoderm of the embryo (page 294), the others are derived from the ectoderm.

**Origin of the Germ Cells.**—The primitive germ cells in many insects are set apart from the body cells at the beginning of embryonic development and migrate to their eventual position in the reproductive organs, and, though this has not been demonstrated for most species by actual observation, the evidence from known cases is sufficient to warrant the assumption that the germ cells of all insects originate in a similar manner. Within the reproductive organs the germ cells undergo all or most of their development into their mature forms—the *spermatozoa* in the male, the eggs or *ova* in the female.

**Reproduction.**—All animals, except those that reproduce by division or budding, grow from at least one cell, the egg, and almost all from a combination of the egg with a spermatozoon. The uniting of these two cells is called *fertilization*. But there are many insects that normally reproduce new individuals from an egg cell alone without union with the male element. This form of reproduction is known as *parthenogenesis*. In most cases, however, parthenogenesis occurs in a cycle of alternating generations in which at some period all the eggs are fertilized. Unfertilized eggs that develop usually give rise to females, but with the honeybee parthenogenesis produces males, and male bees have never been known to come from fertilized eggs.

**Castes of the Honeybee.**—The males of the honeybee are called *drones*, the females are known as *queens* or *workers* according to their structure and their functions in the hive. In the queens the egg-producing organs are very highly developed; in the

workers the ovaries are ordinarily rudimentary, though under certain circumstances they produce mature eggs; but, on the other hand, the workers have the mouth parts, the honey stomach, and the pollen-gathering organs much better developed than the queens. The two castes of females differ correspondingly in their instincts. A single active queen in each hive normally produces all the eggs of the colony, while all the work of collecting and storing food, of building the comb, of keeping the hive in order, warding off enemies, attending the queen, and rearing the brood is done by the numerous workers. The females of most insects lay their eggs at some place where the young will be able to find proper food when they hatch, but the mother never in any way feeds or protects her offspring, in most cases she dies before her progeny emerge from the eggs. The wasps, the bees and the ants, however, are different in that with nearly all of them the females make a nest of some sort for the protection of the young, and in which they place a store of food for them to eat. With 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. But in some of the wasps, such as hornets and yellow jackets, the first females of the new brood that mature in the spring help their mother to provide for her next brood by increasing the size of the nest and by gathering and storing a larger supply of provisions. These females, moreover, appear to be designed for this purpose since they are all sterile but retain their maternal instincts. There is here, therefore, a suggestion of that division of labor which is carried much farther in the honeybee, and which reaches its highest development in the ants. The queens and workers of the honeybee are all apparently produced from the same kind of fertilized eggs, the different development of the two castes is supposed to be due to a difference in the food given to the larvæ, but a more thorough investigation of the subject is needed before we can accept this explanation as final.

### 1. THE MALE ORGANS

The reproductive organs of the male bee consist of the two *testes* (Fig. 93 A, *Tes*), their ducts or *vasa deferentia* (*VDef*) including the sperm reservoirs or *vesiculæ seminales* (*Ves*), the *accessory* or *mucous glands* (*AcGl*), the single *ductus ejaculatorius*

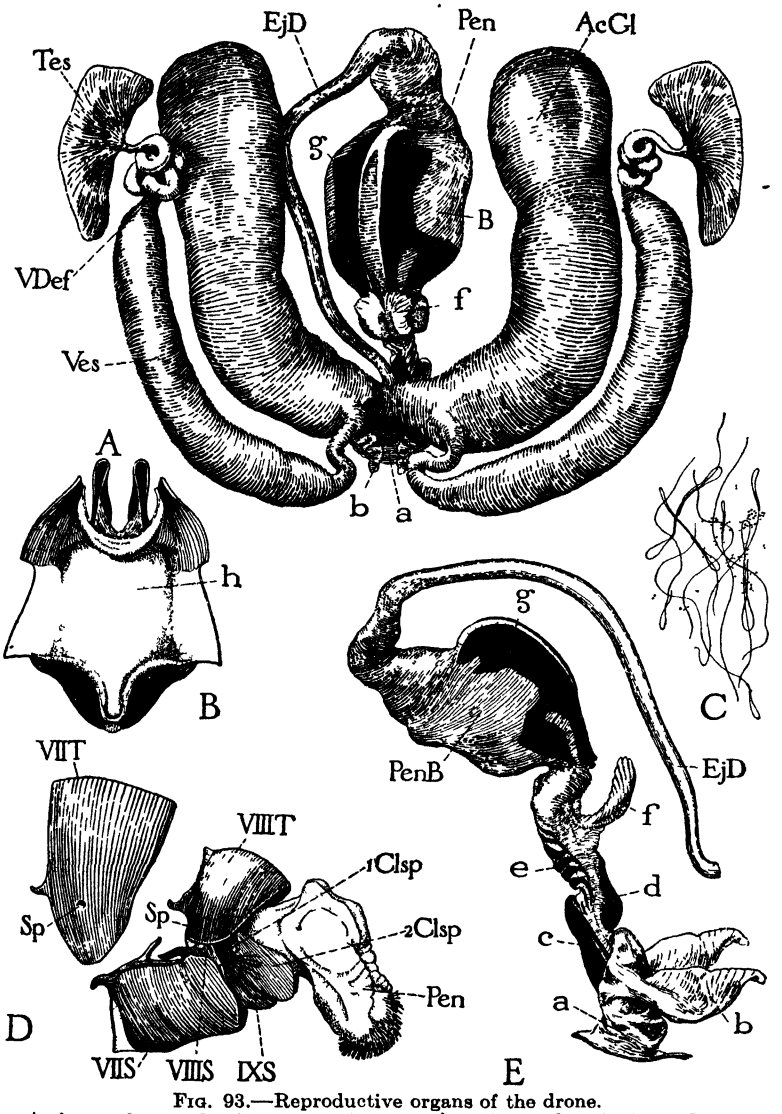



FIG. 93.—Reproductive organs of the drone.

A, internal reproductive organs in natural position, dorsal view. B, inner surface of dorsal wall of bulb of penis. C, group of spermatozoa. D, terminal segments of male abdomen, seventh tergum (*VIIT*) separated from its sternum (*VIIS*), showing lateral claspers (*1Clsp*, *2Clsp*) of ninth segment, and penis (*Pen*) partly everted. E, lateral view of penis entirely invaginated into abdomen, and ejaculatory duct (*EjD*).

*a*, base of penis; *b*, pneumophyses; *c*, ventral basal plate of penis; *d*, dorsal basal plate of penis; *e*, transverse ventral plates in middle section of penis; *f*, dorsal lobe of penis at base of bulb; *g*, dorsal plates of bulb of penis; *h*, gelatinous thickening of inner dorsal wall of bulb of penis.

(*EjD*), and the *penis* (*Pen*), the last being ordinarily inverted within the abdominal cavity.

The testes, the vasa deferentia, including the vesiculæ, and the accessory glands are formed in the embryo as internal parts derived from the mesoderm, and have at this stage no connection with the exterior. The ejaculatory duct, on the other hand, is a tubular ingrowth of the ectoderm which meets the rear ends of the mesodermal tubes and eventually unites with them. In the honeybee the ejaculatory duct does not open into the cavity of the glands until the intervening thin partition is ruptured at the time of copulation.

**The Testes.**—In the mature drone the testes (Fig. 93 A, *Tes*) are small, flat, triangular bodies of a yellowish color overlying the upper ends of the great mucous glands (*AcGl*). They attain their greatest development during the pupal stage; according to Bishop (1920), four days before the emergence of the drone the testes reach a length of 5 millimeters and are then of a bean-like shape with a creamy-yellow color. After emergence they shrink, become flattened in form and acquire a greenish-yellow color. When the drone is functionally mature, 12 days after emergence, the testes have become so reduced that they are less than one-third their maximum length. Each testis consists internally of a large number of small tubules which open into a common chamber at the end of the *vas deferens*. The primitive germ cells are contained within these tubules and in them they undergo most of their development into the spermatozoa (Fig. 100), but they pass down into the seminal vesicles to attain their final form. This migration of the sperm is followed by the degeneration of the testes.

**The Vasa Deferentia and Seminal Vesicles.**—Each vas deferens is differentiated into three regions; an uppermost part consisting of a short, tightly coiled duct (Fig. 93 A, *VDef*); a long median enlarged part constituting the seminal vesicle (*Ves*); and a short terminal tube opening into the dorsal wall of the base of the accessory gland (*AcGl*) of the same side. The epithelial walls of the vas deferens consist of glandular cells. According to Bishop (1920) the cells of the upper and lower narrow tubular parts are cubical in form, but those of the vesicula are very long and narrow with the nuclei in their basal halves. The epithelium is covered by two muscle layers, an inner layer of circular fibers

and an outer layer of longitudinal fibers, and these are invested by an external membranous envelope.

**The Mucous Glands.**—The accessory or mucous glands are two great curved sacs (*AcGl*) which come together at their bases to form a U-shaped structure connected with the median ejaculatory duct (*EjD*). Each gland has an internal epithelial wall of glandular cells similar to those of the vesiculæ, but, according to Bishop, about twice the length of the latter, each being twenty or thirty times as long as its width. The epithelium is surrounded by three muscle layers, as described by Bishop, an outer layer of longitudinal fibers and a median layer of circular fibers corresponding with the two layers of the vesiculæ, and in addition an innermost layer consisting of three bundles of longitudinal fibers extending from the base of each gland more than half way to its anterior end. The last throws the glandular epithelium of the organ into three corresponding lengthwise ridges. The musculature of the glands is heaviest around the entrances to the ejaculatory duct.

**The Seminal and Mucous Secretions.**—The secretion in the epithelium of the vesiculæ and glands, is, according to Bishop, discharged by a constriction of the ends of the cells accompanied by the dissolution of the cell substance. Bishop says:

> The dense granular area at the tip of the cell widens, the granules increase in size, in refractiveness, and in density of staining, and finally vacuoles may appear among them. The end of the cell rounds up into a globule of secretion, which sloughs off into the lumen of the organ. This process is most pronounced in the gland, where the secretion retains its coarse granular character. These granules are transformed to highly refractive globules of somewhat larger size, as if by absorption of some of the fluid; the mass of the secretion at the same time becomes more viscous. In the seminal vesicle the granules are smaller and soon dissolve to a pale plasma. In the narrow portions of the vas deferens, at either end of the vesicle, neither the granulation nor the strangulation are apparent.

This method of secretion results in a shrinkage in the size of the epithelial cells and a consequent enlargement of the cavities of the organs, the change progressing from before backward. Bishop says:

> When the process has reached an advanced stage, it leaves the walls of the organs characteristically sculptured. In the gland the cells entirely disappear anteriorly, leaving a very thin membranous bulb-like

sac which expands with mucous secretion. Posteriorly . . . the ends of the cells protrude into the gland's lumen in fringed and ragged patches.

In the vas deferens and seminal vesicle the effect is more elaborate. Commencing at the anterior end of the vas deferens the cells break down unevenly and in such a manner as to leave the surface of the epithelium in very definite ridges. This is much more clearly defined and regular here than in the gland. This condition is described in the mature insect by Koschevnikov as "in Ringwalzen eingereiht;" but a close inspection of a cleared whole mount or hemisection reveals an arrangement as of a spiral screw with four successive threads. There are about 70 turns, each "thread" making 15 to 20 turns of the spiral, though occasionally one ridge ends and is replaced by a new one. As will appear later the function is apparently to increase the surface for attachment of the spermatozoa.

The commencement of this secretory and erosive process in the vas deferens overlaps the period of spermiogenesis in the testis. As the lumen enlarges it becomes filled with fluid. The sperms pass into it and through it into the seminal vesicle; here as the sperms descend the cells also break down into a secretion. This process in the seminal vesicle serves three purposes: provides a medium for the spermatozoa by dissolution of the glandular elements, renders the rather firm glandular wall flexible and capable of considerable distention, and allows the enclosing muscles to act easily at the time of ejaculation of sperm.

The sperms, still grouped in bundles as they left the cysts of the testicular tubules, attach themselves by the heads to the ribbed surface of the vesicle, and the tails project into the lumen. When spermiogenesis is complete and all the sperms have become attached, a cross-section of the organ shows, inside the muscular ring, first a ring of nuclei following the contour of the inner surfaces of the spiral ridges, then a distinct line of sperm heads at the surface of the epithelium, and finally the remainder of the lumen almost filled with the sperm filaments radially arranged, extending outward from a narrow central space. The spermatozoa even after attachment show a grouping into bundles.

The contents of the vesiculæ seminales now consist, according to the description of Bishop, of a very little lymph-like fluid densely packed with spermatozoa. The spermatic fluid, he says,

. . . mixes readily with any bland aqueous medium, salt, sugar, or lymph solution, but any dilution seems to decrease the activity of the sperms for a long time, though without necessarily killing them. Sperms on a slide under a cover-glass in salt solution were not killed by two hours' contact with ice, and fertile females have been frozen to −2° C.

for fifteen minutes without rendering subsequently laid eggs infertile. The spermatic fluid and the glandular secretion are miscible in the penis before exposure to the air, and the sperms are intensely activated by the secretion of the gland. Particles of the vesicular wall stimulate them similarly.

The accessory glands continue to increase in size, Bishop states, during the first nine days after the emergence of the drone. "The secretion changes in character from fluid to viscous, and acquires increasingly the property of immediately coagulating to a tough, cheesy or doughy mass." It is slightly alkaline in reaction and, in contrast to the spermatic fluid of the vesiculæ, coagulates on contact with air or water or any bland reagent.

**The Ejaculatory Duct.**—The ejaculatory duct (Fig. 93 A, *EjD*) is a long slender tube reaching from the anterior end of the inverted penis (*Pen*) posteriorly to the united tips of the mucous glands. Being of ectodermal origin the inner surface of the duct is lined with thin cuticula. Its walls have no muscles. Its anterior end divides where it comes in contact with the junction of the two mucous glands and a short branch penetrates the muscular wall of each. Around and particularly just anterior to the orifice of the vas deferens, Bishop (1920) says, "The muscular wall of the gland is greatly thickened, and projects into the gland's cavity as a lip or valve guarding the entrance of the vas deferens." This valve cuts off a posterior pocket of the lumen of the gland. The vas deferens opens into the dorsal wall of the pocket and the corresponding branch of the ejaculatory duct applies itself to the floor of the pocket directly beneath the orifice of the vas deferens. Bishop shows very good evidence for believing that there is never any communication established between the cavities of the glands and the lumen of the duct prior to the time of copulation, and that the openings are then produced as ruptures of the thin separating walls caused by the violent contraction of the muscles about the bases of the glands. This contraction at the same time brings the mouths of the vasa deferentia against the openings newly formed into the duct. Zander (1911), on the other hand, claims that all the spermatozoa are forced through the ejaculatory duct and into the bulb of the penis (Fig. 93 E, *PenB*) during the first days after the emergence of the drone, and that here, with mucous from the accessory glands, they form a sperm packet ready for discharge. Bishop, however, says that

. . . in a young drone (up to four or five days) the chitinous blind end of the ejaculatory duct is still reinforced with layers of glandular and hypodermal cells; the walls of both mucous gland and seminal vesicle are stiffened with unresolved glandular epithelium; the sperms are either still in the testis tubules or are firmly attached to the vesicular wall, and are incapable of the activity which later characterizes them. After the fifth or sixth day, the reinforcing cells over the end of the ejaculatory duct have withdrawn; the mucous is more viscous; the sperms release themselves more and more readily from the vesicle and are extremely active; the glandular walls of the organs are thin and pliable, and the sperm content of the vesicle is discharged through the ejaculatory duct ahead of the mucous content of the accessory gland.

According to the investigations of Bishop, then, the spermatozoa and seminal fluid and the mucous "remain in their respective receptacles until copulation, and do not mingle before that time." Finally, he demonstrates by fresh dissections of drones, in which the organs are stimulated to activity, that it is sometimes possible actually to see the mucous of the glands following the sperm down through the ejaculatory duct; and he claims that a microscopical study of such specimens killed immediately "shows that in the base of the gland the mouth of the vas deferens has been forced against the blind end of the ejaculatory duct."

**The Copulatory Organ.**—The penis (Fig. 93 A, *Pen*, E) is an unusually large structure in the bee and is ordinarily inverted and thus concealed within the cavity of the abdomen. Morphologically it is an ectodermal outgrowth of the invaginated ventral part of the ninth abdominal segment, and when it is everted it protrudes from this segment (D) beneath the anal opening. The surrounding parts, including the claspers (1*Clsp* and 2*Clsp*) have already been described in connection with the external anatomy (page 112). The walls of the penis present a number of curious differentiations. The part which is innermost in the inverted condition is enlarged into a bulb (A, *B*, E, *PenB*) having two large irregular but symmetrical chitinous plates (*g*) in its dorsal wall, beneath which is a thickening of the wall having a gelatinous consistency (B, *h*). Posterior to the bulb the penis is more tubular. A double pinnate lobe (A, E, *f*) projects from the dorsal wall of this part near the base of the bulb; below this, on the ventral wall, is a series of close-set, transverse plates (E, *e*); and below these are large dorsal and ventral plates (*d* and *c*). The terminal part of the inverted penis

forms a thin-walled chamber (A, E, *a*), from which project posteriorly and dorsally two very large membranous pouches known as the *pneumophyses* (*b*).

The entire penis is capable of being turned inside out, and when thus reversed the end of the ejaculatory duct everts beyond the bulb, and the exposed lumen of the duct becomes the terminal orifice of the penis. Both Shafer (1917) and Bishop (1920, 1920*a*) show that a complete eversion of the organ most probably takes place during copulation. At the same time the several hollow lobes (*f* and *b*) are also reversed and project from the external surface. The probable action of the different parts of the penis will be discussed in connection with the description of the female organs. The penis has no muscles in its walls nor any attached to it; its eversion is accomplished by the contraction of the abdominal walls and the resulting pressure of the blood and surrounding tissues upon it.

## 2. THE FEMALE ORGANS

The several parts of the reproductive system of the female are separable, as are those of the male, into two groups of organs according to their origin in the embryo from the mesoderm or the ectoderm. The first group includes the *ovaries* and the *oviducts*. The ovaries are the female organs that correspond with the male testes, being those in which the female germ cells undergo most of their development into mature eggs. The oviducts are the conduits from the ovaries corresponding with the vasa deferentia of the male. The second group includes the *bursa copulatrix*, which is an external pouch, the *vagina*, analogous to the ejaculatory duct of the male, and the *spermatheca* or receptacle for the spermatozoa. The organs of the second group, being derived from the ectoderm by invagination of the body wall, consist of an epithelium continuous with the hypodermis, and are lined with a cuticular intima continuous with the external covering of the body wall.

**The Ovaries.**—In insects the ovaries consist of two groups of egg tubules, the *ovarioles*, that diverge from the anterior ends of the two oviducts. The tubules taper to narrow threads at their anterior ends where those of each group unite into a single terminal thread, which is attached to the ventral wall of the heart. The number of egg tubules in the ovaries differs much in different species of insects. In the queenbee (Fig. 94, *ov*) there

is a large number of them in each ovary (*Ov*), the two groups forming two gourd-shaped masses having their distal, curved

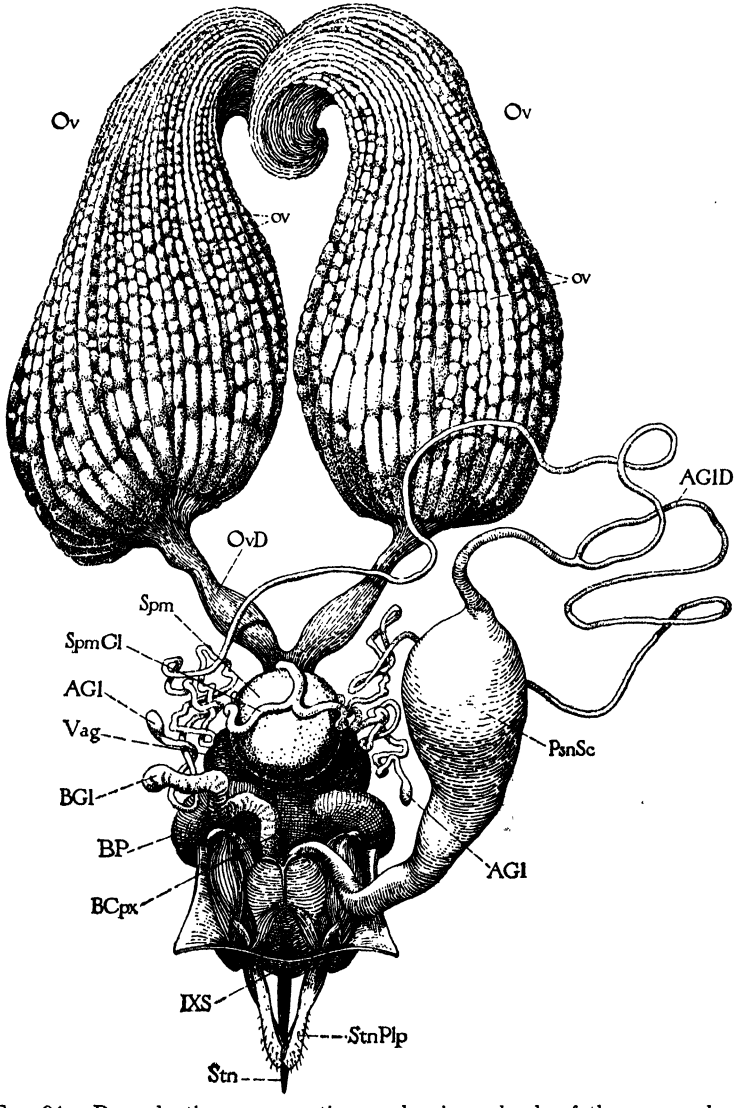



FIG. 94.—Reproductive organs, sting, and poison glands of the queen, dorsal view.

ends attached to each other. According to Nelson (1915) the ovaries of the honeybee arise from mesodermal cells that form

two ridges in the dorso-lateral parts of the body from the second to the seventh segments of the abdomen. Later these *genital ridges* separate from the surrounding mesodermal tissues and become invested in an epithelium, also of mesodermal origin, and this, toward the end of the embryonic period, becomes attached to a ventral ridge of the heart.

Each ovariole (Fig. 94, *ov*) is a long slender tube throughout most of its length, the walls of which consist of a single layer of cells invested in a thin membrane; only the extreme upper, thread-like end has no lumen and consists of a solid row of cells. The tube gradually enlarges in diameter posteriorly and presents a continuous series of swellings which increase in size from before backward. These swellings are due to the contained eggs in successive stages of development together with their accompanying nutritive cells. Since the queenbee lays eggs throughout a long period of time, her ovaries always contain eggs in all stages of growth, and consequently the ovaries of different individuals do not differ so much in appearance as they do in those insects that ripen their eggs in several lots or all at the same time. The details of the structure of the ovarioles and the growth of the eggs within them will be described in the next chapter.

**The Oviducts.**—The oviducts (Fig. 94, *OvD*) are wide tubes receiving the ovarian tubules into their anterior ends. They enlarge posteriorly and converge to open into the anterior end of the median ectodermal duct or vagina (*Vag*). Their inner walls are thrown into folds which allow ample distension to accommodate the eggs, and their outer surfaces are covered with a sheathing of very fine lengthwise muscle fibers.

**The Vagina.**—The vagina (Fig. 94, *Vag*) is a short wide tube lined with cuticula and covered externally by thick muscle layers. It opens posteriorly by a transverse orifice into the anterior wall of the bursa copulatrix (*BCpx*). Its posterior part is flattened, its middle part enlarged, and its anterior part narrowed. An opaque globular sac, the *spermatheca* (*Spm*), and its two associated tubular glands (*SpmGl*) open by a short duct (Fig. 95 A, *d*) into the dorsal wall of the middle part of the vagina. A detailed description of the three regions of the vagina is given by Bishop (1920*a*). The first, he says, is flattened dorsiventrally and opens into the bursa, from which it is separated by a very definite constriction; the middle region, with the orifice of the spermathecal duct in its dorsal wall, has a prominent tongue-

like organ arising from its floor; the anterior part receives the two oviducts into its distal end and has a narrow median groove on its floor which deepens anteriorly where it extends slightly beyond the apertures of the oviducts to terminate in a short blind pocket projecting between them.

**The Copulatory Pouch.**—The bursa copulatrix is the wide cavity at the anterior end of the sting chamber in the end of the abdomen. The base of the sting is lodged within it and its shape is modelled to fit over the somewhat bilobed form of the sting base. Its lower lip forms a free fold across the floor of the sting chamber above the seventh abdominal sternum, and its side walls are continuous with the anterior edges of the spiracle-bearing plates of the eighth tergum (see Fig. 56, *VIIIT*), though the parts are somewhat different in shape in the queen from those of the worker, and the bursa does not show in this drawing of the worker. The bursa is therefore to be regarded as an invagination either of the eighth sternum or of the intersegmental membrane between the seventh and eighth sterna. At the middle of its anterior vertical wall there is a wide, transverse, thick-lipped opening. This is the orifice of the vagina. On either side of the vaginal orifice and below it are two other slit-like apertures. These open into a pair of large pouches which form two flat, bean-shaped lobes (Fig. 94, *BP*) standing out in the body cavity from the sides of the bursa and meeting below it. The rear surfaces of these pouches are membranous, but their anterior walls are covered with heavy layers of thick muscle fibers extending from the base to the crest on each. Otherwise the walls of the bursa have no muscles.

**Mating.**—The mating of the honeybee is always accomplished during flight high in the air, and consequently the actual process has not been observed. The copulatory organ of the male, however, holds so firmly in the genital orifice of the female that it is torn away from the male and remains in the queen until it is extracted by workers in the hive. From a study of the structure of the male and the female organs Bishop (1920*a*) describes the probable function of the parts of the male organ in copulation as follows:

> The pneumophyses first dart into the bursa pouches, and by their expansion depress the ventral floor of the bursa, and thus pull open the vaginal orifice. As the next region of the penis, the median tubular portion with its modifications, proceeds to unfold, the pneumophyses

are forced back and withdrawn, opening the vagina as they retract to the widest possible extent, and probably allowing this tubular section to enter the orifice temporarily. If the contraction of the drone's abdomen is violent enough to cause the eversion of the bulb, the medial tubular section must be withdrawn for the bulb itself is too large to be able to enter the vagina. Its size, however, serves to keep this orifice open until the final portion, the tapering end of the ejaculatory duct adjoining the bulb, everts through the bulb and enters the vagina.

The long pneumophyses of the drone do not correspond at all with the transversely widened, bean-like shape of the bursal pouches, but this may be no argument against the idea that they act as supposed in the above description.

The studies made by Bishop on the disposal of the male fluids in the female corroborate the inference he deduces from the structure of the male organs, that the mucous of the accessory glands and the spermatic fluid of the seminal vesicles do not mix when discharged. The mucous has two functions: First, by following the spermatozoa in the spermatic fluid, it forces the latter into the anterior part of the vagina and into the lower ends of the oviducts; and second, by coagulating instantly in the torn end of the copulatory organ of the male, it prevents the backward escape of the secretion when this organ is detached. Bishop says:

> The bulk of the sperms have entered the spermatheca within four and one-half hours after copulation; practically all of them may enter within six and one-half hours. Their manner of getting there has not been determined, though their progress is not altogether passive, and it is possibly guided by a chemotaxis.

**The Spermatheca.**—The organs of special interest in this connection to students of the honeybee are those by which the queen is able to give out the spermatozoa to the eggs as they pass through the vagina, or to withhold them, for on this potency of the queen depends fertilization or nonfertilization of the eggs, and therefore the determination of the sex of the bees that are to hatch from the eggs. The apparatus that controls the discharge of the spermatozoa is a part of the duct of the spermatheca.

The spermatheca and its accessory parts include the globular seminal sac or spermatheca proper (Figs. 94, 95 A, *Spm*), a pair of tubular glands (*SpmGl*) and the spermathecal duct (Fig. 95 A, *d*). The distal end of the duct connects with the sac and receives

also the duct of the glands (*b*); its proximal end opens into the roof of the middle part of the vagina (*Vag*). The same duct serves both as entrance and exit for the spermatozoa. The latter, as already described, eventually make their way into the spermathecal sac, from which they are given out again in small numbers to the eggs. When the supply is exhausted, the queen becomes infertile and her eggs can develop only into drones; but usually before an old queen reaches this stage she is replaced

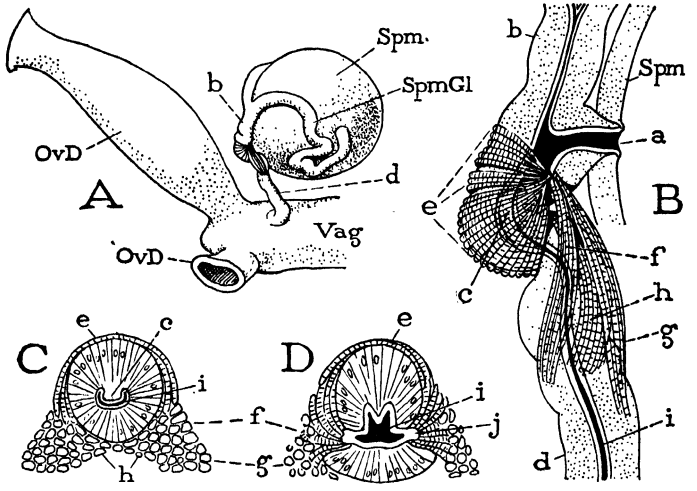



FIG. 95.—Structural details of spermathecal pump of queen (*from Breslau*, 1906.) A, anterior end of vagina (*Vag*) with right oviduct and base of left oviduct (*OvD*, *OvD*), showing spermatheca (*Spm*), its glands (*SpmGl*), and its duct (*d*) opening into dorsal wall of vagina. B, upper end of spermathecal duct, showing orifice (*a*) into spermatheca, and muscles on its surfaces. C, cross-section through upper part of duct showing fold (*c*) of its anterior wall. D, section of duct through muscle attachments.

*a*, orifice of spermathecal duct into spermatheca; *b*, duct of spermathecal glands; *c*, fold of anterior wall of spermathecal duct; *d*, spermathecal duct; *e*, semicircular muscles on upper curve of spermathecal duct; *f*, *g*, longitudinal muscles inserted laterally on upper end of spermathecal duct; *h*, longitudinal muscles inserted on posterior surface of spermathecal duct beneath upper loop of S-shaped curve.

in the hive by a young queen newly fertilized. The spermatozoa, however, remain alive in the spermatheca throughout the lifetime of the queen, which is ordinarily about four years.

It has been shown by Breslau (1906) that the spermathecal duct is formed in such a way that a part of it constitutes a *sperm pump* for the discharge of the spermatozoa from the sac. The upper part of the duct, just below its entrance into the sperm sac (Fig. 95 B, *a*), makes a large S-shaped bend, of which the

dorsal loop is much more strongly convex than the ventral. The lumen of the main tube (*i*) receives the lumen of the duct of the glands (*b*) at the upper end of the S and then turns abruptly backward as a wide passageway to the orifice (*a*) in the spermatheca (*Spm*). The lumen in the upper bend of the S has a deep fold (*c*) projecting from its convex forward wall, which reduces it to a narrow transverse crescentic slit (C, *i*).

Several sets of muscles are disposed upon the outer surface of the curved part of the duct. One set consists of a single layer of semicircular fibers separated into three groups but together forming a cap (Fig. 95 B, *e*) over the convex side of the upper loop of the S. The ends of these fibers converge on each side where they are attached to a chitinous ridge on the outer surface of the duct. Each ridge is a thickening of the cuticular intima over a pocket-like extension of the lumen of the duct (D, *j*), and the muscles of the duct are attached directly to it just as the skeletal muscles are attached directly to the cuticula of the body wall (Fig. 63). The other muscles are stretched lengthwise along the sides and the rear surface of the S part of the duct but do not follow its curvatures. They comprise two paired lateral muscles and one median muscle. The two lateral muscles (B, *f*, *g*) arise from the outer wall of the duct at the lower end of the S and go upward to be inserted on the same chitinous ridge (D, *j*) to which the ends of the semicircular muscles are attached. The median muscle (B, *h*) lies against the rear wall of the duct and arises also below the lower bend of the S, where its edges are visible on each side between the ends of the lateral muscles (*f*, *g*). It is inserted on the posterior surface of the duct at the upper end of the lower loop of the S.

The semicircular muscles are termed the *compressors* by Breslau, the paired lateral muscles the *flexors*, and the single median muscle the *extensor*. Breslau's idea of the working of the pump is as follows: The contraction of the flexors (B, *f*, *g*) pulls the ends of the S together and increases the curvature, especially that of the upper loop, and thereby expands the lumen in this part of the duct. The fold (*c*) in the anterior wall of the lumen being thus lifted acts as a piston and sucks a small bundle of spermatozoa into the upper end of the duct (*a*) from the spermatheca (*Spm*). A contraction now of the extensor (*h*) flattens the bend of the S and the fold (*c*) again closes the lumen. A simultaneous contraction of the semicircular compressors (*e*), especially if their fibers act

in succession from above downward, would then drive the sperm through the duct into the vagina below. The sperm in the extreme upper end of the duct, however, would be driven back into the spermatheca, and thus the apparatus would appear to regulate the number of spermatozoa discharged at each stroke of the pump and to reduce their number to a minimum. Breslau claims, furthermore, that the action of the sperm pump can be demonstrated by means of sections through the organs of queens killed at successive periods of egg-laying. Such sections, he says, show all the stages of the pumping process and the passage of the sperm through the duct as above described.

Another idea of the mechanism of the sperm pump is given by Adam (1913), who, though he accepts Breslau's description of the structure of the apparatus, believes that the curvature of the S and the dilation of the duct is maintained by the elasticity of the thick cuticular lining of the duct. All the muscles, according to Adam, act as compressors; the sperm are sucked into the duct by its automatic distension when the muscles relax, and a successive contraction of the three sets of muscles from above downward drives the sperm through the duct into the vagina. Cheshire calculated that the sperm sac holds only about four million spermatozoa, and concluded that the queen could not spare more than four to each fertilized egg. Breslau did not believe that the pump could select such a small number, and suggested 75 or 100 sperm discharged on each egg as a more likely number. Adam, however, would again reduce the estimate to 10 or 12 which he thinks are as many as the pump can deliver at one time. A point of more interest, however, than matters of detail concerning the exact mechanism of the pump or the precise number of spermatozoa discharged at each stroke would be some information on how the queen controls fertilization. So far as we know at present the working of the sperm pump depends upon the "will" of the queen, though some future investigator may find an explanation more in harmony with modern insect psychology which reluctantly concedes voluntary acts to insects.

Immediately beneath the orifice of the spermathecal duct in the roof of the vagina there is a tongue-like elevation on the floor of the vagina having its free end directed posteriorly. Though Breslau regarded this structure as a valve to prevent an upward suction in the duct from the vagina when the sperm pump is in action, it seems more reasonable to accept the explanation of

Adam that the tongue is rather for the purpose of holding the egg, while on its way through the vagina, close against the orifice of the spermathecal duct in order to insure the discharge of the sperm upon its upper end. The "upper" end of an insect's egg is that end which was anterior in the ovary, and is the one on which is located the *micropyle* or pore in the shell through which the spermatozoa must enter the egg. Adam points out that the nonfertilization of an egg in the bee must depend on the simultaneous cessation of activity by the sperm pump and relaxation of pressure by the tongue. A muscle inserted within the tongue apparently acts as a depressor. The accidental fertilization of an egg now and then may account for the occasional "mistake" made by queens of placing a fertile egg in a drone cell. There is no reason to doubt, however, as we shall see in the next chapter, that all bee eggs that develop form males if they are not fertilized, and females if they are fertilized.

**Number of Eggs Laid by One Queen.**—Various ideas on the number of eggs laid by the queen have become fixed in the minds of beekeepers from time to time and have passed as authentic with little or no evidence based on actual observations of the performance of an individual queen. Earlier writers estimated the daily output of a single queen at from 3,000 to 6,000 eggs, and Cheshire (1886) calculated that a queen may lay as many as 1,500,000 eggs during her lifetime. Recent investigators, however, find that the daily average number of eggs laid by a queen in the prime of her life and during the height of the egg-laying season, which is during the greatest honey flow, is not more than 2,000. Nolan (1924), for example, using a photographic method of study in which counts of all sealed brood were made over twelve-day periods (twelve days being the average time during which worker brood remains sealed) reports a maximum average daily record of 1,908 eggs. This represents the output, during the greatest honey flow, of a queen mated the year before. For 26 days the same queen maintained a daily average of not less than 1,640 eggs. Records from other queens give a daily average of from, 1,587 to less than 1,000. Other recent investigators, whose work is reviewed by Nolan, obtained daily averages ranging from 1,468 to 857.

The actual number of eggs that a queen may lay on one day very probably exceeds these figures, but in any case the number

recorded cannot represent a daily average during the season, because, as Nolan points out, there is a remarkable correlation between the number of eggs laid and the honey flow, and the records were all made during the maximum honey flow. In an earlier study Nolan found the daily average number of eggs for the entire season but slightly over 900.

# CHAPTER XII

## DEVELOPMENT: FROM GERM CELLS TO LARVA

In describing the anatomy of the adult bee it has been necessary to make frequent reference to the origin of the different parts in the embryo in order to explain clearly the structure and relationships of the organs in their final form. The facts of anatomy are dependent on embryology for correct interpretation. This chapter on the development of the bee is, therefore, included for reference, and the student will find it profitable to read it in connection with the preceding chapters, or along with his studies of the adult bee.

Since development depends on the multiplication of cells by division and starts, in most cases, with the union of two cells from individuals of opposite sex, we should understand the structure of a typical cell, the manner of its division, the evolution of the germ cells, the difference between male and female cells, and the processes involved in fertilization, before taking up embryology, which has to do with the development of the form and parts of the body. Furthermore, the germ cells of bees depart from the usual in several of these respects, drones, for example, develop from unfertilized eggs, and hence it becomes necessary to know the "normal" activities of typical reproductive cells before studying the activities peculiar to these cells in bees.

### 1. GENERAL DESCRIPTIONS

The subjects treated in this chapter involve so many things not included in general anatomy that a few preliminary descriptions on the structure of a cell, its methods of multiplication, and the processes of maturation and fertilization in germ cells will probably make it more readable to those who are not specialists in these subjects.

**The Structure of a Cell.**—Cells are the anatomical protoplasmic units of living matter. All the tissues of the body of an animal or a plant either consist of cells or are secreted by them. Most cells are of microscopic size too small to be seen by the naked

eye; they have various shapes in different tissues, but a free cell not influenced by pressure from surrounding cells is usually oval or elliptical (Fig. 96). Each is surrounded by a *cell wall* (*a*) and contains a smaller body known as the *nucleus* (*Nu*). The protoplasm of the body of the cell is called the *cytoplasm*, and in this there is generally to be distinguished a denser, clear outer or cortical layer, the *ectoplasm* (*b*), and a darker, more liquid inner part, the *endoplasm* (*c*). Both parts may be of a granular texture, but in typical cells the endoplasm is traversed by fine strands of *spongioplasm* (*d*) forming all through its substance a network or *reticulum*. The cytoplasmic liquid, or

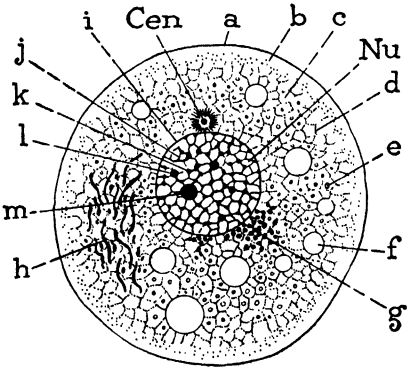



FIG. 96.—Structure of a cell.

*a*, cell wall; *b*, ectoplasm; *c*, endoplasm; *Cen*, centrosome; *d*, network or reticulum of spongioplasm; *e*, granule of deutoplasm; *f*, liquid globule; *g*, chromidia; *h*, mitochondria; *i*, nuclear membrane; *j*, network of linin threads; *k*, net-knot; *l*, karyosome; *m*, nucleolus; *Nu*, nucleus.

*hyaloplasm*, within the meshes of the reticulum may contain small bodies (*e*) of nutritive material or *deutoplasm*, such as yolk, or it may contain grains or liquid globules (*f*) of materials elaborated within the cytoplasm. Often there are small particles called *chromidia* (*g*) which appear to be extrusions from the nucleus into the cytoplasm where, as in the fat cells, they may form the basis for certain cell products. Other bodies in the cytoplasm are known as the *mitochondria* (*h*). These usually have the form of irregular grains or threads, and they appear to have intimate relations with many of the cell activities, though their nature and functions are as yet not well understood. Finally, the cytoplasm of normal cells may contain pigment granules and foreign bodies, even living organisms resembling bacteria, yeasts, and protozoa.

The nucleus (*Nu*), which is ordinarily separated from the cytoplasm by a *nuclear membrane* (*i*), is the most important part of the cell from the standpoint of reproduction, because the division of the cell depends upon special activities which take place within it. The protoplasm of the nucleus is distinguished as the *nucleoplasm* or *karyoplasm*, and it contains a reticulum of strands called *linin threads* (*j*) perhaps continuous with the strands of the cytoplasmic reticulum. In stained cells the nucleus is usually characterized during periods of inactivity by a speckled appearance due to scattered grains and masses of a substance known as *chromatin*, so-called on account of its affinity for basic dyes. The smaller particles attached to the intersections of the linin threads are called *net knots* (*k*), larger ones are designated (*karyosomes* (*l*), and still larger masses form one or more conspicuous *nucleoli* (*m*).

In the cytoplasm just outside of the nucleus there is a body known as the *attractive sphere* which appears to direct the activities of the nucleus in most cases during cell division. This body consists of a central granule, the *centrosome* (*Cen*), which sometimes contains a still smaller *centriole*, of a clear *centrosphere* surrounding the centrosome, and of an outermost zone of radiating lines, the *astral rays*. The centrosome sometimes breaks up into a number of small granules that scatter through the cytoplasm.

**Cell Division.**—Cell division may take place by two methods, one known as *mitosis*, the other as *amitosis*. The second is the simpler and more direct method, consisting principally of a separation of the nucleus into two parts, followed by a corresponding constriction and division of the cell. The centrosome plays no part in this form of division. The process of mitosis is the usual method by which cells divide. It involves activities of the directive spheres and complicated changes in the nucleus which, briefly, are as follows: The centrosome divides (Fig. 97 A, *Cen*) and the two halves, each with its own corona of rays, move to opposite sides of the nucleus (B); the nuclear membrane disappears and opposing rays from the centrosomes form a spindle through the nucleoplasm. At the same time the larger chromatin masses disintegrate, the scattered grains assemble into a long, twisted strand, the *spireme* (A, *Spi*), this strand then breaks up into pieces called *chromosomes* (B, *Chr*), and these arrange themselves in an equatorial plane across the middle of the astral

spindle (C). Now each chromosome splits lengthwise into two equal pieces and the halves move toward opposite centrosomes (D), where soon all are assembled in two compact groups (E), which are to become the two new nuclei. The chromosomes of one nucleus are counterparts of those of the other since each is derived from half of a chromosome of the original nucleus. A layer of granules next appears across the middle of the spindle, the cell constricts opposite to it (E) and then divides through this plane (F), resulting in the production of two new cells, each with a nucleus and a centrosome. The chromosomes finally break

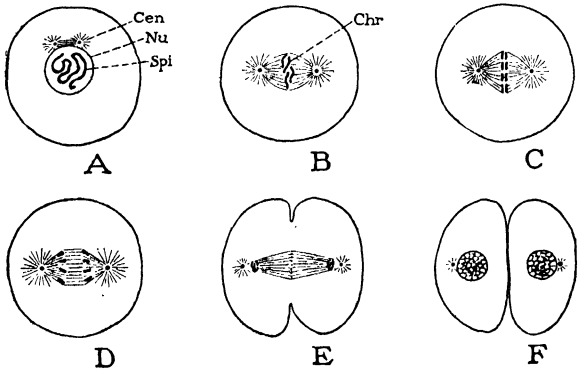



FIG. 97.—Diagram of mitotic cell division.

A, chromatin of nucleus (*Nu*) assembled in a spireme (*Spi*), centrosome (*Cen*) divided and halves moving apart.

B, nuclear membrane has disappeared, centrosome rays form spindle through nucleus, spireme broken into chromosomes.

C, chromosomes in equatorial plane of spindle, and each split into two.

D, chromosome halves moving toward opposite centrosomes.

E, two new nuclei forming, each with full number of chromosomes, cell constricting between them.

F, cell completely divided, nuclear membranes re-formed, chromatin dispersed in each nucleus.

up again into small masses and grains which scatter through the nuclear reticulum as in the resting cell before mitosis began (Fig. 96). The remnants of the spindle shrink to form a body called the *spindle-remains* or *interzonal body*, a part of which may remain outside the cell or be extruded from it.

**Maturation.**—The above description applies in general to all mitotic cell divisions except to one that takes place with the reproductive or germ cells during the course of their development into spermatozoa and eggs, in which the spireme breaks up into less than the typical number of chromosomes. This is therefore known as a *reduction division*. Here, now, it will be necessary to

explain two things: first, that though the number of chromosomes in the cell nuclei vary in different species of animals, they are usually constant and characteristic for each; and second, that the cells of male animals generally have an odd number of chromosomes and one less than the cells in the female of the same species, or occasionally the same number but of which one is much smaller than the others. The chromosomes usually have individual shapes and sizes and ordinarily a pair of chromosomes in the female corresponds with the odd chromosome of the male. These in both sexes are distinguished as *accessory chromosomes*, *heterochromosomes*, or as the *x-chromosomes*. The others are the *orthochromosomes*. Preceding a reduction division, only half the ordinary number of orthochromosomes is formed; the *x*-chromosomes remain as before. When division takes place, moreover, the *x*-chromosomes do not divide. The result is, therefore, that each of the new female cells has just one half the original number of chromosomes, including one *x*-chromosome, but that, while one of the male cells has the same reduced number of chromosomes as the female cells, the other has one less since it lacks an *x*-chromosome. A second division follows immediately after the reduction division, but this one is of the ordinary sort, accompanied by a splitting of all the chromosomes. These two divisions of the germ cells are known as the *maturation divisions*, since after their completion the male cells are ready to become spermatozoa, and the female cells are ready for fertilization. All the matured germ cells have the reduced number of chromosomes, and the spermatozoa are of two kinds according to whether they have an *x*-chromosome or not. Otherwise the process of maturation is essentially the same in the two sexes, but the final results differ again since in the male all of the cells usually develop into functional spermatozoa, while in the female only one of each four produced from the original cell develops into an egg, the others being minute rudimentary cells known as *polar bodies*, which are either extruded from the egg or absorbed within it. With insects, however, some of the sperm cells also are degenerate in some species, and in bees only one spermatozoon develops from the maturation of each drone germ cell.

**Fertilization.**—Fertilization consists of the union of a maturated egg nucleus with a maturated sperm nucleus (Fig. 98 A). The fertilized eggs, therefore, are necessarily of two sorts, female and male, according as they happen to contain the full even number

of chromosomes or the full odd number of chromosomes, the two kinds of spermatozoa are hence known as male-determining and female-determining sperm. But here again the honeybee (Fig. 98 B) departs from the usual (A), and both maturation and fertilization become complicated by the fact that the bee's eggs will all develop parthenogenetically, *i.e.*, without fertilization. Therefore the student should first thoroughly understand the usual or "normal" processes and for further details should consult some up-to-date text on histology.

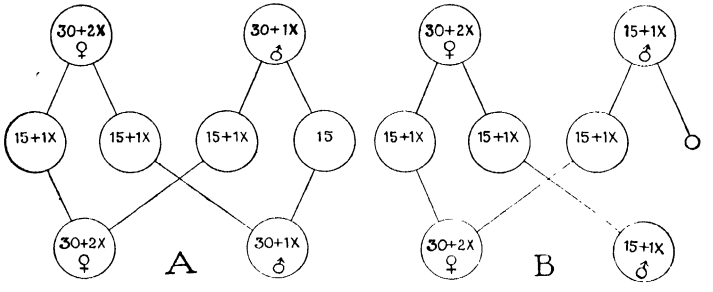



FIG. 98.—Diagram of reduction of chromosomes in maturation, and difference between fertilized and unfertilized parthenogenetic eggs.

A, usual maturation reduction of chromosomes in egg cell with 32 chromosomes, and sperm cell with 31 chromosomes, and normal fertilization resulting in female and male eggs.

B, maturation in honeybee resulting in chromosome reduction in egg cell, but not in sperm cell. All eggs being potentially parthenogenetic after maturation, unfertilized eggs can produce only males, fertilized eggs produce females.

### 2. FROM GERM CELLS TO EGG IN THE BEE

The cells that are destined to form new individual insects are lodged in the upper ends of the egg tubes of the ovaries in the female, and in the sperm tubes of the testes in the male. The primitive germ cells must in each case, however, undergo a growth and special processes of development before they become functional ova or spermatozoa. The process in the case of the egg cells involves *oogenesis* and *maturation;* in the case of the male cells it involves *spermatogenesis*, *maturation*, and *spermiogenesis*. The production of a new individual ordinarily requires the union of a spermatozoon with an ovum; the ovum, however, may develop independently, the spermatozoon never does.

**Oogenesis.**—The ovarioles or egg tubes of the ovary of the adult queenbee (Fig. 94, *ov*) are slender tubules, the walls of which consist of a single layer of small flat epithelial cells. According to Paulcke (1901) the extreme upper part of each tubule is

filled with a multinucleate protoplasmic mass in which cell boundaries are not visible. But a little farther down lines appear between the nuclei; and sections of a tubule (Fig. 99 A) show, enclosed in a distinct epithelial sheath (*Epth*), a solid series of narrow transverse cells (*Oog*), each with one distinct chromatin granule in its nucleus. These cells are the *primary oogonia* (*Oog*),

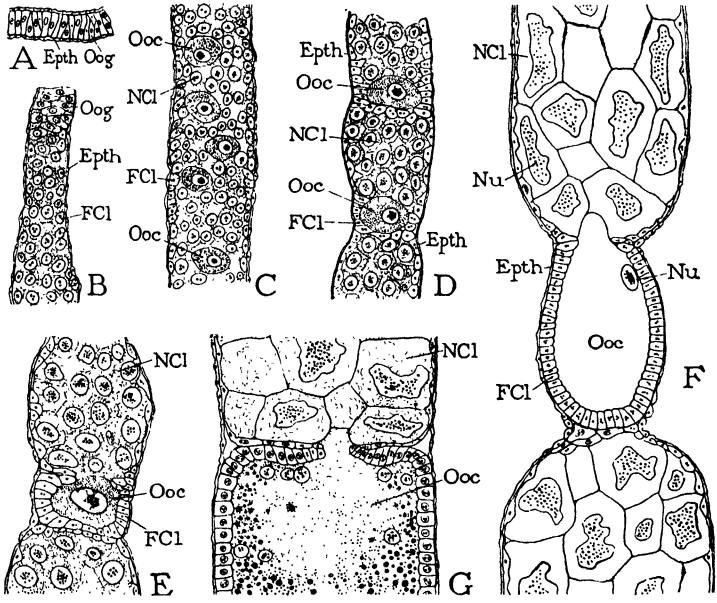



FIG. 99.—Oogenesis in the queen honeybee.

A, upper end of an egg tubule of ovary, showing epithelial sheath (*Epth*) and undifferentiated oogonial cells (*Oog*).

B, farther down in tubule, oogonia multiplied and differentiated into large central cells, and small follicle cells (*FCl*).

C, still farther down, central cells have become egg-cells or oocytes (*Ooc*) and nurse cells (*NCl*).

D, formation of follicles within epithelium (*Epth*) of tubule by follicle cells (*FCl*) surrounding group of nurse cells above (*NCl*) and egg cell (*Ooc*) below.

E, later stage, follicle divided by constriction into nutritive chamber containing nurse cells (*NCl*), and egg chamber containing egg cell (*Ooc*).

F, still later stage of same.

G, upper end of egg cell (*Ooc*) nearing maturity in lower part of egg tubule, and adjoining nurse cells (*NCl*).

or cells from which the eggs are to be formed. Still farther along in the tubule (B) the row of oogonia breaks up into an irregular mass of larger cells having polygonal forms, while the diameter of the tube increases to accommodate the added bulk of its contents. It is to be noted now, also, that there are two

sorts of cells in the tubule, smaller external ones (*FCl*) lying against the tube wall (*Epth*), and larger central ones with big, clear nuclei containing from one to three distinct chromatin granules. At first these central cells appear to be all alike except for differences in the number of granules in the nuclei, but beyond this part of the tubule some of them show an increase in size and have a single dense mass of chromatin grains in their nuclei. Next, these cells form an irregular row of large, oval, darkly stained bodies (C, *Ooc*) scattered through the middle of the tube, each easily distinguished from the surrounding cells by its size and by its large clear nucleus with a dark mass of chromatin. These cells are known as the *primary oocytes* (*Ooc*), being the first stage of the differentiated egg cells.

The eventual disposition and relation of the three kinds of cells now present in the egg tubules are seen in sections a little farther down (D). The egg cells or *oocytes* (*Ooc*) are here regularly spaced in each tube and the intervals between them are filled with the other central cells (*NCl*). The latter have also increased in size and their large clear nuclei now contain many dark grains. The small superficial cells (*FCl*) form capsules about the central cells, each enclosing an egg cell and the mass of cells between this egg and the one next above. These capsules are the *ovarian follicles*. The cells massed above the egg cell in each follicle are known as the *nutritive* or *nurse cells* (*NCl*) because they are destined to nourish the egg and finally to be absorbed by it. The follicle cells are particularly large and closely packed around each egg cell. In the ovarioles of the honeybee it appears that the three kinds of cells are all descended from the primary oogonia, though in some insects the follicle cells and the nurse cells are said to have an independent origin. In such cases the oogonia produce oocytes or egg cells only.

The follicles and their contents pass downward through the egg tubules as the new elements multiply in the upper ends of the latter. Soon the wall of each follicle forms a constriction between the contained oocyte and the mass of nurse cells (E), and this divides the follicle into an *egg chamber* and a *nutritive chamber*, except for a central opening left between the folds of the constriction. The nurse cells now grow rapidly and the nutritive chambers become much larger than the egg chambers (F). The follicle cells (*FCl*) form a thick columnar layer investing the egg cell (*Ooc*), but are drawn out into a thin sheet of attenu-

ated cells over the nurse cells (*NCl*). The large nuclei of the nurse cells become filled with many granules and take on strange, irregular shapes, but the egg cell nucleus preserves its oval outline and its single mass of chromatin. The upper end of the egg cell protrudes through the opening into the nutritive chamber as a blunt plug abutting against the adjoining nurse cells.

Next, a reversal in the relative sizes of the egg chambers and the nutritive chambers takes place, for not only does each oocyte increase rapidly in size but the accompanying mass of nurse cells decreases. Hence, beyond the middle of the tubes the egg chambers equal or surpass the nutritive chambers, while in the lower parts the eggs have acquired an enormous size and the nurse cells are reduced to mere remnants or have disappeared entirely. In later stages each oocyte acquires a great number of darkly staining yolk globules which fill its protoplasm except at the upper end, where there is always a clear space immediately behind the opening from the nutritive chamber (G). The position and appearance of this clear space suggests that it is due to an influx of finely granular matter from the nurse cells, and that the latter secrete and discharge a nutritive substance into the egg, as described by Paulcke (1901). The final disappearance of the nurse cells appears to be due to their total absorption into the oocytes when the latter reach the lower ends of the egg tubes, and during the later stages the oocytes always contain many small grain-filled globules which look like fragments of nurse cell nuclei. Paulcke says that large masses of the latter are to be found in the upper ends of the mature oocytes, but sections examined by the writer do not show this.

The final absorption of the nurse cells by the egg unites into one cell all of those that occupied a single egg follicle. Paulcke believes that all of these cells are produced from one original cell. According to his idea each primary oogonium of the queen-bee forms first four cells, by two consecutive divisions, one of which becomes an oocyte while the other three, by four consecutive divisions, produce 48 nurse cells, the approximate number in each nutritive chamber. When the oocyte is fully formed, the 49 cells are reunited into one which becomes the egg. Paulcke states that he never observed cell division by mitosis in the egg tubes, and he believed that this form of division did not take place in the germ cells of the bee, but Nachtsheim (1913) claims that mitosis may be observed in the cells differentiating in the

upper parts of the tubules, though division proceeds rapidly, and Hegner (1914) concludes from a review of the subject in other insects that amitotic division of the germ cells has not been demonstrated in any case. Nachtsheim says that the nuclei of the dividing oogonia appear to have only 16 chromosomes, but that in reality each is bivalent or double, as becomes evident later at the time of fertilization.

In the lower part of the egg tube each egg is invested in a thin coating of some tough substance supposed to be secreted by the follicle cells enclosing it. This forms the *chorion* or shell of the insect egg. The inner faces of the follicle cells are individually rounded and press into the egg surface, leaving their imprints on the chorion to be retained when the latter becomes dry and hard as a network of raised lines enclosing polygonal spaces (Fig. 103). The follicle does not close over the upper end of the egg until the nurse cells are absorbed, and here there is usually left a minute opening in the chorion. This pore is called the *micropyle.* Later it serves as an entrance to the egg for the spermatozoa. The eggs of some insects have several micropyles. At last the fully formed oocyte or egg breaks through the follicle, passes into the oviduct, goes down into the vagina, and so on to the exterior. What becomes of the follicle cells has not been noted, but they probably degenerate as the next egg and its follicle crowd down to take the place of the egg just discharged. For the present let us leave the egg in the oviduct while we trace the development of the male germ cells into spermatozoa.

**Spermatogenesis.**—The testes of the honeybee drone, as described by Meves (1907), consist each of a mass of many long cylindrical tubules, the upper ends of which contain small globular bodies, the *spermatocysts*, four to six of which are to be seen in cross-sections (Fig. 100 B). In the larva each cyst is filled with pyramidal cells that have their bases against the cyst wall and their inner ends converging at the center of the cyst where they are connected by granular masses (the interzonal bodies) extending from them. These cells are the *spermatogonia*, or cells from which the spermatozoa are to be evolved. All the spermatogonia of a single cyst appear to be descendents of one ancestral cell. Their origin in the bee, however, has not been observed, but it has been determined in other insects and is well described by Davis (1908) in the grasshopper. According to Davis all the spermatozoa of each cyst are derived from one cell,

and these original cyst cells or *primary spermatogonia* are arranged about an "apical cell" in the upper end of the tube. Each primary spermatogonium divides into a group of secondary spermatogonia, and these become surrounded by a cellular envelope to form a spermatocyst. The covering cells of the cysts are functionally analogous to the follicle cells of the egg tubes, and some investigators believe that they too are derived from the germ cells. But Davis says that in the grasshopper they are connective tissue cells of independent origin, since a

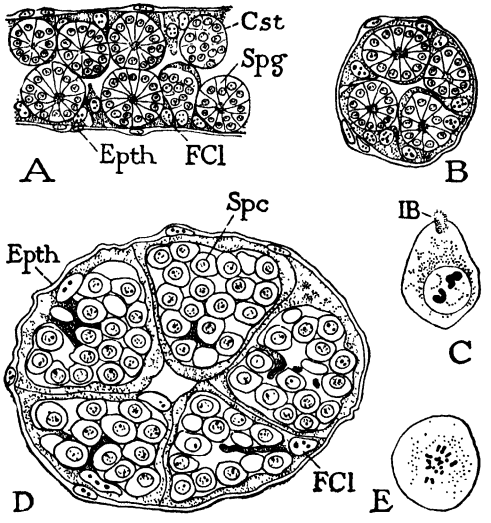



FIG. 100.—Spermatogenesis of the honeybee (*from Meves*, 1907).
A, longitudinal section of sperm tubule of testis, showing outer epithelium (*Epth*), sperm cysts (*Cst*), spermatogonia (*Spg*), and follicle cells (*FCl*). B, cross-section of same. C, a spermatogonium with interzonal body (*IB*) partly extruded. D, cross-section of sperm tubule, showing later stage of development, cysts containing spermatocytes (*Spc*) and surrounded by follicle cells (*FCl*). E, equatorial section of a spermatogonium in division, showing 16 chromosomes.

mass of them occurs in the upper ends of the sperm tubes ready to invest the newly formed spermatogonia. Meves describes and figures the investing or follicle cells of the spermatocysts in the honeybee (Fig. 100 A, B, *FCl*) but he does not discuss their origin. The spermatocysts pass downward through the sperm tubes in the same manner that the egg follicles pass down the egg tubes of the female. The encysted spermatogonia in the course of their progress divide into a large number of smaller cells, until these finally reach the stage where they are to be

prepared for their transformation into spermatozoa. The sperm cells are now called *spermatocytes* (D, *Spc*). The next period in their development is that of *maturation.*

**The Maturation of the Sperm.**—In the honeybee, the maturation of the germ cells in the drone, and the development of the male eggs of the queen do not conform exactly to any of the general rules for these processes because the drones develop from eggs that are not fertilized, and this has brought about

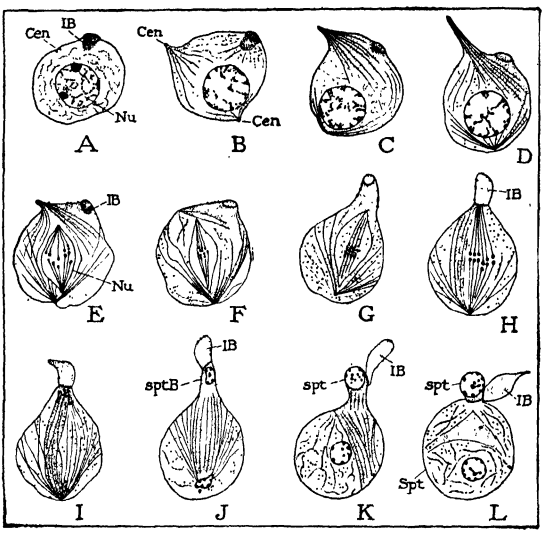



FIG. 101.—Maturation of the sperm cell of the honeybee (*from Meves*, 1907, *but re-lettered and differently interpreted*).

A, primary spermatocyte; *Cen*, centrosome; *IB*, interzonal body; *Nu*, nucleus. B, beginning of first maturation activity. C-D, formation of first maturation spindle, accompanied by elongation of cell, but not by division. E, F, retraction of cell neck, and formation of second maturation spindle. G, H, extrusion of interzonal body (*IB*). I, division of nucleus in second maturation division. J, formation of bud of rudimentary spermatid (*sptB*). K, cell in process of second maturation division. L, end of maturation process, resulting in formation of one functional spermatid (*Spt*), and one rudimentary spermatid (*spt*), and in extrusion of spindle remains or interzonal body (*IB*).

the elimination of male-determining spermatozoa. Meves (1907) and Mark and Copeland (1907) agree that the germ cells of the male honeybee always contain 16 chromosomes at all stages, there being no reduction of the number in maturation, and this has been verified by Nachtsheim (1913). The maturation of the spermatocytes in the honeybee has been described by Meves (1903, 1907), by Doncaster (1906, 1907) and by Mark and Copeland (1907). There is essential agreement in all the accounts,

but that of Meves (1907) is the most complete, and briefly is as follows: At the beginning of maturation the centrosomes in each spermatocyte (Fig. 101 A, *Cen*) move apart and become drawn out on two unequal conical outgrowths from opposite ends of the cell (B). The nucleus (*Nu*) takes a position near the small cone, but the latter soon flattens and disappears. The other, however, lengthens and becomes a long, slender, tapering, finger-like process with its centrosome in its tip (C, D). Radiating lines now spread from the two opposite centrosomes and form a spindle in the cytoplasm enveloping the nucleus, while the chromosomes of the latter separate as if cell division is about to take place. But the nuclear membrane remains intact, the finger-like lobe retracts and finally disappears as did the other, and nothing comes of the cell activity, which, however, is very suggestive of an aborted mitotic division.

Before the cell has regained its even contour another series of changes begins. A small granular mass, the remnant of a former division spindle, called the "spindle remains" and "interzonal body" (A, E, *IB*), has been lying within the cell against one side just below a circular scar on the cell wall where the last division took place. This part of the cell now begins to swell (E) and soon projects as a thick lobe containing the interzonal body, though the outline of the latter becomes indistinguishable from the cytoplasm (F, G). Meves says that the centrosome from the former finger-like lobe and a number of centrosome granules now migrate into the new outgrowth. This lobe then becomes constricted at its base (H, *IB*) where a division ring forms between it and the main body of the cell. The bud thus formed is finally separated from the mother cell, (K, L), but not until another outgrowth (J, *sptB*) is formed beneath it. The growth of this second bud, however, is accompanied by a normal splitting and separation of the nuclear chromosomes to form two nuclei (I, J, K) with 16 chromosomes each. One nucleus remains in the cell and the other goes into the second bud. The latter is then constricted at its base (K), and finally both buds are separated from the parent cell (K, L). According to Meves the first non-nucleated bud (*IB*) degenerates, the second (*spt*) begins to develop into a small spermatid, but its growth is soon checked and it never matures. Only the large cell (L, *Spt*) in the honeybee becomes a functional spermatid that develops into a spermatozoon.

Ordinarily the maturation of the sperm results in the production of four equal-sized spermatids. Meves believes that the extrusion of the first degenerate, nonnucleate bud from the germ cell of the honeybee is for the purpose of maintaining the 16 chromosomes, for, as Giglio-Tos (1905) points out, since the males are produced from unfertilized eggs containing only 16 chromosomes, any reduction of this number in their germ cells would render the latter incapable of fertilizing the female eggs. Mark and Copeland (1907), however, believe that the formation of the first, nonnucleated bud is merely the extrusion of the interzonal body, and they doubt, therefore, that the following division is a maturation process. But these writers did not distinguish in their investigations the two separate activities of the cell described by Meves—first, the formation of the long tapering cone (Fig. 101 D) with the centrosome in its tip; and second, the production of the first bud (F, G, H) after the retraction of the cone. Meves, on the other hand, ascribed no special significance to the outgrowth and retraction of the slender cone. These two conflicting views, therefore, suggests a third, as follows: The protrusion and retraction of the long finger-like cone with accompanying spindle formation and nuclear activity (B-E) represents the aborted first maturation division; the production of the first bud (F-H, *IB*) is merely the extrusion of the interzonal body, as claimed by Mark and Copeland; while finally, the separation of the second or nucleated bud (J-L, *spt*) is the true second maturation division, normal except for its inequality which results in the production of one small degenerating spermatid (L, *spt*) and one large functional spermatid (*Spt*).

The formation of only one functional spermatid from the maturation of the spermatocyte appears to be characteristic of the bee family (Apidæ), for Meves says that the same is true of the bumblebee, and Nachtsheim states that it is likewise true of two other bee genera (*Osmia* and *Xylocopa*). On the other hand in wasps, ants, and other Hymenoptera that produce males parthenogenetically, though the first maturation division of the sperm is aborted as in bees, the second results in the formation of two equal-sized spermatids, both of which develop into functional female-determining spermatozoa.

**Spermiogenesis.**—The egg cell or oocyte acquires its complete growth in the egg tubes *before* maturation and is ready for fertilization immediately afterwards. The spermatocytes, however,

are changed by maturation into *spermatids* which have ordinary cell forms and which must yet be evolved into the ripe spermatozoa by a complicated series of transformations sometimes distinguished as *spermiogenesis*. This final metamorphosis of the sperm cell, however, will not be described here, since it has not been followed in detail for the honeybee, and the student may find typical examples given in most any textbook on histology. The mature spermatozoa of insects usually have the form of long motile threads with a small swelling or head at one end containing the nucleus.

Spermatogenesis, or the evolution of the spermatocytes from the spermatogonia, maturation of the sperm cells, or the change of the spermatocytes into spermatids, and spermiogenesis, the transformation of the spermatids into spermatozoa, all take place in the tubules of the testes. According to Bishop (1920) spermiogenesis in the honeybee is accomplished during the four days previous to the emergence of the drone from the comb cell. As the spermatozoa are formed they go down the vasa deferentia into the seminal vesicles and attach themselves by their heads to the walls of these receptacles. Three days after the emergence of the drone the vesicles are full of spermatozoa, but the drone does not attain functional maturity until from nine to twelve days after emergence. The spermatozoa remain in the vesicles until the time of copulation. Then they are forced out in a small amount of thin liquid secreted by the vesicles, and are driven down the lower parts of the vasa deferentia by the contraction of the muscles in the walls of the vesicles and the ducts. At the same time the muscles on the lower ends of the accessory glands contract and bring the mouths of the sperm ducts in their dorsal walls against the thin coverings of the ends of the ejaculatory duct pressed against their ventral walls. These points of contact then break through, and the spermatozoa are discharged directly into the ejaculatory duct and out of its distal end through the everted penis into the vagina of the queen. Then there follows a discharge of mucous from the accessory glands which presses the spermatozoa against the walls of the vagina. The mucous coagulates in the orifice of the vagina and in the end of the penis. The last is now torn from the male and remains in the genital opening of the queen. The spermatozoa probably make their way by their own activity into the duct of the spermatheca and finally into the spermathecal sac where they are stored until used

up in the fertilization of the eggs. The queen normally mates only once during her lifetime and then receives from one male enough spermatozoa to last ordinarily about four years. After that she is capable of producing only drone eggs, but she is usually replaced by a new queen before she reaches this condition.

**Fertilization and Maturation of the Egg.**—We may now resume the history of the egg, which was interrupted just after the egg had slipped into the oviduct from its discarded follicle (page 274). As it goes down into the vagina on its way to the exterior the egg must pass the orifice of the spermathecal duct. Ordinarily as it does so a small mass of spermatozoa is discharged upon its upper end as described in the last chapter (page 259). Here one or more of the motile threads find the micropyle and force at least their nucleated heads into the cytoplasm of the egg.

In the honeybee, according to Nachtsheim (1913), from 3 to 7 spermatozoa or sometimes as many as 10 normally enter each egg that is to be fertilized, and it is claimed by Adam (see page 262) that only about 10 or 12 sperm are discharged upon each egg as it passes the orifice of the spermathecal duct. Nachtsheim furthermore shows that, in the case of the bee, the entire spermatozoon enters the egg, both head and tail being clearly visible in the egg cytoplasm, though the tail is somewhat shorter and thicker than in spermatozoa of the sperm receptacle, as if it had been contracted. As the spermatozoon goes deeper into the egg its head swells and takes on a spiral form, and the sperm slowly winds its way inward amongst the yolk globules by a screw-motion, disturbing the plasma on both sides of it, which becomes marked by transverse lines, the so-called sperm-radiations. The sperm tail, however, soon degenerates and disappears, while the head takes on first a dumb-bell form and then masses into a great ball, from which eccentric radiations extend outward in the egg plasma. The several spermatozoa in each egg scatter about in its upper end and their radiations never interfere.

In the meantime the egg, which left the ovarian tubule still in the primary oocyte stage, has been undergoing its maturation. This process in the female consists, as with the male cells, of two consecutive divisions accompanied by a reduction of the chromosomes to half the number present in the original germ cells. But with the egg, as already explained, the products of maturation are always one large cell, which is the egg, and two or three small degenerate cells called the *polar bodies*. Nachtsheim says

that the first polar spindle is already formed in the egg of the honeybee by the time the egg is laid, and that each chromosome group contains eight dyads or double chromosomes. The outermost group is separated as the first polar body which remains at the surface of the egg cytoplasm. The second maturation division immediately follows the first, and during this division the first polar body divides, so that four equal chromatin groups result. The innermost becomes the *pronucleus* of the egg. The two middle groups—the second polar body and the median half of the first polar body—unite with each other to form the so-called polar copulation nucleus ("Richtungskopulationskern"). This body may divide several times, but according to recent investigators the products of its division eventually degenerate and disappear, though Petrunkewitsch (1903) believed they became in the male the germ cells. The outer half of the first polar body also degenerates and there remains only the egg pronucleus with its 16 chromosomes (or eight double chromosomes). The pronucleus now travels inward from the polar protoplasm of the egg and, in a fertilized egg, soon encounters a male pronucleus, with which it unites and establishes the final *segmentation nucleus* of the fertile egg in which the normal number of 32 chromosomes is restored. The fertilized eggs, therefore, develop into female bees—queens or workers according to later influences. The other sperm nuclei in the egg quickly degenerate and are absorbed.

If the egg is not a fertilized one, Nachtsheim says, the migrating female pronucleus continues its course without interruption until it traverses the egg transversely and comes to rest against the opposite or concave side. Here it begins the divisions that are to produce the embryo, which will be a male since the female pronucleus contained but 16 chromosomes and no others have been added. Nachtsheim points out that the male and the female eggs thus differ with regard to the point at which development begins. It has been reported by several investigators that the number of chromosomes in the body or somatic cells of the bee, especially of the drone, is not constant and appears to vary from 8 to 64, but it is always some multiple of 8, the normal being 16.

### 3. PARTHENOGENESIS

The occurrence of parthenogenesis in insects and other animals, and the evidence establishing the fact that the males of the honey-

bee are produced from unfertilized eggs, as first claimed by Dzierzon in 1845, have been well reviewed by Phillips (1903) and are confirmed by all subsequent investigations (see Nachtsheim, 1913).

Parthenogenesis in bees is merely the property that the eggs have acquired of developing after maturation without fertilization. It cannot be explained at present why the eggs do not need the union with the male element, but they appear to be released from some inhibiting influence that ordinarily checks the activity of a mature germ cell until it is united with another. The fact that all the maturated eggs develop into males unless fertilized, however, may be explained on a basis of what is now known about the sex-determining influence of $x$-chromosomes; and the departures of the drone cells from the usual, both with respect to the number of chromosomes they contain and in the exceptional features of their maturation, are mere corollaries from the parthenogenesis of the maturated eggs. While it is true that $x$-chromosomes have not been visibly distinguished as such in the Hymenoptera, yet it may be assumed, as Armbruster (1913) points out, that an $x$-element of some sort is present in the cells. This then implies the farther assumption that the female and the male cells differ in the usual manner, that the 32 chromosomes of the queen, therefore, are to be expressed as $30 + 2x$, and the 16 of the drone as $15 + 1x$ (Fig. 98 B). After maturation, all the eggs, since they undergo a reduction division, must then contain $15 + 1x$ chromosomes, and the normal spermatozoa, which suffer no chromosome reduction, must likewise be of only one sort containing also $15 + 1x$ chromosomes.

We must believe, now, that parthenogenesis was not a primitive character with bees, in as much as it is not a characteristic of insects in general, and that the male cells originally contained the usual proportion of chromosomes, which would be $30 + 1x$ (Fig. 102 A, ♂). In this case the males must have produced spermatozoa of the ordinary two sorts—female determinants with $15 + 1x$ chromosomes, and male determinants with 15 chromosomes. As long as sexual reproduction prevailed, the union of eggs and sperms gave the combinations $(15 + 1x) + (15 + 1x)$, or $30 + 2x$, and $(15 + 1x) + 15$, or $30 + 1x$, the first being females, the second males. But, as Nachtsheim points out, whenever the bee eggs acquired the power of developing without fertilization after maturation, they could produce only drones

since they all at this stage have the chromosome formula of $15 + 1x$—the presence of the single $x$-chromosome being male determining (Fig. 102 B). With no check on fertilization, how-

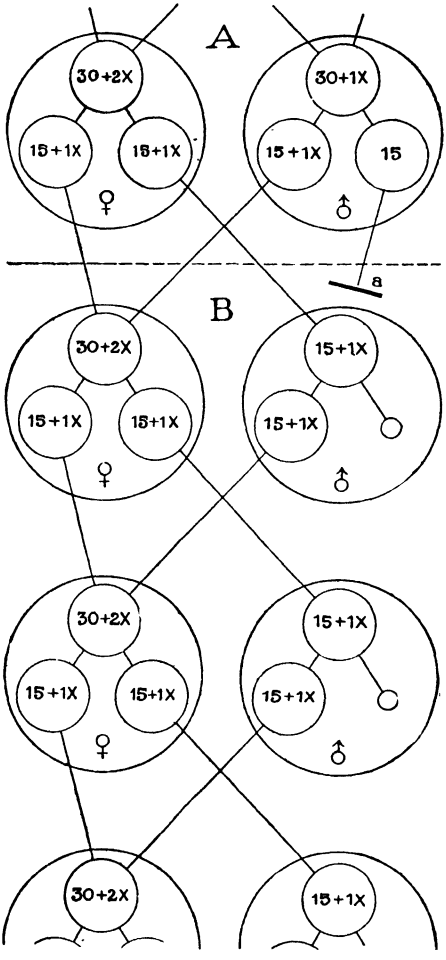



FIG. 102.—Diagram illustrating production of females from fertilized eggs, and males from unfertilized eggs that develop parthenogenetically after maturation.

A, theoretical ancestors of the bee, with both males and females produced from fertilized eggs (see Fig. 98 A). B, modern bees, with eggs developing parthenogenetically after maturation, showing that females must result from fertilization of eggs, but that all eggs unfertilized must produce males.

ever, all the eggs might be fertilized and therefore become females. Hence, as expressed at *a* of Fig. 102, the queen must have some

instinct or apparatus for the control of fertilization in order to allow males to develop. This control she has in the sperm pump of the spermathecal duct, and in some instinct or reflex for using it or not as the eggs pass through the vagina. When parthenogenetic males, now, produce germ cells, the chromosomes of these cells cannot be reduced since the normal double assortment has not been restored. The first maturation division, therefore, is abortive in all Hymenoptera studied (wasps, ants, bees) whose eggs develop parthenogenetically after maturation. There is, however, no reason why the second maturation division should not take place, since with it the chromosome division is always of the normal type preceded by an equatorial splitting of all the chromosomes; but all the spermatids produced are necessarily alike in that each contains only one $x$-chromosome. Consequently they are all female-determinants. In the wasps and the ants the two spermatids formed from each spermatocyte are of equal size and both develop into functional female-determining spermatozoa. In bees, however, one of the two spermatids has become rudimentary and degenerative, but this fact cannot be connected with parthenogenesis except in so far as parthenogenesis may have reduced the need for spermatozoa. Finally we must assume that males from parthenogenetic eggs eventually replaced those developed from fertilized eggs, and that the species thus lost the power of producing male-determining sperms, since only males with reduced chromosomes were left. If this theory is correct, the full normal number of chromosomes can never be restored in the drones, and bees must continue to produce males by parthenogenesis.

As a consequence of the development of male bees from the parthenogenetic eggs, the drones have no fathers, but each has one grandfather on his mother's side. The male inheritance of the drones, therefore, is through alternate generations, and this fact must be taken into consideration in any experiment on selective breeding of bees by controlled mating or by artificial fertilization.

### 4. DEVELOPMENT

There is no other thing in the field of biology so impressive as the development of a complex animal from a single cell. The egg cell divides, the daughter cells divide and redivide, the resulting cells arrange themselves without visible guidance but according to a definite plan into tissues and organs that finally

assume the structure and form of the mature animal. The progress of development from egg cell to adult may be continuous or intermittent, and either direct or indirect. The creature within the egg is termed an *embryo*. The development that takes place in the egg is known as *embryonic development*, that after hatching as *postembryonic development*.

With insects, development in the egg may be intermittent; postembryonic development is nearly always intermittent and in many cases indirect. The postembryonic life of the insect is, therefore, divided into a series of *stages* during each of which the insect changes but little. The stages are separated by brief periods of rapid growth, which may involve structural changes and which are normally accompanied by a shedding or molting of the cuticula. Each stage of the insect is known as an *instar*. Where development is indirect, the form of the young insect departs more or less widely from that of the parent and may be different in succeeding instars. All such changes of form constitute *metamorphosis*. The application of this term, however, is usually limited to the final development of the adult from the last immature stage, a change often accompanied by a dissolution of temporary tissues. If a special transformation stage or *pupa* intervenes between the last immature stage and the fully mature stage, the young insect is termed a *larva*. If there is no pupal stage it is known as a *nymph* or *naiad* according as its development is direct or indirect. Larvæ are typically worm-like in form, and common types of them are distinguished as caterpillars, grubs, and maggots. The young bee is a larva of the grub form. The metamorphosis of the bee will be described in the next chapter; its embryology is briefly reviewed in the following section of this chapter.

### 5. FROM EGG CELL TO LARVA

While the true egg or ovum is a cell, the term "egg" is commonly applied to the egg capsule and its contents regardless of development, and the "egg stage" of an insect is reckoned as the period from the time the egg is laid or is ready to begin its development until it hatches. Properly speaking, however, this is the embryonic stage in its growth.

**The Egg of the Bee.**—The egg of the honeybee (Fig. 103) is elongate oval in form, 1.53 to 1.63 millimeters or about one-sixteenth of an inch in length, a little larger at one end, and

slightly curved. Its color is pearly white. The surface of the shell or chorion is marked by a network of raised lines, the imprint of the follicle cells, which form pentagonal areas all over it except at the smaller end where the lines fade out and disappear. At the larger end the lines converge to a point where the micropyle should be situated, but no actual perforation has been discovered in the covering of the bee's egg, though this is probably due to the difficulty of making perfect sections through this part of the chorion.

The queenbee ordinarily places one egg in each cell of the comb, the worker eggs in cells like those that are to receive the nectar and pollen, the male eggs in larger cells built for the rearing of drones, and the queen eggs in the special queen cells constructed usually along the lower edges of the combs. Each egg is attached by its smaller end to the wall of the cell, adhering to the latter by a gummy substance on its surface. Usually it is fastened to the inner vertical wall of the cell, but the queens seem often to be careless in their egg-laying and sometimes stick the eggs anywhere inside the cell, occasionally even placing two or several in the same one. Since the cell, however, is designed to accommodate only one larva, the workers usually remove the extra eggs before they hatch.

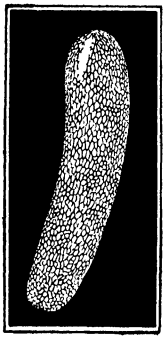


FIG. 103.—Egg of the honeybee. (× 24.)

The interior of the egg (Fig. 104 A) contains the original egg cytoplasm and a large volume of nutritive matter or *deutoplasm* usually called "yolk" (*Y*). A small island of cytoplasm near the upper end of the egg contains the nucleus (*Nu*); the rest forms a network of fine strands amongst the yolk globules, and a denser layer on the outside of the latter called the *cortical layer* (*CL*). This is covered by the *vitelline membrane* (*Vit*) which is the true egg wall, outside of which is the chorion (*Cho*) supposed to have been deposited from the follicle cells.

**Cleavage and the Blastoderm.**—Immediately after the fertilization of the female egg of the bee, the new or segmentation nucleus (Fig. 104 A, *Nu*) and its containing mass of protoplasm begin to divide. The resulting cells again divide and redivide forming a group of *cleavage cells* (B, *CCl*) which scatter through the yolk and migrate in all directions to the surface. Here they sink

into the cortical layer of protoplasm and form a layer of cells covering the surface of the egg inside the vitelline membrane and enclosing the yolk (C). This hollow oval of cells having the form of the egg is the *blastoderm* (*Bl*), the beginning or first stage of the embryo.

We may not here trace all the details of the transformation of the blastodermic sac into the larva of a bee. For a complete account of the complicated evolutions involved the student is referred to Nelson's "The Embryology of the Honey Bee" (1915), from which the following brief sketch is taken.

**The Germ Band.**—The blastoderm is completely formed in from 20 to 30 hours after the egg is laid. The part of the convex side of the egg, which is to be the ventral or under surface of the future bee, is the part in which the most important features of the development take place. The larger end of the egg, which is the end that was uppermost in the egg tube of the ovary, is to be the head end of the embryo and is known as the *anterior* or *cephalic pole* of the egg, while the smaller end is called the *posterior* or *caudal pole* of the egg. The cells of the under side of the blastoderm soon become much thickened and those of the upper side very thin and flat (Fig. 104 D). The original simple blastodermic layer is thus early differentiated into a thin dorsal blastoderm (*DBl*) and a thick ventral blastoderm or *germ band* (*GB*). The latter reaches from one end of the egg to the other and curves upward at the two poles (E).

**The Germ Layers.**—The germ band grows upward on the sides of the egg at the expense of the dorsal blastoderm, reducing this to a narrow *dorsal strip* (F, *DS*). But a slender band of blastodermic cells on each side between the dorsal strip and the germ band remain distinct from both and are known as the *amnion cells* (*Am*) because they are to produce later the embryonic envelope called the *amnion*.

On the ventral surface of the egg there now appear two lengthwise ridges that enclose between them a narrow median strip of the germ band which begins to sink inward along the inner margins of the ridges. The germ band is thus differentiated into a ventral *middle plate* (F, *MP*) and into two *lateral plates* (*LP*).

The middle plate of the germ band, however, is not destined to remain on the surface of the embryo; it continues to sink into the yolk, and at the same time the lower edges of the lateral plates grow together beneath it, beginning near the anterior

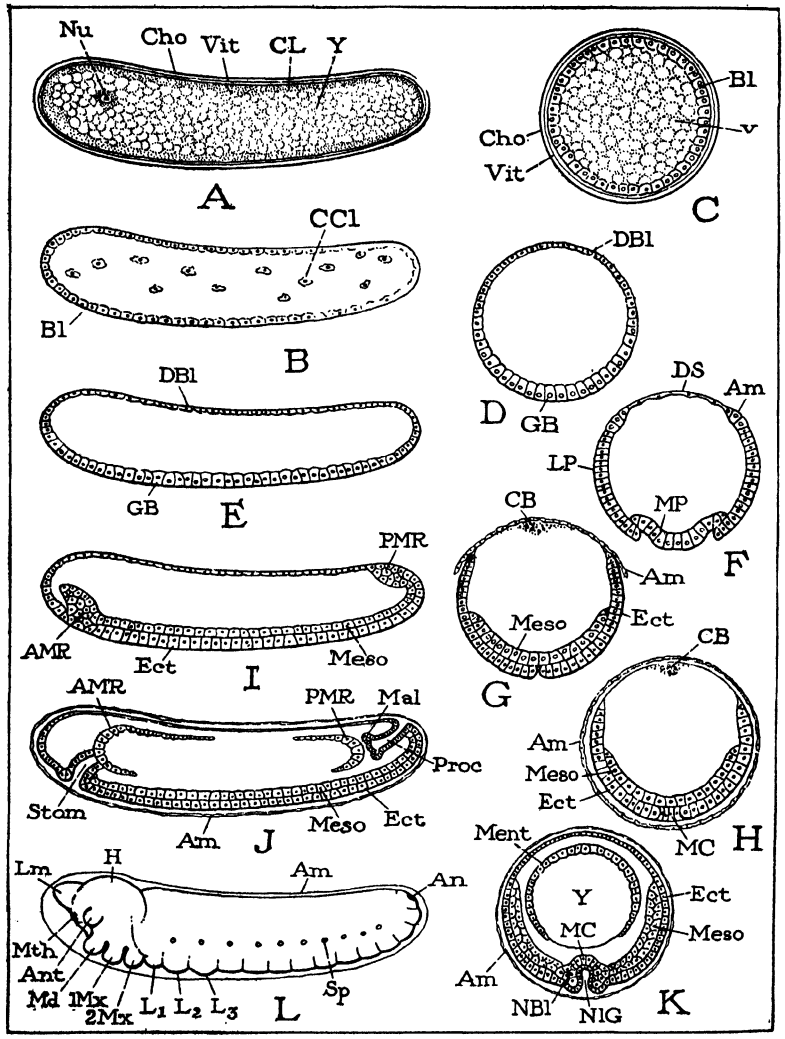



FIG. 104.—Embryology of the honeybee. (*Diagrams based on text and figures of Nelson*, 1915.)

A, the egg. B, formation of blastoderm. C, cross-section of blastoderm and egg coverings. D, formation of germ band, cross-section. E, the same, longitudinal section. F, differentiation of middle plate (*MP*), lateral plates (*LP*), and amnion cells (*Am*). G, formation of mesoderm (*Meso*), and beginning of growth of amnion (*Am*). H, completion of amnion, differentiation of median cord (*MC*) in ectoderm (*Ect*). I, formation of anterior mesenteron rudiment (*AMR*) and posterior mesenteron rudiment (*PMR*). J, growth of mesenteron rudiments (*AMR*, *PMR*), and formation of stomodeum (*Stom*) and proctodeum (*Proc*). K, formation of neural groove (*NlG*) and neuroblasts (*NBl*); yolk (*Y*) nearly surrounded by mesenteron (*Ment*). L, embryo 52 to 54 hours old, showing rudimentary appendages of head and thorax.

end and progressing backward, till finally the middle plate is shut into the inside of the egg by the union of the two lateral plates below it. In this way the young insect embryo comes to consist of *two* germ layers both formed from the original ventral plate of the blastoderm. The outer layer is the *ectoderm* (G, *Ect*), the inner the *mesoderm* (*Meso*).

**The Mesenteron.**—While the middle plate is in process of differentiation from the rest of the germ band, the cells of the latter at each end of it form cellular masses by cell migration that bulge into the yolk. These masses are the *anterior mesenteron rudiment* (I, *AMR*) and the *posterior mesenteron rudiment* (*PMR*), destined to form the middle division or *mesenteron* of the alimentary canal (Fig. 65, A, *Ment*). The fact that the two mesenteron rudiments and the middle plate arise in the bee at the same time by an inward movement of the median ventral cells of the germ band suggests that the three formations are modifications of one process of invagination. But the mesenteron rudiments are formed in various other ways in other insects, and it is as yet impossible to establish any certain homology between the inner germ layers of an insect and those of other animals that develop in a more typical manner.

The mesenteron rudiments are at first solid cell masses, but they soon become hollowed on their inner faces and later each sends out a long flat tongue over the top of the yolk, one backward the other forward (Fig. 104 J). The two strips eventually meet and unite and then spread downward around the sides of the yolk and join below it, finally enclosing the yolk in a sac formed of a single layer of flat cells. This sac is the *mesenteron* (Figs. 104 K, 65 A, *Ment*) of the embryo and becomes the stomach of the adult (Fig. 65 B, *Vent*); but at this stage it is still closed at both ends and contains the yolk of the egg which henceforth must be absorbed through its walls and from them passed on to the other tissues in the process of development and growth.

**Growth of the Mesoderm.**—The mesodermal layer formed from the middle plate of the germ band grows upward on each side of the body (Fig. 104 K, *Meso*) in the space between the lateral ectodermal plates (*Ect*) and the mesenteron (*Ment*), when the latter is completed. From it are to be derived the muscles, the heart, the fat cells, and the blood cells.

**Segmentation.**—During the time that the two germ layers are being formed the embryo becomes marked in surface view by

a series of narrow, transverse pale lines separating wider dark areas. This is the beginning of *segmentation.* The lines appear first at the anterior end of the body and increase in number backward, each being due to a crosswise constriction that effects both ectoderm and mesoderm. The entire embryo is finally divided into a series of segments, as already described and shown diagrammatically in Fig. 3. All insect embryos, however, do not show the typical maximum number of segments, and the segmentation of the head is seldom as distinct as that of the thorax and abdomen.

**The Amnion.**—At this same period of embryonic growth the amnion cells (Fig. 104 F, *Am*), which have been inactive thus far, begin the formation of the sheath or *amnion* which is to enclose the embryo till the time of hatching. First there is a widening of the bands of amnion cells (F, *Am*); then each band grows upward over the dorsal strip of the blastoderm (*DS*), which latter becomes submerged in the yolk; while finally the two unite and form a continuous layer across the back (G). At the same time the ventral edges of the amnion bands separate from the germ band at the anterior end of the egg and grow over it in the form of a hood. This separation of the amnion bands from the germ band progresses backward accompanied by an extension of the head fold in the same direction till the anterior half of the embryo is enclosed in it. Now a second similar amniotic fold forms at the rear end of the egg and grows forward. The two folds finally meet and unite. In the meantime the dorsal amnion has separated from the yolk, and thus finally the embryo is completely enclosed in a thin sac, which is the amnion (H, *Am*).

The amnion of the honeybee consists of a *single layer of cells.* In other insects it is commonly formed from double folds of the amnion cells that grow around the germ band and unite beneath it, thus producing two separate envelopes. In such cases the inner one is called the *amnion proper* and the outer is distinguished as the *serosa.* Usually the two membranes break apart again along the under side of the body before the insect hatches, shrink upward, and are absorbed into the yolk on the back. The method both of formation and of destruction of the amnion differs much in different insects, but the subject needs no further discussion here since the organ has nothing to do with the development and final form of the embryo. The amnion of

the bee embryo remains intact until it is ruptured and broken up by the movements of the young larva just before hatching.

**The Stomodeum and Proctodeum.**—After the amnion has become a closed sac, a depression appears at each end of the embryo which grows inward as an invagination of the ectoderm. The one at the anterior end is the *stomodeum* (Figs. 65 A, 104 J, *Stom*), the one at the rear end the *proctodeum* (*Proc*). The first applies itself to the outer surface of the anterior mesenteron rudiment (Fig. 104 J, *AMR*). In the bee, according to Nelson, the inner wall of the stomodeum consists of mesenteron cells. The last become reduced to a thin membrane and at about the time of hatching the inner end of the stomodeum invaginates into the mesenteron, the separating membrane ruptures, and the cavities of the two organs become continuous. The stomodeum differentiates in the adult into the pharynx (Fig. 65 B, *Phy*), the œsophagus (*OE*), the crop (*Cr*), and the proventriculus (*Pvent*), while its point of origin becomes the mouth (*Mth*). The proctodeum grows forward in the same manner from the posterior end of the body, and unites with the rear end of the mesenteron, to form the intestine. It becomes differentiated into small intestine (Fig. 65 B, *SInt*) and rectum (*Rect*), while its point of origin is the anus (*An*). The Malpighian tubules (Figs. 65 A, 104 J, *Mal*) grow out as evaginations from its anterior end. Ordinarily the opening between the proctodeum and the mesenteron is established in the embryo, but in the bee the two parts remain separate until the end of the larval stage.

Since the stomodeum and the proctodeum are formed as ingrowths of the ectoderm all the parts derived from them in the adult are lined with a chitinous cuticula continuous with that of the hypodermis of the body wall. But also the tracheal tubes, the salivary glands, all hypodermal glands, and the ejaculatory duct and vagina of the reproductive organs are formed likewise from ectodermal invaginations and are lined with cuticula.

**The Tracheæ.**—The tracheal invaginations, according to Nelson, arise as eleven pairs of pits, ten of which later become the spiracles of the adult. The inner end of each depression gives off branches internally which are the tracheal tubes, the longitudinal trunks being formed by the union of anterior and posterior branches from consecutive spiracles. The first pair of invaginations are in the sides of the first maxillary segment and their branches form the tracheal tubes of the head,

but the maxillary pits themselves later close and never form spiracles. The other depressions are on the sides of the second and third thoracic and the first eight abdominal segments, and become the ten pairs of spiracles of the adult.

**The Salivary Ducts.**—The apertures of the salivary glands, which are the silk glands of the bee larva, appear first just behind the bases of the second maxillæ. But as these appendages move together and fuse to form the labium, the gland apertures also approach each other and unite into a common median orifice which is finally situated on the labium in the larva of the bee.

**The Endoskeleton.**—The entire endoskeleton of the head and body and the appendages, including the muscle tendons, the furcæ, the phragmas, the pleural ridges, and all other internal arms and ridges known in general as apodemes are but ingrowths of the ectoderm and its covering cuticula.

**The Nervous System.**—To trace the development of the nervous system we must go back again to the time when the germ layers are about completed (Fig. 104 H ). The median ventral cells of the ectoderm now become distinguished from the rest of the ectodermal plates by having larger and clearer nuclei, and constitute a ventral band called the *median cord* (*MC*). Then the adjoining edges of the lateral plates become thickened to form two longitudinal ridges with a narrow furrow, the *neural groove* (K, *NlG*), between them and below the median cord (*MC*). Next, the cells of the ridges themselves become differentiated into a superficial layer and into a deeper mass in each ridge. The former remain as the hypodermal cells of this region while the latter become the *neuroblasts* (*Nbl*), or cells that are to form the ganglia and longitudinal commissures of the ventral nerve cord. Each ganglion is, hence, double in its origin, the transverse commissures that eventually connect the parts formed from the neuroblasts being derived from the median cord.

The first six primitive ganglia belong to the head segments, the first three of which consolidate in all insects to form the brain above the œsophagus, and the next three to form the subœsophageal ganglion below the œsophagus. The body ganglia may remain separate or unite in various combinations in different insects, though there is never a separate ganglion beyond the thirteenth segment of adult insects. According to Nelson (1918) the newly hatched larva of the honeybee has 12 body ganglia,

the last one being a compound ganglion, composed of the primitive ganglia of the ninth, tenth and eleventh abdominal segments. This terminal ganglion is situated in the ninth abdominal segment of the larva, but in the adult it has moved forward and combined with the ganglion of the eighth segment (Figs. 72, 86, 7*Gng*). In the adult bee there are, however, only seven body ganglia in all, the second and third thoracic ganglia having combined with the first and second ganglia of the abdomen to form a large ganglionic mass situated in the thorax (2*Gng*), and the sixth and seventh having united to form the penultimate ganglion of the abdomen.

**The Œnocytes.**—The œnocytes, as described in Chapter IX, are derived from the ectoderm. Nelson says that they are given off as free cells from the inner ends of ectodermal invaginations along the sides of the body in the first eight abdominal segments. The invaginations are in line with those that form the tracheæ, and are formed in the middle of that part of each segment behind the latter.

**The Appendages.**—The rudiments of the appendages appear during the stage when the stomodeum and proctodeum are forming. Nelson says that there are in the bee embryo rudiments of antennæ (Fig. 104 L, *Ant*), mandibles (*Md*), first maxillæ (1*Mx*), second maxillæ (2*Mx*), and legs ($L_1$, $L_2$, $L_3$), but no trace of abdominal appendages. The bee larva has no antennæ or legs, and, according to Nelson, the rudiments of these appendages in the embryo become reduced to hypodermal thickenings prior to hatching. The corresponding organs of the adult redevelop in the pupal stage from the embryonic remnants.

**Mesodermal Organs.**—The mesoderm forms only organs that are strictly internal, such as the muscles, blood cells, fat cells, and the internal parts of the reproductive systems. The formation of the mesoderm by the in-sinking of the ventral middle plate of the blastoderm (Fig. 104 F, *MP*) has already been given, and its growth was traced (G, H, K) till it consisted of two lateral plates (K, *Meso*) lying between the ectoderm and the mesenteron. In some of the lower insects and in the Myriopoda a series of segmental cavities appears in the mesoderm along each side of the body. These are known as the *cœlomic sacs*. They later unite to form the body cavity which, in such cases, seems to correspond with the body cavity in other animals. But in the higher insects no such mesodermic sacs are formed, the body cavity of the adult

begins as a free space that appears beneath the yolk and spreads upward over the sides of the latter as the yolk contracts and becomes surrounded by the mesenteron rudiments.

The lateral parts of the mesoderm plates, however, split into two layers, an outer or *somatic* layer and an inner or *visceral* layer, and their history in the bee as described by Nelson is as follows. From the somatic layers are formed the muscles of the body wall and the fat cells of the pericardial cavity. The visceral layers form the muscles of the mesenteron and, in the honeybee, the fat cells of the fat body, but this last is exceptional since in other insects the fat body arises from the somatic layers. The cells along the upper edge of each mesoderm plate, those at the union of the somatic and visceral layers, become differentiated as the *cardioblasts* or cells that are to form the heart. They become detached from the mesoderm layers as two longitudinal strips which then approach each other and unite above and below a median dorsal space, thus forming the tubular heart. Flat sheets of cells extending outward on each side from the cardioblasts become the dorsal diaphragm, which later is attached to the body wall at the anterior edge of each segment (Figs. 72, 74). The ventral diaphragm is formed from muscle fibers derived from the somatic layer of the mesoderm.

The ventral part of the mesoderm layer, which is not affected by the splitting into somatic and visceral layers, breaks up into a mass of loose cells that become the *leucocytes* or blood corpuscles and disperse in the liquid or blood of the body cavity.

**The Reproductive Organs and the Germ Cells.**—The reproductive organs of insects first appear as the *genital ridges* situated near the back in the abdomen on each side of the heart, and at their earliest stage they appear to belong to the mesoderm. But in many insects the true germ cells have been traced back to a much earlier period and found to originate from special cells of the blastoderm set apart before the germ layers are formed. Nelson says that there is no evidence of such an origin of the germ cells in the honeybee, but that, on the other hand, it could not be disproved that they do not descend from some of the original cleavage cells produced at the time the blastoderm itself is being formed. Petrunckevitsch (1901, 1903) believed that he could trace the germ cells of the drone bee to a cell produced by the union of two of the polar bodies, but later (1916) saw that this was not substantiated by other investigations. A good résumé

of the subject of the origin of the primordial germ cells in insects is given by Hegner (1914). He shows that there is very commonly present at the posterior pole of the egg a disk of special protoplasm, the "Keimbahn" or *germ tract,* and that the cleavage nuclei that pass into this protoplasm become the reproductive cells of the future insect. The protoplasm of the germ tract is distinguished from the normal cytoplasm of the egg by the presence in it of coarse granules which appear to be either themselves the *germ cell determinants* or their visible accompaniments.

**The Young Larva.**—The egg of the bee hatches in about 76 hours. The young larva becomes active shortly before its emergence and curves itself in the opposite direction from the curvature of the egg, thus reversing the position it has held during its embryonic growth, and assuming that which it will maintain during most of its larval life.

## CHAPTER XIII

## METAMORPHOSIS: FROM LARVA TO ADULT

Nearly every animal changes structurally in some way as it develops from youth to maturity. During their embryonic growth all go through a definite series of changes, but there is no fixed time at which an animal must leave the protection of the egg shell or its mother's body. Some are cast upon the world to shift for themselves at a much earlier stage than others.

**Divergence in Form between Young and Adult.**—In general it is believed that the immature forms through which an animal goes during its individual development represent, in a modified way, the forms that its ancestors have passed through in their evolution. So long as the young creature is protected it can follow this normal course of development, but when it must gain its own living as a free animal, exposed to the inclemencies of nature and in open competition with other animals, it is likely to acquire characters that will be of advantage to it which its ancestors in the adult form never possessed. Hence, nearly every species with precocious hatching or birth departs more widely from the ancestral path in its postembryonic stages than in its embryonic stages: and the earlier it enters upon its post embryonic life, the greater its departure is likely to be.

This rule has applied particularly to insects, especially to those that leave the egg at an early period of development. The form of the caterpillar of a moth or butterfly, for example, of the maggot of a fly, or of the grub of a wasp or bee cannot be held to represent the form of any ancestor in the history of the species; these larval forms are specialized forms that have been acquired secondarily by way of adaptation to the needs of the larvæ and their individual ways of living. In other words, the larvæ of insects have digressed, along paths of their own, from the regular roads their adult ancestors have followed. In the higher orders much of the departure of the larvæ from the direct line of their evolution has been due to the fact that to them has been

delegated the major part of the function of obtaining food, the adults having conserved and perfected the function of reproduction. In such cases the larvæ must eat not only for their own sustenance, but also for that of the adult, providing for the latter by storing up nutriment in their bodies greatly in excess of their individual needs. As a result the organs of feeding, digestion,

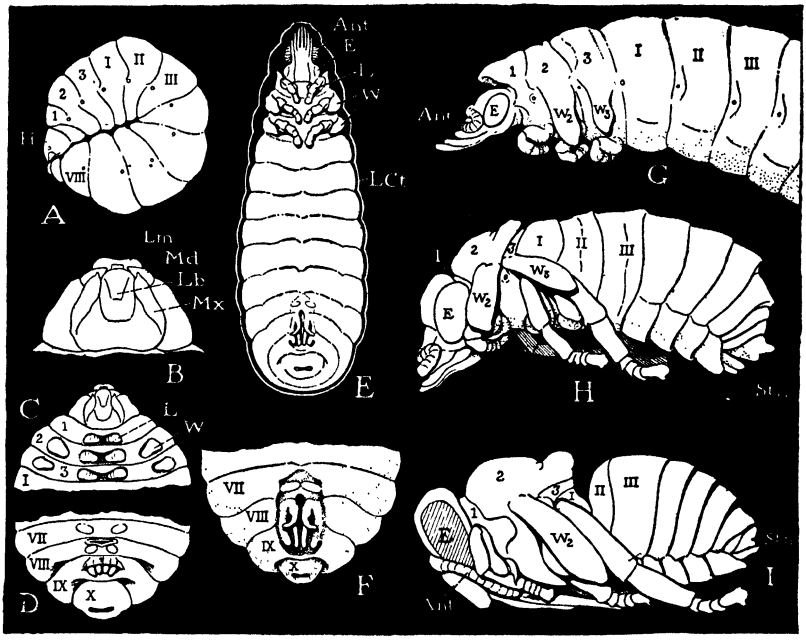



FIG. 105.—External changes of the bee during metamorphosis from larva to pupa.

A, mature larva still coiled in cell. B, ventral surface of head of larva. C, ventral surface of head and thorax of mature larva, with buds of legs (*L*) and wings (*W*) everting beneath transparent cuticula. D, ventral surface of last four segments of mature larva, with rudiments of ovipositor showing through cuticula. E, early stage of propupa within larval cuticula (*LCt*). F, terminal segments of propupa, with rudiments of ovipositor more developed than at D. G, lateral view of propupa (same stage as at E). H, late stage of propupa, just before shedding of last larval cuticula. I, fully formed pupa, after shedding of larval cuticula.

and storage have been highly developed in the larvæ, while these parts in the adults have usually become adapted to the needs of a special diet or, in extreme cases, have become entirely rudimentary.

With a large number of the Hymenoptera the larva lives parasitically in some other insect, protected by the body of its

host and surrounded by an abundance of food, where, in its evolution, it has returned almost to embryonic conditions. In the social Hymenoptera the larva lives within the security of a cell and *is fed by the adult females.* The adults in this group, therefore, require a large amount of well-balanced food, which they must procure for themselves, while the larvæ need eat only so much as will assure them of their own maturity and carry them through their transformations into adults.

The change of the larva to the imago is, in any case, merely the inevitable return to the final form, for the distance from germ cell to adult must be transversed whether by the direct course or by a roundabout one. With the higher insects, the larva and the imago have separated so far along divergent paths that the larva must at last suffer a violent reorganization, which it undergoes in a special stage called the pupa.

**Definition of Metamorphosis.**—This brings us to the subject of metamorphosis, which may be defined as *any change of form or structure that an animal undergoes which is not in line with direct development, or which results from a deviation from it.* There may be, therefore, various degrees of metamorphosis, or no metamorphosis at all; there may be embryonic metamorphosis and larval metamorphosis, besides that from larva to imago. Most insects have no adult metamorphosis, since, with rare exceptions, they do not change after reaching the adult form. In the bee, metamorphosis is practically limited to that between the last larval stage and the imago, most of which is accomplished in the pupa.

**Molting and Growth of the Honeybee Larva.**—It is recorded by Koehler (1923) and by Bertholf (1924) that the larva of the honeybee sheds its skin, or the outer layer of its cuticula, five times during the course of its growth. Throughout its feeding period the larva lies against the inner wall of its cell, curved first in the form of a crescent, then doubling more and more as it enlarges, until at last it is tightly molded into the hexagonal shape of its cell, with its head slightly overlapping the end of the abdomen on the side toward the cell entrance (Fig. 105 A). At each molt, Bertholf says, the skin splits over the head, and in less than half an hour the larva wriggles out of it, pushing it off over the rear end of the body into the surrounding food, on the surface of which the pellicle floats till it is covered by a fresh supply of food from the nurses. After the fourth molt the larva

does most of its growing, gaining 40 per cent of its final weight in the last two days of its life.

**The Larva in the Capped Cell.**—At about the end of the fifth day from hatching the larva is given its last food, and then its cell is sealed over with a capping of wax put on by the attendant workers. Koehler (1923) says that the cell is closed on the sixth day, and in general the records given by German writers extend the uncapped larval period to six days, but probably variations of the actual time account for the different statements by different writers. After the larva has eaten its food, its stomach and its excretory or Malpighian tubules make connection with the intestine, as explained on page 163, and both now for the first time discharge their contents through the intestine into the cell. The delay in opening the intestinal passage until after the feeding period is evidently to prevent the larva from contaminating its own food.

*Spinning the Cocoon.*—Having finished with alimentary functions, the larva relaxes and turns lengthwise in the cell to begin its last larval activity, the spinning of the cocoon about itself. The fabric of the cocoon is formed from the fluid silk of the silk glands, which open on the lower lip. The silk is woven over the walls of the cell, probably as soft, gummy threads that run together until they finally form a parchment-like capsule completely enclosing the larva. According to Bertholf, a worker larva finishes its cocoon about 24 hours after the sealing of its cell. Now, as if exhausted, it stretches out on its back full-length on the floor of the cocoon, in which position it lies quiet for about 24 hours. During this time a liquid appears to accumulate beneath its cuticula, especially at the base of the head, a sign that the fifth and last molt is about to take place.

*The Last Molt of the Larva.*—Bertholf states that the fifth or last molt of the worker larva occurs on the third day after the capping of the cell; Koehler says that two days intervene between the two events. But Bertholf allows in this case only five days to the uncapped larva, Koehler giving six; either reckoning makes the true larval period one of eight days. "The old larval skin," Bertholf says, "is pushed back to the base of the cell where it mixes with the yellow feces, given off by the larva during or just after the spinning of the cocoon, and the whole sticks to the base of the cell as a yellow flake." According to Koehler the feces of the larva are excluded from the interior of the cocoon and

lie in the space between the cocoon and the cell wall, only the last larval skin remaining within the cocoon. This is the condition common with other insects; but with the bee larva it is likely that a part of the fecal matter becomes enclosed between the layers of the cocoon wall and that some of it remains inside the cocoon.

**The Pupal Stage.**—The creature which is disclosed at the fifth molt is no longer a larva; it has already acquired most of the characters of an adult bee (Fig. 105 I), though the wings are short and all the appendages are pressed close to the sides and under surface of the body. In fact, the larva has already changed to a pupa.

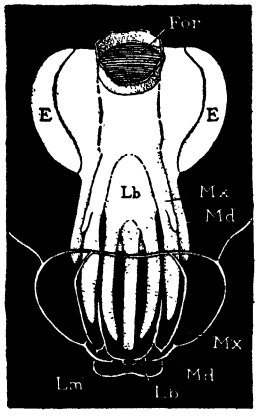



FIG. 106.—Head of propupa of worker, ventral view, and outline of larval head, showing formation of pupal mouth parts in corresponding parts of larva.

*External Changes during Metamorphosis.*—The transformation, however, has not been so abrupt as it would appear; much has been going on beneath the skin of the quiescent larva before the molt occurred, some of the changes being plainly visible through the skin. Even while the larva is yet coiled in the feeding position (Fig. 105 A) small buds of the future wings (C, *W*), legs (*L*), and ovipositor (D) can be seen protruding beneath the cuticula from pockets of the hypodermis. During the quiescent or prepupal stage of the larva, when the molting liquid accumulates beneath the skin, the head of the creature within draws back from the capsule of the larval head, while the mouth parts rapidly lengthen and take on forms suggesting those of the adult (E). Each new appendage, however, is formed at first within the corresponding one on the larval head (Fig. 106, Cf. Fig. 105 B), though with the retraction of the head some of the shorter members, such as the mandibles (*Md*), become entirely separated from the larval parts. At the same time the compound eyes (*E*) swell out on the sides of the head, and a pair of large antennæ grow out from the face in the space beneath the larval cuticula. On the thorax, the wings (Fig. 105 E, *W*) enlarge, and the legs (*L*) elongate and show that they are already divided into the principal joints they will have when mature. On the abdomen (E, F) the parts of the sting lengthen to slender lobes crowded

together at their bases, but as yet scarcely suggestive of the effective weapon they will eventually form. The creature within the larval skin is, in fact, now well advanced toward the pupal stage, and in this early phase it may be designated a *propupa*. But the propupa is not designed for practical purposes. By artificially removing the skin it may be seen what a really grotesque thing it is (G), half worm and half bee, a myth if it were not a fact.

The development of the propupa proceeds rapidly; the head enlarges and turns downward, the eyes (*E*), antennæ (*Ant*), and mouth parts increase in size, the wings become long flaps, the legs take on the adult characters, the abdomen contracts, the sting is drawn into its pouch between the terminal ventral plates, and, shortly before the skin is normally shed, the creature reaches a stage (H) in which it is clearly on its way to becoming a bee.

When at last the larval skin is cast off, the fully formed pupa appears (I). The head is now turned ventrally and posteriorly underneath the front of the thorax, the wings overlap against the sides, the legs are rough models of those of the adult, and the abdomen is sharply separated from the thorax by a deep constriction. The most interesting changes in the later development have taken place, however, in the thoracic region itself. In the early stage of the propupa (G) the three segments of the thorax (*1*, *2*, *3*), are of approximately equal length, as they are in the larva (A), and the first segment of the abdomen (*I*) does not differ from the others. But, toward the end of development (H), the middle thoracic segment (*2*) has greatly increased in size, especially on the back, while the other two have correspondingly contracted, the first (*1*) forming a mere collar back of the head, and the third (*3*) being reduced to a narrow band between the second thoracic and the first abdominal segment. The latter (*I*) is distinctly crowded forward against the thorax above, while its ventral part is much restricted. When the pupa is fully formed (I) this segment is incorporated with the three in front to form the thorax of the adult bee, while the constriction separating the thorax from the abdomen has formed between segments *I* and *II*, which were originally the first and second segments of the propupal and larval abdomen (G and A). Thus, the propodeum (*I*), though originally a segment of the abdomen, becomes a part of the middle body region, and the Hymenoptera

are shown to be descended from insects with a normal three-segmented thorax.

The pupa (I) is clearly a *pro-imago*, a preliminary stage of the adult, separated from the mature adult by another molt. Yet, it has characters of its own, which are not retained by the adult. On its legs, for example, there are prominent spurs (Fig. 107), one projecting from the under side of the coxa, another from the trochanter, and one from the distal end of the tibia. All these spurs are lost in the adult, except the one at the end of the tibia on each front leg (*g*), which apparently becomes the tibial spur of the antenna cleaner (Fig. 39 A, *g*), and possibly the one at the end of the middle tibia, which may form the spine situated here on the adult leg. The presence of the other spurs on the legs of the pupa, however, suggests that recent ancestors of the bees in the adult stage were provided with corresponding spurs or spines.

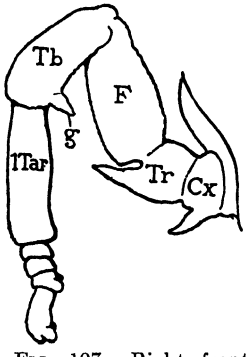



FIG. 107.—Right front leg of a bee pupa, showing spines on coxa (*Cx*) trochanter (*Tr*), and tibia (*Tb*). That of tibia (*g*) becomes spur of antenna cleaner of adult (Fig. 39 A, *g*)), the others disappear.

*Internal Changes during Metamorphosis.*—The physiological business of the pupa is the reconstruction of the adult, and, while the pupa will not change externally after acquiring its final form (I), except in color, much goes on within it. Not only are the imaginal details of outward form perfected within the crude shapes of the pupal members, but the internal organs of the larva are either reorganized into those of the adult, or they are completely broken down while imaginal organs are built up anew from the débris.

We shall not here go into all the details of the internal metamorphosis, especially since the details are not thoroughly known in the bee. Aside from the paper on the metamorphosis of the wasp and the bee by Anglas (1901), very little has yet been done on the histological processes that transform the larva of the bee into the adult; and it must be remembered that changes in the form or structure of any organ, whether external or internal, proceed from a deep-seated physiological activity in its tissues. At the beginning of the metamorphic period, which we have seen in the bee is even before the larva has finished its active life, certain organs suddenly start into an active renewal of their

growth, while others suffer a degeneration in the tissues of their cells which results often in their complete disorganization and disappearance. In the first case, the larval organ simply develops into the corresponding adult organ, with perhaps considerable changes; in the second case, the adult organ is built up anew from certain groups of cells, the *imaginal buds* or *histoblasts*, which probably in some cases are the rudiments of the adult organs, and in others normal regenerative tissues. Metamorphosis is, therefore, a period of very active histolysis and histogenesis.

All the remodeling of the external shape depends on a reconstructive growth in the hypodermis. In the higher insects the larval hypodermal cells degenerate and are supplanted by new ones that spread out from the bases of the appendage buds and from other groups of cells on the segments that have no appendages. At the same time the parts of the alimentary canal derived from the stomodeum and the proctodeum, which are but ingrowths of the body wall (Fig. 65 A, *Stom*, *Proc*), are reconstructed in the same way from histoblasts in their walls. The salivary glands are likewise remodeled, but the tracheal system, also of ectodermal origin, usually grows directly, without much histolysis, into the tracheal system of the adult. The ectodermal tissues, however, never lose their continuity, the change is accomplished by a gradual replacement of the cells; the body wall is never lacking at any point, the alimentary canal never loses its unity.

The muscles, on the other hand, may undergo complete histolysis before the new muscles are formed. In the flies and the Hymenoptera few of the larval muscles persist, almost all the adult muscles are newly formed in the pupa. As the muscles break up, their fragments appear to be ingested in some insects by the amœboid blood corpuscles, the leucocytes, or *phagocytes* as they are called when their function as scavengers becomes particularly apparent. But the phagocytic activity of the leucocytes in metamorphosis is not as important as it was formerly supposed to be. The heart muscles are said to undergo but little histolysis, though the reorganization of the heart of the adult may involve considerable change in that of the larva.

The epithelium of the larval ventriculus or stomach is cast off into the lumen of the organ at the beginning of metamorphosis, and a new lining is generated from groups of cells, which Anglas

(1901) says appear at an early stage in the wasp beneath the larval layer. In other insects, it is claimed, the replacement proceeds from the same cells that continually regenerate the cells lost in the digestive processes. The discarded epithelium is digested and absorbed by the new.

The role of the fat body in metamorphosis has been fully described in Chapter IX. Upon its proper functioning as an elaborator and conserver of nutrient and energy-forming materials depends the ability of the insect to go through its reconstuctive processes during the fasting period of the pupa. An insufficiency of food during the larval period probably results directly in a scanty store of provender in the fat body, and consequently in the production of undersized adults, or in the loss of power to complete the transformation.

**The Molt of the Pupa.**—As the bee pupa ages it begins to show color externally on various parts of the body, but particularly on the eyes, which first become pinkish, then darken to purple, and finally turn brown. The transformation of the pupa to the adult, as that from larva to pupa, is accompanied by a molt, though, of course, the real changes of the organs to the adult forms precede the actual casting of the pupal cuticula. The final molt of the worker bee, according to Bertholf (1924), takes place about 20 days from the time the egg was laid, or 9 days after the last molt of the larva. Immediately the young imago begins to chew its way out of the cell, and it usually emerges on the same day or the day following its molt.

**Length of Stages of Worker, Queen, and Drone.**—Certain differences in the times of molting by the different castes of the honeybee are noted by Bertholf. With the queen, he finds, the last molt of the larva takes place at the end of the tenth day after the laying of the egg, while the molt of the pupa occurs on the fifteenth day. The pupal period of the queen is, therefore, one of but five days instead of nine days as with the worker. The queen emerges from the cell on the sixteenth day. With the drone the prepupal period of the larva lasts four days, the fifth larval molt being on the fourteenth day after the egg was laid. The pupal stage of the drone, therefore, lasts eight or nine days, with the final molt on the twenty-third day after hatching.

The time of the various events in the lives of the three castes of the honeybee may be tabulated as follows from Bertholf's

records, giving the approximate periods in days after the laying of the egg in each case:

| | Worker Days | Queen Days | Drone Days |
|---|---|---|---|
| Hatching of the egg | 3 | 3 | 3 |
| First larval molt | 3½–3¾ | 3½–3¾ | 4 |
| Second larval molt | 4½ | 4½ | 5 |
| Third larval molt | 5½ | 5½ | 6 |
| Fourth larval molt | 6½ | 6½ | 7 |
| Capping of the cell | 8 | 8 | 10 |
| Spinning of the cocoon | 9 | | |
| Fifth larval molt | 11 | 10 | 14 |
| Molt of pupa | 20 | 15 | 22½ |
| Emergence of adult | 21 | 16 | 24 |

**The Nature and Meaning of Metamorphosis.**—In its higher manifestations metamorphosis has the aspect of a miracle; in its simpler forms it is a mere alteration of growth during a molt.

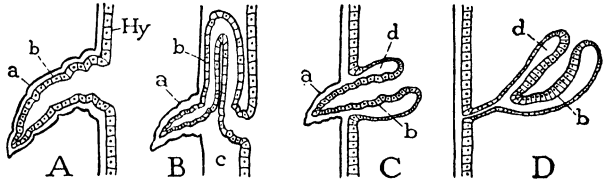



Fig. 108.—Diagram showing evolution of an imaginal bud.
A, formation of a new appendage (*b*) within old cuticula of larval appendage (*a*) of same size. B, growth of larger adult appendage (*b*) beneath larval cuticula, with only its tip in reduced larval appendage (*a*). C, growth of an adult appendage in open peripodal pocket (*d*) of imaginal hypodermis, but with its tip still in rudimentary larval appendage (*a*). D, larval appendage completely obliterated, adult appendage (*b*) forming in closed peripodal cavity (*d*) of imaginal hypodermis.

At any molt between larval stages a new member usually duplicates the old, except in size, and is formed within the limits of the latter (Fig. 108 A), as in the leg of a caterpillar. When the old cuticula is loosened a new organ grows, but it *may* also take on a different form. If it is to be much longer than the old (B, *b*), perhaps only its tip can develop within the latter (*a*), the rest must either find accommodation in the space (*c*) beneath the skin, or it must retreat into the hypodermis. In the second event (C) it forms a depression (*d*) in the body wall, known as a *peripodal cavity*. If, finally, the original appendage has disappeared completely in the larval stages, through being reduced to a disc of cells in the hypodermis during the evolution of the species, but is to be restored in the adult stage of the individual,

the disc of cells, or imaginal bud, must either make its growth entirely beneath the skin, or it must begin its development in a pouch of the body wall (D). In this case the bud or histoblast, being unhampered by any responsibility to larval parts, may begin its growth precociously at any time during earlier larval or even embryonic stages, and this it sometimes does.

The metamorphosis that has occurred in the evolution of the larva was a progressive change toward a larval goal, the metamorphosis that now occurs in the pupa is the resumption of normal development, greatly complicated and distorted by the aberrations of the larva.

The meaning of the metamorphosis of insects, and the nature of the physiological activities that actually bring it about in the individual are two quite different subjects for research. Though a few investigators have begun to study the chemistry of the insect in process of transformation with a view toward finding the physical cause of metamorphosis (Bishop, 1923*a*), the subject is still mostly in a speculative stage, and is one on which discussion may be more profitably left to the future.

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