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MORPHOLOGY OF THE HONEYBEE LARVA¹

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INTRODUCTION

The observations here recorded seem desirable for several reasons. In the first place, it has been the policy of the Office of Beekeeping Investigations to secure, as far as possible, comprehensive and detailed information regarding all phases of the life history of the honeybee. An account of the development of the honeybee in the egg already having been completed (*36*)², a study of the postembryonic development appears next in order, and this involves necessarily a thorough and intimate knowledge of the structure of the larva. Moreover, an account of the structure of the bee larva ought not to be entirely without interest to intelligent beekeepers. Finally, such an account will unquestionably prove valuable to investigators of the pathology of brood diseases of the honeybee.

No complete description of the structure of the larva of the honeybee has yet been published. This is especially surprising in view of the attention bestowed on the structure of the imago. Leuckart and Nitsche (*31*) have included the bee larva in the series of types illustrated by their wall charts. These illustrations, however, convey but a meagre amount of information on this subject and in some respects are incorrect. Anglas (*1*) gives a description of the bee larva in his account of the metamorphosis of the wasp and that of the honeybee, but here again the description of the morphology of the larva is only incidental and for the most part brief and superficial. Moreover, some organ systems, such as the nervous system, are left almost untouched.

In the following account the larva has been treated as if it constituted a single stage. The larval period, it is true, embraces a series of stages, differing from one another and representing a continuous process of development, but the principal morphological features peculiar to the larva as such remain surprisingly constant. Since a sketch of the structure of the newly-hatched larva has already been published by the writer in connection with the embryonic development, and, since it is especially important to know the structural conditions immediately preceding pupation, especial attention is here paid to the larva which has virtually attained its full growth. The following descriptions therefore apply to such a larva, unless otherwise stated. Wherever important changes in larval structures accompany growth, these are taken into consideration.

EXTERNAL FORM

In general appearance the bee larva much resembles many other cruciform larvae. When removed from the cell the full-grown larva (Pl. 1, D) is fusiform, the posterior end being the larger. Younger larvae are more slender and more nearly cylindrical, while the head is much larger in proportion to the trunk. In those recently hatched the body differs in its proportions from the bodies of

¹ Received for publication Apr. 22, 1924—issued Nov., 1924.

² Reference is made by number (*italic*) to "Literature cited," pp. 1208-1212.

older larvae in that the anterior end is the larger, the body tapering toward a pointed posterior end. In old larvae the posterior end is blunt and rounded. In larvae of all ages the body is strongly flexed toward the ventral side. In marked contrast the larvae of the Vespidae have bodies which are nearly straight.

In color the larva is ivory white. As seen in the comb it appears to be pure white by contrast with the brown comb, but when removed and placed on a white surface it takes on a yellowish or brownish tinge.

A series of sharply defined constrictions divides the body into 13 segments, 3 thoracic and 10 abdominal.³ In antero-posterior extent the three thoracic segments are subequal and slightly inferior to the adjacent abdominal segments. The latter are also subequal in extent, with the exception of the 9th and 10th. The 9th is short and has a somewhat discoid form, as shown in the figure. The 10th is quite small and also discoid and bears in its center a low papilla on which is situated the anal opening.

The ventral or sternal surface is marked off from the lateral surfaces by a deep groove, the ventrolateral suture (Pl. 1, D, *VLS*), which extends from the 1st to the 8th abdominal segments, being absent on the three thoracic and the last two abdominal segments. The lateral surfaces of the abdominal segments, with the exception of the last two, are raised to form rounded lobes, the epipleural lobes (*EpL*). These lobes, while sharply marked off from the ventral surface by the ventrolateral suture, merge almost imperceptibly into the dorso-lateral surfaces of the body. The epipleural lobes are often more or less confluent, producing the appearance of a beaded ridge on each side of the body. The abrupt termination of these ridges at the posterior boundary of the third thoracic segment produces the appearance of "shoulders" noted by White (50).

Ten pairs of spiracles are present, belonging as usual to the 2d and 3d thoracic and the first eight abdominal segments. They appear externally as minute circular apertures, each of which is surrounded by a narrow chitinous ring, the peritreme. They are located at the same level on all of the segments, about half way between the dorsal mid-line and the ventrolateral suture, and lie close to the anterior edges of their respective segments in depressions confluent with the intersegmental constrictions. In the thoracic region the first pair of spiracles has the appearance of belonging to the 1st instead of to the 2d thoracic segment, this appearance being due to the somewhat peculiar outline of the contiguous margins of these two segments (see fig. 4, A). Below the spiracles of the 2d and 3d thoracic segments the oval outlines of the wing rudiments (*WngR*) may be somewhat indistinctly seen. On all of the segments bearing spiracles a shallow linear depression or suture arises in the neighborhood of each spiracle and takes an oblique course dorsad and caudad across the dorso-lateral surface of the segment toward the dorsal mid-line, where it disappears, thus separating the dorsal half of the segment into anterior (*Prs*) and posterior (*Scs*) divisions. Comparison with coleopterous larvae, such as those of *Dendroctonus* (17), makes it evident that the anterior division corresponds to the prescutum, while the posterior, which is confluent laterally with the remainder of the segment, corresponds to the scutum and scutellum together, which in the coleopterous larva are separated by a suture. These divisions, and in fact the entire contour of the body, are intimately related to the internal structure, as will be more completely explained in the description of the muscular system.

The head (Pl. 1, F, G), with regard to its general outline, may be described as bluntly conical, the base of the cone being formed by the head capsule, the apex by the labrum and the other mouth parts. The head is joined to the

³ Embryological evidence indicates that there are actually 12 segments represented in the abdomen of the bee larva (36, 38).

trunk by nearly its entire width, a sharp and narrow constriction representing the neck region. Normally the head is retracted into the prothoracic segment, thus forming a deep fold between the two. The ventral third of the head, including the labium, maxillae, and that part of the head capsule to which they are attached, is sharply separated from the remainder of the head, which constitutes the head capsule (*26*), by a deep furrow which extends on each side from between the bases of the mandibles and maxillae to the posterior limits of the head. This may be conveniently designated as the *lateral furrow*.⁴ Its posterior end, on each side, is continuous with the lumen of the posterior arms of the tentorium (*2Ten*). In face view the head capsule is seen to be divided dorsally into two equal lobes by a median cleft (Pl. 1, F). On the convex surface of each of these lobes is a small rounded elevation (*Ant*), representing the distal end of the antennal rudiments. Springing from the head capsule in the mid-line, between the antennal rudiments and directed cephalad and ventrad is the cushion-shaped common rudiment of the labrum and clypeus (*Clp+Lm*). Its distal end is free from the head capsule and its tip slightly indented in the mid-line.

In *Vespa*, according to Kirmayer (*26*), the labrum is distinguishable from the clypeus, but apparently this is not always possible, since the two areas are represented as distinct in Kirmayer's figure 30, but not in his figures 28 and 29. In the bee larva they are not always readily distinguishable on the exterior, but in many preparations of the head of advanced larvæ the rudiment of the clypeus and labrum is seen to be crossed by a delicate and distinct fold, dividing it into a distal and a proximal part, which can only be labrum and clypeus, respectively (Pl. 1, F). These two parts are also evidently indicated by the arrangements of the muscles. (Pl. 6, C.)

Beneath the labrum is the mouth opening (*Mth*), on each side of which are the conical mandibles (*Md*), curved in such a way that their pointed tips lie beneath the labrum. The maxillæ (*Mx*), which are attached to the ventral part of the head capsule, are situated somewhat farther apart than the mandibles. They are also longer and of larger diameter, converging a trifle toward the mid-line, cylindrical in form, slightly tapering toward their apices, which are rounded and tipped each with a small spine. The labium (*Lb*), which springs from the ventral part of the head in the mid-line, is of relatively large size, projecting beyond the other mouth parts, bluntly conical in form, rounded at the apex, on which is a transversely elongated elevation bearing the slit-like common opening of the silk glands (*SilkDO*). On each side of the latter, and slightly ventrad to it, is a small spine, similar to those on the maxillæ. The upper surface of the labium is separated from the lower surface of the labrum by a narrow cleft, forming the mouth opening (*Mth*) which is bounded laterally by the mandibles and maxillæ. All of the mouth parts are soft and fleshy and covered only by thin chitin, with, of course, the exception of the small spines already mentioned.

Above the common rudiment of the clypeus and labrum, on each side of the mid-line, a shallow depression is found. These depressions represent the insertions of muscles on the inner surface of the head capsule. Above each of the antennal rudiments is a smaller but somewhat more sharply marked triangular depression; these also mark points where muscles are inserted.

⁴ A study of the figure by Kirmayer (*26*) of the head of the wasp at different stages makes it evident that the "lateral furrow" of the wasp larva corresponds very closely with the margins of the fossa of the proboscis in the imago and this of course must be also true in the honeybee. It would appear, therefore, that the ventral part of the larval head lying between the two lateral furrows becomes later differentiated into the various structures included in the fossa of the proboscis—mentum, submentum, cardines, etc., and also that part of the occipital region ventrad to the foramen.

The description above given applies to a bee larva four or five days old, after removal from the cell. The larva is never permitted to assume this form, however, until after the cell is sealed, when it undergoes the important changes preliminary to pupation. The actual shape assumed by the bee larva of from four to five days old is shown in Plate 1, E. The specimen from which this drawing was made was fixed and hardened in the normal position in the cell, from which it was afterwards extracted. As can readily be seen, the larva is bent ventrad in the shape of the letter U, head and anus being brought close together, and fits its narrow quarters so completely and so snugly that it forms a veritable cast of the interior of the cell, the prismatic six-sided form of the latter being plainly reproduced by the larva, which not only takes nourishment and grows in this compressed state, but on being withdrawn from the cell can immediately assume the plump, rounded form shown in figure 1, the only remaining perceptible evidence of its close confinement being a slight asymmetry of the 8th abdominal segment, the lateral fold on this segment being more turgid on the side turned toward the bottom of the cell. This is evident in Plate 1, E. In all the specimens of larvæ fixed and hardened within the cell the head lies somewhat closer to the mouth of the cell than the anus, the long axis of the larva thus being spirally curved. In some larvæ the right side is outermost, in others the left.

Kellogg (24) has given a brief account, accompanied by two figures, of the head and mouth parts of the honeybee in connection with a study of the metamorphosis. It is of interest to note here that the spines on the maxillæ were found to represent the minute one-segmented maxillary palpi of the adult. This may readily be seen in stained and cleared preparations of the head of larvæ about to pupate. Kirmayer (26) has given a detailed account of the structure of the head of *Vespa* in connection with the changes taking place during the metamorphosis. Kirmayer's excellent figures of the head of the larva of *Vespa* show that while it is similar to that of the honeybee, it differs much in details, and particularly in the proportions of the various parts. It may be noted that in general the head of the larva of *Vespa* is both shorter and narrower than that of the bee larva, the labrum being indented ventrad and even a trifle caudad. (Pl. 10, A.) The labium is relatively much smaller, while the head capsule lacks the conspicuous median dorsal cleft seen in the honeybee.

HYPODERMIS AND CUTICLE

The hypodermis, which, together with the cuticle secreted by it constitutes the body wall, is a simple one-layered epithelium, differing in thickness in different parts of the larva. These differences are indicated in many of the illustrations, but it may be said that in general both hypodermis and cuticle are thin over the entire extent of the trunk, the hypodermis being as a rule thinner at the middle of the segments and increasing in thickness in the intersegmented regions, and therefore ranging from the squamous to the cuboidal type. In the head the hypodermis has a considerably greater average thickness than in the trunk (Pl. 2, B, and 3, D). The hypodermal cells here have as a rule a prismatic form, and are in many places so slender and so closely crowded together that the nuclei are compelled to lie at different levels, giving the impression of a many-layered epithelium. It should be noted that in the larva there is no thinning of the hypodermis or cuticle at the borders of the segments or at the bases of the mouth parts. Such a thinning would correspond to the articular membranes of the imago.

The rudiments of the antennæ, wings, legs, and genitalia remain to be mentioned, since they are hypodermal structures. The antennal rudiments of old larvæ are ovoid in form and are situated in deep depressions or cavities (peripodal

cavities) on either side of the labrum. They are directed cephalad and slightly mesiad, their smaller ends directed outward, and are attached by the mesial side of their larger inner ends to the head capsule on the mesial side of the peripodal cavities. The long axis of the rudiments is therefore actually bent through an angle of about 90 degrees (Pl. 2, D). The cavities themselves are closed only by the chitinous cuticle, which is continuous over their external openings. The tips of the antennal rudiments project slightly above the general surface of the head and produce the small rounded elevations visible from the exterior (Pl. 1, F and G, *Ant*). The segments of the antennæ are indicated by the wavy contour of their hypodermis as well as by the distribution of the antennal nerve. (Pl. 2, D, *AntNv*.)

The leg rudiments (fig. 1 and 4, A, *1L-3L*) are short fusiform or ovoid in shape, like the antennæ, and are also situated in deep open depressions covered externally only by the cuticle. The leg rudiments are directed caudad and mesiad. The segments of the imaginal legs are indicated by annular constrictions. The wing rudiments are flat hollow outgrowths of the hypodermis of the mesothoracic and metathoracic segments and are situated in shallow depressions low down on these segments, close to the ventral surface and at a considerable distance ventrad to the stigmata of these segments (fig. 1, Pl. 1, D, and fig. 4, A, *WngR*). In outline the wing rudiments are heart-shaped.

The rudiments of the genitalia (fig. 1, *1G-3G*) are six in number, one pair being situated on the sternite of the 8th abdominal segment and two pairs on the 9th abdominal segment, as described by Dewitz (9). At this stage they are small knob-like outgrowths situated in open depressions.

While the cuticle of the trunk is thin and elastic, that covering the cranium is much thicker and forms a more or less rigid capsule for the protection of the contained brain and other organs. The chitin covering the mouth parts is, as has already been said, thin and relatively flexible.

The rigidity of the head capsule is further increased by the cranial endoskeleton or tentorium, formed during the embryonic period by invaginations of the ectoderm (36). In the imagoes of insects the tentorium is evident as a framework of chitinous bars, but in the bee larva the embryonic conditions persist so that the tentorium consists of tubular ingrowths of the hypodermis lined with chitin, the hypodermal portion being relatively well developed as compared with the imago, in which the hypodermis forms a relatively insignificant layer. Lying between the oesophagus and the suboesophageal ganglion, transverse to the long axis, is a wide tube lined with a thick layer of chitin, compressed in a dorsoventral direction and slightly curved, the convex side being directed cephalad. This tube is subdivided—on embryological evidence—into three nearly equal parts, a central body (Pl. 1, A, and 6, D, *Ten*), and two lateral arms, the "posterior" arms (*2Ten*). The latter become continuous with the walls of the head capsule at the posterior ends of the deep lateral furrows of the head. These infoldings, or at least their posterior part, may in fact be considered as the expanded distal ends of the posterior arms, the furrows leading at their posterior ends directly into the lumen of the posterior arms, which, together with the lumen of the central body, forms a continuous open passageway from one side of the head to the other. At the junction of the central body with the lateral arms arise the anterior arms (Pl. 1, A, *1Ten*) which extend cephalad and dorsad to the anterior wall of the head capsule, with which they are united. These points of junction are marked on the exterior by two minute pits, situated above the bases of the mandible at the sides of the labrum (Pl. 1, F, *1Ten*). The anterior arms are also tubular but are much more slender than the posterior arms and are round in section. Halfway between their anterior and posterior ends each of the anterior arms gives off a

slender spur dorsad and laterad. These serve as the tendonous insertions of short muscles inserted on the anterior wall of the cranial capsule.

The mandibular apodemes also claim attention here. These are slender tapering chitinous spines which arise from the base of each mandible on its mesial side and are directed caudad and dorsad (Pl. 1, A, *RAp*). These, as their name indicates, serve as tendonous insertions for the large adductors of the mandibles. These spines are hollow for a considerable part of their length and are both accompanied and produced by corresponding involutions of the hypodermis.

White (50) has already called attention to the minute spines of the larval cuticle. These are more or less irregularly scattered over the surface of the cuticle of the head and trunk, the distance between them varying from 5 to 30 microns. Their length does not exceed the thickness of the cuticle, which is 5 to 6 microns. On the mesial surface of the tips of the maxillae these spines are however quite numerous, while the extreme tip of the labrum is clothed with thick-set chitinous spines, longer and more slender than those found elsewhere.

The head capsule and endoskeleton of the head of the bee are, except for slight differences in proportion, identical with those of the larva of *Vespa*, as described by Kirmayer (26).

NERVOUS SYSTEM

The general features of the nervous system of the bee larva have already been described in an earlier publication (36). These features indicate on the whole a conformity to the simple type found in many insect larvae. In the bee larva this simple type persists throughout larval existence, although histological changes are continually taking place, especially in the brain, in the direction of the imaginal condition. In comparison with certain other insect larvae, such as *Corydalis* (13), the nervous system of the bee seems deficient, particularly with regard to the sympathetic nervous system. This may, however, only argue a deficiency in observation. The small size of the bee larva and the abundance of fat tissue, which more or less completely fills all the spaces of the body cavity, clinging tenaciously to whatever organs lie adjacent, constitute no small obstacle to successful dissection, while the tracing of nerves in sections has not been found satisfactory.

The nervous system of the bee larva has never been described or illustrated in detail. Probably the only figures worth mentioning are those of Brandt (5), and the one shown in the Leuckart and Nitsche wall charts (31), a figure widely copied in text books and evidently borrowed from Brandt. These show little more than the general plan of the nervous system, the shape and proportions of the brain and circumoesophageal connections being incorrectly represented. Brandt's figure shows correctly the number and relative size of the ganglia in the ventral chain, and also the paired connections and lateral nerves.

In describing the nervous system it may be conveniently divided into the brain, the ventral nerve cord, and the stomatogastric nervous system. The following description, unless otherwise stated, is to be understood as applying to the mature, or nearly mature, larva.

BRAIN

The brain is of relatively large size, almost completely filling the upper part of the head capsule (fig. 1, *Br*; Pl. 1, B, C). It is divided symmetrically into two expanded crescentic halves united on their convex borders by the supraoesophageal commissure (Pl. 1, B, *Sup Com*). Seen in face view, each half presents a mesial pyriform division, the slender inferior ends of which form the *crura cerebri* (*CCer*) connecting the brain with the suboesophageal ganglion (*SoeGng*); above these follow in order the small but prominent tritocerebrum (*3Br*), the

deutocerebrum, olfactory or antennal lobes (*AntL*), and the large protocerebral lobes (*1Br*). Laterad and caudad the protocerebral lobes merge into the broad auriculate optic lobes (*OpL*), which lie almost precisely in the transverse plane. Their edges are quite thin and their posterior faces almost perfectly flat. The two lobes of the tritocerebrum are recognizable externally as distinct swellings most evident in profile view (Pl. 1, C, 3Br); those of the deutocerebrum, however, are to be identified externally only by the antennal nerves which spring from them. On the anterior faces of each of the optic lobes, near their ventral margins, and involving also the antennal lobes, is a well-marked depression, of a somewhat hemispherical outline. These depressions are produced by the peripodal cavities of the antennal rudiments, which in mature larvae are of large size.

Two pairs of nerve trunks arise from the brain. The first of these, the antennal nerves (Pl. 1, B and C, *AntNv*) spring from the anterolateral faces of the antennal lobes. They then take a lateral course to the base of the antennal rudiment, where each divides to form three branches. Two of these branches innervate the adjacent masses of mesodermal cells surrounding the base of the antennal rudiment, and are therefore evidently motor nerves. The third or sensory branch enters the cavity of the antenna and passes along its lateral margin, sending off a tuft of nerve fibers to each segment. This is well illustrated by Plate 2, D, which shows the antennal rudiment in longitudinal section with the nerve (*AntNv*) giving off branches to each of the six segments seen in the section. The labrofrontal nerve (Pl. 1, B and C, and 2, B, *LmNv*) springs from the anterior face of each of the two halves of the tritocerebrum. This nerve is, as its name

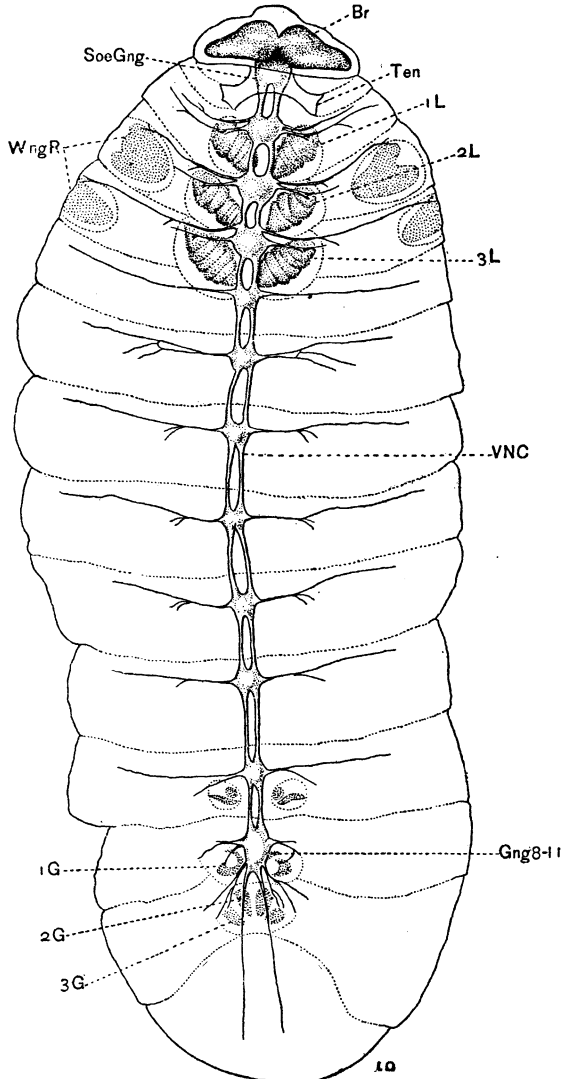


FIG. 1.—Nervous system and ventral body wall of mature honeybee larva, drawn from a dissection. $\times 16$

indicates, a double one, and near its point of origin it divides into its component parts, the frontal nerve (Pl. 1, B and C, *FtNv*), which turns mesiad to unite with the stomatogastric or frontal ganglion (*FtGng*), and the labral nerve (*LmNv*). The latter takes a cephalad course, entering the clypeus at its extreme lateral border, and runs close under the hypodermis to the tip of the labrum, where it divides into several branches innervating the hypodermis.

The two halves of the tritocerebrum are united by the suboesophageal commissure (*SoeCom*), a relatively thick strand of nerve tissue which forms a loop below the oesophagus. Its two ends are joined to the two halves of the tritocerebrum on their ventral sides, just anterior to the crura cerebri.

In the imago of the honeybee two other pairs of nerves have been described which, however, appear to be absent in the larva. These are the tritocerebral nerve, discovered by Janet (19) in the ant *Lasius*, which issues from the inner faces of the tritocerebral lobes and innervates the inferior dilator muscles of the pharynx, and the salivary nerve (Kenyon, 25), which also issues from the tritocerebrum and innervates the salivary gland. Jonescu (21) has shown that the roots of both of these nerves lie in the suboesophageal ganglion.

The suboesophageal ganglion (Pl. 1, B and C, 2, B, and 3, A, *SoeGng*) is lenticular in form, somewhat broader at its anterior end, and turned obliquely with respect to the long axis of the larva, its anterior end being directed dorsad as well as cephalad to meet the crura cerebri. It gives rise to four pairs of nerves, as follows:

1. The mandibular nerves (Pl. 1, B and C, *MdNv*). These arise from the antero-lateral angles of the ganglion, just below the crura cerebri. Each of these nerves pursues a cephalad course, turning slightly dorsad and laterad, just below and parallel to the anterior arms of the tentorium, to the base of the mandible, where it divides into branches which are distributed to this appendage.

2. The maxillary nerves (Pl. 1, B and C, *MxNv*). These arise from the ventro-lateral face of the ganglion, a short distance behind the mandibular nerves. These nerves run ventrad, laterad, and cephalad to the anterior surface of the depressors of the maxillae (see p. 1190). Here each of these nerves divides into three branches, one of which supplies the depressor, a second the flexor of the maxilla, while the third pursues a cephalad course into the interior of the maxilla, where it branches among the mesoderm cells situated there.

3. The labial nerves (Pl. 1, B and C, *LbNv*). These arise from the ventral face of the suboesophageal ganglion, near its lateral borders, and about two-thirds of its length from the anterior end. Each of these nerves runs ventrad and laterad to the major retractor, where each nerve divides into two branches, one of which supplies the retractor muscle while the other continues cephalad to the tip of the labium.

4. X nerves of Jonescu (Pl. 1, C, *x*). These arise from the lateral faces of the ganglion close to its posterior end. Although taking their rise from prominent papillate elevations on the side of the ganglion, these nerves in old larvae are excessively slender and correspondingly difficult to trace. The evidence obtained by examination of several series of sections seems, however, to indicate that the X nerves pursue a fairly direct course ventrad and laterad, reaching the hypodermis close to the origin of the major retractors of the labium. In sections of recently hatched larvae these nerves are relatively much larger than in older larvae and in fact are very easily distinguished. Their course is directly laterad to the ventral margin of the junction of the posterior arms of the tentorium with the hypodermis of the neck region. No indication of a connection with the silk gland was seen. It appears therefore that in the bee larva this nerve is purely sensory. Jonescu (21) has described this nerve in his account of the brain of the imaginal honeybee, but is silent regarding its course and destination. The

writer has also seen it in sections of material of the imaginal bee, but has been unable to follow it to its termination. As in the larva, it is insignificant in size, although plainly evident at its point of departure from the ganglion. Janet (18) has described a fourth pair of nerves arising from the suboesophageal ganglion in the ant *Myrmica rubra*, and Krauss (28) and Hammar (13) have described a pair of nerves in the *Corydalis* larva arising from the caudo-lateral portion of the ganglion just cephalad of the junction of the connectives with the ganglion. In *Myrmica rubra* the nerve corresponding in position to the X nerve, termed by Janet "the labial sympathetic nerve (*nervus sympatheticus labi*)" gives rise to a complex system consisting of a ganglion and three branches on each side of the mid-line. These innervate the labial gland and also adjacent muscles and tracheae. In *Melanoplus* (39), *Corydalis* larva (13), *Forficula* and certain other insects (29) a pair of nerves make their exit from the lateral faces of the suboesophageal ganglion near its posterior end, generally known as "salivary gland" nerves. In the bee larva no connection between the X nerves and the salivary (silk) gland could be established, but it nevertheless is possible in view of the close correspondence in the point of exit from the suboesophageal ganglion of the salivary gland nerves in *Melanoplus*, *Corydalis*, etc., the labial sympathetic nerves in *Lasius*, and the X nerves in *Apis*, that these are all homologous. Pietschker (42) has described a nerve in the ant which he terms "*nervus accessorius*." It springs from the suboesophageal ganglion about half way between the labial nerve and the connectives and runs toward the labium, where it ends in depressions of the hypodermis, possibly representing sense organs. This nerve in its point of exit and its termination closely approximates the X nerve of the bee larva. The accessory nerve of Pietschker is entirely distinct from the salivary nerve which was also observed and makes its exit from the dorsal side of the ganglion. It is also not to be identified with the labial sympathetic nerve of Janet.

The brain and suboesophageal ganglion of the mature larva, with reference to their external form, differ slightly from those of the young larva, and very materially from those of the imago. In the newly hatched larva (36) the two lobes of the protocerebrum (including the optic lobes), as compared with those of the mature larva, are shorter and thicker, and are bent caudad instead of lying in a plane transverse to the long axis of the larva. Moreover, they show clearly a subdivision into three lobes, as described by Viallanes (49) for Orthoptera. The antennal lobes, although not prominent, are present as distinct swellings, while the tritocerebral lobes are scarcely differentiated externally from the antennal lobes on the one hand and the thick *crura cerebri* on the other. The latter merge caudad into the elongate suboesophageal ganglion, which is divided externally into three swellings representing its three component pairs of ganglia.

As compared with the brain of the larva that of the imago (21) shows striking differences. Superficially there is a certain resemblance between the two, principally on account of their flat expanded form and the large size of the optic lobes. In the imago, however, the protocerebral lobes become high bilobed elevations separated from the optic lobes by well marked constrictions, and the antennal lobes become conspicuous rounded swellings projecting from the anterior face of the brain; while the tritocerebral lobes, which are fairly distinct in the larva, become almost indistinguishable. Moreover, in the imago the suboesophageal commissure becomes so fused with the suboesophageal ganglion as to be indistinguishable externally, while the frontal ganglion sinks to insignificant proportions. On the other hand, the suboesophageal ganglion of the mature larva differs but little in form, size and general external appearance from that of the imago. It is scarcely necessary to remark that most of these differences, such as the difference in size of the antennal lobes, may readily be

correlated with the differences in the environmental conditions of the two forms, yet some of these differences, such as the reduction in size and relative importance of the tritocerebrum and of the suboesophageal commissure, represent developments in the direction of specialization. In other words, notwithstanding its relatively specialized form, the brain of the larva is appreciably nearer the primitive type, as represented in the lower orders of insects, than is that of the imago.

VENTRAL NERVE CORD

The ventral cord consists of 11 ganglia united by rather widely separated connectives (fig. 1, *VNC*). All of these ganglia, with the exception of the eleventh, or terminal ganglion, are situated in the anterior half of their respective segments. In form the ganglia are more or less lenticular, the first three, or thoracic, being much larger than the abdominal ganglia. The latter are subequal in size, with the exception of the eleventh or terminal ganglion, which is elongate in form and much larger than the others. Unlike the other ganglia, this one is situated in the middle of its segment, the eighth abdominal. This ganglion, as usual, is compound, consisting of three ganglia and the rudiment of a fourth (6, 38), representing, respectively, the neuromeres of the 8th, 9th, 10th and 11th abdominal segments.

Each thoracic ganglion gives off two pairs of lateral nerves (fig. 1 and 4, A). The first pair arises from the antero-lateral margin of the ganglion close to the point where the latter joins the connectives. In the prothorax these nerves run laterad in the anterior half of the segment, close to the hypodermis. In the mesothorax and metathorax these nerves also run laterad, giving off a branch to the ventral trunk muscles, and, continuing onward, skirt the anterior margin of the wing rudiments. At the antero-lateral border of the latter each of these again bifurcates, one branch going to the wing rudiment while the other passes dorsad and laterad to the viscera.

The second of the two pairs of nerves given off arises from the lateral margin of the ganglion about midway of its length. The course and distribution of these nerves is the same in all three thoracic segments. Each passes laterad and slightly caudad to the leg rudiment (*1L-3L*) of the corresponding segment, sending a branch to the base of the rudiment. It then continues laterad and is lost to view among the muscles and fat cells.

Each of the abdominal ganglia, exclusive of the terminal ganglion, possesses but one pair of lateral nerves (fig. 1 and 4, B, *LNv*). These nerves run directly laterad, giving off branches to the ventral trunk muscles, as shown in Figure 4, B, and become lost to sight among the trunk muscles and viscera.

The 8th abdominal or terminal ganglion gives off four pairs of nerves (fig. 1). The first pair arises from the lateral margins of the ganglion near its anterior end and passes laterad to the muscles and viscera of the 8th abdominal segment. The second pair of lateral nerves originates so close behind the first pair that these two pairs can be regarded as having a common root. These two pairs of nerves go to the first pair of genital rudiments (*1G*). The third pair of lateral nerves runs caudad into the 9th abdominal segment, breaking up meanwhile into several branches, some of which supply the second pair of genital rudiments (*2G*). The fourth and last pair arises from the posterior margin of the ganglion, and these nerves run almost directly caudad to the 10th segment, where they break up into branches supplying the viscera and muscles of this segment. Three segments, the 8th, 9th, and 10th abdominal, are therefore represented in the terminal ganglion on the basis of the number and distribution of the lateral nerves. The fourth segment, the 11th abdominal, is represented by only an insignificant ganglionic rudiment, and its corresponding segment disappears about the time embryonic development is completed.

STOMATOGASTRIC NERVOUS SYSTEM

In the bee larva, so far as known, this is the sole representative of the so-called sympathetic nervous system. It consists of the frontal or stomatogastric ganglion and the nerves associated with it. The frontal ganglion is of relatively large size, in comparison with the imago, and is more or less pyriform in shape, its smaller end directed caudad (Pl. 1, B and C, and 3, A, *FtGng*). It is situated above the oesophagus and just in front of the brain. Its sole connection with the brain is made by means of the frontal commissures or nerves (*FtNv*), which are rather stout bundles of fibers arising from the two sides of the ganglion near its anterior end. From this point they run laterad and caudad to the anterior faces of the two halves of the tritocerebrum, joining there the roots of the labral nerves, as already described. From the anterior end of the frontal ganglion a small nerve is sent off, sometimes called the "frontal nerve." This term, however, is objectionable, since it is also commonly applied to the commissures connecting the frontal ganglion with the tritocerebrum. The nerve in question (Pl. 3, A, *SPhyNv*) runs cephalad along the dorsal surface of the oesophagus to the epipharynx, where it divides into several branches, some of which go to the epipharyngeal muscles. Twigs are also apparently sent to the tip of the labrum. In view of its terminations, Janet (18) has termed the corresponding nerve in *Myrmica rubra* "nerf des muscles supérieurs du pharynx situés en avant du ganglion frontal." This descriptive term the writer for convenience ventures to abbreviate to "superior pharyngeal nerve" (*SPhyNv*). In *Myrmica rubra* there is another nerve to the posterior superior muscles of the pharynx. This nerve apparently is not represented in the bee larva. The posterior smaller end of the frontal ganglion is continued caudad as the stomatogastric or recurrent nerve (Pl. 3, A, *StgNv*). This nerve passes caudad in close contact with the dorsal wall of the oesophagus, meanwhile rapidly diminishing in caliber, to the posterior part of the head. Here it bifurcates, and a little farther caudad the two forks break up into branches too small to be successfully traced. In young larvae, and even in those as much as three days old, the two bifurcations of the recurrent nerve lead to flat discoid cell masses, closely applied to the sides of the oesophagus. These cell masses have been interpreted as the pharyngeal ganglia (36). In mature larvae they are no longer present, their places being taken by branches of the recurrent nerve, as stated above.

HISTOLOGY

The histology of the nervous system of the bee is too complex to be treated here in detail, but there are nevertheless certain outstanding features which deserve consideration.

The outer neurilemma or sheath consists of a layer of cells, usually single, limited on each side by a delicate but distinct membrane, and forms the outer covering layer of the brain, the various ganglia, the connectives, and at least the roots of the peripheral nerves. In both its thickness and in the form of its component cells the neurilemma differs much in character at different points. On the dorsal surface of the suboesophageal ganglion, for example (Pl. 2, B, *SoeGng*) the neurilemma (*Nlm*) often has the appearance of being only a single membrane, the two component membranes being actually brought very close together and the neurilemma cells being thin, flat, and spaced widely apart. At certain other points, in particular the posterior surface of the protocerebral lobes (Pl. 2, B, *Nlm*), the neurilemma is, on the other hand, very thick, and its cells, irregular and mesenchymatous in form, are seemingly disposed in several layers. Usually the neurilemma cells form a regular epithelial layer (Pl. 3, B and C, *Nlm*). Their cytoplasm, however, commonly presents a more or less shrunken and vacuolated

appearance, while the nuclei frequently stain very intensely with iron haematoxylin (Pl. 3, C, *Nlm*). An inner neurilemma is present as a more or less regular layer of small cells lying between the ganglion cells and the fibrous substance. It is best developed and most early seen in the brain (Pl. 2, B, *INlm*), and less so in the smaller ganglia. (Pl. 3, C, *INlm*.)

The brain and other parts of the central nervous system present in sections the usual core of nerve fibers and the cortical zone of nerve cells. (Pl. 2, A and B.) In the larval brain many of the features of the imaginal brain are plainly recognizable. This is particularly true of the broadly expanded optic lobes, which in transverse sections clearly display a division into inner, middle, and outer fibrillar masses (Pl. 2, A, *fm3*, *fm2*, *fm1*), while the cells and their fibrous processes show a distinct radial arrangement. In Plate 2, A, a layer of fibers intermingled with small cells is seen situated near the lateral faces of the optic lobes, between the latter and the hypodermis. These are evidently the developing postretinal fibers (*PrF*). They enter the optic lobes on the posterior surface of the latter, near their lateral margins, and may be traced around their lateral margins to the optic plates. The latter comprise two crescentic thickened areas of the hypodermis (ectoderm), one on each side of the head, their extent and relation to the remainder of the head capsule being indicated by Plate 2, C, *OpPl*.

The ocelli are present at this stage as hypodermal thickenings. Those for the two lateral ocelli are shown in Plate 2, A, *O*. The rudiment of the median ocellus lies farther cephalad, in the median groove (*43*).

Centrad and somewhat cephalad of the optic lobes, the rounded protocerebral lobes (Pl. 1, B, *IBr*) are seen to contain well-developed mushroom bodies, which are essentially similar to those of the imago (Pl. 2, B, *MB*). These bodies were found to be recognizable in a larva three days old.⁵

The deutocerebral or antennal lobes, although not evident externally, are distinguishable in sections by corresponding enlargements of the fibrous core (Pl. 2, A and B, *AntL*), and the relatively prominent tritocerebral lobes are similarly characterized (*3Br*).

The internal structure of the ganglia of the ventral nerve cord of the bee larva is simple, offering no striking peculiarities, and may probably be considered as fairly typical of the condition generally found in the simpler types of insect larvae. As seen in Plate 3, B, which represents a transverse section through the fifth abdominal ganglion, each ganglion is divided externally into right and left halves, representing the two members of the pair of primitive single ganglia. The outer surface of the ganglion is covered by a well-defined neurilemma (*Nlm*). Internally each lateral half consists of a central mass of nerve fibers, continuous with that of the connectives and surrounded by ganglion cells (*NvF*). These two central masses of nerve fibers are connected with one another by two parallel transverse strands of nerve fibers, the commissures (Pl. 3, B and C, *Com*). These are, as shown in Plate 3, C, situated somewhat cephalad of the middle of the ganglion. On the left side, in Plate 3, B, a strand of fibers (*LNvF*) is seen passing laterad from the central mass of fibers. On the right side the ganglion is seen to extend itself laterally into the lateral nerve of this side, in which is seen a strand of fibers (*LNvF*) corresponding to that of the opposite side. On the right side, however, the connection of the nerve fibers of the lateral nerve with the central mass is not shown in this section.

⁵ The duration of the feeding period of the larva is from four and one-half to five and one-half days. Larvae taken at or near the end of this period are considered mature, and it is to such larvae that the description above applies, unless otherwise stated.

The suboesophageal and the terminal, or 8th, abdominal ganglia are, as already mentioned, compound ganglia. The threefold nature of the suboesophageal ganglion is evident in sagittal sections such as that represented in Plate 3, A. At first glance four segments appear to be indicated by the presence of four commissures and four corresponding groups of ganglion cells. Examination of other sections of this series, however, as well as of the sagittal sections of other larvae of the same age, and also of younger larvae, shows that the last two bundles of transverse nerve fibers, together with the last two cell groups, belong to the labial segment. This component of the suboesophageal ganglion shows from the first two well-defined transverse commissures, like those of the succeeding trunk ganglia (36, fig. 45), while the mandibular and maxillary divisions never show clearly more than one. In the terminal ganglion three double commissures are distinguishable, being those of the 8th, 9th, and 10th abdominal segments (38). The same condition is found in embryos of *Forficula* (14, fig. 44).

One detail in the cellular composition of the nervous system should be noted. In the peripheral region of the brain and ganglia of the ventral cord of mature larvae are to be seen here and there cells of large size, which in their mode of division and other characters are plainly to be identified as neuroblasts. This observation corresponds with those of Bauer (2) on the larvae of *Vespa*, *Formica*, and other insects. Hilton (15) also reports the presence of neuroblasts in the brain and ventral cord of the larva of *Corydalid*.

CORPORA ALLATA

The corpora or so-called "ganglia" allata have, as is now well known, no intimate connection or relation with the nervous system, but since they have also no connection with other organ systems it is convenient to follow the time-honored custom of considering them at this point. They have in the mature larva the same structures and relations as in the newly hatched larva (36). They are spherical bodies (Pl. 2, B, *CorAll*), about 0.85 mm. in diameter, situated one on each side of the mid-line, close behind the brain, lying on the dorsal side of the anterior arms of the tentorium, near their posterior ends, and in close contact with the lateral walls of the aorta. Each is composed of a compact mass of polyhedral cells having finely granular and deep-staining cytoplasm, and nuclei with abundant chromatin in the form of subspherical granules. Surrounding the corpora is a delicate membrane secreted by the outer layer of cells. Just cephalad of the corpora, on each side of the aorta, is a tuft of tracheoles. Two or three of these enter the corpora allata and may be seen here and there between the cells of the latter.

TRACHEAL SYSTEM

The external openings of the tracheal system, the spiracles (fig. 2, A, Pl. 1, D, *Sp*), are 20 in number, or 10 pairs, each of the 10 segments from the 2d trunk (thoracic) segment to the 10th (8th abdominal), inclusive, bearing one pair. They are arranged on each side in a row parallel with the long axis of the body, and very nearly midway between the ventral and dorsal mid-lines. The mesothoracic spiracles are placed near the anterior limits of that segment; in the older larvæ they are located so far cephalad that they have frequently the appearance of coming within the limits of the prothorax. The spiracles of the succeeding segments are also located near the anterior borders of their respective segments at the bottom of shallow depressions, which are continuous with the adjacent intersegmental constrictions. Each spiracle is a minute, round aperture situated in the middle of a small circular elevation of the surface, the stigma. The spiracles are connected by short branches, the spiracular branches (Pl. 3, D,

SpBr), to the tracheal trunk (fig. 2, A, *TraTr*) of the corresponding side. Each of these trunks traverses the body cavity, about midway between the hypodermis and mid-intestine, slightly ventrad to the line formed by the spiracles of that side. The tracheal trunk of a mature larva has an inside diameter of about 0.1 mm. in its posterior and larger half; in the three anterior segments its diameter is reduced to about one-half of this caliber. The anterior ends of the tracheal trunks of opposite sides meet to form a loop, the anterior transverse commissure (fig. 2, A and B, *ATraL*), in the region of the neck and above the oesophagus; a similar loop, the posterior transverse commissure (fig. 2, A, *PTraL*), is formed by the posterior ends of the tracheal trunks. This latter, however, is situated ventrad of the posterior end of the mid-intestine, near its junction with the hind intestine. The two tracheal trunks are also united by a segmentally arranged series of transverse commissures, which lie in the ventral half of the body cavity, close to the body wall, passing below the ventral nerve cord. In a larva three days old or more the prothorax is seen (fig. 2, A) to possess one commissure, while the mesothoracic, metathoracic, and first abdominal (propodeal) segments each possess two commissures. These, however, become confluent just before their junction with the tracheal trunks. It should be noted that the commissures in the thoracic segments are quite slender, while those in the 1st abdominal segment approximate the diameter of the tracheal trunks at this point. In the 2d to the 8th abdominal segments the transverse commissures are single and of large diameter, the most anterior being largest, while the transverse commissure of the 9th abdominal segment is relatively slender and its course somewhat oblique. The prothoracic commissure joins the tracheal trunks just in front of the branches from the mesothoracic spiracles, those of the mesothorax just behind these branches. The commissures of the other segments, except that of the 9th segment, join the tracheal trunks either close to or slightly caudad to the corresponding spiracular branches.

Throughout their length the tracheal trunks give off numerous branches which supply the various regions of the body. Three branches on each side supply the head. The more anterior of these (fig. 2, B, *Bra1*) arises from the anterior transverse commissure close to the mid-line and runs cephalad to the brain, passing beneath the base of the optic lobes. It then turns abruptly dorsad, and supplies the anterior face of the brain and the region immediately adjacent (*a*). In the latter part of its course it passes close to and in contact with the spine, which arises from the anterior arm of the tentorium on each side. The second branch (*Bra2*) is much larger and arises from the anterior face of the transverse commissure a short distance ectad of the branch just described. Near its base it gives off a secondary branch (*b*) which passes mesiad and cephalad above the brain between the two halves of the protocerebrum, and supplies the aorta and the brain in the region of the mushroom bodies. The main branch takes a straight course cephalad and slightly ventrad, below the optic lobe, to the anterior region of the head, where it divides into three secondary branches. One of these (*c*) curves abruptly dorsad and breaks up into a large number of tracheoles at the base of the antennal rudiment. Before terminating its course, however, it gives off a twig to the mandible and one to the labrum. The second secondary branch passes mesiad to the head cavity underlying the supraoesophageal ganglion. The third secondary branch (*d*) supplies the maxilla.

In the prothorax the only tracheal branch worth noting is one (fig. 2, B, *e*) which arises on each side from the single tracheal commissure of this segment near its junction with the tracheal trunk, and passes mesiad and cephalad to supply the walls of the salivary glands in the region of the neck. In the remaining trunk segments, exclusive of the 9th and 10th abdominal, the number and arrangement of the tracheal branches is virtually identical. Springing from the

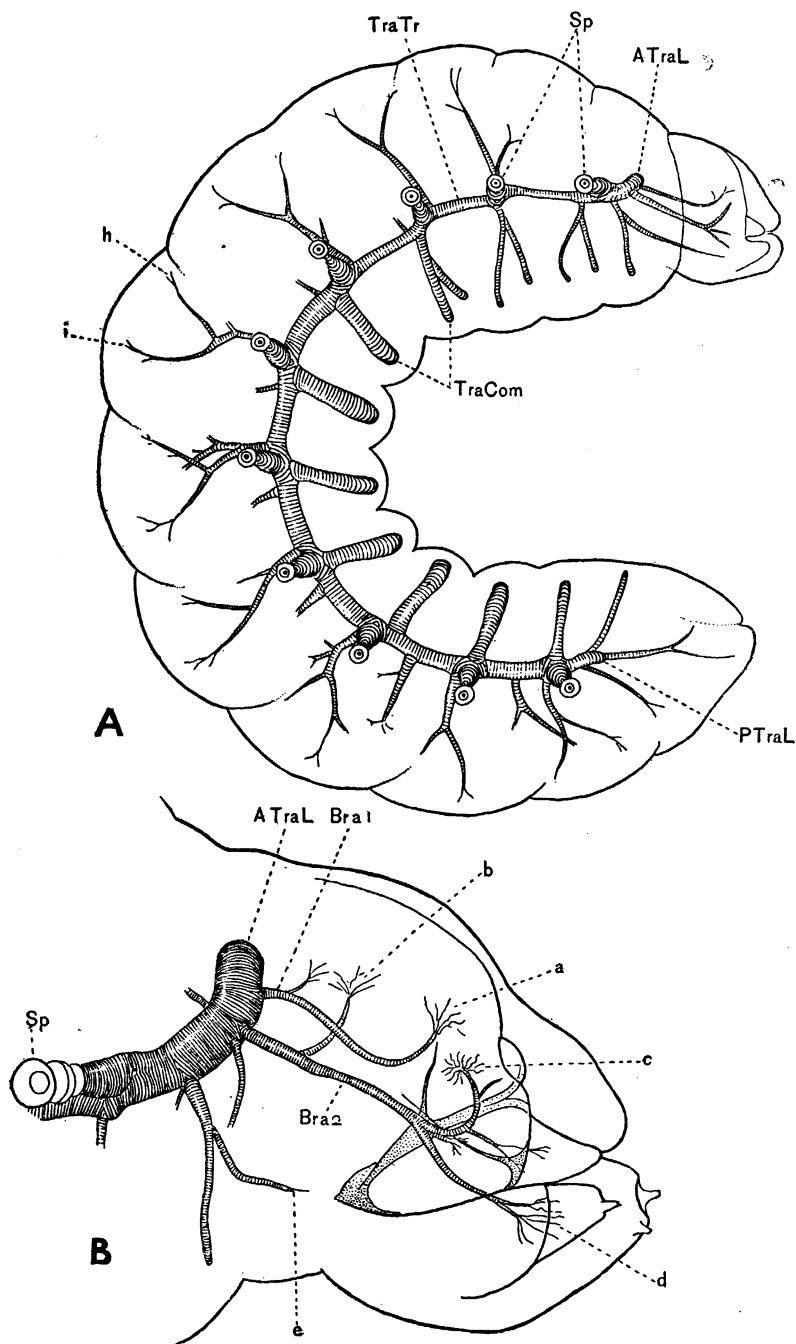


FIG. 2.—A, honeybee larva treated with caustic potash, showing tracheal system, side view, $\times 18$; B, head of larva treated with caustic potash, right side, showing distribution of tracheae, $\times 44$

dorsal side of the tracheal trunk on each side close to the spiracular branches is a stout branch which runs dorsad for a short distance, and then divides into two secondary branches. One of these (fig. 2, A, *h*) runs dorsad along the line of separation from the segment next preceding and supplies the pericardial cells of this region. The other secondary branch (*i*) takes an oblique course along the suture separating the prescutum and the scutoscuteum, and enters the pericardial cavity in the middle of the segment opposite the valves of the heart in the pericardial intersegmental sinus. Here the branch breaks up into a few tracheoles which are distributed to the walls of the heart. The dorsal branches just described may be designated as "superficial," in contradistinction to other ("deep") branches which supply the viscera. They are branches of considerable size springing from the dorsal side of the tracheal trunks in the intervals between the spiracular branches. In addition to these, each of the superficial branches usually gives off near its base a twig to the viscera. The viscera in

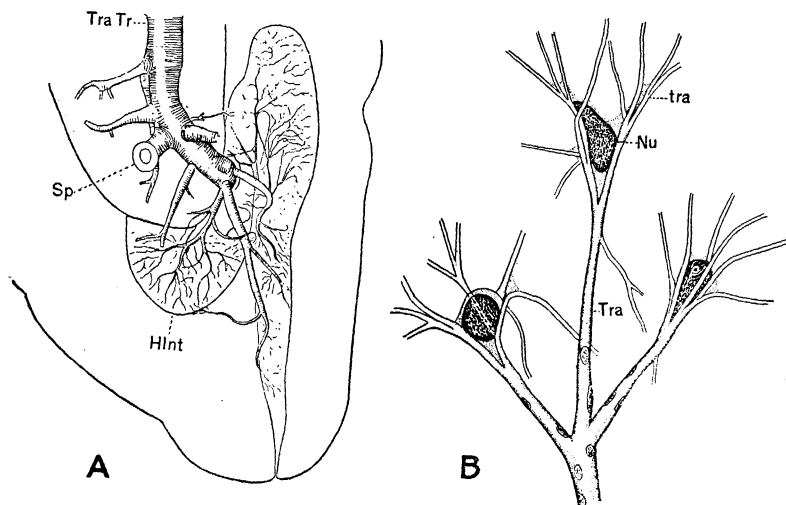


FIG. 3.—A, posterior end of a honeybee larva treated with caustic potash, seen from right side, showing distribution of tracheae to hind-intestine (*HInt*), \times ca 33; B, distal end of tracheal branch (*Tra*) showing tracheoles (*tra*) and nuclei of tracheal end cells (*Nu*), \times 195

the lower half of their segments are supplied by small twigs given off by the transverse commissures and not shown in the figures. In the 9th abdominal segment a superficial branch is given off caudad of the last pair of stigmata, while from the two ends of the posterior transverse commissure two or three deep branches are given off which supply the hind-intestine, as shown in Figure 3, A.

As in all insects, the tracheae are simple in structure, being merely thin-walled tubes composed of small flat epithelial (pavement) cells and lined with a chitinous intima which is thickened in the form of fine transverse spirally-wound threads, the taenidia. The size of the taenidia is at least approximately proportional to the size of the trachea of which they form a part, while the size of the tracheal cells themselves remains nearly constant in the same individual. Taenidia are found in the tracheal branches up to their termination in tracheal end cells. The structure of the spiracular branches, however, differs somewhat from that of the tracheae proper. At each point where the hypodermal epithelium turns inward to become the wall of a spiracular branch it forms a sharp fold, thus somewhat reducing the mouth of the aperture (Pl. 3, D). The chitinous cuticle also folds

upon itself at every such point, the fold extending toward the middle of the opening in such a way that only a small circular aperture remains. The cells of the wall of the spiracular branch next to the hypodermis, although long-prismatic in form, are of the same size as the latter, and are also covered internally by a smooth layer of cuticle. A short distance within, however, the internal surface of the wall becomes raised up into annular ridges, thus again reducing the diameter of the lumen of the branch so that a distinct antechamber is made, more or less spheroidal in form, bounded externally by the chitinous fold bordering the spiracular opening, and internally by the ridges just mentioned. The section or zone of the branch bearing the ridges comprises about a half of the total length of the branch. The cells are here much larger than elsewhere and usually much vacuolated, particularly at their bases. The ridges are here formed not so much by thickenings of the cuticle as by the contour of the inner ends of the cells themselves, except toward the inner end of this zone, where a number of coarse taenidia are found which in sections present a more or less pinnatifid form. These intergrade with the taenidia of the usual type which are found farther centrad within the branch. Centrad the zone of large cells rather suddenly gives place to the flat pavement type of cells common to tracheae in general. The description just given applies to the larva of intermediate size, about three days old. In mature larvae the zone of large cells is even more sharply differentiated, but the cells no longer combine to form annular ridges on their inner surface. They are very much vacuolated at their bases, and this portion of the spiracular branch presents the appearance of having contracted, reducing the lumen to little more than a cleft (fig. 3, B). The significance of this reduction of the lumen is not evident. The general aspect and the arborescent mode of branching of the tracheae is shown in Figure 3, A. At their tips the branches break up rather suddenly into a tuft of delicate filaments, the tracheoles. At the point of origin of the tracheoles and surrounded by them is a nucleus, of large size as compared with those of the tracheae and of somewhat irregular form (fig. 3, B, *Nu*). Its chromatin is abundant and distributed in the form of coarse granules of fairly uniform size. Surrounding the nucleus is an exceedingly delicate layer of cytoplasm, which accompanies each tracheole and in fact forms part of its wall. This is most clearly seen in transverse sections of tracheoles. The intima, however, is that which gives to the tracheoles their sharp contour, and since they are still visible in caustic potash preparations it is to be inferred that this intima is chitinous. Near their point of origin the tracheoles frequently branch; farther on in their course branching becomes infrequent. The tracheoles of course vary in length. In a preparation of the muscular layer of the mid-intestine of a mature larva a single tracheole was traced for a distance of 0.548+ mm. In the pericardial cavity the tracheoles are much shorter than this (about 0.300 mm.). After the preliminary branching a tracheole is quite uniform in diameter, and decreases gradually until the double contour is lost, the tracheole finally terminating in a slender point. The course taken by a tracheole differs in accordance with the structure of the organ or tissue supplied by it. For example, on the outer surface of the mid-intestine, which is very richly supplied with tracheoles, the latter run in straight lines or in gentle curves, the majority being parallel with the circular fibers. In the fat body, on the other hand, they pursue a sinuous course, winding in and out between the fat cells.

The relation of the tracheoles to the organs and tissues of the honeybee larva is essentially the same in every case, since nowhere has a tracheole been seen to penetrate a cell, the statements of Leydig (32), Kupffer (30), Lidth de Jeude (33), Gilson (12), and Holmgren (16) to the contrary notwithstanding. In the case of the alimentary canal and the heart the tracheoles simply spread out over

the external surface. On the other hand, the brain, ventral cord, and ovaries are not only penetrated by the tracheoles but not infrequently by the finer tracheal branches also, the latter terminating in end cells, which therefore lie within the tissues of the nervous system or of the ovaries, as the case may be. Anastomosis of the tracheoles to form a meshwork, as reported by Wielowieyski (51), Von Wistinghausen (54), Petersen (41), Williams (53), and others was not observed.

The tracheal system of the bee larva offers nothing of special interest in its general form and relations and conforms to the type usual in the higher insects. As compared with the imago the tracheal system is simpler and more generalized. In the abdomen of the imago, however, particularly in segments 3 to 7, the tracheal trunks and their metamericly arranged commissures and branches may easily be recognized, although now enlarged to form air sacs (46). The posterior commissure is wanting. In the thorax the tracheal system is more greatly modified, and the larval type correspondingly obscured.

ALIMENTARY CANAL, MALPIGHIAN TUBULES, AND SILK GLANDS

ALIMENTARY CANAL

The alimentary canal comprises a short and slender fore-intestine (Pl. 4, A, *Oe*), a voluminous mid-intestine (*MInt*) and a relatively short hind-intestine, having a sigmoid flexure (*HInt*).

The fore-intestine shows the usual differentiation into three subdivisions, mouth, pharynx, and oesophagus.

The mouth (Pl. 2, B, *Mth*) is a narrow transverse slit bounded above by the clypeus, below by the labium, and laterally by the mandibles. It opens immediately into the pharynx. This is a somewhat ill-defined region, comprising the anterior end of the fore-intestine and extending caudad to about the point where the crura cerebri cross the fore-intestine. The epithelium of the mouth and pharynx (with the exception of the roof of the latter) is precisely similar to the hypodermis of adjacent parts of the head, being composed of closely crowded prismatic cells with flat external ends (Pl. 2, B, and 4, C). On the roof of the pharynx is a conspicuous and well developed epipharynx (Pl. 3, A, and 4, C, *Ephy*), which extends from the mouth well back into the oesophagus. It is broad and flat at its anterior end (Pl. 3, A, *Ephy*), scarcely rising above the level of the adjacent epithelium of the roof of the mouth, but in the pharyngeal region it becomes a highly convex fold of the dorsal wall, projecting ventrad into the lumen of the pharynx and giving the latter a crescentic outline in transverse section (Pl. 4, C, *Ephy*). The cells constituting this fold are very different from those of the remainder of the pharyngeal wall, being of small size and elongated, pyriform or club-shaped in form, their larger ends directed toward the lumen of the oesophagus. On the dorsal surface of the pharynx the cavity of the epipharyngeal fold is crossed by a large number of muscle fibers which unite the two lateral edges of the fold. These are shown in Plate 4, C, and in section in Plate 3, A, *EphyMcl*. Beneath these are a few longitudinal muscle fibers.

On the floor of the pharynx, at its external end, is a small papillate elevation, provisionally labeled the hypopharynx (Pl. 3, A, *Hyphy*).

In addition to the muscles of the epipharynx, the pharynx is provided with other muscles, which are described in this paragraph. In the clypeus a pair of small muscles take their origin from the dorsal wall and are inserted on the epipharyngeal fold close to the median plane. Some four or five pairs of similar muscles are ranged behind one another, having their origin on the dorsal wall of the labrum. These are the levators of the epipharynx (Pl. 4, C, and 6, C, *LevEphy*). Their action is evidently directly opposed to those crossing the

epipharyngeal fold, which, by drawing together the two edges of the fold, force the epipharynx down into the lumen of the pharynx and thus occlude it, while the levators, on the other hand, virtually serve as dilators. A larger pair of muscles having their origin on the dorsal wall of the labrum are inserted on the oesophagus at the lateral margins of the epipharynx, the levators of the pharynx (Pl. 4, C, *LevPhy*). Just ectad of these are inserted still another pair of muscles which are attached to the cranial wall on each side of the base of the labrum, the superior dilators of the pharynx (Pl. 4, C, *SDilPhy*). On the ventral side of the pharynx is a group of muscles having their origin on the anterior face of the central body of the tentorium, which are inserted on the ventral wall of the pharynx. These are the inferior dilators of the pharynx (Pl. 3, A, *DilPhy*). This list comprises the total equipment of muscles possessed by the pharynx.

The pharynx passes without material change in caliber into the oesophagus. This is a cylindrical tube, its walls continuous with those of the pharynx, but formed of cells of a somewhat different character, these being much less crowded than those of the pharynx and varying in form from cuboid to long columnar. Their central ends are rounded instead of flat. This epithelial layer, however, does not always form a true hollow cylinder, being generally more or less in-folded at the sides, top and bottom, and the cells being higher at these points, so that the lumen of the oesophagus is frequently quadrangular in section (Pl. 2 A, *Oe*), or even in some cases rosette-shaped. A chitinous cuticle, continuous with that covering the external surface, lines the oesophagus as well as the mouth and pharynx. In the anterior part of the fore-intestine this corresponds in thickness with the external cuticle, but toward the posterior end of the fore-intestine it becomes thinner, and in sections has a much wrinkled and torn appearance. It usually extends a short distance into the lumen of the mid-intestine, forming the "funnel" (Trichter) of Schneider (45). On its external surface the oesophagus is clothed with a single layer of circular (transverse) muscle fibers. Longitudinal muscle fibers appear to be virtually absent. The caudal end of the oesophagus, where it joins the anterior end of the mid-intestine, is reflected back on itself to form an oesophageal valve (Pl. 3, A and 5, C, *OeVlv*) similar to that found in many other insects. The cells of that part of the valve which is reflected back are notable for their attenuated, almost linear form. Muscle cells are lacking between the two folds of the valve.

The mid-intestine (Pl. 4, A, *MInt*) has the form of a long hollow cylinder with rounded ends, and in mature larvae has a diameter about one-third of that of the body. It extends from the prothorax to the ninth abdominal segment. It is hardly necessary to state that structurally the mid-intestine is a blind sac, the posterior end being completely closed. It is anchored in place by numerous tracheae which extend mesiad from the longitudinal trunks. The finer branches of these tracheae terminate in tracheal end cells upon reaching the surface of the mid-intestine. From these end cells numerous tracheoles are sent out enveloping the external surface of the mid-intestine. If the muscular coat of the intestine be stripped off, as can be done in favorable cases, its surface is seen to be closely and uniformly dotted with tracheal end cells, one of which is represented in Plate 5, D, *TraECl*.

The walls of the mid-intestine are composed of a thick single-layered epithelium covered externally by a delicate meshwork of muscle fibers. The cells composing the epithelium (with the exception of a few cells around the anterior end, next to the oesophageal valve) are all alike, being relatively large and having in general a short and rather cubical form, their mesial margins, however, being slightly convex (Pl. 5, B). Here and there are to be seen cells which are pyriform, with their larger ends directed centrad and projecting into the lumen.

There is, however, no evidence that cells or parts of cells of the epithelium are set free in the lumen, as described by Snodgrass (46) for the imago. The cytoplasm of the cells of the mid-intestine is always deeply stained in sections (Pl. 5, A, *MInt*) and has the appearance of being traversed by numerous parallel fibrillae which run at right angles to the surface of the epithelium. A similar appearance is found in the secreting cells of the silk gland in certain Lepidoptera (12) and in the epithelial cells of the mid-intestine of Ptychoptera (11). The nuclei are spherical, as a rule, and contain a large number of chromatin granules. In fixed material, at least, these granules, along with the achromatic material, are agglomerated into a dense spherical mass within the nuclear membrane, leaving a peripheral space vacant. This condition may, however, be an artifact. On their mesial surfaces the cells of the mid-intestinal epithelium show a well-developed striated border (Pl. 5, B, *StrBor*) similar to that observed in Ptychoptera (11) and other insects. Wedged in between the bases of the cells, next to the basal membrane (intima) triangular groups of minute cells are seen here and there. These are the imaginal cells of the mid-intestine (Pl. 5, B, and C, *ImCls*).

The mid-intestine is lined throughout by a homogeneous layer of unknown chemical nature, apparently of gelatinous consistency, and having a thickness two or three times that of the epithelium, the so-called "peritrophic membrane" (Pl. 5, C, *Pmb*). In sections it is more or less finely granular in structure. Peripherally it is in intimate contact with the epithelium of the intestine; centrally it is sharply demarcated from the enclosed food mass. Not a little has been written concerning this somewhat problematical structure in various insects, but a full review of the literature will not be attempted here. Rengel (44) has described it in the larvae of the wasp (*Vespa*) and honeybee, Strindberg (47) in the ant embryo, and Snodgrass (46) and Petersen (41) in the adult honeybee. Rengel states that in larvae the peritrophic membrane has a laminated structure consisting of several concentrically arranged membranes, as is plainly the case in the adult, but in all of the writer's preparations of this membrane he has never observed this structure except at the anterior end of the mid-intestine. Elsewhere the membrane is thick and homogeneous, but here the epithelial cells grow rapidly and progressively smaller, forming a ring around the oesophageal valve (Pl. 5, C, *x*) and are separated from the latter by a narrow space. These cells also differ from those of the remainder of the mid-intestine not only in being of smaller size but also in lacking, at least to a large extent, the striated appearance of the cytoplasm. From the surface of these cells thin streams of secretion can plainly be seen running caudad and joining with the principal mass of the peritrophic membrane within the mid-intestine. Streams of this material also appear leading inward from the three rows of epithelial cells next to the ring of smaller cells, as shown in Plate 5, C, and this appearance is characteristic of all of the sagittal sections examined, including preparations of both young and old larvae. It suggests that the cells of the anterior rim and those of the two or three adjacent rows are responsible for the secretion of the peritrophic membrane; an interpretation precisely in line with the view advanced by Van Gehuchten (11) in the case of the dipterous larva Ptychoptera and Cuénot (8) in Orthoptera. Strindberg, however, has advanced against this view the fact that in the ant larva peritrophic membrane is continuous over the closed posterior end of the mid-intestine, which, he states, could not be the case if the membrane were secreted by an anterior rim of cells. This objection, however, would have less weight if, as seems probable, the peritrophic membrane is fluid or semi-fluid, since from its nature it would tend to form a uniform layer over the area of contact and therefore would flow together over the posterior end. It should be noted that the peritrophic membrane described above has nothing whatever to do with the cuticle secreted by the oesophagus, the free

posterior ends of which frequently project far into the anterior end of the mid-intestine (Pl. 5, C, *Ctl*).

The external surface of the mid-intestine, as already stated, is covered by a delicate network of muscle fibers. A small portion of this sheet, stripped off from the mid-intestine, is shown in Plate 5, D. The central or inner surface is uppermost. The inner layer (*LMcl*) is composed of branched muscle cells whose delicate processes, connecting adjacent cells and thus forming an anastomosing plexus, tend to run in a longitudinal direction. Below these, and morphologically outside of them, is a layer of transverse muscle fibers (*TMcl*). These are closely and uniformly spaced, and are also quite uniform in caliber. The nuclei of the cells composing this layer are much smaller than those of the inner layer. The muscle cells of the transverse layer are also interconnected by extremely delicate protoplasmic processes, some of which are indicated in the figure.

The hind-intestine (Pl. 4, A, *HInt*) is a cylindrical tube of fairly uniform diameter except at its anterior end, where it shows a funnel-like or bell-shaped expansion, the larger end of which is applied to the posterior end of the mid-intestine. From this point it bends ventrad, taking a cephalad course to the sixth abdominal segment, where it bends sharply upon itself and takes a direct course caudad to its termination on the tenth abdominal segment. The hind-intestine of the honeybee larva exhibits a simpler structure than that of the ant larva, in which the posterior portion of the hind-intestine is enlarged, narrowing again near the anus, three divisions being thus formed, small intestine, large intestine and rectum (35). This condition also exists in the larva of the beetle *Anobium* (23).

As already stated, the anterior end of the hind-intestine exhibits a funnel-like or bell-like enlargement (Pl. 4, A). The end of the funnel is, however, not open, but is closed by an extremely thin layer of minute cells (Pl. 6, A, *dph*), which is continuous around the margin of the funnel with the epithelial wall of the mid-intestine. This epithelium, on the sides of the funnel-like enlarged portion, is thick and composed of a large number of slender club-shaped cells (Pl. 6, A, *HInt*). These give place, at the neck of the funnel, to larger prismatic or columnar cells. The remainder of the epithelium of the hind-intestine is formed of cells of this type. This is thrown into deep folds, as shown in Plate 5, E, projecting almost to the center of the lumen and giving the latter a stellate aspect in section. Relatively stout muscle fibers (*TMcl*) encircle the hind-intestine, being found from the margin of the funnel-like expansion to the anus. These are for the most part arranged in a single layer, but toward the posterior end they become more numerous and are arranged in two or even three layers. Outside of the transverse muscles are a few irregularly arranged longitudinal fibers (Pl. 5, E, *LMcl*). In the 10th segment numerous slender muscle fibers run between the lateral hypodermis and the lateral walls of the hind-intestine.

The posterior termination of the hind-intestine, the anus, is a simple transverse slit situated on a slight elevation in the center of the 10th abdominal segment.

The mode of attachment of the mid- and hind-intestines in the larvae of the aculeate Hymenoptera is of special interest and has been studied and described in detail by Rengel (44) in the wasp (*Vespa*), in the ant (*Lasius*) and in the honeybee. With the exception of minor details, it is the same in the three groups. As shown in Plate 6, A, at the extreme posterior end or fundus of the mid-intestine there is an outpushing (*st*) of the epithelium, thus forming a rounded projection on the external surface of the fundus. In *Vespa* this projection is quite prominent, forming the "stalk" (*Stiel*) of Rengel. In the honeybee larva it is externally merely a low rounded eminence; internally it is represented by a depression of the epithelium, the bottom of which is formed by a heap of irregular transparent cells,

smaller than those of the adjacent epithelium. The muscular investment of the mid-intestine (*MclEnt*) ceases abruptly at the margin of the "stalk." As already stated, the enlarged anterior end of the hind-intestine is closed by a thin layer of minute cells, forming a circular structure (*dph*) which may conveniently be termed "the diaphragm." The central part of the diaphragm is closely adherent to the stalk, as described by Rengel. In larvae of *Vespa* and of ants the diaphragm is relatively much thicker than in those of the honeybee, judging from the figures given by Rengel (44), Karavaev (22) and Pérez (40), but otherwise the relations are essentially similar.

MALPIGHIAN TUBULES

The Malpighian tubules are four in number and lie, two on each side, between the lateral faces of the mid-intestine and the body wall (Pl. 4, A and 5, A, *Mal*). They pursue a winding course, being thrown into numerous loops and folds, and extend from about the last thoracic to the 9th abdominal segment. In the newly hatched larva the tubules are slender and of nearly uniform diameter throughout; in the mature larva their anterior ends only are slender, the tubules widening gradually caudad, reaching their maximum diameter, which is about one-half that of the mid-intestine, in the region of the 7th abdominal segment (Pl. 4, A, *Mal*). From this point they taper rapidly to their caudal (or central) ends, which are inserted, two on each side, between the mid-intestine and hind-intestine where the two latter have their junction. These central ends are exceedingly slender and pointed, composed of relatively small cells, and become closely attached to the thin epithelium closing the anterior end of the hind-intestine, with their tips abutting on the stalk of the hind-intestine (Pl. 6, A, *Mal*). The lumen of the Malpighian tubules becomes greatly reduced here and finally ceases, the central ends of the tubules therefore ending blindly, contrary to the statements commonly found in the literature on this subject (44). The writer (36) stated that in the newly hatched larva the Malpighian tubules open into the mid-intestine, but renewed investigation shows that there is no basis for the statement, since in all the sections examined, both cross and sagittal, the central ends of the tubules disappear in the relatively thick layer of cells closing the anterior end of the hind-intestine. Sections of a larva two days old also fail to disclose any connection between the lumen of the Malpighian tubules and that of the hind-intestine.

The walls of the Malpighian tubules consist of a single layer of epithelial cells. In very young larvae the wall of the tubules is relatively thick and the centrally placed lumen correspondingly small. In mature larvae the cells composing the walls are flat, thin, and pavement-like in character (Pl. 5, A, *Mal*, and Pl. 4, B and D). This condition exists even in the slender anterior ends, clearly indicating that the tubules are distended by internal pressure. The nuclei are discoid (Pl. 4, D, *Nu*), being flattened in a plane normal to the surfaces of the tubules, and contain abundant chromatin in the form of subequal spherules. The cytoplasm of the cells displays no fibrillae, as in the case of the cells of the mid-intestine and silk glands, and appears to be finely granular. The margins of the cells at the point of junction with one another are uniformly vacuolated, as shown in Plate 4, D, thus giving the tubules, stained or unstained, a characteristic mottled appearance in surface view (Pl. 4, B). The tubules are lined within by a cuticular intima, possibly chitinous, which stains much less densely than the cytoplasm (Pl. 4, D, *Int*).

The condition just described is characteristic of larvae shortly before the capping of the wax cell. Younger larvae show intermediate conditions, that is, the diameter of the tubules is relatively smaller and the walls thicker. The

next phase in their development takes place subsequent to capping and is directly correlated with the establishment of communication between the lumina of the mid- and hind-intestines, and the consequent evacuation of the feces. This takes place some time during the twenty-four hours subsequent to capping, and has been treated at length by Rengel (44). In brief it consists, as shown in Plate 6, A and B, in an outpushing (caudad) of the fundus of the mid-intestine, that is, of the stalk, into the lumen of the anterior enlarged end of the hind-intestine and the subsequent perforation of the stalk and also of the diaphragm to form a tubular opening through which the fecal accumulations of the mid-intestine are forced by contractions of the latter. This mass of feces is omitted in Plate 6, B. In larvae of this stage the central ends of the Malpighian tubules no longer end blindly, but each now opens into the hind-intestine by a minute pore-like aperture. These openings are close to the junction of the mid- and hind-intestines, as shown on the left side in Plate 6, B, *Mal*. The appearance of this and other preparations suggests that the central ends of the tubules were perforated the diaphragm while at the same time their lumina became extended to communicate with that of the hind-intestine. A curious feature of the efferent ducts of the Malpighian tubules of this stage is the appearance of structures which in fixed preparations resemble motile cilia. That the Malpighian tubules are now emptying themselves of their contents is strikingly shown by sections of the tubules at points more or less remote from the place of attachment. Whereas in sections of mature larvae prior to the establishment of communication between the mid- and hind-intestines the Malpighian tubules have in general the appearance of thin-walled tubular sacs, they now show a much diminished caliber and the cells forming the walls are no longer flat, but are cubical in form.

The accumulation of solid excreta in the blind mid-intestine of the bee larva is therefore paralleled by the accumulation of fluid excreta (urates?) in the blind Malpighian tubules. Both discharge their accumulations at the same time. The advantage of this in the life history of the larvae is obvious.

The imaginal Malpighian tubules appear just previous to capping (Pl. 6, A and B, *mal*), as outgrowths of the anterior enlarged section of the hind-intestine (*I*).

SILK GLANDS

The silk glands comprise a pair of slender cylindrical tubules, thrown into numerous short convolutions, and extending from the posterior border of the mesothoracic segment to the neighborhood of the sixth abdominal segment (Pl. 4, A, *SilkGl*). Their location, relative to the other organs, is shown by Plate 5, A, *SilkGl*. They lie, one on each side of the mid-line, closely surrounded by fat cells, about halfway between the mid-intestine and the ventral body wall. At about the posterior margin of the mesothoracic segment the glands, strictly speaking, terminate, and each gland here opens cephalad into a thin-walled duct which pursues a straight course into the head, passing close to the ventral wall and beneath the suboesophageal ganglion, where it meets its mate from the opposite side. The two ducts unite to form a common duct (Pl. 2, A, *SilkD*) which terminates on the tip of the labrum. The common duct is cylindrical with the exception of its anterior end, where it rather suddenly widens out laterally and opens by a narrow transverse slit on an elevation, also transversely elongated, situated on the tip of the labrum (Pl. 1, F, and 3, A, *SilkDO*).

The finer structure of the silk glands is illustrated by Plate 5, F and G. Plate 5, F, represents an oblique transverse section through one of the silk glands near its posterior end. The cells forming the wall of the tube are in many respects similar to those forming the mid-intestinal epithelium, although much smaller, the nuclei of the walls of the silk gland having a diameter scarcely more than a

third of that of the nuclei of the mid-intestinal epithelium. The cells forming the walls of the silk gland are like those of the mid-intestine in the deeply-staining character of their cytoplasm, which usually stains so densely in comparison with the other tissues as to be almost totally opaque, as shown in Plate 5, A, *SilkGl*. Other points of similarity are the form of the cells, whose breadth and height are approximately equal, the striated or fibrillated aspect of the cytoplasm, noted also in the cells of the silk gland of Lepidoptera and Trichoptera (12), and the spherical nuclei, each containing a compact mass of chromatin granules. Near their anterior ends the character of the cells forming the wall changes somewhat. Here the walls are thicker, the cells composing them being smaller and long-columnar in form. The cytoplasm stains less deeply and no longer shows well-marked fibrillae. The lumen of this portion of the gland shows within it coagulated secretion, although the larva in question was scarcely mature.

The ducts of the silk glands are thin-walled and otherwise histologically precisely similar to the tracheae, this similarity extending to the possession of a chitinous intima, thickened spirally to form taenidia.

MUSCULAR SYSTEM

MUSCLES OF THE HEAD

The muscles of the bee larva may be divided for descriptive purposes into muscles of the head and muscles of the trunk, since these two sets are totally different. The principal muscles of the head are as follows:

MANDIBLES

Each of these is provided with an extensor and a flexor muscle. The extensor (Pl. 6, C and D, *EMd*) is inserted on the inner surface of a papillate elevation of the hypodermis located on the ectal side of the base of the mandible. From this point it passes directly caudad to its origin on the fold of hypodermis separating the head and trunk (neck fold) close to the outer end of the transverse arm of the tentorium. The flexor muscle (Pl. 6, C and D, *RMd*), which is the largest in the head, is inserted on a long and pointed hollow spine, the mandibular apodeme (Pl. 1, A, and 6, D, *RAp*), which arises from the mesial side of the base of the mandible (*Md*). From this a stout bundle of muscle fibers passes caudad parallel to the fibers of the extensor muscle to an origin just dorsad of them. Another and larger group of fibers breaks up into small subequal bundles, passing behind the brain. These are attached at regular intervals along the neck fold between the point of origin of the extensor muscle and the mid-dorsal line of the head (Pl. 6, C, *RMd*).

MAXILLAE

Mesial and dorsad of the base of each maxilla, below the apodeme for the extensor of the mandible, there is a papillate elevation of the hypodermis, on the inner surface of which is inserted the flexor muscle of the maxilla. This is of small size (Pl. 6, C, *RMx*), and originates on the neck fold, just ventrad of the origin of the extensor muscle of the mandible. The maxillae have no extensor muscles corresponding morphologically to those of the mandibles. They are, however, provided with a pair of strong muscles which appear to be functionally extensor muscles. Each of these takes its origin as a broad band from the ventral surface of the anterior arm of the tentorium of the corresponding side, close to the posterior end of the arm, and from here passes ectad and ventrad

to an insertion on the ventro-lateral surface of the head, just caudad of the base of the maxilla (Pl. 6, C, *EMx*). It apparently serves to rotate the maxilla outward.

LABIUM

The labium is provided with two pairs of retractors. The larger or major retractors (Pl. 6, C, *IRLb*) take their origin from the neck fold just ventrad of the external ends of the transverse arms of the tentorium. From there they run cephalad, converging meanwhile, and are inserted, a short distance apart on either side of the ventral mid-line, on the posterior margin of the labium. These muscles by their contraction withdraw the labium into the ventral part of the head. The minor retractors (Pl. 6, C, *2RLb*) are slender muscles which have their origin directly cephalad of the insertions of the major retractors. From here they run cephalad, converging at the same angle as the major retractors, to the tip of the labium where they are inserted on the wall of the common duct of the silk gland. These muscles serve to retract the tip of the labium. The two sets of retractors, when seen from the ventral surface, form a figure resembling the letter V, inverted.

LABRUM

At the base of the clypeus is a pair of well defined muscles (Pl. 2, B, and 6, C, *ClpMcl*), each of which takes its origin from the head capsule at the dorsal margin of the line of junction with the anterior arms of the tentorium. From these points the two muscles pass dorsad and slightly mesiad to insertions on minute apodemes on the dorsal wall of the head capsule, near the mid-line, at the base of the clypeus. These insertions are marked on the exterior by shallow depressions of the surface (see Pl. 1, F). Immediately cephalad of the insertions of these muscles, a second pair of muscles, the retractors of the labrum (Pl. 3, A, and 6, C, *RLm*), have their origin. These are inserted on the posterior edge of the clypeus in the dorsal mid-line.

Certain other muscles located in the labrum and clypeus and associated with the pharynx are described in the section on the alimentary canal (see p. 1184).

CRANIAL MUSCLES

Two other pairs of muscles are found in the head which pass from the tentorium to the cranial wall. The muscles of the first pair are slender, and originate on the dorsal surface of the anterior arms of the tentorium, near the junction of the latter with the transverse bar. These two muscles then pass dorsad on either side of the oesophagus, between the two halves of the brain, and are inserted on the median fold of the dorsal cranial wall. It is worthy of note that in preparations of larvae which have completed their growth these muscles appear to have lost their attachment to the dorsal cranial wall. This change is presumably related in some way to the approaching metamorphosis. The muscles of the second pair are also well developed in young larvae, but insignificant in older ones. Each of these muscles takes its origin from a long spur on the dorsolateral face of each of the anterior arms of the tentorium (Pl. 1, A, *ApTen*). These spurs are directed dorsad and laterad. In the young larvae the muscle fibers are directed dorsad and laterad, diverging meanwhile, and have broad insertions on the lateral walls of the head capsule, laterad of the cerebral lobes (*36*). In old larvae the spurs are long and directed cephalad and dorsad, extending nearly to the anterior cranial wall (Pl. 6, D), the short gap being bridged by a few muscle fibers inserted on the anterior wall of the cranium just dorsad of the antennal rudiments. The points of insertion are marked externally by well-defined circular depressions (see Pl. 1, F). Kirmayer (*36*) finds similar spurs on the tentorium and corresponding muscles in the head of the *Vespa* larva.

MUSCLES OF THE TRUNK

The muscles of the trunk have a strictly metameric arrangement and conform more or less closely to a definite and typical arrangement in all segments. The arrangement of the muscles in the thorax differs slightly from that of the abdominal muscles. In the abdomen the same arrangement of muscles prevails in all the segments with the exception of the 10th. In the 10th segment the muscles characteristic of the other segments are almost entirely wanting, the only

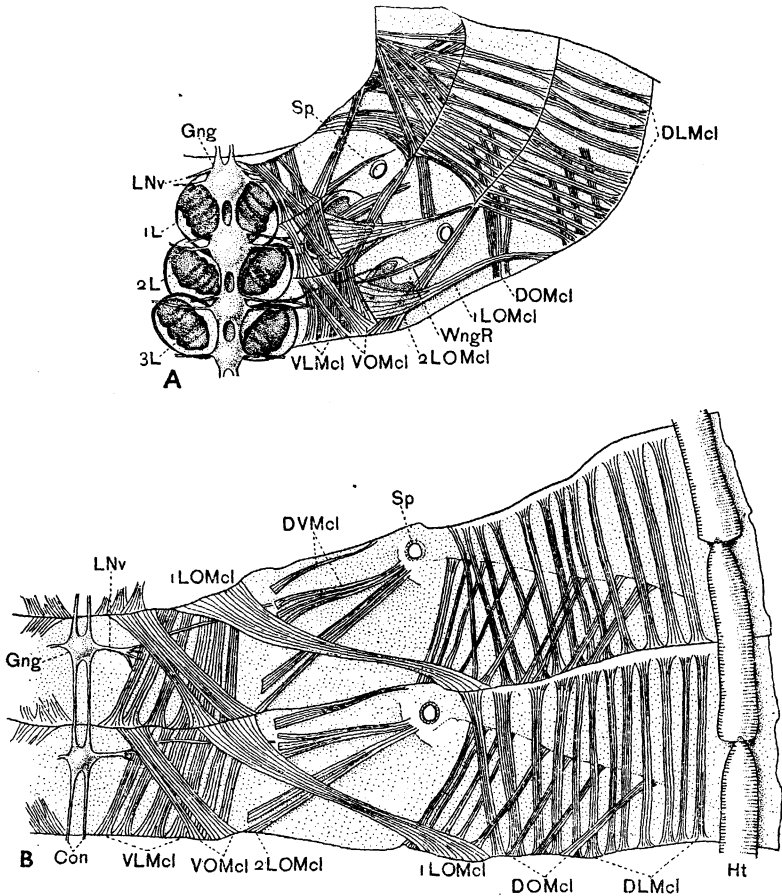


FIG. 4.—A, inner surface of right half of body wall of thoracic segments, showing musculature, $\times 10$; B, inner surface of right half of body wall of fourth and fifth abdominal segments, showing musculature, $\times 10$

trunk muscles present being a few fibers running from the lateral border of the anus to the anterior (lateral) borders of the segment.

The trunk muscles, taking the 4th and 5th abdominal segments (fig. 4, B) as typical, are the ventral longitudinal, ventral oblique, lateral oblique, dorso-ventral, dorsal longitudinal, and dorsal oblique.

VENTRAL LONGITUDINAL MUSCLES

These muscles (fig. 4, B, *VLMcl*) are not, strictly speaking, longitudinal, since they diverge slightly from the long axis of the larva in a cephalo-laterad direction.

The total effect of their action is, however, to contract the ventral surface in a longitudinal direction. They are flat bands, 10 or 12 in number, disposed on either side of the ventral mid-line, close to the hypodermis, and extend between the anterior and posterior margins of each segment.

VENTRAL OBLIQUE MUSCLES

These (*VOMcl*) overlie the ventral longitudinal muscles, crossing them at an angle of about 45 degrees and running in a cephalo-mesial direction, also connecting the anterior and posterior borders of the segment. Each consists at its anterior end of a broad band of fibers which splits into two subequal bands at its posterior end.

LATERAL OBLIQUE MUSCLES

These include two sets of muscles, which may be designated as major oblique (*1LOMcl*) and minor oblique (*2LOMcl*). The major oblique muscles are of large size and connect the anterior and posterior borders of their respective segments. Their anterior ends are attached to the body wall directly adjacent to the line of attachment of the posterior ends of the ventral oblique muscles of the segment preceding. From this point each of these muscles runs laterad and caudad, spanning the lateral fold of that side, to an attachment on the posterior border of the segment approximately on a line with the spiracles. The minor lateral oblique muscles (*2LOMcl*) comprise two small bands lying close to the body wall under the major oblique muscles. One of these small bands is attached to the posterior margin of the segment just dorsad (ectad) of the posterior attachment of the ventral oblique muscle; the other band is attached to the body wall close in front of this point. These two bands take a dorsad and cephalad course, meanwhile diminishing in breadth to a point on the body wall just ventrad of the spiracle (*Sp*).

DORSO-VENTRAL MUSCLES

Two pairs of dorso-ventral muscles (*DVMcl*) are present in each segment. The muscles of the smaller pair run close to the anterior margin of the segment from a point just dorsad (ectad) of the anterior attachment of the major oblique muscle to an attachment on the intersegmental body wall about on a line with the spiracles. The second set of dorso-ventral muscles comprises three small muscle bands on each side of the segment, having their ventral attachment to the body wall just caudad of that of the smaller muscles just described, about one-fourth of the width of the segment from its anterior margin. Their dorsal attachment is close beside that of the minor lateral oblique muscles, below the spiracles.

DORSAL LONGITUDINAL MUSCLES

These (*DLMcl*) comprise a set of narrow bands, from 10 to 12 on each side, underlying the dorsal body wall and divided by the heart into two bilateral groups. Their arrangement is truly longitudinal and the area occupied by them extends ventrad on each side almost as far as the spiracles. These muscles connect the anterior and posterior margins of the segments.

DORSAL OBLIQUE MUSCLES

The dorsal oblique muscles (*DOMcl*) include a row of from 10 to 12 slender bands on each side. Their posterior ends are attached to the posterior margin of the segment, the line of attachment extending dorsad from a point about midway between the dorsal and ventral mid-lines halfway to the dorsal mid-line. From here these muscles run cephalad and dorsad, diverging slightly, and are attached

to the dorsal body wall of each side along the suture separating the prescutum from the scuto-scutellum and in fact determining this sutural line.

In the thoracic region (fig. 4, A) the musculature is slightly different from that of the abdomen. The ventral longitudinal and oblique muscles (*VLMcl*, *VOMcl*) are readily recognized, although here their lateral extent is reduced, especially in the prothorax. The dorsal longitudinal muscles (*DLMcl*) are present in all three thoracic segments. In the prothorax there are present two groups of dorsal oblique muscles whose arrangement may be gathered from the figure. In the mesothorax and metathorax the dorsal oblique muscles are divided into two parallel groups. A strong muscle (*2LOMcl*) crosses the lateral face of each of the three segments, running from its posterior border cephalad and dorsad to its anterior border. This muscle is absent in the abdominal region. In the meso- and metathorax a very large muscle (*1LOMcl*) is attached by a broad line of attachment to the ventral side of the segment, mesiad of the leg rudiments (*1L-3L*), and runs laterad and caudad to the posterior margin of the segment near the lateral margin of the area occupied by the dorsal longitudinal muscles. This muscle evidently corresponds to the major oblique muscles of the abdomen. In all three thoracic segments the minor lateral oblique muscles (*2LOMcl*) connect the anterior and posterior margins of their respective segments, crossing the lateral body wall in an oblique direction. It seems doubtful whether these muscles are truly homologous with the minor lateral oblique muscles of the abdominal segments. In the mesothorax and metathorax a dorso-ventral muscle spans the imaginal wing disks. This muscle is much larger in the prothorax than in the metathorax.

The effects of the contraction of the various trunk muscles may be inferred from their size, direction, and attachments. These effects may readily be seen, however, on the external surface of the larva. If the figure showing the external features of the larva (Pl. 1, D) be compared with figure 4, B, it will readily become evident that the superficial contour of the larva is determined principally, if not exclusively, by the trunk muscles. The evident division of the trunk into segments is not, as in the imago, due to the formation of sclerites, but is produced principally by the longitudinal trunk muscles, aided, of course, by the ventral oblique, the major lateral oblique, and the smaller dorso-ventral muscles. The epipleural lobes are referable to the action of the major oblique muscles, the sharp demarcation of these lobes from the sternal area being apparently due to a certain amount of rigidity imparted to the body wall in this region by the ventral longitudinal and oblique muscles, since the area occupied by these coincides with this area. The depressions in which the spiracles are located are produced by the action of the minor lateral oblique muscles, aided, of course, by the posterior set of dorso-ventral muscles. The sutural lines obliquely traversing the dorso-lateral surface of the segments are plainly to be identified with the anterior insertions of the dorsal oblique muscles.

Detailed accounts of the muscular systems of hymenopterous larvae are lacking. The account by Carrière and Bürger (7) of the muscular system of the mason bee and that by Anglas (1) of the muscular systems of *Vespa* and the honeybee are extremely brief. Both merely recognize dorsal and ventral longitudinal muscles, and a set of obliquely arranged dorso-ventral muscles. An examination of the accounts of the muscular systems of the larvae of other orders, such as that recently given by Forbes (10) for lepidopterous larvae, discloses no basis for comparison with the bee larva. The muscles of the latter are, in comparison, few and simple, as might be inferred from its mode of life.

Anglas (1) states that some of the larval muscles, more particularly those of the abdomen, persist with slight modification through nymphosis into the imago. A study of the muscles of the abdomen of the imago shows them to be so different

in number and arrangement from the trunk muscles of the larva that identification of any given muscle or set of muscles of the imago with those of the larva proves to be impossible without a knowledge of the intervening stages.

The general features of the histology of the larval muscles has already been given (36). This description applies to the newly hatched larva, but no essential changes take place during larval growth. In this account it is stated that the muscles of the young larva are not striped. However this may be, in the old larvae cross-striped muscles are the rule. Mention should be made of the constant occurrence of very distinct fibrillae, "tomomitosomes," Maziarski (34), "filaments de resistance," Janet (20, p. 54), in the hypodermal cells at the points of attachment of muscles. These fibrillae frequently assume a brush-like form, as shown in Plate 6, D, at both of the ends of the dilator of the pharynx and at the posterior ends of the mandibular muscles. The filaments bind muscle, hypodermis, and cuticle firmly together, as shown in fixed material by the clinging of the cuticle, elsewhere loosened, to the hypodermis at the points where muscles are inserted.

HEART AND BLOOD CELLS

HEART

The heart of the larva is in most respects like the less differentiated portion of the imaginal heart which is situated in the abdomen. The heart consists essentially of a slender thin-walled tube situated in the mid-line close beneath the dorsal hypodermis. It is widest (about 0.25 mm.) at its posterior end and gradually diminishes in caliber up to the anterior border of the 2d trunk (the mesothoracic) segment. Here the heart leaves the dorsal body wall and bends downward, passing beneath the anterior tracheal loop (Pl. 3, A, A₀), at the same time diminishing rapidly in diameter, and is continued cephalad as the aorta. The aorta is not strictly tubular but is open on the ventral side, having in transverse section the form of an inverted letter U, the free edges hanging down on each side of the oesophagus and becoming clothed on the exterior with a layer of tracheoles. At the posterior side of the brain the aorta becomes reduced in its dorso-ventral diameter to enter the narrow cleft between the oesophagus and the upper ends of the crura cerebri and finally terminates at the anterior face of the brain. The posterior end of the heart terminates blindly in the 9th abdominal segment. In life the heart is transparent, and since it is bounded on either side by the relatively opaque white fat cells, it produces externally the appearance of a dark band along the dorsal mid-line of the larva.

At the middle of trunk segments 2 to 11, inclusive, the heart is sharply constricted and is thus divided into 11 chambers. These constrictions, however, do not affect the dorsal and ventral walls of the heart, but only the lateral walls, which are in fact indented by a series of pairs of opposite V-shaped indentations the open ends of which are directed slightly caudad. At the bottom of each indentation is a linear slit; these slits constitute the ostia (fig. 5, B, *Ost*). The ostia are not, however, precisely normal to the long axis of the heart, but are slightly oblique, their dorsal ends being slightly caudad of their ventral ends.

The action of the heart is simple and similar to the heart action of many other insects. The heart walls bordering on the ostia form valvelike flaps projecting inward which allow a free inrush of blood during diastole, but which automatically close the ostia during systole. The posterior pair of flaps project inward far enough also to close the posterior ends of the heart chambers during systole, preventing a backward flow of blood. Moreover, the thickened margins of the ostia share in the contractility of the heart wall, so that probably these also possess the ability to contract the ostia and the posterior ends of the heart chambers as well, thus acting as sphincter muscles.

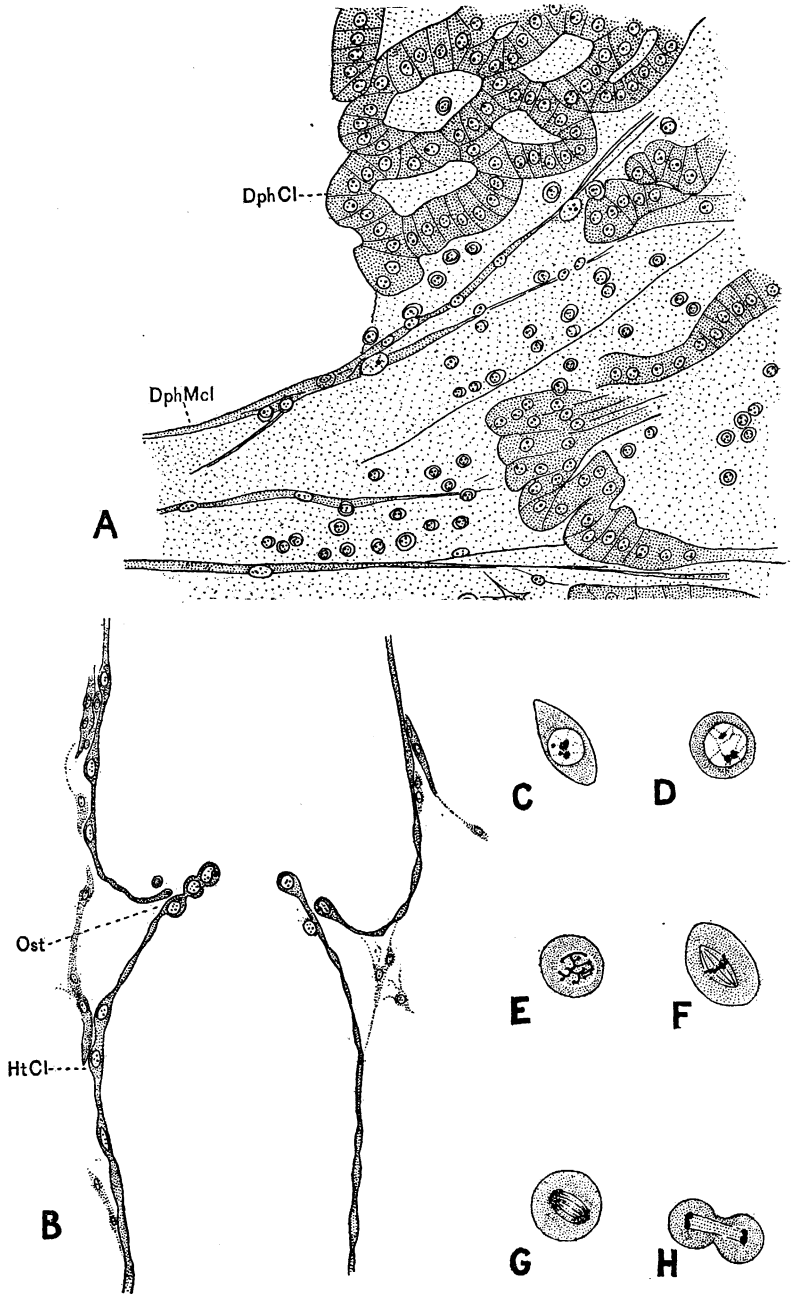


FIG. 5.—A, part of dorsal diaphragm of old larva, showing diaphragm cells (*Dph Cl*) and muscle fibers (*Dph Mcl*), $\times 66$; B, longitudinal (coronal) section of heart in the region of the second thoracic segment, showing ostia (*Ost*) and valves. $\times 260$; C—H, blood cells (lymphocytes), $\times 600$

The wall of the heart is exceedingly thin, as shown by the figures, and is composed of a double row of cells, corresponding to the cardioblasts of the embryo, the two rows constituting the right and left sides of the heart, respectively. These cells have the form of the half of a radially compressed ring (Pl. 7, B). At the middle of its length each cell is thickened and at this point a large discoid nucleus is found. Traversing each of the heart cells lengthwise, that is, at right angles to the long axis of the heart and mesiad of the nucleus, is a bundle of delicate fibrils, few in number, usually visible only under high magnification. They are most readily seen in cross sections of the heart cells, that is, in longitudinal sections of the heart itself, which have been counter-stained with eosin, the muscle fibrils of the heart cells, like those of other muscles in the larva, readily taking this stain. Their appearance in section is shown in figure 5, B, where they are represented in black. An attempt to represent these in lateral view is made in Plate 6, E, but they are actually less evident than here represented. In suitably stained preparations this bundle of fibers is plainly seen to be transversely striated (Pl. 6, F). The heart cells are therefore muscle cells, essentially similar structurally to other muscle cells in the bee larva, for example the trunk muscles, but in which the fibrillae (myofibrils) are more feebly developed. Similar conditions of structure are found in the cells of the heart wall of the larva of *Tipula* (48) and of those of *Vespa* (1) and *Aeschna* (55). Since the heart of all insects is contractile, it seems probable that further investigation will show such a differentiation to be general. In the larva of the honeybee, the myofibrils may easily escape notice, since larvae stained to show other structures to the best advantage scarcely show them at all. A deep and heavy stain with iron haematoxylin is necessary to reveal the myofibrils in face view; that is, in tangential sections of the heart. The arrangement of the heart cells in a double row is evidently not unique, since in addition to being characteristic of insect embryos it has been described for the *Tipula* larva by Viallanes and for the *Aeschna* larva by Zawarzin (55).

The heart is clothed externally by a loose meshwork of minute branched connective cells, the meshes tending toward elongation in a longitudinal direction (Pl. 6, E and F, *ConCls*). This meshwork serves to strengthen the heart wall and also to anchor the heart in position, since many of the processes of the connective tissue cells extend out to the hypodermis and to the adjacent fat cells.

DORSAL DIAPHRAGM

The dorsal diaphragm of the larva is well developed only in the posterior region, from the 4th to the 9th abdominal segments, inclusive, and here it is very similar in structure to that of the imago. In these segments it forms a continuous sheet, attached to the heart on its ventral surface (Pl. 7, A, B, *DDph*) and extending laterad, parallel with the dorsal body wall on either side of the dorsal midline, a distance somewhat less than one-eighth of the entire circumference of the larva. It partitions off a narrow dorsal space, the dorsal sinus or pericardial cavity. The lateral margins of the dorsal diaphragm are free except where they cross the lines of separation of the segments, and here the margins are attached to the body wall. Between these points the membrane is somewhat retracted mesiad, giving the margins a wavy contour (Pl. 7, A). The dorsal diaphragm terminates in the anterior half of the 9th abdominal segment with a free border. Angas (1) states that the two delicate membranes ensheathing the diaphragm cells are reflected in the median plane below the heart to form a sort of septum which does not reach ventrad to the mid-intestine. This membrane, or septum, which is termed the "cloison médiane," is said to separate the fat body into two symmetrical halves. This account, as regards the bee larva, appears to be incor-

rect in several particulars. The "cloison médiane" is restricted to the anterior segments of the trunk; it does not form a continuous membrane; it does sometimes become attached to the muscular coat of the mid-intestine; it does not divide the fat body, since this is already divided mesially by a space or sinus dorsad to the mid-intestine; and it does not appear to be continuous with the two halves of the dorsal diaphragm, but represents delicate processes of connective tissue cells attached to the ventral surface of the heart. It is apparently absent in mature larvae and is probably a structure of minor importance.

Structurally the dorsal diaphragm consists of two very delicate membranes, having the appearance of basement membranes and possibly being chitinous. These membranes are attached to the ventral wall of the heart in the mid-line. Between the two membranes are situated the diaphragm cells (fig. 5, A, *DphCl*). These are small cells, quadrangular in form, each having a spherical nucleus which occupies the greater portion of the cell. The diaphragm cells are arranged in single rows or strings which are bent in a sinuous form and frequently anastomose, forming a sort of lacework and giving the dorsal diaphragm in surface view a curious vermiculated pattern (Pl. 7, A). These cells are not found anterior to the middle of the fourth abdominal segment. The diaphragm cells are closely covered on their dorsal and ventral faces by the two membranes, which here have the appearance of limiting membranes secreted by the cells (Pl. 7, B, *DDph*). Elsewhere, in the open spaces between the diaphragm cells, the two membranes are generally evident, but are often found in close apposition, giving the appearance of a single membrane.

The diaphragm cells have a general resemblance to the blood cells in size and staining reaction, and in the large size of the nucleus as compared with that of the cell body. For this reason Angas (*1*) has assumed that the diaphragm cells give rise to blood cells (leucocytes). This may perhaps be possible, although the diaphragm cells are as a rule slightly larger than the blood cells. Moreover, the latter show such frequent mitoses that an independent origin for them need not be assumed.

Accompanying the dorsal diaphragm and forming an integral part of it are extremely delicate muscle fibers (fig. 5, A, *DphCl*), the so-called alary muscles, apparently unicellular and corresponding histologically to the fibrillae of other muscles. These fibers or fibrils are attached at more or less regular intervals to the ventral wall of the heart, the line of attachment coinciding with that of the membranes. The fibers corresponding to each chamber of the heart converge to their intersegmental points of attachment of the diaphragm on the body wall, thus giving the fibers the well known fan-like arrangement (Pl. 7, A). The relation of the diaphragm muscles to the membranes of the diaphragm does not seem to be uniform. At some points the muscles appear to run between the two membranes, at others dorsad to them. Thus far the description of the structure of the dorsal diaphragm of the larva corresponds with the account given by Snodgrass (*46*) for the imago. In the latter, however, the dorsal diaphragm terminates in the 7th abdominal segment, since the segments remaining are highly modified. The histological elements are the same in both, except that this structure in the imago is much more robust than in the larva, and can easily be seen on dissection, while in the larva it is so delicate that special methods are necessary to demonstrate it. In regard to one feature, a discrepancy exists between the two accounts. Snodgrass speaks of the diaphragm cells as situated upon the membrane, whereas in both cases they undoubtedly lie between two membranes.

The dorsal diaphragm anterior to abdominal segment 4 is less well defined than in the segments posterior to this point, and does not form a continuous sheet, being entirely absent in the middle of the segments and restricted to triangular areas corresponding with the diaphragm muscles (Pl. 7, A). These

areas naturally diminish in size with the diminishing size of the trunk segments. The whole of this anterior half of the dorsal diaphragm is, however, so exceedingly delicate that it is difficult to determine accurately its structure in detail. In preparations showing the dorsal diaphragm in surface view, such as that from which Plate 7, A, was taken, in the segments anterior to the 5th abdominal segment the dorsal diaphragm appears as a cobweblike structure in which only the radiating muscle fibers can be clearly discerned. In sections the muscle fibers may occasionally be found, and here and there are indications of an exceedingly fine structureless membrane; but the most conspicuous elements of the anterior half of the dorsal diaphragm are certain cells which may be called the anterior diaphragm cells. These are of relatively large size, and of pale appearance in stained preparations. The cytoplasm, besides being more transparent or less deeply stained, offers no peculiarities, and has a rather finely granular appearance. The nuclei are elliptical and, unlike those of the posterior diaphragm cells, are rather small as compared with the cytoplasm. In form these cells are irregular, although always flattened in a dorso-ventral direction. Their distribution is apparently scattered and irregular; some are found close to the heart wall, some at a considerable distance from it. Occasionally two or more are found associated together in small groups, attached end to end, but usually they occur singly. They never occur in long bands, as do the posterior diaphragm cells. Although they are frequently found crowded in among fat cells, it is usually possible to discern a connection with either the diaphragm muscles or the diaphragm membrane, if not with the heart itself.

The homology and function of these cells is unknown. On the basis of a study of the dorsal diaphragm, the writer (36), following Carrière and Bürger (?), thought that but two kinds of cells, exclusive of muscle cells, were found in the dorsal diaphragm; small epithelial cells, forming the major portion of the diaphragm, and a smaller number of large cells, assumed to be homologous with the "paracardial" cells found by Heymons (14) in certain Orthoptera. The conditions found in older larvae, as described above, make this view untenable. Definite information regarding the function and homologies of the two kinds of diaphragm cells in the larva of the honeybee will undoubtedly demand extended investigation.

VENTRAL DIAPHRAGM

The ventral diaphragm is well developed in newly-hatched larvae (36) and in the imago (46) and forms a continuous sheet made up of transversely arranged muscle fibers overarchng the ventral nerve cord and partitioning off a ventral (perineural) sinus. In older larvae it becomes merely a vestigial structure confined to the abdominal segments, and composed of more or less isolated delicate muscle fibers crossing the body cavity above the ventral nerve cord. They are entirely too few in number to form anything even approaching a membrane in structure, and constitute only a very loose and insignificant meshwork (Pl. 5, A, *VDph*).

BLOOD

The blood comprises a transparent fluid, the plasma, watery and only slightly viscid, and the blood cells (blood corpuscles, leucocytes) or amoebocytes. In the feeding larva the latter are of one sort only and correspond to the young amoebocytes of Cuénot (8). The amoebocytes of the bee larva are scattered throughout the spaces filled by the blood, but are usually more numerous in the dorsal sinus in the region of the heart. They vary in form from ovoid or ellipsoid to spherical, but the latter form is assumed only by cells preparing to divide. The ovoid form (fig. 5, C) is the one most frequently assumed by resting amoebocytes. In narrow spaces these are sometimes found slightly deformed by

pressure from the adjoining tissues, but no evidence of a true amoeboid movement was observed. Unlike the cells of many other organs and tissues of the larva, such as those of the mid-intestine and of the fat body, the size of the amoebocytes remains nearly constant throughout the life of the larva, and is from 6 to 9 microns wide and 7 to 12 microns long. The cytoplasm stains moderately with the usual chromatin stains and normally presents no evident differentiations or inclusions. The nucleus is relatively very large, is spherical in form, and contains a few small chromatin granules. Cells in mitosis are quite frequent (fig. 5, D-H) and it is easy to find a series representing the different phases. This seems to be the normal if not the only mode of increase, since there is no good evidence of a special blood-forming tissue in the bee larva.

Angas (1) describes a second type of blood cell "lymphocyte," larger, and with the cytoplasm finely vacuolated. This type apparently does not appear in the larva prior to capping.

The action of the heart and the flow of the blood are very similar to those of the imago, as described by Snodgrass (46), except that the sole propulsive organ is the heart. Except in very young larvae, the ventral diaphragm is so poorly developed that its action must be practically negligible. In a mature living larva, removed from the cell, successive waves of contraction are seen to pass cephalad over the heart at the rate of about one per second at room temperature, driving the blood into the head cavity. From here the blood flows caudad, filtering back through the channels formed by the various spaces between the fat body and the viscera. Some of these spaces are sufficiently well defined to deserve to be called blood sinuses. The most conspicuous of these is the ventral sinus (Pl. 5, A, VS), a tubular space extending the entire length of the larva above the ventral nerve cord and bounded laterally and dorsally by lobes of the fat body. As the figure shows, it is not limited dorsally by the ventral diaphragm (VDph), as it is in other insects. Another considerable space is found between the heart and the alimentary canal, while a continuous space exists around the mid-intestine, permitting a free flow of blood over the external face of the latter. Around the tracheal trunks and their principal branches are also narrow spaces free from fat cells, which form blood channels. The pericardial chamber is more or less completely filled with fat cells (the pericardial fat cells) except in the middle of each segment, where there is a space on each side of the heart, opposite the ostia, which is unoccupied by fat cells. These spaces extend laterad from the heart a short distance, and each receives one of the dorsal tracheal branches (fig. 2, A), being thus connected with the blood channel accompanying this branch. In the living larva blood may be seen flowing dorsad along this path. The pericardial blood lacuna just described may be seen in Plate 7, A, in which the round pericardial cells are represented in dotted outline. It should be stated, however, that these cells actually extend farther laterad than is shown, many of them having been removed in dissection. In the living larvae, and even in some fixed specimens, these pericardial lacunae are evident externally as short dark bands extending right and left from the heart in each segment (see Pl. 1, E).

FAT CELLS, OENOCYTES, EXCRETORY CELLS

FAT CELLS

At all stages except the earliest, fat cells, constituting collectively the so-called fat body, occupy approximately a half of the body cavity not already occupied by the other viscera. In life the fat cells are nearly opaque and colorless. Since they underlie the transparent hypodermis over the greater portion of the body they are largely responsible for the ivory-white tint of the larva. In general, the fat cells adhere together in flat lobular masses or strings, supported by tracheae

and projecting centrad into the body cavity (Pl. 5, A, 1-3*F*). In the arrangement of these masses a certain amount of bilateral symmetry exists. Carrière and Bürger (7), in their description of the larval mason bee, divide the fat body into three sections: (1) That part, situated dorsad to the lateral tracheal trunks and below the dorsal diaphragm (Pl. 5 A, 1*F*); (2) that part situated ventrad to the lateral tracheal trunks (2*F*); (3) that part situated above the dorsal diaphragm and comprising one to three layers of cells (3*F*). These divisions are only incompletely separated and are merely of topographic value, since there are no differences in the morphological character of the cells themselves. As shown in Plate 5, A, the fat cells are most abundant peripherally, next to the body wall, a considerable space around the alimentary canal being left vacant (see p. 1184). In advanced larvae fat cells are abundantly present in contact with the hypodermis, but not attached to it, throughout the trunk, crowded between the hypodermis and muscles and also beneath the ventral nerve cord. A few fat cells are likewise present in the head, lying against the posterior surface of the brain and below the suboesophageal ganglion. The various open spaces in the fat body, constituting channels for the flow of blood, have been described in a previous section (see p. 1199).

Bishop (4) has published a detailed account of the structure and development of the fat cells of the honeybee larva, to which the reader is referred for more extended information on this subject. In quite young larvae the deutoplasm of the fat cells (Pl. 8, D and E, *F*) is commonly found represented in each cell by a single relatively large vacuole (*y*), while the nucleus is still more or less spherical. In larvae three to four days old the deutoplasm of the fat cells (Pl. 8, F, *y*) is scattered throughout the cytoplasm in the form of vacuoles of various sizes; at the same time the nuclei begin to show distortion. Plate 8 illustrates a typical fat cell (*F*) from a mature larva, in which the nucleus has assumed the shrunken and branching form characteristic of this stage.

OENOCYTES

The oenocytes of the honeybee have been described by Wielowieysky (52), Koschevnikov (27), Anglas (1), and the writer (36). They are very conspicuous in sections, on account both of their large size and their great affinity for stains. They are rare in the thoracic segments, but are found abundantly throughout the abdomen, always occurring singly, never in groups, and generally, if not invariably, in more or less intimate contact with fat cells. In mature larvae the oenocytes closely approximate the fat cells in size, but this is not true of younger larvae. In a larva two days old, for example, the average diameter of the oenocytes is about twice that of the fat cells (Pl. 8, D, *Oen*). The rate of growth of the fat cells therefore greatly exceeds that of the oenocytes. Generally speaking, the oenocytes are more or less ellipsoid in form, but modifications of this are frequent and of such a kind as to afford plain evidence of the amoeboid, wandering nature of these cells. The oenocyte represented in Plate 8, B, is deformed to accommodate itself not only to the two adjacent fat cells (*F*, *F*) but also to a blood cell (*BIC*). It is to be noted that the contour of the fat cells is not evidently altered. Many oenocytes are found with a pointed process at one end—evidently a pseudopodium—extending between the adjacent fat cells, as though wedging them apart, while other oenocytes possess two such processes which are applied to and partially surround one or more of the adjacent fat cells. One instance of the amoeboid character of the oenocytes, as seen in sections, was particularly striking; here an oenocyte had assumed the form of a crescent embracing a fat cell between its horns, thus irresistibly suggesting the movements of an amoeba preliminary to ingesting its prey. The oenocytes, however, never

contain food vacuoles, nor do they in fact give any good evidence of being phagocytic in character. This is in accord with the observations of Anglas (1) on the wasp and honeybee and Pérez (40) on the ant.

The nuclei of the oenocytes are spherical or ellipsoid and contain a large number of subequal chromatin granules uniformly distributed (Pl. 8, B, *Oen*). The cytoplasm is dense, staining intensely in both haematoxylin and eosin, and exhibits variations in density which give it a characteristic mottled or marbled appearance.

EXCRETORY OR URATE CELLS

In the mature larva of the honeybee these cells, as stated by Anglas, occur only in small number. They are found in the abdomen, interpolated singly here and there among the fat cells, with which they are always closely associated. As shown in Plate 8, C, *u*, they are cells of somewhat irregular form, having a diameter about half that of the fat cells. The nucleus is spherical and contains a relatively scanty amount of chromatin in the form of small granules. The cytoplasm has a fine and regular alveolar structure, and in sections usually appears pale, having slight affinity for stains. In a very young larva (two days old) the excretory cells (Pl. 8, D, *u*) appear to be more numerous than in older larvae, and may be found in groups or clusters. They are here rendered more conspicuous both by their relatively greater size, which is equal to that of the fat cells, and more particularly by the greenish-yellow color of their cytoplasm. Under high magnification (1/12 homo. immers.) minute refractive greenish particles may be seen within the alveoles.

The general resemblance of the excretory cells to the fat cells and their close association with them at this stage argues strongly for a community of origin, as assumed by both Pérez (40) for the ant and Anglas (1) for the wasp and bee. Berlese (3) suggests that the excretory cells and the oenocytes have had a common origin. In Plate 8, D, an oenocyte from the same section as the other cells is introduced for comparison. The discrepancy in size and in other characters between this cell on the one hand and the fat and excretory cells on the other is sufficiently obvious. Moreover, the oenocytes are well differentiated and possess most of their distinctive characters even at the time of hatching (36).

RUDIMENTS OF GONADS

OVARIES

In the mature worker larva the ovarian rudiments are two small flat structures, one situated on either side of the dorsal mid-line in the 5th abdominal segment (Pl. 8, G, *Ov.*). In side view each of these rudiments (Pl. 8, I) presents a trapezoidal outline, the dorsal and ventral margins being parallel, while the two ends are abruptly narrowed to form slender tapering filamentous processes which extend cephalad and caudad along the ventral side of the heart into the 4th and 6th abdominal segments respectively. Exclusive of these processes, the length of the rudiment does not exceed half of that of the segment in which it lies. The ventral margin is thickened, the dorsal margin thin, so that in section each rudiment presents a pyriform outline (Pl. 8, G and H, *Ov.*).

Histologically each rudiment is composed principally of a close network of minute branching connective tissue cells (Pl. 8, H) enclosed by an epithelium made up of minute flat cells and covered externally by a cuticular tunic. From the dorsal border delicate cell-strands, clothed with a membrane continuous with the tunic, pass to the ventral wall of the heart on either side of the mid-line, thus acting as suspensory ligaments. The dorsal borders of the rudiments lie close to the mid-line, but their ventral borders lie farther apart, so that the mesial surfaces

of the rudiments are inclined at an angle of about 45 degrees to the median plane (Pl. 8, G, *Ov.*). The ventral half of each rudiment is traversed at right angles to its long axis by a large number of slender parallel columns or strings of cells with deeply stained cytoplasm, each column consisting of several rows of such cells (Pl. 8, H). These columns are assumed to be the rudiments of the ovarian tubules of the imaginal ovary. Their ventral ends extend to the ventral borders of the ovarian rudiments; the spaces between them are filled with branched connective tissue cells.

Along the ventral margin of each ovarian rudiment is a groove, at the bottom of which is located a ridge (Pl. 8, H, *Ovd*) composed of minute vacuolated cells. The base of this ridge is closely associated with the ventral or distal ends of the ovarian tubules. Near the posterior end of the rudiment the ridge becomes separated off as a solid cord of cells, taking a ventrad and caudad direction (Pl. 8, I and K, *OvD*), evidently becoming the rudiment of the oviduct.

Numerous tracheoles are found within the connective-tissue matrix surrounding the ovarian tubules. In some cases end cells have been observed within the rudiments of the ovaries.

In a mature larva, reared in a queen cell, the rudiments of the ovaries are long reniform structures (Pl. 8, L, *Ov*) measuring about 2.25 mm. in length and attached to the ventral wall of the heart in the 5th abdominal segment. The anterior ends of these rudiments, which lie on the boundary between the 4th and 5th abdominal segments, are each prolonged to form slender pointed processes like those found in the worker larva. With the exception of these insignificant processes the entire ovarian rudiment of the queen larva is composed of transverse parallel columns of dark-staining cells, assumed to represent the future ovarian tubules, similar to those of the worker larva but far more numerous, of larger diameter, and extending from the ventral to the dorsal margin. These are of course united by a connective tissue network. The (presumptive) rudiments of the oviducts are similar to those of the worker larva.

TESTES

These are relatively enormous structures, measuring about 3.75 mm. in length and 1.25 mm. in breadth, and lie on either side of the heart in the 4th, 5th and 6th abdominal segments, close to the dorsal body wall. They are elongate reniform in outline (Pl. 8, J, *Tes*) and somewhat compressed in a dorso-ventral direction. Like the ovarian rudiments, those of the testes are made up of numerous parallel transverse cell strands bound together by connective tissue. The (presumptive) rudiments of the vasa differentia (*VDef*) are similar to those of the oviducts in the worker and queen larvae, but more delicate and more difficult to demonstrate.

TECHNIQUE

Several fixing fluids were tried for killing and fixing bee larvae, but none gave as general satisfaction as Carnoy's acetic-alcohol mixtures. Their success is largely due to their superior power of penetration, since the chitinous cuticle of the larva, although very thin and delicate, is almost impenetrable by aqueous solutions.

The study of the internal organs by dissection is made difficult by the short and curved form of the larva, its small size, the abundance of fat cells and the general delicacy of the tissues. The preparation represented by Plate 4, A, was made from a larva fixed in Carnoy's fluid, stained over night in Mayer's carmalum and heavily destained (4 to 6 hours) in acidulated alcohol. The body wall, muscles, coagulated blood, etc., were then removed bit by bit with a needle, the stain rendering possible the identification of the different organs and tissues.

This method of dissection was the one usually employed. Fresh material was not found satisfactory. Very successful entire preparations of separate parts, such as the head, were made by staining for 18 to 24 hours in carmalum and afterwards destaining in acidulated alcohol (0.1 per cent) for about the same length of time. To demonstrate the dorsal diaphragm, the larva was first killed and the body wall and muscles fixed by immersion in absolute alcohol for five minutes. The dorsal body wall was then removed with the aid of fine scissors, spread out on a slide, ventral surface uppermost, and the fat body gently pushed away from either side of the dorsal mid-line, thus uncovering the dorsal diaphragm. The latter was then fixed with any convenient fixing fluid, stained rapidly (5 minutes) with Ehrlich's haematoxylin, dehydrated, cleared, and mounted, together with the dorsal body wall, to which it remains attached.

Sections were made in the usual manner. Celloidin sections 30 to 40 microns thick were found very useful in determining the relation and size of organs. Sections of material imbedded in paraffin were cut 6 to 8 microns in thickness, since the completeness of the series was usually more important than extreme thinness of individual sections. Prior to embedding, the larvae were either cut in half, or, when sagittal sections were desired, an aperture of considerable size was made in the lateral body wall. Infiltration is complete in 4 to 6 hours, if xylol has been used for clearing.

Iron haematoxylin proved to be the only satisfactory stain for sections of material embedded in paraffin, the other haematoxylin stains being too diffuse in their action. A counter stain such as Orange G or alcoholic solution of eosin is useful in differentiating certain structures, such as nerve fibers or the albuminoid granules of the fat cells. Material intended for celloidin sections was stained in bulk with Mayer's carmalum.

SUMMARY

(1) The bee larva has a fusiform shape, the posterior end being the smaller, and is flexed ventrad. Its color is ivory white. The larva is divided by constrictions into a head and 13 segments, 3 of which belong to the thorax, the remainder to the abdomen. The sternal surface of the abdomen is sharply demarcated from the lateral surfaces by the ventrolateral suture. The ventrolateral region of abdominal segments 1 to 9 is raised to form a series of rounded swellings, the epipleural lobes.

Ten pairs of spiracles are present, situated on the lateral faces of the 1st and 2d thoracic and the first eight abdominal segments, near their anterior limits. The head is short and blunt and the neck constriction is a narrow fold. The labium is prominent, bluntly conical, slightly compressed dorso-ventrally, and bears on its tip the common opening of the silk glands. The maxillae and mandibles are papillate, the mandibles being more pointed than the maxillae and curved mesiad. A well-defined groove, the lateral furrow, runs from between the bases of the mandibles and maxillae caudad to the neck constriction. The labrum is broad and flat, slightly bilobed at its apex, and is indistinctly marked off from the clypeus. The labrum and labium are separated by a narrow cleft-like space, the mouth opening, which is bounded laterally by the mandibles and maxillae. On each side of the clypeus the antennal rudiments are evident as circular papillate elevations.

(2) The body wall consists of a single epithelial layer of small cells, the hypodermis, clothed externally by a delicate cuticle. The hypodermis differs greatly in thickness in different parts of the body but its average thickness is greatest in the head. The cuticle also is here thicker and more rigid than elsewhere. The antennal rudiments are ovoid in form and situated in deep bipodal cavities,

only the peripheral ends of the rudiments projecting above the surface of the head. The peripodal cavities of the antennae as well as of the other appendages are closed externally only by cuticle. The wing rudiments are small, flat, heart-shaped, hollow outgrowths of the hypodermis situated in shallow depressions low down on the second and third thoracic segments. The leg rudiments are ovoid in shape and are situated in deep peripodal cavities on the ventral side of the three thoracic segments, close to the mid-line. The genital rudiments are six in number, one pair being situated on the 8th abdominal segment and the other two pairs on the 9th. They are knob-like in form and lie in shallow open depressions.

(3) The rigidity of the head capsule is increased by the tentorium, which consists of a system of tubular ingrowths of the hypodermis lined by chitin. It comprises two short and broad posterior arms which are attached to the cranial wall at the junction of the lateral furrows with the neck fold; a transverse central body, continuous with the lateral arms; and two slender anterior arms joining the ends of the central body to the cranial wall at the sides of the clypeus. On the lateral face of each of the anterior arms is a spine for the attachment of a muscle. At the base of each of the mandibles, on its mesial side, is a hollow spine-like apodeme for the insertion of the adductor muscle.

(4) The nervous system is simple and primitive as compared with that of the adult and consists, in the mature larva, of a brain, a nerve chain comprising 11 ganglia joined by paired connectives and a stomatogastric ganglion with its accompanying nerves. The brain includes a pair of large somewhat crescentic or auriculate optic lobes, situated in the transverse plane, well-developed protocerebral lobes, and small antennal lobes (deutocerebrum) and tritocerebral lobes. The two halves of the latter are united by a distinct suboesophageal commissure which is not fused with the suboesophageal ganglion. Two pairs of nerves spring from the brain proper: the antennal nerves, which connect the antennal lobes with the antennal rudiments, and the labrofrontal nerves, which spring from the tritocerebral lobes. Each of these last mentioned nerves divides near its point of origin into the frontal nerve, which runs mesiad to the frontal ganglion, and the labral nerve, which innervates the labrum. The suboesophageal ganglion, attached to the brain by slender crura cerebri, is somewhat lenticular in form, broader at its anterior end. It represents three pairs of simple ganglia and gives rise on each side to four nerves: mandibular, maxillary, labial, and the X-nerve of Jonescu. The last mentioned possibly corresponds to the salivary gland nerve in other insects. In the bee larva it is difficult to trace but appears to terminate in the superficial hypodermis at the base of the labium. The 11 ganglia of the ventral cord are lenticular in form and are connected with one another by distinct parallel connectives. The ganglia are not located in the middle of the segments but are near their anterior ends. The three thoracic ganglia are the largest, those of the following seven abdominal segments being subequal; the 8th abdominal ganglion is, however, elongate and comprises three pairs of simple ganglia and the rudiment of a fourth. All of the abdominal ganglia are provided with well-developed lateral nerves which divide into branches supplying the viscera, muscles, etc. The stomatogastric system comprises a well-developed stomatogastric ganglion situated above the pharynx and connected to the brain by the frontal nerves. Anteriorly it gives off a single nerve, the superior pharyngeal nerve, supplying the superior pharyngeal muscles and the tip of the labrum. Posteriorly the stomatogastric ganglion gives off a stout nerve which passes caudad, diminishing in caliber meanwhile, along the dorsal surface of the oesophagus. It finally breaks up into small branches.

The nervous system of the larva is histologically similar to that of the imago but is of course less specialized. The central nervous system displays the usual

division into an outer and cortical zone of ganglion cells surrounding an inner central core of nerve fibers (punk-substanz). Among the ganglion cells large actively dividing neuroblasts, like those of embryos, may frequently be recognized. An outer neurilemma is always distinguishable; an inner neurilemma is probably also constantly present, but less evident. In the brain of the larva many of the typical features of the imaginal brain may be readily recognized, such as the arrangement of the cells of the optic lobes to form inner, middle and outer fibrillar masses, and the presence of well-developed mushroom bodies.

(5) The corpora allata are spherical bodies about 0.85 mm. in diameter, situated one on each side of the mid-line, close behind the brain, lying on the dorsal side of the anterior arms of the tentorium, and in close contact with the walls of the aorta. Each is composed of a compact mass of polyhedral cells. Tracheoles may be seen to enter these bodies and penetrate between their component cells.

(6) There are ten pairs of spiracles, following the rule for insect larvae, located on the 2d and 3d thoracic and the first eight abdominal segments. The spiracles of each side open by short branches into a longitudinal trunk. The two trunks are united anteriorly by a loop or commissure in the region of the neck, above the oesophagus, and posteriorly by a similar loop below the hind-intestine. The longitudinal trunks are also connected by segmentally arranged commissures which run close to the ventral body wall. Two pairs of tracheal branches from the anterior tracheal loop supply the brain, antennal rudiments and other parts of the head. Segmentally arranged branches springing from the longitudinal tracheal trunks supply the muscles, heart and viscera. The tracheae terminate in typical tracheal end cells from which arise the tracheoles. The latter never branch or anastomose and have never been observed to penetrate the cytoplasm of other cells.

(7) The alimentary canal comprises a short and relatively slender fore-intestine, a large cylindrical mid-intestine and a hind-intestine. The fore-intestine includes mouth, pharynx and oesophagus, these three divisions being somewhat ill-defined. The mouth is a wide transverse slit passing immediately into the pharynx. The latter is provided with a well-developed epipharynx which consists essentially of a fold of the dorsal wall of the pharynx, and which is provided with numerous transversely arranged muscles uniting the lateral margins of the fold and also with levator muscles which are attached at the dorsal ends to the dorsal wall of the clypeus and labrum. In addition, the pharynx itself is provided with two sets of dilator muscles and a pair of levators. The pharynx leads directly into the tubular oesophagus, which opens into the anterior end of the mid-intestine. Here the wall of the oesophagus is reflected upon itself to form a fold which projects into the anterior end of the mid-intestine, thus constituting an oesophageal valve similar to that found in many other insects. The oesophagus is provided with a muscular coat composed mainly of transverse fibers. The mid-intestine is very capacious, cylindrical in form, about one-third of the diameter of the body and extends from the prothoracic to the 9th abdominal segment. Its walls are thick and composed of large cubical cells displaying the usual striated border. A peritrophic membrane, apparently gelatinous in consistency, lines the mid-intestine. This layer appears to be secreted by those cells of the mid-intestine lying next to the oesophageal valve. The mid-intestine possesses a muscular coat composed of an inner layer of delicate longitudinal fibers and an outer layer of transverse fibers. The muscle fibers of both layers are branched and anastomose with one another. This is more conspicuously seen, however, in the case of the inner longitudinal layer. The posterior end of the mid-intestine is completely closed and its extremity is not covered by the muscular coat. The hind-intestine is a relatively slender tube, doubled on itself

and of uniform diameter except at its anterior end, which is enlarged and closed anteriorly by a thin diaphragm-like membrane which is closely applied to the extreme posterior end of the mid-intestine. The hind-intestine is clothed with a well-developed muscular coat composed of an inner layer of circular (transverse) muscle fibers and an outer layer of longitudinal fibers. Posteriorly the hind-intestine terminates in a slit-like anus. Here the hind-intestine is provided with muscle fibers which act as dilators.

(8) The Malpighian tubules are long and winding, extending cephalad to the region of the metathorax. Their tapering and pointed posterior (central) ends are blind and are inserted between the posterior extremity of the mid-intestine and the thin epithelial layer closing the anterior end of the hind-intestine. In young larvae the Malpighian tubules are slender, with a small lumen and relatively thick walls; in old larvae they attain a relatively large diameter and possess very thin walls, being obviously much distended. After the cell occupied by the larva has been sealed and communication between the mid- and hind-intestine has been established, permitting the discharge of feces, each of the Malpighian tubules acquires an opening into the mid-intestine by means of a minute canal perforating the annular remains of the epithelial layer which formerly closed the anterior end of the hind-intestine. The discharge of the fluid excreta of the Malpighian tubules thus occurs simultaneously with the discharge of solid excreta from the mid- and hind-intestines.

(9) The silk glands comprise a pair of slender tubes, thrown into numerous short convolutions and extending nearly the entire length of the larva, below the mid-intestine. Their anterior ends unite to form a thin-walled duct, lined with chitin, which opens by a slit-like aperture on an elevation situated on the tip of the labium.

(10) The trunk muscles are the same in all the abdominal segments except the 10th, and are (1) ventral longitudinal, a group occupying the sternal region of each segment and connecting its anterior and posterior margins; (2) ventral oblique, a pair of flat bands running obliquely cephalad and mesiad across the sternal region and also connecting the anterior and posterior margins of each segment; (3) lateral oblique, comprising one stout band crossing the lateral region of each segment in a cephalad and mesiad direction and connecting the two margins of the segment, and a small band crossing the lateral region in the opposite direction and having its dorsal end attached to the body wall in the region of the spiracle; (4) two small dorso-ventral bands; (5) dorsal longitudinal muscles connecting the anterior and posterior dorsal margins of the segments; (6) dorsal oblique muscles running from the posterior margin of each segment, in the dorso-lateral region, obliquely cephalad and mesiad to an oblique line of attachment on the body wall, the sutural line separating the prescutum and the scutoscuteillum. Since the body wall is nowhere rigid, the arrangement of the muscles is responsible, to a large extent at least, for the external contour of the larva.

(11) The heart is a thin-walled tube, blind at its posterior end and running the entire length of the body in the mid-line close to the dorsal body wall, and continuous cephalad as the aorta, which enters the head. The structure of the larval heart closely resembles that part of the imaginal heart lying in the abdomen. It possesses a pair of valvular ostia in every segment except the 1st (possibly also the 2d) thoracic segment and the 9th and 10th abdominal segments. The heart is composed of two rows of flat cells on each side of the mid-line. The cytoplasm of these cells is differentiated to form striped muscle fibers. Externally the heart is clothed with a network of branching minute connective tissue cells. A dorsal diaphragm is present which is especially well-developed in the 4th to the 9th abdominal segments, where it is composed largely of sinuous bands of small

cells, as in the adult. Anterior to this region a few cells of medium size, of unknown significance, are found attached to the ventral border of the heart. The ventral diaphragm is well developed in young larvae, consisting of a sheet formed of transverse muscle fibers, spanning the lower portion of the body cavity. In old larvae, however, there remain only a few scattered muscle cells. The blood cells of the larva are all of one kind, of minute size and ellipsoid form. Many are found in division, indicating that this is the chief, if not the only, method of increase, since no blood-forming tissue is found.

(12) The fat body is voluminous, occupying a large part of the body cavity. Certain spaces are, however, left open for the flow of blood. The most evident of these are, (1) a tubular space extending longitudinally beneath the alimentary canal; (2) an annular space around the mid-intestine; (3) a tubular space extending longitudinally above the alimentary canal; (4) a set of transverse spaces in the dorsal region of the body, one in the middle of each segment and communicating with the ostia of the heart. Excretory (urate) cells are present in limited number, scattered among the fat cells. Oenocytes are very abundant and conspicuous because of their large size and staining reaction. They are found scattered throughout the trunk, but are most abundant in the abdomen. They are evidently amoeboid wandering cells, but no evidence of phagocytic activities was found.

(13) The rudiments of ovaries in the worker larvae are very small and situated in the 5th abdominal segment, attached to the ventral border of the heart and consisting principally of connective tissue, in which are embedded transverse strands of minute cells. These strands are presumably rudiments of ovarian tubes. Rudiments of oviducts are present as delicate solid strands of cells. The rudiments of ovaries in the queen larva are much larger than in the worker larva, showing that their development is greatly accelerated during the later larval stages. Their structure is similar to that of the worker larva except that the presumptive rudiments of ovarian tubes are both more numerous and longer. The rudiments of testes in the drone larva are relatively enormous, lying in the 4th, 5th and 6th abdominal segments, and are composed of very numerous transversely arranged strands of cells united by connective tissue. Rudiments of vasa deferentia are present.

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EXPLANATION OF SYMBOLS USED IN PLATES AND TEXT FIGURES

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| <i>AntL</i> , Antennal lobe. | <i>fm2</i> , Middle fibrillar mass of optic ganglion. |
| <i>AntNv</i> , Antennal nerve. | <i>fm3</i> , Inner fibrillar mass of optic ganglion. |
| <i>Ant</i> , Antennal rudiment. | <i>FtGng</i> , Frontal ganglion. |
| <i>Ao</i> , Aorta. | <i>FtNv</i> , Frontal nerve. |
| <i>ApTen</i> , Spur on anterior arms of tentorium. | <i>1G-3G</i> , First second, and third pairs of genital rudiments. |
| <i>ATraL</i> , Anterior tracheal loop. | <i>Gng</i> , Ganglion. |
| <i>BIC</i> , Blood cells. | <i>HInt</i> , Hind intestine. |
| <i>Br</i> , Brain. | <i>Ht</i> , Heart. |
| <i>1Br</i> , Protocerebral lobes. | <i>HtCl</i> , <i>HtCls</i> , Pericardial cell, pericardial cells. |
| <i>3Br</i> , Tritocerebral lobes. | <i>Hyp</i> , Hypodermis. |
| <i>Bra1</i> , <i>Bra2</i> , Tracheal branches to head. | <i>Hphy</i> , Hypopharynx. |
| <i>CCer</i> , Crura cerebri. | <i>ImCls</i> , Imaginal cells of mid intestine. |
| <i>Clp</i> , Clypeus. | <i>INlm</i> , Inner neurilemma. |
| <i>Com</i> , Commissure of ventral nerve cord. | <i>In</i> , Intima. |
| <i>Con</i> , Connective of ventral nerve cord. | <i>1L</i> , <i>2L</i> , <i>3L</i> , Thoracic legs (rudiments). |
| <i>ConCls</i> , Connective tissue cells. | <i>Lb</i> , Labium. |
| <i>CorAll</i> , corpora allata. | <i>LbNv</i> , Labial nerve. |
| <i>Cil</i> , Cuticle. | <i>LevEphy</i> , Levator muscle of epipharynx. |
| <i>DDph</i> , Dorsal diaphragm. | <i>LevPhy</i> , Levator muscle of pharynx. |
| <i>DilPhy</i> , dilator muscles of pharynx. | <i>Lm</i> , Labrum. |
| <i>DLMcl</i> , Dorsal longitudinal muscles. | <i>LMcl</i> , Longitudinal muscles of alimentary canal. |
| <i>DOMcl</i> , Dorsal oblique muscles of trunk. | <i>LmNv</i> , Labrofrontal nerve. |
| <i>dph</i> , Diaphragm closing anterior end of hind intestine. | <i>LNv</i> , Lateral nerve. |
| <i>DphCl</i> , Diaphragm cells of heart. | <i>LNvF</i> , Lateral nerve fibers. |
| <i>DphMcl</i> , Muscle fibers of dorsal diaphragm. | <i>1LOMcl</i> , Major lateral oblique muscles of trunk. |
| <i>EMd</i> , Extensor muscle of mandible. | <i>2LOMcl</i> , Minor lateral oblique muscles of trunk. |
| <i>EMx</i> , Extensor muscle of maxilla. | <i>Mal</i> , Malpighian tubules of larva. |
| <i>EpL</i> , Epipleural lobes. | <i>mal</i> , Malpighian tubules of imago. |
| <i>Ephy</i> , Epipharynx. | <i>MB</i> , Mushroom bodies. |
| <i>EphyMcl</i> , Epipharyngeal muscles. | <i>MclEnt</i> , Muscular layer of alimentary canal. |
| <i>1F-3F</i> , Fat cells. | |
| <i>f</i> , Fatty globules of fat cells. | |
| <i>fm1</i> , Outer fibrillar mass of optic ganglion. | |

- Md*, Mandible.
MdNv, Mandibular nerve.
MInt, Mid intestine.
Mth, Mouth.
Mx, Maxilla.
MxNv, Maxillary nerve.
Nbl, Neuroblasts.
Nlm, Neurilemma (outer).
Nu, Nucleus.
NvF, Nerve fibers.
O, rudiment of ocellus.
Oe, Oesophagus.
OeCom, Circumoesophageal commissure.
Oen, Oenocyte.
OeVlv, Oesophageal (proventricular) valve.
OpL, Optic lobe.
OpPl, Optic plate.
Ost, Ostia of heart.
Ov, Ovary.
OvD, Oviduct.
Pmb, Peritrophic membrane.
PrF, Postretinal fibers.
Prs, Prescutal area.
PTraL, Posterior tracheal loop.
qq, Food matter in mid intestine.
RAp, Retractor apodeme of mandible.
1RLb, Major retractor muscle of labium.
2RLb, Minor retractor muscle of labium.
RMd, Retractor (adductor) muscle of mandible.
RMx, Retractor muscle of maxilla.
Scs, Scuto-scutellar area.
SDilPhy, Superior dilator muscles of pharynx.
SlkD, Common duct of silk glands.
SlkDO, External opening of common duct of silk glands.
SlkGl, Silk glands.
SoeCom, Suboesophageal commissure.
SoeGng, Suboesophageal ganglion.
Sp, Spiracle.
SpBr, Tracheal branch to spiracle.
SPhyNv, Superior pharyngeal nerve.
st, Stalk, or projection of fundus of midintestine.
StgNv, Stomatogastric nerve.
StrBor, Striated border of the epithelium of the midintestine.
SupCom, Supraoesophageal commissure.
Ten, Central body of tentorium.
1Ten, *2Ten*, Anterior and posterior arms of tentorium.
Tes, Testis.
TMcl, Transverse muscles of alimentary canal.
Tra, Trachea.
tra, Tracheoles.
TraCom, Tracheal commissure.
TraECl, Tracheal end cell.
TraTr, Tracheal trunk.
U, Urate or excretory cell.
VDef, Vas deferens.
VDph, Ventral diaphragm.
VLMcl, Ventral longitudinal muscles.
Vls, Ventrolateral suture.
VNC, Ventral nerve cord.
VOMcl, Ventral oblique muscles of trunk.
VS, Ventral sinus.
WngR, Rudiments of wings.
X, Nerve designated as "X" by Jonescu.
y, Food reserve in fat cells.

PLATE 1

Larva of the honeybee

A.—Head of mature larva, treated with caustic potash, showing endoskeleton, viewed from dorsal surface. $\times 26$.

B.—Brain and suboesophageal ganglion of mature larva, face view. Drawn from a wax model reconstructed from sections and verified by dissections. $\times 40$.

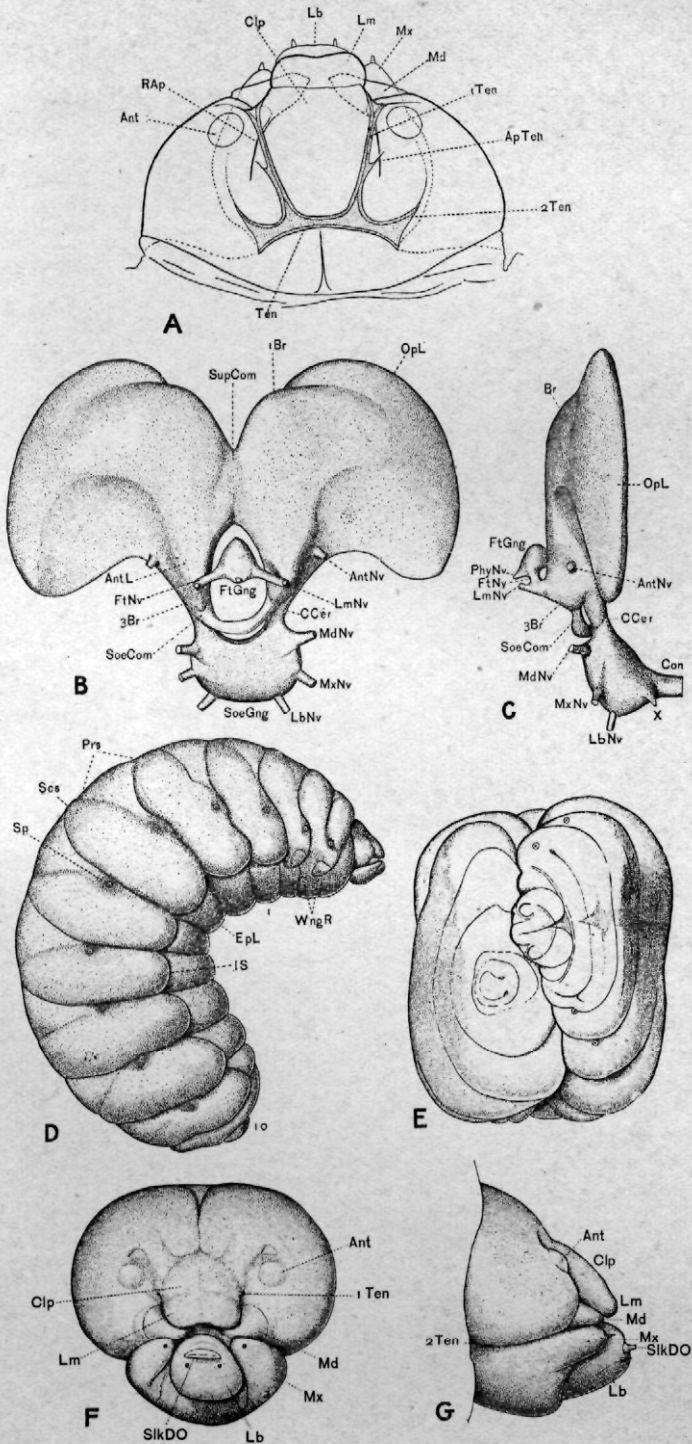
C.—Same as B, side view. $\times 40$.

D.—Mature worker larva, removed from cell, viewed from the right side. $\times 6$.

E.—Mature worker larva, fixed within the cell and afterwards removed, showing the compressed hexagonal form assumed while within the cell. The head and anus are both turned toward the observer, the body being bent in the shape of the letter U. $\times 6$.

F.—Face view of head of mature larva. $\times 20$.

G.—Head of mature larva, side view. $\times 20$.



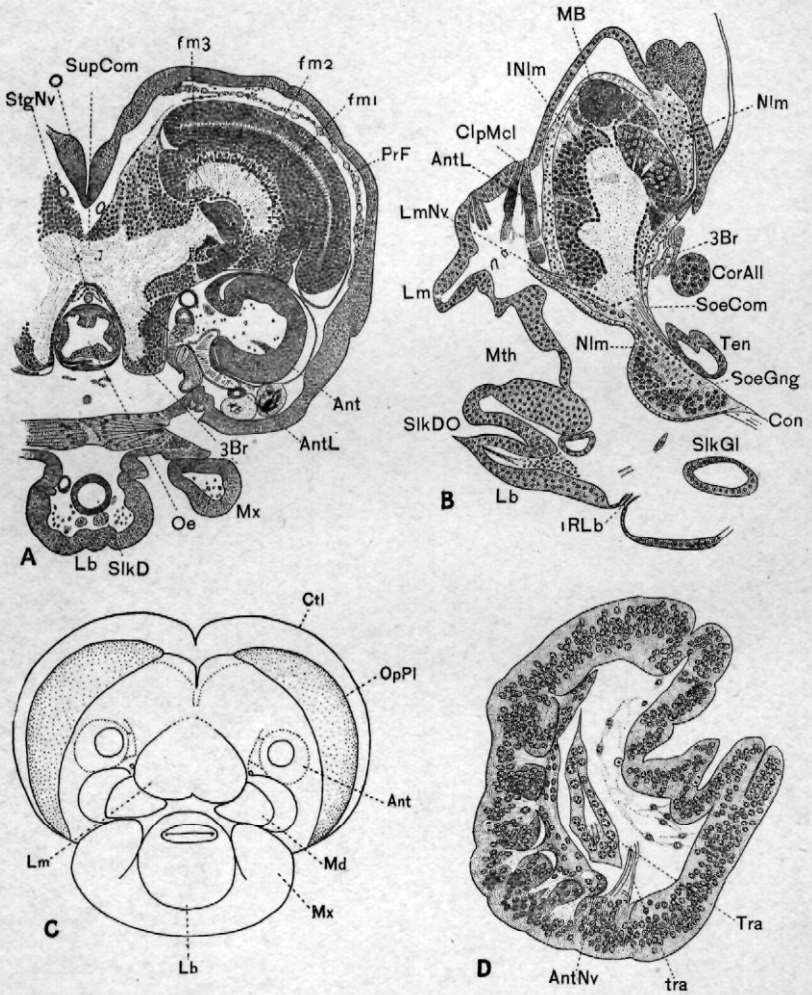


PLATE 2

Larva of the honeybee

A.—Cross section of head of mature larva, intersecting the optic lobes (*fm 1-3*) and antennal lobes (*AntL*). × 60.

B.—Longitudinal section of head of mature larva, passing through one of the suboesophageal commissures (*SoeCom*). × 60.

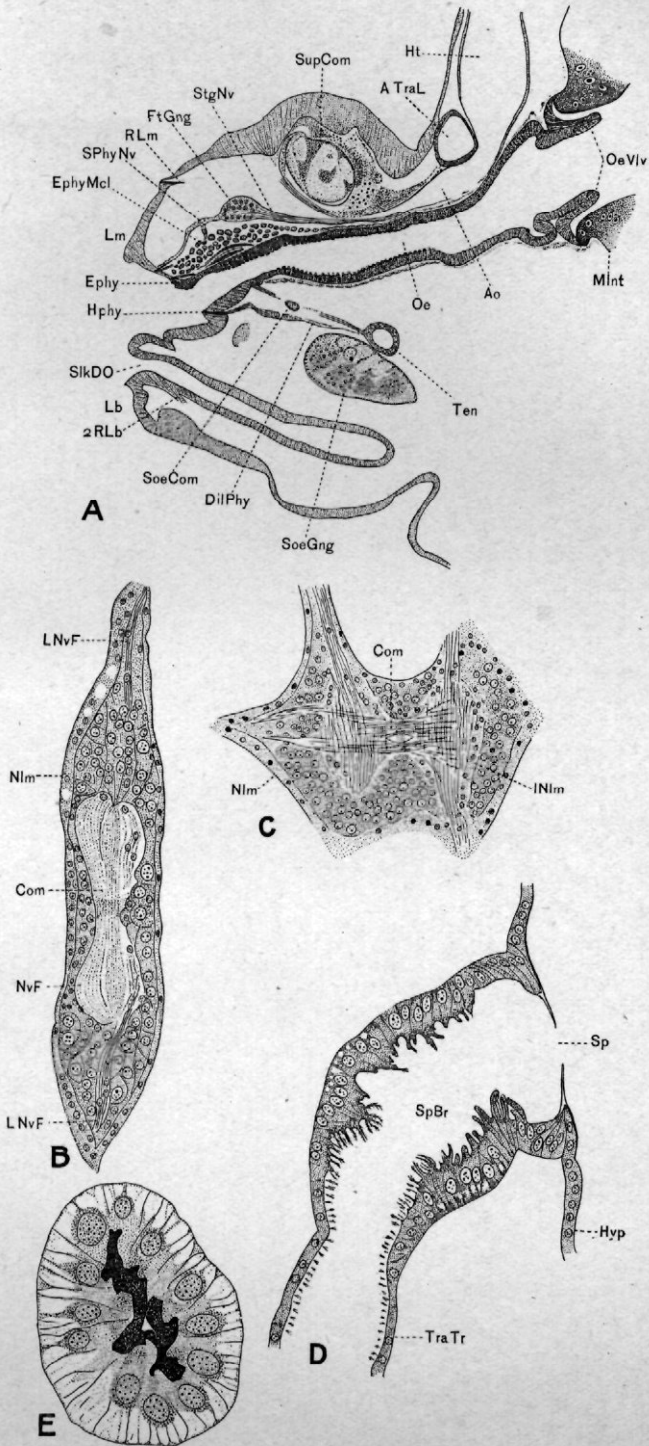
C.—Head of larva, face view, showing the optic plates (*OpPl*) and rudiments of antennæ (*AntR*). × 40.

D.—Longitudinal section of one of the antennal rudiments. × 156.

PLATE 3

Larva of the honeybee

- A.—Sagittal section through head of mature larva. × 57.
- B.—Cross section of a thoracic ganglion. × 205.
- C.—Horizontal (coronal) section of a thoracic ganglion. × 153.
- D.—Longitudinal section of a spiracular branch, intersecting spiracle (*Sp*).
× 195.
- E.—Cross section of a spiracular branch of a mature larva. × 195.



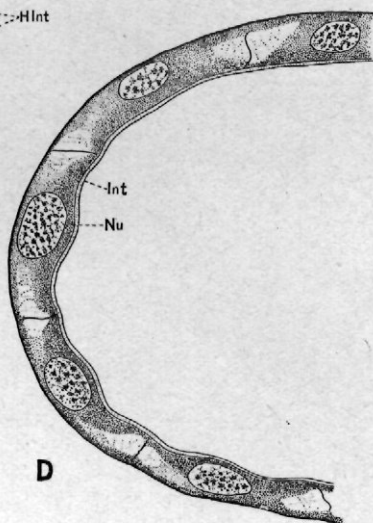
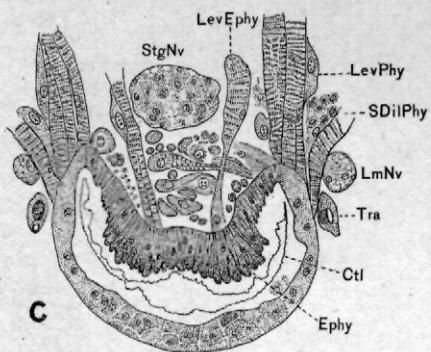
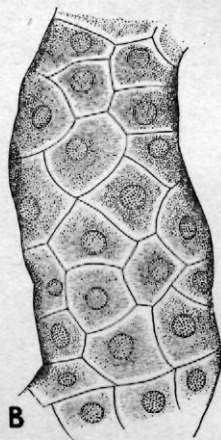
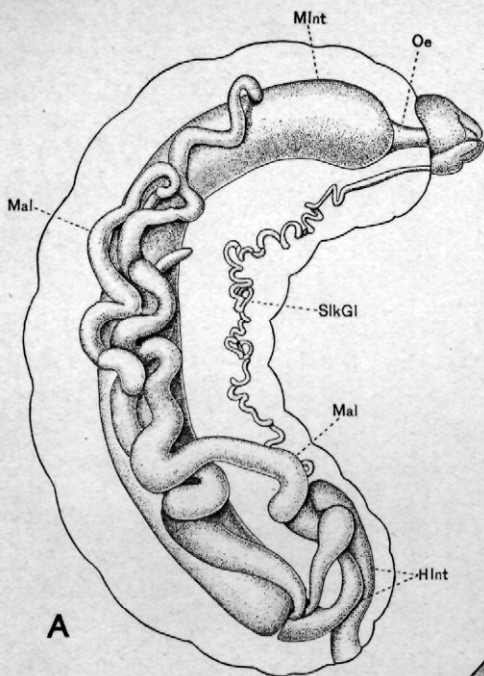


PLATE 4

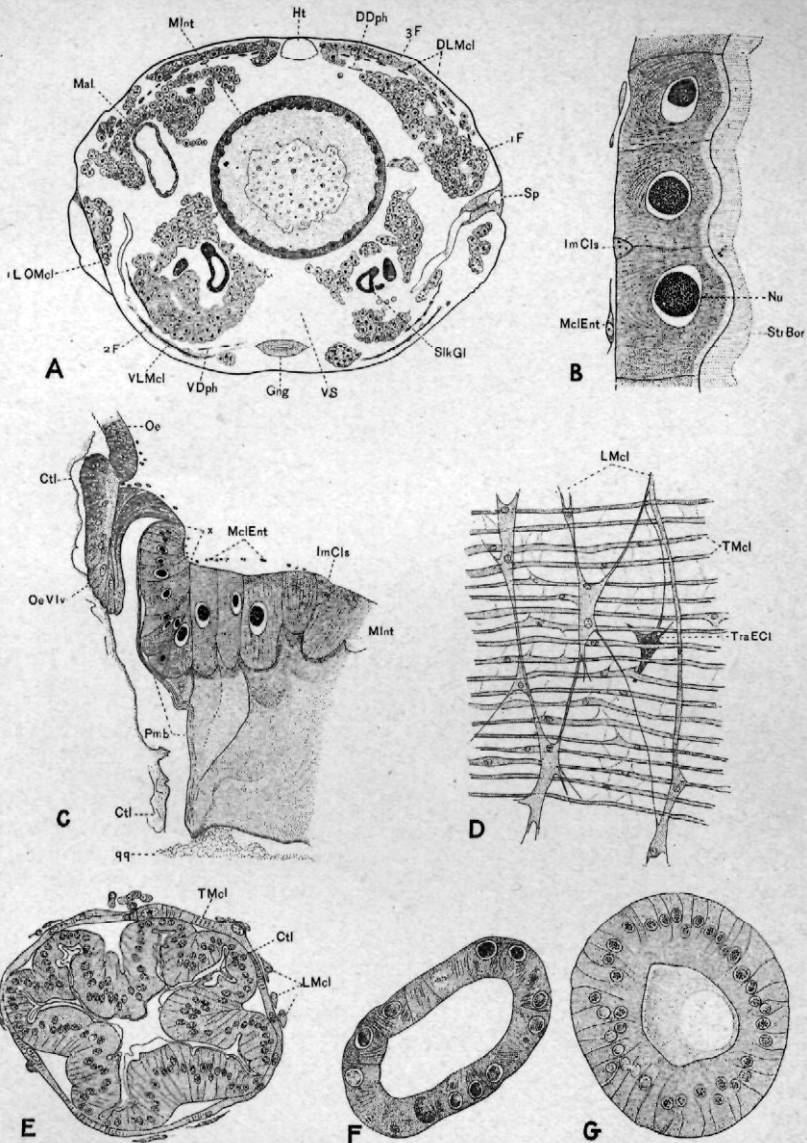
Larva of the honeybee

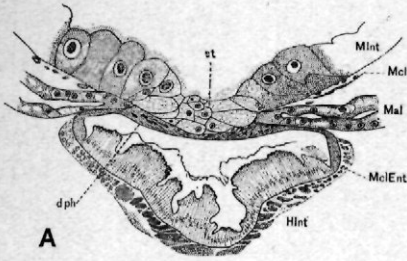
- A.—Alimentary canal, silk glands (*SilkG*), and Malpighian tubules (*Mal*) of a mature larva, drawn from a dissection. $\times 10$.
- B.—Surface view of a short section of a Malpighian tubule. $\times 75$.
- C.—Cross section of pharynx, just caudad of frontal ganglion. $\times 152$.
- D.—Cross section of Malpighian tubule. $\times 300$.

PLATE 5

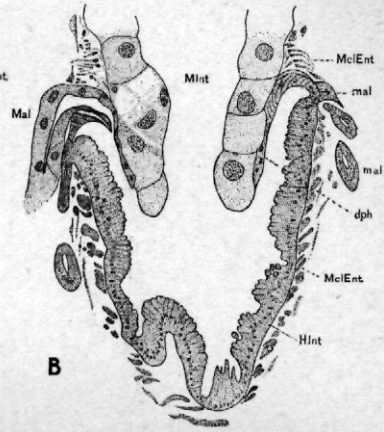
Larva of the honeybee

- A.—Cross section through the first abdominal segment of mature larva. $\times 20$.
- B.—Section of wall of mid-intestine of old larva, showing imaginal cells (*ImCls*) and striated border (*StrBr*). $\times 235$.
- C.—Junction of wall of mid-intestine and oesophagus, longitudinal section, showing one-half of oesophageal valve (*OeVlv*). $\times 120$.
- D.—Muscles of mid-intestine, seen from their inner (central) surface. $\times ca\ 80$.
- E.—Cross section of hind intestine, showing folds. $\times 144$.
- F.—Cross section of silk gland, near the fifth abdominal segment. $\times 235$.
- G.—Cross section of silk gland, near its anterior end. $\times 235$.

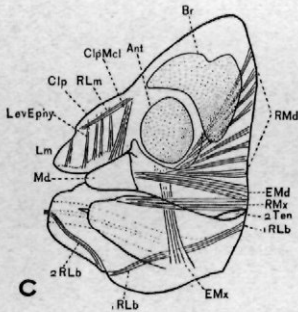




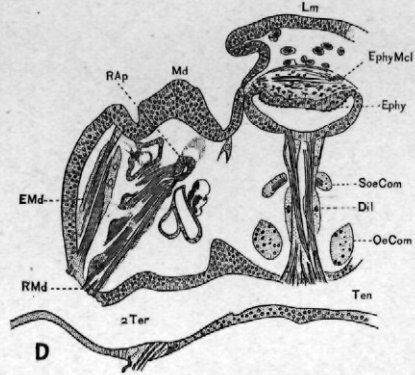
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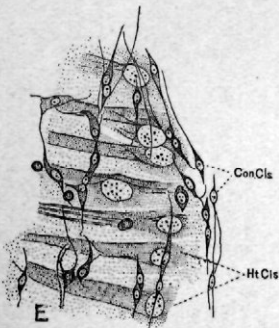
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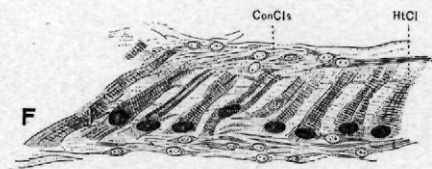
C



D



E



F

PLATE 6

Larva of the honeybee

A.—Longitudinal section through the junction of mid-intestine and hind intestine of mature larva just prior to capping of the cell. The section passes through the central blind ends of two Malpighian tubules (*Mal*), one on each side. $\times 92$.

B.—Longitudinal section through the junction of mid-intestine and hind intestine of a larva 12 hours after capping, showing the establishment of communication between the mid-intestine, hind intestine, and Malpighian tubules. The opening of one of the latter into the hind intestine is to be seen on the left side. $\times 92$.

C.—Head of larva, left side, showing musculature. From a stained and cleared preparation. $\times 26$.

D.—Coronal section of head of mature larva, intersecting the posterior arms of tentorium (*2Ten*). $\times 60$.

E.—Tangential section of wall of heart, showing cells of wall (*HtCls*) and connective tissue (*ConCls*). From the region of the fourth abdominal segment. $\times 300$.

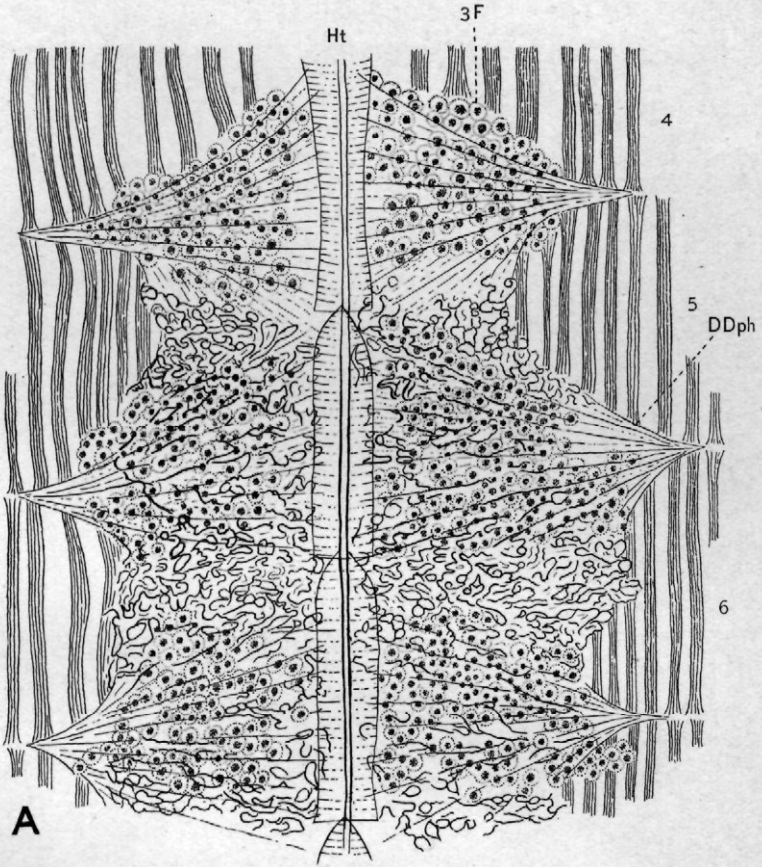
F.—Tangential section of anterior end of heart. $\times 300$.

PLATE 7

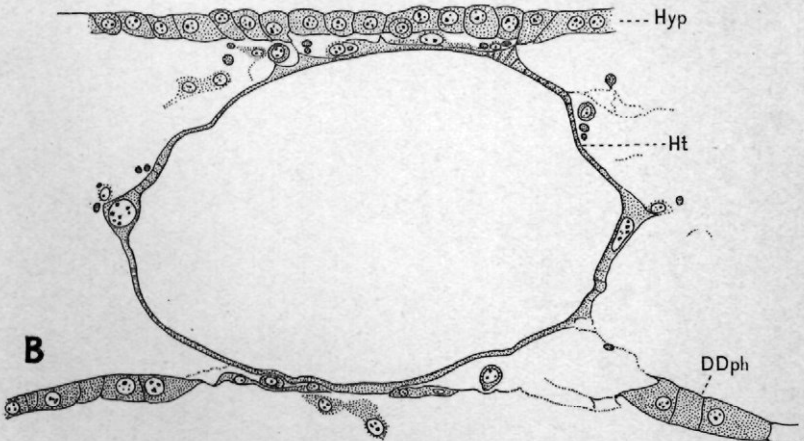
Larva of the honeybee

A.—Dorsal diaphragm and heart, fourth, fifth, and sixth abdominal segments, viewed from the inner surface. Diaphragm cells represented by heavy wavy lines. $\times 63$.

B.—Transverse section of heart (*Ht*), taken near the anterior end of the abdomen. $\times 315$.



A



B

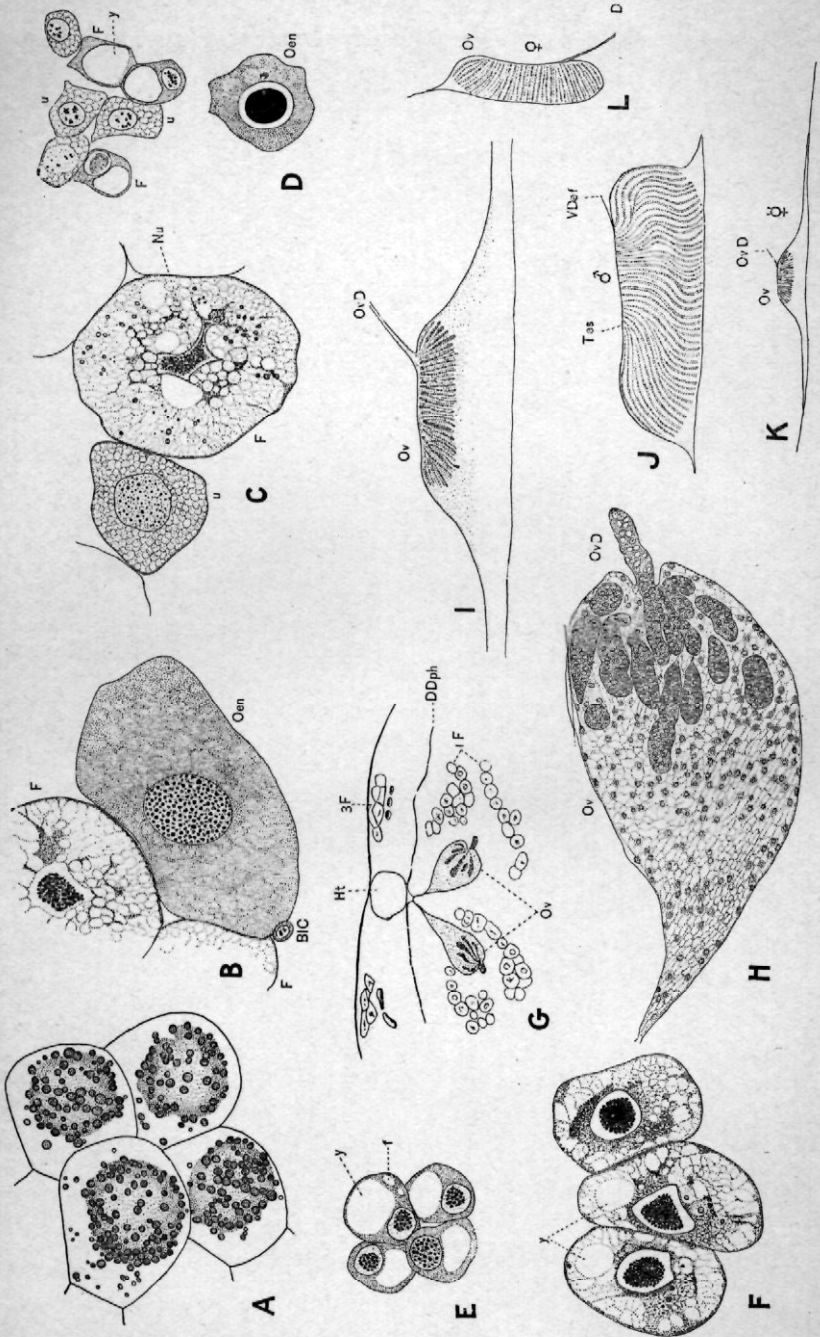


PLATE 8

Larva of the honeybee

A.—Four fat cells from advanced worker larva, showing fat globules blackened by osmic acid.

B.—Oenocyte (*Oen*) and fat cell (*F*), from a mature larva. × 406.

C.—Urate cells (*u*) and fat cell (*F*), from a mature larva. × 406.

D.—Fat cells (*F*), oenocytes (*Oen*), and urate cells (*u*), from a larva about two days old, showing the crowding of the nuclei toward the side of the cells. × 406.

E.—Four fat cells from a larva 3 days old. × 406.

F.—Three fat cells from a larva 3 to 4 days old. × 406.

G.—Transverse section through heart (*Hi*) and rudiments of ovaries (*Ov*) of a mature worker larva. × 18.

H.—Transverse section through the rudiment of an ovary of a mature worker larva, taken near the posterior end of the rudiment. × 176.

I.—Side view of rudiment of ovary of mature worker larva, showing rudiment of oviduct (*Ovd*). × 28.

J.—Rudiment of testis of drone larva, side view. × 9.

K, L.—Rudiments of ovary of worker larva and queen larva, respectively. × 9.