similar to those of *Tabanus*. When spread out flat they form an oval disc (B, *La*) crossed by the pseudotracheal channels (*b*), and enclosing centrally an opening (*a*) at the posterior end of the anterior cleft between the component lobes. This opening, which leads into the food canal of the proboscis, is known as the "oral aperture," but it must not be confused with the functional mouth aperture of the fly, which, as we have seen, lies at the upper end of the food canal between the bases of the labrum and hypopharynx. The cleft between the labellar lobes anterior to the aperture of the food canal is known as the *prestomum*. Its inner walls in some flies are armed posteriorly with several rows of small *prestomal teeth*.

The morphology of the muscoid proboscis is difficult to understand in all its details, and there are many features in the structure and musculature of this complex feeding apparatus which show that it is a highly specialized composite organ. The parts of the proboscis distal to the rostrum are clearly the homologues of corresponding elements in the mouth parts of the horse fly, including the premental region and terminal lobes of the labium, together with the labrum and the hypopharynx. The composition of the rostrum, however, is less easy to determine, but it apparently includes the base of the labium and a part of the clypeal region of the head.

The inverted V-shaped plate of the anterior wall of the rostrum (Fig. 174, C, D, *clp*) bears upon its lateral arms the origins of the dilator muscles of the cibarial pump (D, *3*). There can be little question, therefore, that this sclerite represents at least the median part of the clypeus in the head of *Tabanus* (Fig. 171 B, *clp*). The lateral walls of the pump in the muscoid flies, however, are attached by wide apodemal inflections to the margins of the V-shaped clypeal plate, and for this reason anatomists have often regarded the latter as a part of the sucking mechanism. The pump, the clypeal plate, and the connecting apodemes are described as a stirrup-shaped structure which, in the special terminology of the fly head, is called the *fulcrum*, because certain muscles attached upon it serve to flex the proboscis (see Lowne, 1890–1895; Graham-Smith, 1930). Frew (1923) recognizes "this exposed part of the fulcrum" as the clypeus. Peterson (1916), on the other hand, attempted to explain the anterior plate of the rostrum as derived from the tormae, which are sclerotic processes in the base of the epipharyngeal wall of the labrum. The attachment of the dilator muscles of the cibarial pump on the arms of the V-shaped rostral plate, however, clearly demonstrates the clypeal origin of this sclerite, and confirmatory evidence of its homology with the median clypeal region in *Tabanus* is seen in the fact that a pair of labral muscles (Fig. 174 D, *2*) take their origin on its dorsal part. The smaller sclerite above the V-shaped clypeal plate

(C, *c*) is either a part of the clypeus or a secondary sclerotization hinging the latter to the lower margin of the face. We must, then, assume that the rostrum of the fly's proboscis includes at least a part of the clypeus, which has become detached from the head walls and shifted ventrally.

The origin of the maxillary palpi (Fig. 174 C, *MxPlp*) from small sclerites in the ventral part of the rostrum shows that the last has also absorbed the basal parts of the maxillae. The remaining major part of the rostrum is apparently to be attributed to the basal part of the labium.

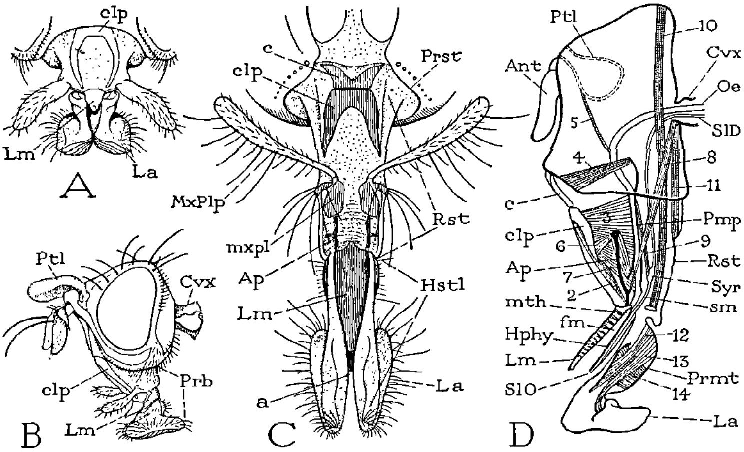

FIG. 174.—Proboscis of a fruit fly and a blow fly. A, *Rhagoletis pomonella*, proboscis, anterior view. B, same, head and proboscis, lateral view. C, *Calliphora erythrocephala*, proboscis, anterior view. D, same, head and proboscis, lateral view, showing muscles. (*Adapted from Graham-Smith*, 1930.)

Within the rostrum lie the sucking pump, the salivary duct with its syringe, and a pair of long rodlike apodemes arising from the basal angles of the labrum (Fig. 174 C, D, *Ap*). The sucking pump of the blow fly does not differ from that of the horse fly, except for the connection of its lateral walls with the margins of the clypeus and in details of its form. The rostral apodemes appear to belong to the labrum, but some writers have regarded them as remnants of the maxillae. Muscles are inserted upon them which have no apparent homologues in the head of biting insects.

The musculature of the proboscis is somewhat complex (Fig. 174 D) but is not difficult to study. Most of the muscles, however, appear to be special adaptations to the functions of the fly proboscis, and they cannot be satisfactorily homologized with the muscles of the mouth parts in biting insects.

For a full account of the structural details and musculature of the head and mouth parts of muscoid flies the reader is referred to the elaborate paper on the proboscis of the blow fly by G. S. Graham-Smith (1930), and to that on the head and mouth parts of the tsetse fly by Jobling (1933), though the many special terms used by these writers, taken largely from Lowne (1890–1895), will be somewhat confusing to the student of general insect morphology.

The blow fly *Calliphora erythrocephala*, according to the observations of Graham-Smith, has several different methods of feeding, which involve a use of the labellar lobes in as many corresponding different positions. In the nonfeeding position, the lobes are flexed posteriorly against the haustellum with their pseudotracheal surfaces in apposition. When the fly feeds on a film of liquid the labella are spread out flat like the leaves of a book, but only the parts of their surfaces covered by the pseudotracheae are applied to the food substance; the liquid is then sucked up through the pseudotracheal openings ("interbifid grooves"), and "all particles too large to pass through them are filtered out and rejected." This way of using the labella is termed by Graham-Smith the *filtering position.* In some cases the edges of the lobes are turned down, producing a marginal rim around the labellar disc, thus giving a second or *cupping position.* By a separation of the labella the prestomal teeth may be partly exposed and used to some extent while the liquid food is still being filtered through the pseudotracheae. This gives an *intermediate position* leading to the next, or *scraping position,* in which the labellar lobes are turned upward until the prestomal teeth are fully exposed for the purpose of rasping. In this position the pseudotracheal surfaces are out of action. Finally, there is the *direct feeding position,* produced by folding the labella upward and outward against the sides of the haustellum, in order that the aperture of the food canal may be applied directly to the food, thus allowing not only the liquid but particles in the liquid to be freely ingested.

In some of the nonpiercing Muscidae the prestomal teeth are large and strong, as in *Musca crassirostris,* which attacks cattle and obtains blood from them by scratching the skin with its powerful labellar armature.

The Piercing Type of Muscoid Mouth Parts.—Muscoid flies having the "biting" type of mouth parts are principally the stable flies, the horn flies, and the tsetse flies, that is, members of the genera *Stomoxys, Haematobia,* and *Glossina.* The piercing organ of these flies is the proboscis (Fig. 175 A, *Prb*), which consists of the same parts as does that of the nonpiercing muscoids. The haustellum, however, is elongate and rigid, swollen at the base to accommodate the contained muscles, and tapering toward the extremity. The labellar lobes (C, *La*) are small, flat, and densely horny, and the prestomal teeth are well developed. The labrum is almost circular in transverse section (B, *Lm*) and is firmly locked within the upturned edges of the labium (*Lb*), the two parts forming thus a tubular food channel (*fm*), within which lies the slender hypopharynx (*Hphy*) traversed by the salivary channel (*sm*). The beaklike proboscis is forced into the flesh of the victim by a strong thrust of the head and body of the fly, and the blood is sucked up directly through the food canal. The salivary secretion of *Glossina* is said to prevent clotting of the blood.

For further information on the structure of the mouth parts and the feeding mechanism of the piercing muscoid flies, the student should consult the works of Cragg (1912), Hansen (1903), Jobling (1933), Minchin (1905), Patten and Evans (1929), Stuhlmann (1907), and Vogel (1920).

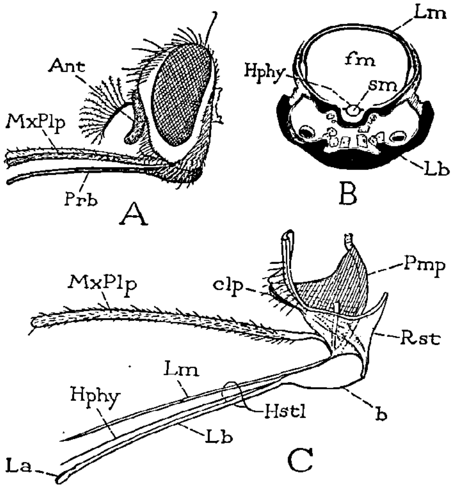

Fig. 175.—Head and mouth parts of a tsetse fly. A, *Glossina palpalis*, male, head and proboscis. B, *G. fusca*, cross section of proboscis. (*From Vogel*, 1920.) C, *G. palpalis*, mouth parts and sucking pump.

7. THE MOUTH PARTS OF SIPHONAPTERA

The mouth parts of the fleas appear to be of the dipterous type of structure, but they are more generalized than those of any adult fly. None of the usual pieces is lacking, and both the maxillae and the labium retain long, segmented palpi. The mandibles are said to be the cutting and piercing organs of the fleas, and the preoral food canal lies between them and the concave under surface of the labrum, as it does in the Tabanidae. The essential characters of the flea mouth parts, as described by Patten and Evans (1929), are as follows: The labrum is long and slender but is blunt at the apex; its lateral edges are rolled downward between the mandibles, forming the anterior wall of the food canal. The mandibles are long, sharp-pointed blades armed distally with minute teeth. The maxillae are short, rather wide plates, bearing each a long, segmented palpus. The labium consists of a short median body, hollowed anteriorly, bearing distally a pair of segmented palpi. The short hypopharynx projects into the proximal end of the food canal between the bases of the mandibles; upon it opens the duct of the salivary glands, the secretion of which is conveyed to the wound through a channel between the posterior edges of the mandibles.

8. THE FEEDING MECHANISM OF THYSANOPTERA

There are few insects so isolated from other orders by some peculiar feature of their anatomy as are the Thysanoptera and the Hemiptera in the form and structure of their mouth parts. It has often seemed to entomologists that the Hemiptera in particular must be a group but distantly related to other insects, and yet such an assumption is discredited in all parts of their organization except the mouth parts. It is true, however, that the members of these two sucking orders possess a piercing mechanism, at least, that has no counterpart in any other group of insects, though some of its features are suggested in certain structures found in the Psocidae and Mallophaga.

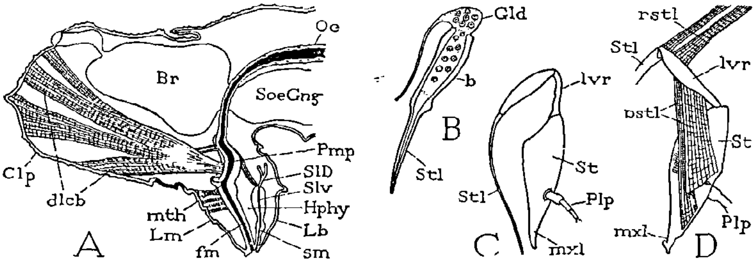

FIG. 176.—Mouth parts and sucking apparatus of Thysanoptera. A, *Heliothrips femoralis*, section of head and beak, showing food meatus (*fm*) between labrum and hypopharynx, and sucking pump (*Pmp*) with its dilator muscles. B, same, mandible. C, *Frankliniella tritici*, maxilla. D, *Heliothrips haemorrhoidalis*, maxilla and muscles. (A, B, C *from Peterson*, 1915; D *from Reyne*, 1927.)

The mouth parts of the thrips, while aberrant in some respects, are distinctly more generalized than are those of the Hemiptera, and studies of their development give us an insight into the nature of the unusual modifications that have produced the distinctive characters of both the Thysanoptera and the Hemiptera. The most important papers on the mouth parts of the thrips are those of Peterson (1915) and Reyne (1927).

The curiously distorted head of the Thysanoptera, which usually is produced forward from the thorax with the facial area turned ventrally (Fig. 176 A), bears a short, thick, conical beak projecting downward from the posterior part of the under surface. Externally the beak is formed by the labrum in front (*Lm*), the maxillae on the sides, and the labium behind (*Lb*). Within the beak is contained a single mandible, which is the left one, two piercing stylets associated with the bases of the maxillae, and the hypopharynx (*Hphy*). All the elements of the piercing mechanism and the lower parts of the head wall are subject to an asymmetry of shape, and they may differ in details of form in the two thysanopterous suborders, the Terebrantia and Tubulifera, but their essential structure is the same in both groups.

The Labrum.—The labrum (Fig. 176 A, *Lm*) is a broad, triangular lobe, usually of irregular form, covering the anterior surface of the beak. Between its wide base and the lower edge of the facial region of the head is an asymmetrical triangular sclerite which is probably a basal part of the labrum, since, for reasons to be given presently, the writer would regard the clypeus as being contained in the large facial region of the head capsule (*Clp*).

The Mandible.—The mandible developed on the left side of the head is contained in a *mandibular pouch* invaginated within the head from the basal angle between the contiguous surfaces of the labrum and the left maxilla. The mandible is an elongate piercing organ (Fig. 176 B), consisting of a wider basal part (*b*) and a slender distal stylet (*Stl*). On the base are inserted retractor muscles arising on the head wall, but protractor muscles are said to be absent. A functionless rudiment of the right mandible, according to Peterson (1915), is present on the right side of the head.

The Maxillae.—The maxillae of the thrips, with their associated stylets, are of particular interest because of the light they have thrown on the obscure morphology of the maxillae in the Hemiptera. Each maxilla consists of an elongate, triangular plate (Fig. 176 C, *St*) forming the lateral wall of the conical beak. Near its distal end it bears a short palpus (*Plp*) of two or more segments. From the inner side of the base of the maxillary plate there is given off mesally (in the Terrebrantia at least) a short bar (*lvr*), which supports a long, slender *maxillary stylet* (*Stl*) with an enlarged base, which is contained in a pouch of the ventral head wall. It is shown by Reyne (1927) that the maxillary stylet is formed in the embryo from the body of the maxilla. The latter, at the end of the sixth day of development, is still a simple lobe, but soon a cleft appears in the maxillary rudiment, which separates the basal part from the rest, and later from this basal part the stylet is formed as an outgrowth. Retractor muscles from the head wall (D, *rstl*) become inserted on the bar (*lvr*) connecting the stylet with the lateral plate, and protractor muscles (*pstl*) are developed in the tissue between the bar and the inner face of the plate. The lateral part of the maxilla bearing the palpus is clearly the stipes, which terminates in a single lobe (*mxl*) representing the fused galea and lacinia. The stylet, according to Reyne, is of the nature of a large cuticular spine produced from the mesal part of the maxillary base, secondarily split off from the region of the cardo and stipes.

The structure of the thrips maxilla, as we shall presently see, is almost an exact duplicate of that of the hemipterous maxilla (Fig. 181 B), in which the part representative of the stylet is usually drawn out into a long slender bristle (*MxB*). Furthermore, the "mouth forks" of the Psocidae and similar rods associated with the maxillae in some of the Mallophaga appear to be structures analogous at least with the thysanopterous maxillary stylets. All these anomolous organs Hansen (1930) would derive from the superlinguae and not from the maxillae. Hansen, however, entirely ignores the import of Reyne's studies of the development of the mouth parts in the Thysanoptera, and he gives no weight to Reyne's assertion that the maxillary stylets are actually split off from the maxillary rudiments during embryonic growth.

The Labium and Hypopharynx.—The labium of the Thysanoptera is a wide triangular appendage forming the posterior surface of the beak (Fig. 176 A, *Lb*). Distally it bears a pair of short two-segmented palpi and terminates in one or two pairs of flaps which are evidently the glossae and paraglossae. The hypopharynx (*Hphy*) is a short medium lobe arising from the anterior surface of the base of the labium. Between it and the labrum is the food meatus of the beak (*fm*) leading to the mouth aperture (*mth*) behind the base of the labrum. The duct of the labial glands (*SlD*) opens posterior to the base of the hypopharynx, and the salivary liquid is conveyed to the tip of the beak through a channel, the salivary meatus (*sm*), between the hypopharynx and the labium. The salivarium into which the salivary duct opens has muscles inserted upon it, forming thus a structure suggestive of the more highly evolved salivary syringe of the Hemiptera.

The Sucking Pump.—The sucking organ of the thrips (Fig. 176 A, *Pmp*) is very similar to that of the Hemiptera (Fig. 179, *Pmp*). It is a cibarial chamber enclosed within the head, and its external aperture (*mth*) is directly continuous with the food meatus (*fm*) of the beak. On its dorsal wall are inserted long bundles of dilator muscle fibers (*dlcb*) that take their origin on the anterior part of the facial region of the head capsule. The cranial sutures are obsolete in the Thysanura, but it is evident that the head area on which the pump muscles arise (*Clp*) corresponds to the enlarged clypeal plate in the head of a cicada (Fig. 177 B, *Clp*) or a psocid (A, *Clp*).

9. THE FEEDING MECHANISM OF HEMIPTERA (RHYNCHOTA)

The typical hemipterous feeding mechanism differs from that of the Thysanoptera in the following respects: (1) The beak is usually long and slender and consists principally of the labium, which lacks palpi and terminal lobes, the short labrum covering only its basal part; (2) both mandibles are symmetrically developed, and their apical parts are drawn out into long slender bristles, each movable by retractor and protractor muscles; (3) the lateral plates of the maxillae are mostly incorporated into the head capsule with only their terminal parts free, maxillary palpi are lacking, and the maxillary stylets are long slender bristles similar to the mandibular bristles; (4) the salivary syringe is a well-developed force pump for ejecting the saliva, and its duct transverses the short hypopharynx to its tip; (5) both the food canal and the salivary canal of the beak lie between the closely apposed inner surfaces of the maxillary bristles.

The Structure of the Head.—In a typical homopterous insect, such as the cicada, the head capsule presents anteriorly a prominent convex plate (Fig. 177 B, *Clp*). This plate clearly belongs to the clypeal region of the head, since the dilator muscles of the sucking pump (cibarium) take their origins upon it. The plate is bounded laterally and dorsally by a deep groove (*es*) identified as the epistomal suture by the presence of the pits of the anterior tentorial arms in its lateral parts (Figs. 177 A, 178, *at*). The epistomal suture is strongly arched upward on the face, its transverse dorsal part lying between the bases of the antennae. A comparison of the cicada head (Fig. 177 B) with the head of a procid (A) leaves little doubt of the homologies of the facial plates in the two insects. The frons of the cicada is reduced to the small, imperfectly demarked, triangular area (*Fr*) on the top of the head, immediately above the large clypeal plate, bearing the median ocellus. Between the large clypeal plate and the base of the labrum (*Lm*) there is in the cicada a smaller anteclypeal plate (*Aclp*), but in some of the Homoptera the separation between the two clypeal areas is indistinct or absent. The labrum in the cicada is a small, slender, tapering lobe (*Lm*) closely applied to the anterior side of the base of the beak. It is often called the "epipharynx."

On each side of the head below the compound eye are two lateral plates (Fig. 178, *A*, *B*) separated by a deep membranous groove (*h*), best seen in the soft head of a newly emerged imago (B). The anterior plate (B, *A*), termed the *lorum* by homopterists, might appear from its position to represent the mandible, since its dorsal extremity lies immediately beneath the root of the anterior tentorial arm (*at*) and its lower part is continuous with the lateral wall of the hypopharynx (*Hphy*), but an identity with the mandible is not borne out by studies of the development of this plate. The sclerite, however, is commonly called the *mandibular plate*, since the mandibular bristle is articulated by a leverlike arm with the posterior border of its upper part (Fig. 181 A, *lvr*), and the mandibular protractor muscles (*pmdb*) arise on its lower part. The second lateral plate (Fig. 178, *B*), which is continuous dorsally with the cranial wall, is known as the *maxillary plate.* Its upper part is probably the gena, but its lower extremity (B, *Mx*) and the small tapering appendicular lobe suspended from it (*mxl*) have been shown from embryological evidence to be the basal part of the maxilla fused with the lateral wall of the head. The maxillary bristle is articulated by a lever with the maxillary plate (Fig. 181 B), and the maxillary protractor muscles (*pmxb*) arise on the lower part of the latter.

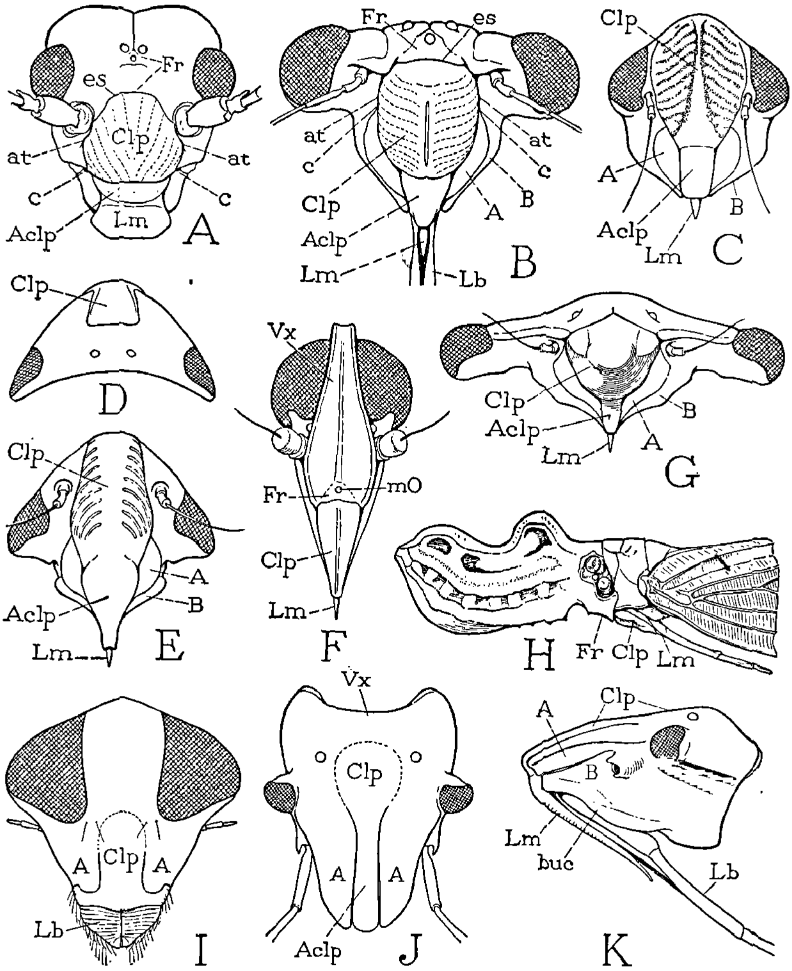

FIG. 177.—Types of head structure in Corrodentia and Hemiptera. A, head of a psocid. B, *Magicicada septendecim.* C, *Deltocephalus simplex* (Cicadellidae). D, E, *Lepyronia quadrangularis* (Cercopidae). F, *Ocleus borealis* (Fulgoridae). G, *Ceresa diceros* (Membracidae). H, *Laternaria* (Fulgoridae). I, *Corixa* (Corixidae). J, K, *Euschistus variolarius* (Pentatomidae).

The posterior part of the cranium is imperfect in the cicada, and the labium is suspended from a large membranous ventral area continuous with the neck.

It is not difficult to identify the cranial areas or sclerites of other Homoptera with those of the cicada if the criterion of muscle attachments is consistently followed. The clypeus (or postclypeus) is in all cases the plate on which arise the dilator muscles of the sucking pump. In Cicadellidae (Fig. 177 C), Cercopidae (E), and Membracidae (G), it has a position similar to that in the cicada; in the cercopids its upper part is reflected beyond the fastigial angle of the cranium and appears as a small sclerite in the dorsal wall of the head (D, *Clp*). The anteclypeus is not always distinctly separated from the postclypeal area (E), and in some Fulgoridae the clypeus is undivided (F, *Clp*). The clypeus of the fulgorids is relatively small and has a ventral (F) or posteroventral position on the under side of the head (H); the vertex, on the other hand, is large and often elongate on the facial aspect of the head (F, *Vx*), in the lanternflies (*Laternaria*) it attains an extreme size and a highly grotesque form (H). In the Psyllidae the head is markedly opisthognathous, the clypeus being ventral, and the beak set far back on the under side of the head. This condition is still more exaggerated in the flattened "sternorhynchous" larval and adult female Coccidae. On the sides of the homopterous head the mandibular and the maxillary plates are in most cases easily recognized (C, E, G, *A*, *B*) or can be identified respectively as the areas on which arise the mandibular and maxillary protractor muscles.

In the Heteroptera the head differs in several respects from that of the Homoptera, and the homologies of its parts are more difficult to determine. The beak usually arises anteriorly (Fig. 177 K), the clypeal area is typically dorsal (J, K, *Clp*), and there is a large ventral area of the head behind the beak, walled by a sclerotic hypostomal bridge (usually called the "gula") between the base of the labium and the foramen magnum. In Corixidae and Notonectidae, however, the mouth parts are ventral and the facial region is directed forward (I). The area of the clypeus is marked by the origins of the dilator muscles of the sucking pump (Fig. 184 A, *dlcb*) and may extend far back on the dorsal surface of the head (Fig. 177 J, *Clp*), but its upper or posterior part is not defined by a suture (I, J). On the other hand, the distal part of the clypeus or anteclypeal region (J, *Aclp*), called the *tylus* by heteropterists, is margined by deep clefts that separate it from lateral lobes of the head (*A*, *A*) known as the *juga*. These paraclypeal lobes appear to be the mandibular plates of the Homoptera, since the mandibular bristles are articulated to their lateral margins and the mandibular protractor muscles arise upon them. In Corixidae and Notonectidae the mandibular muscles arise on the inflected mesal margins of the lobes, which support the sucking pump. The maxillary plates generally have the usual position on the sides of the head (K, *B*), but in Notonectidae they are inflected and mostly concealed at the base of the labium. The heteropterous labrum is relatively long (K, *Lm*), in Notonectidae it is a large triangular flap.

The Beak.—The typical hemipterous beak is formed principally of the slender, segmented, but usually rigid labium (Fig. 178 A, *Lb*), which, in the cicada, hangs freely from the neck membrane behind the lower extremities of the maxillary plates. The basal part of the beak, however, includes the short labrum (*Lm*), and the lateral spaces between the labrum and the labium are closed by the terminal lobes of the maxillary plates (*mxl*). Within the beak are enclosed the mandibular and maxillary bristles (B, *MdB*, *MxB*), which lie in a deep groove of the anterior surface of the labium (Fig. 182 A). The tip of the hypopharynx (Fig. 178 B, *Hphy*) projects into the proximal part of the beak between the bases of the bristles, which issue from pouches of the head wall invaginated between the sides of the hypopharynx and the inner walls of the maxillary plates (Fig. 180 A).

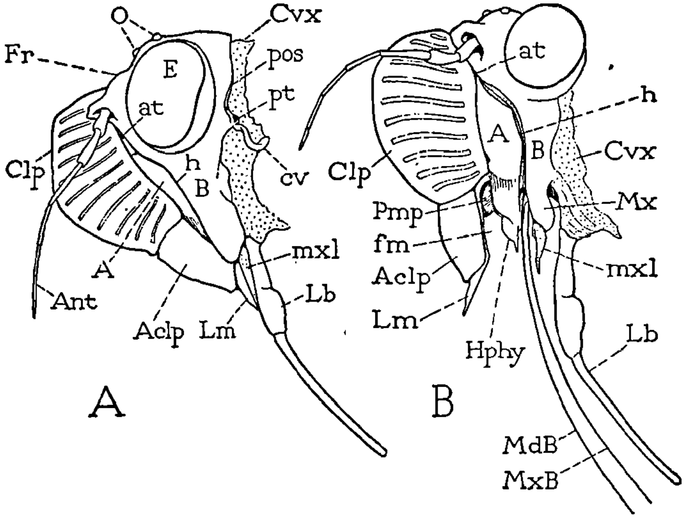

FIG. 178.—Head and beak of *Magicicada septendecim*. A, head of fully matured imago. B, soft head of imago emerging from nymphal skin, with parts separated.

The Hypopharynx.—The hypopharynx of the cicada (Fig. 178 B, *Hphy*) is a median conical lobe of the ventral wall of the head between the lower ends of the mandibular plates (*A*), where in the normal condition it is entirely concealed by the approximation of the surrounding parts (A). The anterior surface of the hypopharynx is continued dorsally into the posterior (ventral) wall of the chamber of the sucking pump (Fig. 179 A, B, *Pmp*). Within the hypopharynx is located the salivary syringe (*Syr*), the terminal duct of which (B, *sm*) opens on the tip of the hypopharynx (Figs. 179 B, 180 B, *SlO*). The sides of the hypopharynx are prolonged upward as two flat, strongly sclerotized plates (Fig. 180 A, B, *hpl*) forming the inner walls of the bristle pouches (*bp*). The upper extremities of these plates are secured to the posterior transverse bar of the tentorium (*Tnt*), the union being so close in the cicada as to make it appear that the plates are united with the tentorial bar.

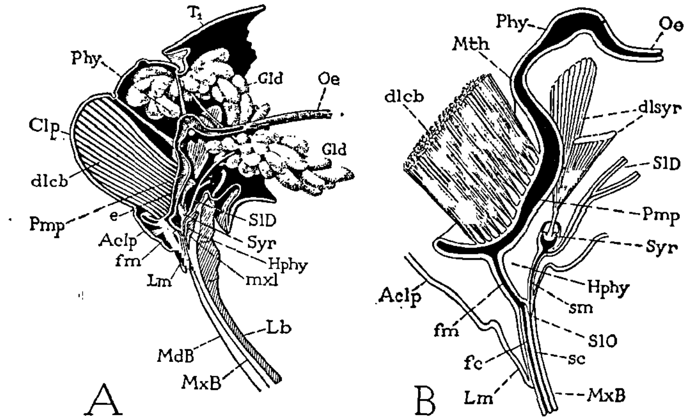

FIG. 179.—The sucking pump and salivary syringe of *Magicicada septendecim*. A, section of the head showing position of the sucking pump (cibarium) with dilator muscles arising on the clypeus. B, section through the mouth region, showing food meatus (*fm*), suck-pump (*Pmp*), and salivary syringe (*Syr*).

The Mouth.—In the soft immature stage of the cicada imago newly emerged from the nymphal skin (Fig. 178 B), there is seen to be a wide, open, transverse cleft between the base of the anteclypeus (*Aclp*) and the hypopharynx (*Hphy*), which exposes the chamber of the sucking pump (*Pmp*). In the fully matured insect the lips of this cleft are always tightly shut by the contact of the anteclypeus against the lower parts of the mandibular plates (A), and by the closure of the epipharyngeal wall of the anteclypeus upon the anterior surface of the hypopharynx. But the surface of the hypopharynx that is thus covered by the epipharynx contains a median groove, and this groove, converted into a tube (Fig. 179, *fm*) by the overlying epipharyngeal wall, remains as the only entrance into the pump chamber and becomes thus the *functional mouth*. The chamber of the sucking pump of the Hemiptera, however, as we shall presently see, represents the preoral cibarium of orthopteroid insects (Fig. 155, *Cb*). The *true mouth*, therefore, is the posterior opening of the pump into the stomodaeum (Fig. 179 B, *Mth*).

The Sucking Pump.—The narrow, tubular functional mouth of the Hemiptera, or channel between the anterior surface of the hypopharynx and the apposed epipharyngeal surface of the anteclypeus (Fig. 179 A, B, *fm*), on the one hand, connects with the food canal between the maxillary bristles (B, *fc*) and, on the other, leads into the cavity of the sucking pump (*Pmp*). The latter in the cicada is a large oval chamber lying almost vertical in the lower part of the head (A). Its posterior and lateral walls are convex and strongly sclerotized. The anterior wall is flexible and is deeply invaginated into the lumen of the chamber. On its midline are inserted the converging ends of two large groups of muscle fibers (A, B, *dlcb*), which have their origins on the entire inner surface of the postclypeal plate of the head wall (A, *Clp*). These muscles are the dilators of the pump. Their contraction lifts the infolded anterior wall of the organ, thus creating an upward suction through the tubular entrance to the chamber; with the relaxation of the muscles, the lifted wall springs back into the lumen by the force of its own elasticity, its lower end descending first. By this mechanism the food liquid is drawn into the pump chamber from the food canal of the beak (B, *fc*) and is expelled upward into the anterior part of the stomodaeum.

The pump chamber of the Hemiptera very evidently represents the preoral cibarium of more generalized insects (Fig. 155, *Cb*), though it has usually been referred to the buccal cavity or to the pharynx. Its floor is formed by the proximal part of the anterior surface of the hypopharynx, and its roof is the epipharyngeal wall of the anteclypeus. In the cicada the lateral walls of the pump are deeply cleft by the wide opening between the hypopharynx and the epipharyngeal surface, as seen in the newly emerged imago (Fig. 178 B), and it is only in the mature condition that the pump cavity is concealed by the firm closure of these opposing parts. The true mouth of the insect is the inner opening of the pump (Fig. 179 B, *Mth*) into the stomodaeum.

The stomodaeum of the cicada extends upward from the inner mouth of the pump in the usual fashion and enlarges into a small sac (Fig. 179 A, B, *Phy*) resting upon the transverse bar of the tentorium (Fig. 180 A). This sac is the true pharynx, as shown by the fact that the frontal ganglion lies on its anterior end. The walls of the pharynx are muscular, and the organ is provided with dilator muscles arising on the postocular region of the head and on the tentorium. Following the pharynx is a long tubular oesophagus (Fig. 179, *Oe*).

The prototype of the hemipterous sucking pump is evidently present in the Corrodentia (Copeognatha), where, as shown by Weber (1933, Fig. 56), the ingestive apparatus includes a pumplike mechanism provided with huge dilator muscles arising on the large postclypeal plate that forms most of the facial area of the head. Though the psocid pump is attributed by Weber to the "pharynx," it is clear from its relations to surrounding parts, and by its clypeal musculature, that it belongs to the cibarial region of the preoral cavity lying proximal to the molar surfaces of the closed mandibles and thus corresponds to the mouth pump of the *Dytiscus* larva, which Weber refers to the cibarium (*Mundhöhle*). The position of the frontal ganglion in the cicada on the muscular pharyngeal sac leaves no doubt that the sucking pump of the Hemiptera is a prepharyngeal structure. The wholly nonmuscular walls of the pump and the origin of the dilator muscles on the clypeus attest that the pump has been evolved from the preoral cibarium. The enlargement and dorsal or posterior extension of the clypeus in Corrodentia, Thysanoptera, and Hemiptera is clearly correlated with the great development of the cibarium and its dilator muscles.

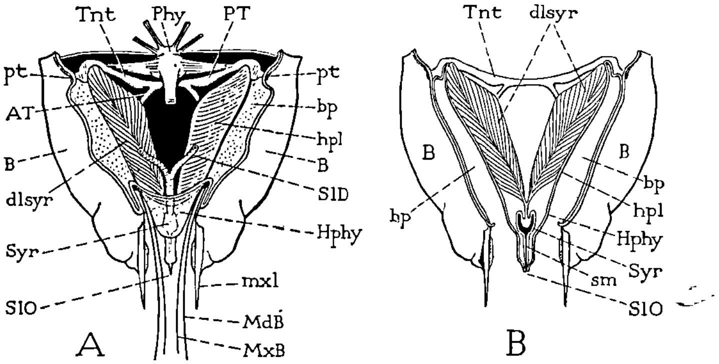

FIG. 180.—The salivary syringe and associated structures of *Magicicada septendecim* A, posterior view looking into back of head between maxillary plates. B, diagrammatic cross section through the maxillary plates (*B*), bristle pouches (*bp*), hypopharynx, and salivary syringe.

The position of the sucking pump within the head varies considerably in different groups of Hemiptera. In the Heteroptera the organ generally lies farther back than in the Homoptera and has a more horizontal position (Fig. 184 A). Its various types of structure and many details in the mechanism of the sucking apparatus have been admirably portrayed by Weber (1928, 1928*a*, 1929, 1930, 1933).

The Salivary Syringe.—The salivary syringe of the Hemiptera is a small, hollow, cup-shaped organ (Fig. 179 B, *Syr*), which at its distal end receives the common duct of the salivary glands (*SlD*), and discharges to the exterior through an outlet tube (*sm*) opening on the tip of the hypopharynx (*Hphy*). The wider inner end of the cup is deeply invaginated and supports a short apodeme on which are inserted a pair of large muscles (*dlsyr*) arising on the mesal surfaces of the long lateral plates of the hypopharynx (Fig. 180 B). The mechanism of the apparatus is very simple: the contraction of the muscles lifts the invaginated end wall of the cup, and the latter springs back by its own elasticity when the muscles relax. Thus the salivary liquid is drawn into the chamber of the cup through the salivary duct and is forcibly expelled through the outlet tube. In some of the Hemiptera at least, as described by Weber (1930), the entrance and exit of the pump chamber are provided with valvular flaps to prevent the backward flow of the liquid. Though the organ is commonly known as the "salivary" pump, or syringe, the secretion of the connected glands, which undoubtedly are the homologues of the labial glands of other insects, probably does not have in all Hemiptera a strictly digestive function.

Structurally the salivary syringe of the Hemiptera is very similar to the corresponding organ of Diptera; in each case the pump chamber is provided with hypopharyngeal muscles only, and the exit duct traverses the hypopharynx to open on the tip of the latter. Morphologically there can be little doubt that the syringe is a highly specialized development of the salivary pocket, or salivarium, of orthopteroid insects (Fig. 155, *Slv*). Its dilator muscles are the dorsal hypopharyngeal muscles of the salivarium (1*s*). Representatives of the ventral labial muscles (2*s*, 3*s*) are absent in both Diptera and Hemiptera. There is no evidence to show how the syringe and its exit duct have become enclosed within the hypopharynx; but if the duct represents the salivary meatus of generalized insects (Fig. 155, *sm*), it is perhaps possible that the apparent posterior wall of the hypopharynx in the Hemiptera is a fold of the labial wall. On the other hand, the whole apparatus may be simply infolded within a closed groove of the hypopharyngeal wall. It is interesting to observe in this connection the much more primitive structure in the Thysanoptera (Fig. 176 A).

The Mandibular and Maxillary Bristles.—The long bristle-like stylets characteristic of most of the Hemiptera arise from the walls of the bristle pouches, which, as already noted, are invaginations of the ventral wall of the head between the inner surfaces of the maxillary plates and the outer surfaces of the hypopharyngeal plates (Fig. 180 B, *bp*). Emerging from the pouches the bristles converge along the sides of the hypopharynx (A, *Hphy*), and, as they enter the groove of the labium, they become adherent to one another in a compact bundle, or fascicle (Fig. 182 A). The bases of the bristles are enlarged; those of the mandibular pair lie anteriorly in the pouches, those of the maxillary pair posteriorly. Within the labium, the mandibular bristles are the outer pair of the fascicle (*MdB*), the maxillary bristles the inner pair (*MxB*).

The mandibular bristles of the cicada are slightly thicker than the maxillary bristles. The enlarged base of each lies in the bristle pouch just behind the lower end of the corresponding mandibular plate (Fig. 181 A) and is produced proximally into two long arms. One arm (*ra*) proceeds dorsally in the inner wall of the pouch (*bp*) and gives attachment to the retractor muscles (*rmdb*) arising on the dorsal wall of the head. The other arm (*lvr*) goes dorsally in the external membranous groove (Fig. 178 B, *h*) between the mandibular and maxillary plates on the side of the head, and its upper part bends forward to articulate with the dorsal end of the mandibular plate (Fig. 181 A, *g*). This arm supports for most of its length a wide, thin apodemal inflection (*ap*), on which are inserted the protractor muscles of the bristle (*pmdb*), which have their origins on the inner face of the mandibular plate (*A*). The protractor arm of the mandibular bristle (*lvr*) thus functions as a lever, and its relations to the mandibular plate and the base of the bristle are very similar to those of the maxillary lever (B, *lvr*) to the maxillary plate and the base of the maxillary bristle. The mandibular lever is differentiated from the mandibular plate during the transformation from the nymph to the imago.

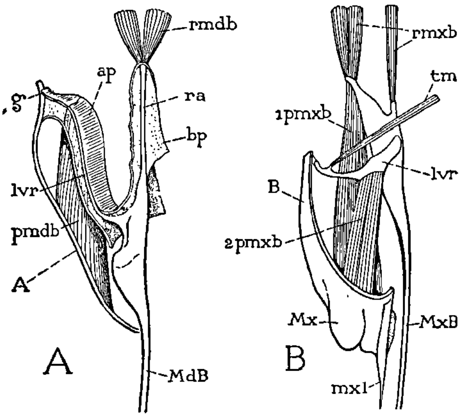

FIG. 181.—Motor mechanism of the mandibular and maxillary bristles of *Magicicada septendecim*. A, base of a mandibular bristle with retractor (*rmdb*) and protractor (*pmdb*) muscles. B, base of left maxillary bristle, posterior view, with retractor and protractor muscles.

The maxillary bristles arise from the walls of the bristle pouches at a higher level than do the mandibular bristles. Upon the base of each (Fig. 181 B, *MxB*) are inserted the retractor muscles (*rmxb*), which arise on the dorsal walls of the head, and also a large protractor muscle (1*pmxb*) having its origin ventrally on the inner face of the maxillary plate (*B*). In addition to these muscles there is a second set of protractor fibers (2*pmxb*) arising on the maxillary plate and inserted on the leverlike sclerite (*lvr*) that lies in the wall of the bristle pouch and connects the base of the bristle with the posterior edge of the maxillary plate.

The two sets of bristles extend out of the bristle pouches along the sides of the hypopharynx, where the maxillary bristles slide upon tracklike ridges of the lateral hypopharyngeal plates. Beyond the tip of the hypopharynx the bristles turn downward to enter the groove of the labium and those from opposite sides converge, the maxillary bristles becoming here interlocked, while the mandibular bristles take their positions at the sides of the maxillary bristles. In the groove of the labium the four bristles are thus assembled in a slender fascicle. The maxillary bristles form the core of the fascicle (Fig. 182, *MxB*) with their inner faces closely applied to each other and usually held firmly together by dovetailing grooves and ridges extending throughout their lengths (C). In some species of Hemiptera the mandibular bristles are similarly locked to the maxillary bristles (C). Between the maxillary bristles there are two minute tubular canals formed by opposing grooves on the inner surfaces of the bristles (B, C, *fc*, *sc*). The position of these canals is such that, where the bristles diverge to enter the bristle pouches, the anterior canal (Fig. 179 B, *fc*) opens into the mouth channel (*fm*), and the posterior canal (*sc*) receives the tip of the hypopharynx, on which is located the aperture of the salivary meatus (*sm*). The anterior canal is, therefore, the food canal (*fc*), and the posterior one the salivary canal (*sc*). In the distal part of the labium the bristle fascicle may become twisted, with a consequent change in the relative positions of the canals.

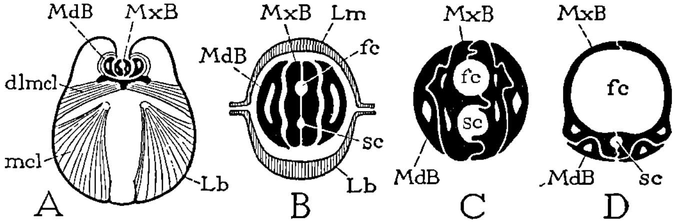

FIG. 182.—Sections of the beak and feeding bristles of Hemiptera. A, *Magicicada septendecim*, labium and bristles. B, *Aphis rumicis*, labrum, labium, and bristles. (*From Davidson*, 1925.) C, *Anasa tristis*, bristle fascicle. (*From D. G. Tower*, 1914.) D, *Cimex lectularius*, bristle fascicle. (*From Kemper*, 1932.)

The Labium.—The labium of the Hemiptera, when well developed, is a long, slender, rigid organ divided into three or four parts, or "segments" (Fig. 179, *Lb*). Its anterior surface is deeply concave to form the channel of the beak containing the mandibular and maxillary bristles (Fig. 182 A, *Lb*). The morphology of the hemipterous labium is not understood. The cranial muscles that move it are inserted on the first or second segment, and it would seem, therefore, that the principal part of the labium of the Hemiptera consists of the prelabium alone, the postlabium being represented by a basal segment or by the ample membranous area at the base of the organ. The cranial muscles act as either retractors or protractors according to whether they are inserted directly on the labial base or on an apodemal arm of the latter. The interior of the labium contains an elaborate musculature, which has been fully described in *Aphis fabae* by Weber (1928*a*) and in *Cimex* by Kemper (1932).

The Piercing Mechanism.—In most of the Hemiptera, and probably in all members of the order, as has been shown by Weber (1928, 1930), the mouth bristles are not moved by simultaneous contractions of their muscles. The mandibular bristles are the chief piercing organs. When the insect begins an insertion of its bristle bundle (Fig. 183, 1), one mandibular bristle is thrust out a short distance in advance of the other to puncture the food tissue (2), and then the opposite mandibular bristle is protracted until its tip meets that of the first (3). Now the two maxillary bristles are lowered together until their tips lie between those of the two mandibular bristles (4). At a single thrust a bristle is extruded no farther than the maximum distance the short protractor muscle can drive it with one contraction. This distance at best is insignificant compared with the depth to which the bristle bundle can finally be sunken into the food tissue. Repeated thrusts, therefore, are necessary (5 to 8). But a repetition of the insertion process necessitates that the protracted bristles be in some way secured in the new position in order to resist the backward pull of the retractor muscles that restores the protractors to their functional lengths. In some cases the bristles are anchored in the food tissue by barbs on their tips; in others they are held in a clasp of the enclosing labium.

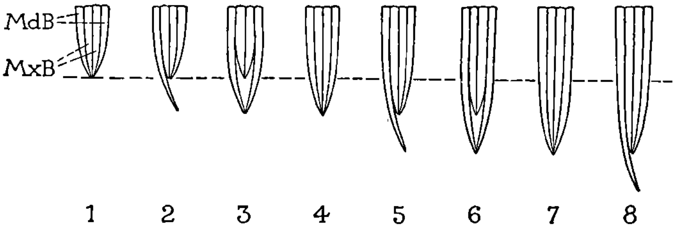

Fig. 183.—Successive stages in the insertion of the feeding bristles of Hemiptera. (*Diagrams based on figures from Weber*, 1928.)

When the mouth bristles are not in use they do not normally protrude from the tip of the labium. With most species, moreover, the bristles are not long enough to be projected from the labium except for the very short thrust given them by the protractor muscles, and in such cases the exposure and insertion of the distal part of the bristle fascicle are made possible by a retraction or folding of the labium that does not involve the bristles.

In homopterous forms having mouth bristles of usual length, the labium is suspended from a membranous area of the head and is often flexible at its base (Fig. 184 C). The exposure of the bristles in such species is brought about by a retraction of the labium or by a backward folding of its basal segments, allowing the head to be lowered as the bristles penetrate the food tissue (D). In some species of aphids an individual in the act of inserting its bristles stands high on its front legs and plants the beak vertically against the leaf (Fig. 185); as the bristles sink into the leaf tissue, the body is lowered anteriorly and the basal part of the labium bends back like the elbow of an arm, while the terminal part retains its grasp on the bristles; finally, when the bristles are in at full length, the insect stands almost on its head. In the adults of Aleurodidae, according to Weber (1928), the labium is equipped with protractor muscles; this provision allows these insects to make a quick departure from a feeding puncture, but the aphids, which have no protractor mechanism for the labium, often have much difficulty in extracting the mouth bristles.

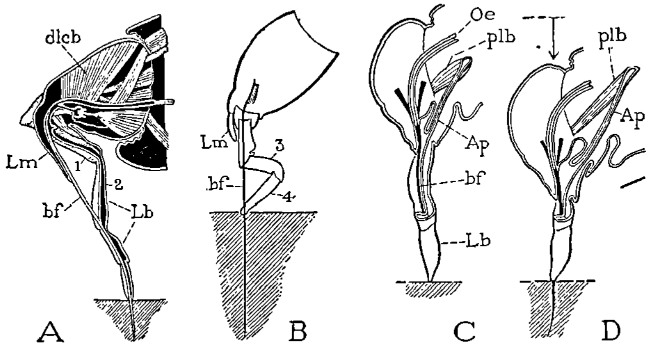

FIG. 184.—Various positions of the hemipterous labium during feeding. A, *Graphosoma italicum.* (*From Weber,* 1930.) B, *Cimex.* (*From Kemper,* 1932.) C, D, *Trialeurodes,* before and after insertion of the bristles. (*Adapted from Weber,* 1928.)

With many of the Heteroptera the long rigid labium is firmly articulated to the head somewhat behind the exit of the bristles from the latter, and in such species it is probable, as shown by Weber (1928), that a preliminary exposure of the tips of the bristles is effected merely by the forward swing of the beak from its horizontal position of repose. The further exposure and the insertion of the bristles are usually accompanied by an elbowlike bend of the labium between the first and second segments (Fig. 184 A), while the base of the bristle fascicle (*bf*) is held in the groove of the labrum (*Lm*). In the bed bug, however, according to Kemper (1932), the labium bends between the third and fourth segments (B) and is further shortened by an invagination of its base into the head, and to a smaller degree by a telescoping of its segments.

It is evident, now, that such simple devices as those just described for the exsertion of the mouth bristles can give effective service only to larger species or to species that obtain their food but a short distance below the surface of the food tissue. Very small sucking insects or those that draw their food from relatively greater depths must have proportionately long mouth bristles. Such species, therefore, are confronted with the problem of storage for bristles often of greater length than the body, and with that of exserting the bristles far beyond the tip of the labium.

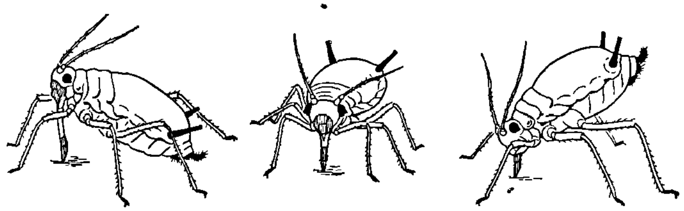

Fig. 185.—Attitudes of an aphis during feeding.

Hemiptera with bristles much longer than the labium include the larvae of Psyllidae and Aleurodidae, larvae and adult females of Coccidae, the Coptosmatidae, and the Aradidae. The problem of bristle storage has been solved by these insects in different ways. With the larval psyllids the bristle fascicle when retracted is projected forward from the base of the labium in a large free loop beneath the head (Fig. 186 A). In the Coccidae and the larvae of Aleurodidae the retracted fascicle is received into a long internal pouch, the *crumena,* extending

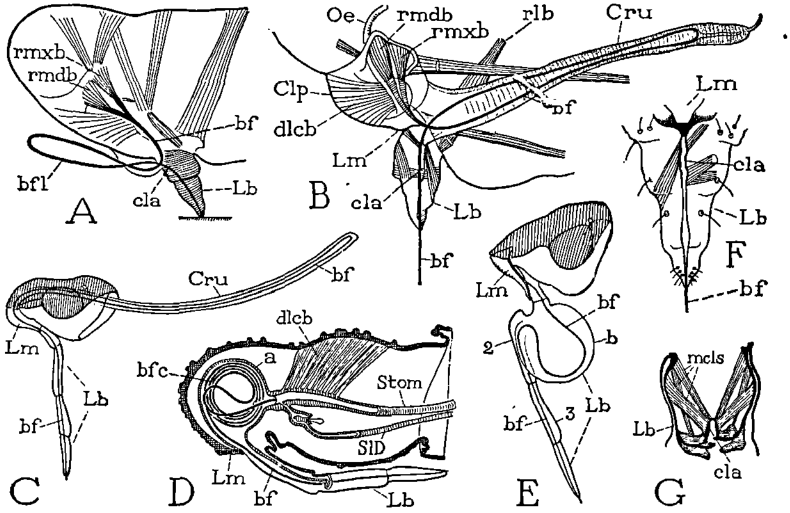

Fig. 186.—Structural details and various devices for the storage of the mouth bristles of long-bristled Hemiptera. A, *Psylla mali* larva, bristles looped outside of head. B, *Pseudococcus* adult female, bristles in crumena. C, *Tropidotylus fasciolatus,* bristles in crumena. D, *Aradus,* bristles coiled in preoral cavity. E, *Bozius respersus,* bristles looped in base of labium. F, *Pseudococcus,* labium and bristle clamp. G, *Psylla mali,* bristle clamp of labium. (A, B, F, G *from Weber,* 1928; D *from Weber,* 1930; C, E *from China,* 1931.)

backward from above the base of the labium into the thorax (B, *Cru*). In some members of the heteropterous family Coptosomatidae (Plataspididae), as shown by China (1931), the retracted bristle fascicle is looped posteriorly in a large membranous diverticulum at the base of the second labial segment (Fig. 186 E), while in others (C) the fascicle is received into a long crumenal sac (*Cru*) resembling that of the Coccidae, extending from the head into the base of the abdomen. The coptosomatids are mostly fungus feeders, and the length of the mouth bristles, as suggested by China, is probably an adaptation for probing lengthwise through the mycelial filaments. In the Aradidae, finally, which are also fungus feeders, the retracted bristle fascicle is coiled in a large chamber of the preoral cavity anterior to the mouth of the sucking pump (Fig. 186 D).

The means by which the long-bristled Hemiptera, particularly the minute Coccidae, are able to protrude their threadlike mouth bristles from the head and to insert them into woody tissues was for a long time an outstanding entomological mystery. Some writers attempted to explain the exsertion of the bristles as brought about by a muscular contraction of the crumena, and others postulated blood pressure against the sac as the active force, but these theories could not apply to larval Psyllidae with the bristles looped outside the head, nor would they in any case account for the retraction of the bristles. A consistent and convincing explanation of the mechanism of protraction and retraction of the mouth bristles in these species, however, has recently been given by Weber (1928, 1930, 1933), and the following descriptions are based on his observations.

Three anatomical facts explain the principle by which the mechanism of exsertion and retraction accomplishes its results. First, the protractor and retractor muscles are able to move the bristles but a very short distance with each contraction; second, the four bristles are firmly interlocked in the fascicle but slide freely upon one another; third, there is some provision for holding the bristles in place, after each protraction or retraction, that prevents the antagonistic muscle from undoing the work of the other. The holding apparatus in the Psyllidae, Aleurodidae, and Coccidae is a clamp in the labium, consisting of a narrowed and strongly sclerotized area in the labial groove with muscles to regulate its pressure on the bristle fascicle (Fig. 186, F, G). In other families the same effect is accomplished by barbs on the ends of the bristles.

The musculature of the mouth bristles is mechanically the same in all cases, and the alternating thrusts and pulls are exerted on the several bristles of the fascicle in the manner already described for the Hemiptera in general (Fig. 183). The only difference in the long-bristled forms is that the retracted fascicle is thrown into a loop or coil somewhere between its base and its extremity (Fig. 187). The loop, however, makes no difference in the movement of the bristles, because the latter are securely held together by interlocking grooves and ridges and slide freely on one another. The successive contractions of the protractor muscles have no effect on the loop (1 to 4), the bristles being moved alike at both ends. But, after each thrust, when the fascicle is held in place by the labial clamp, the simultaneous contraction of the retractor muscles takes up a little of the slack in the loop (5). Hence the bristles penetrate deeper and deeper with the succeeding outward thrusts, while the series of pulls on their bases is expended against the loop, with the result that the latter is gradually shortened, until it is obliterated when the bristles are exserted at full length (6). The looping of the fascicle during retraction of the bristles requires only a reverse action of the labial clamp.

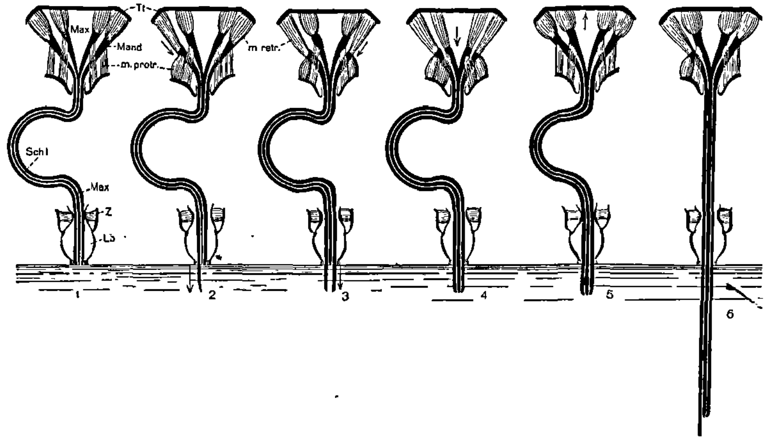

Fig. 187.—The mechanism of insertion of the feeding bristles by Hemiptera having long bristles stored in a loop or coil when retracted. (*From Weber*, 1933.) 1, beak placed against the plant surface. 2, 3, 4, first insertion of the mandibular and maxillary bristles, as in Fig. 183, by contraction of the protractor muscles. 5, fascicle of bristles held in labial clamp while loop shortened by contraction of the retractor muscles. 6, bristles inserted full length after successive repetitions of movements 2 to 5.

It still seems almost beyond belief that the delicate bristles of such small insects as Coccidae can penetrate the bark of trees; but since it is an observable fact that they do so, the feat evidently is not impossible. It is known, however, that the salivary secretion of some Hemiptera has a solvent effect upon plant tissues and thus facilitates the insertion of the bristles. The salivary canal of the beak, it should be recalled, accompanies the food channel throughout the length of the bristle fascicle.

10. THE FEEDING MECHANISM OF ANOPLURA

The feeding equipment of the true lice is a highly specialized piercing and sucking mechanism. The morphology of the piercing organs is not definitely known, and observations on the structure of the mouth parts given by various investigators do not agree in all respects, though details have been minutely described and figured. Our present information on the mouth parts of the Anoplura is contained in the work of Cholodkowsky (1904), Enderlein (1905, 1905*a*), Pavlowsky (1906), Harrison (1914), Sikora (1916), Peacock (1918), Florence (1921), Vogel (1921*a*), and Fernando (1933), while summarized accounts are given by Metcalf and Flint (1928), Patten and Evans (1929), and Imms (1934), though with variations in detail according to the source selected.

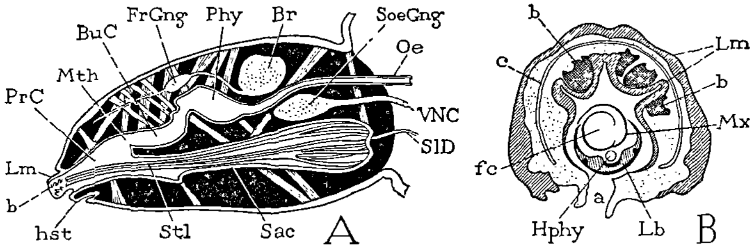

FIG. 188.—The piercing and sucking apparatus of Anoplura. A, section of the head showing buccal and pharyngeal pumps (*BuC*, *Phy*), and suboral sac (*Sac*) containing the piercing stylets (*Stl*). (*Diagram composed from Sikora,* 1916, *and others.*) B, section of the labrum and piercing stylets of *Pediculus vestimenti.* (*From Vogel,* 1921*a*.)

The essential structure of the piercing and sucking apparatus of *Pediculus* appears to be as follows. The elongate head terminates anteriorly in a small, protractile, snoutlike tube, known as the *mouth cone, rostrum, proboscis,* or *prestomum.* The organ appears to be the labrum (Fig. 188, A, *Lm*). It has a terminal aperture continued into a median ventral cleft, and its inner walls are armed with small recurved teeth (*b*), which, when everted, enable the parasite to obtain a hold on the skin of its host. Other members of the mouth parts are not ordinarily visible externally. The ventral channel of the labrum leads into a tubular preoral cavity, the "buccal funnel" (*PrC*), in the anterior part of the head. The head capsule is closed below by a long hypostomal wall, the distal extremity of which forms the lower lip (*hst*) of the preoral cavity. From the posterior end of the preoral cavity the mouth (*Mth*) opens dorsally into a two-chambered sucking pump (*BuC, Phy*), which terminates in a slender oesophageal tube (*Oe*). Ventrally the preoral cavity is extended below the mouth in a long sac (*Sac*) containing a group of slender piercing organs (*Stl*). The first chamber of the sucking pump (*BuC*) is perhaps the buccal cavity, since it lies anterior to the frontal ganglion (*FrGng*); the second (*Phy*) is without doubt the true pharynx; both evidently belong to the stomodaeum since their walls have a sheath of circular muscle fibers. A more careful study of the relations of the dilator muscles to the head wall and to the frontal ganglion connectives may be expected to give more conclusive evidence as to the identities of the several parts of the food passage.

The piercing organs of the louse (Fig. 188 A, *Stl*), according to Vogel (1921*a*), consist of three superposed stylets (B, *Mx, Hphy, Lb*). The stylets arise posteriorly from the walls of the containing sac (A), and, in the retracted condition, their distal ends extend to the base of the labrum in the preoral cavity, where they are ensheathed in folds of the walls of the cavity. The most dorsal stylet appears to be formed of two united appendages (B, *Mx*), the distal parts of which have their free edges rolled upward to form a tubular channel (*fc*), which is the food canal serving to conduct the ingested blood from its source to the mouth. The intermediate stylet (*Hphy*) is a slender rod traversed by the salivary duct (A, *SlD*), which opens on its extremity. The ventral stylet (B, *Lb*) is a broader appendage with distinct dorsal and ventral walls (which have been mistaken for separate pieces). The dorsal wall is deeply grooved by a channel containing the median stylet. Distally the ventral stylet ends in three sharp-pointed, serrate lobes, which are the piercing organs of the louse. The proximal ends of the dorsal and ventral stylets give off long apodemal arms (A), one pair from the former, a dorsal and a ventral pair from the latter, which are imbedded in folds of the wall of the sac and give insertion to protractor muscles arising anteriorly on the sac walls. Other muscles, arising on the head and inserted on the sac, serve for the retraction of the sac and the stylets.

The stylets have been generally assumed to represent in some way the mouth parts of the louse. Investigators are agreed that the mandibles are absent in adult Anoplura or are reduced to a pair of small plates lying at the sides of the preoral cavity. The mandibulate elephant louse (*Haematomyzus*), as shown by Ferris (1931), has none of the special features of the sucking lice and is perhaps to be classed with the Mallophaga. Cholodkowsky (1904) claimed that both the mandibles and the maxillae of the Anoplura disappear during embryonic development, and that the piercing organs are secondary structures concealed by the labium. Enderlein and Vogel, however, from anatomical studies of the adult insect, have contended that the dorsal stylet (Fig. 188 B, *Mx*) represents the united maxillae, that the intermediate stylet (*Hphy*), traversed by the salivary duct, is the hypopharynx, and that the ventral stylet (*Lb*) is the labium. This interpretation appears to be confirmed by the more recent study of Fernando (1933) on the embryonic development of the mouth parts of *Pediculus humanus*.

According to Fernando, the usual gnathal appendages appear on the head of the embryo of *Pediculus*, there being present at an early embryonic stage paired rudiments of mandibles, maxillae, and the labium. The mandibles undergo no development and finally disappear. The maxillary and labial rudiments, however, elongate and those of each pair unite, forming thus two median organs which become the dorsal stylet and the ventral stylet. The stomodaeum is formed in the usual manner as a median invagination between the antennae and the mandibles, and the labrum appears anterior to the mouth. The stylets are now withdrawn into an invagination of the ventral wall of the head behind the mouth, and the lips of the pouch grow out to form the enclosing sac. The intermediate stylet is then formed by an outgrowth between the bases of the maxillary and labial stylets involving the terminal part of the salivary duct and evidently represents the hypopharynx. The labrum becomes the conical snoutlike rostrum embracing the tips of the retracted stylets.

CHAPTER XIII

THE ALIMENTARY CANAL

The organs of alimentation in metazoic animals have to do with the intake of raw food materials, the digestion and absorption of nutrient substances from these materials, the ejection of the unused residue, and the distribution within the body cavity of the absorbed products of digestion to the cellular tissues where they are utilized in the processes of growth and metabolism. The organs of ingestion, digestion, absorption, and egestion are the parts of the alimentary canal and the digestive glands that pour their secretions into it. The medium of distribution is the blood.

Feeding is primarily a matter of getting nutrient materials from the environment through the integument of the organism; assimilation is the utilization of the absorbed materials by the cells of the body tissues. Most metazoic animals in their feeding habits differ fundamentally from such protozoans as the amoeba in that they do not take solid particles of food matter through the body wall; the requisite nutrient substances are dissolved in liquids thrown off from a part of the body and are then absorbed into the latter. The primitive stomach, or archenteron of the gastrula, is simply a food pocket invaginated on one side of the body, the wall of which is formed of specialized digestive cells. The more complex alimentary canal of the higher animals, therefore, must be regarded as merely a more efficient device for holding food materials in proximity to a digestive and absorptive surface, to which have been added special mechanisms for ingestion and egestion. The lumen of the food tract is a part of the environment enclosed within the animal.

1. DEVELOPMENT OF THE ALIMENTARY CANAL

The embryonic development of the alimentary canal, described in Chap. II, gives us a misleading concept of the true nature of the digestive tract of arthropods, especially of insects, for we are induced to think of it as consisting of an endodermal stomach formed entirely within the body, which only secondarily acquires openings to the exterior through an ectodermal stomodaeum and an ectodermal proctodaeum. The ontogenetic development of the digestive tube, however, is clearly an embryonic adaptation to the conditions of life in the egg and is not to be taken as a literal repetition of phylogenetic history. The mesenteron is the primary stomach and there is little probability that it was ever a closed sac in any of the adult ancestors of the arthropods; the stomodaeum and proctodaeum are later ingrowths of the ectoderm at the primitive oral and anal apertures of the mesenteron. The stomodaeal and proctodaeal openings into the stomach, therefore, in a sense, are the true mouth and anus of the arthropod, which have been carried internally by an inward growth of the circumoral and circumanal parts of the ectoderm. According to Henson (1931), the innermost cells of the stomodaeum and proctodaeum in lepidopterous larvae form *interstitial rings* of ectodermal cells that retain the power of mitotic division and at the time of metamorphosis regenerate the epithelium of the stomodaeum and the proctodaeum. During the larval period these parts of the alimentary canal grow by enlargement of the epithelium cells but not by cell multiplication. Though the stomodaeum and proctodaeum are primarily organs of ingestion and egestion, they have come to serve also in various other capacities accessory to the function of the stomach.

The cells of the mesenteron maintain their early acquired activities that particularly adapted them to the functions of digestion and absorption. They are continually subject to disintegrating processes, and some of them, at least, retain the power of mitotic division to replace those depleted by digestive activities, or to regenerate the entire epithelium at the time of metamorphosis or even at the larval moults.

2. GENERAL STRUCTURE OF THE ALIMENTARY CANAL

Since the digestive tract is but an infolded part of the body wall, its own walls have the same essential structure as that of the body integument. They consist of a layer of cells, the *enteric epithelium,* resting upon a *basement membrane* turned toward the somatic cavity and lined internally by a cuticular *intima.* The intima is best developed in the stomodaeum and proctodaeum; in the mesenteron, if present at all, it has a very delicate texture and is often disrupted by the activities of the epithelial cells. All parts of the alimentary canal are usually invested in a muscular sheath, or *muscularis,* derived principally from the splanchnic layer of the mesoderm. Other muscles, probably of somatopleure origin, extend from the body wall to the alimentary canal. These extrinsic muscles are known as the *suspensory* or *dilator muscles,* the second term probably better expressing their function.

In form the alimentary canal of insects is a tube, either straight, or variously looped upon itself if its length exceeds that of the body. In its simplest development the tube shows little differentiation beyond the primary division into *stomodaeum* (Fig. 189, *Stom*), *mesenteron* (*Ment*), and *proctodaeum* (*Proc*). The functional stomach, or *ventriculus,* is the mesenteron. Usually a circular valve-like fold separates the cavities of adjoining sections, that between the stomodaeum and mesenteron being known as the *stomodaeal*, or *cardiac, valve* (*SVlv*), the one closing the entrance to the proctodaeum as the *proctodaeal*, or *pyloric, valve* (*PVlv*).

Few insects, however, have an alimentary canal so simple as that just described. Generally each of the primary sections of the tube, particularly the first and the third, are differentiated into several more or less distinct regions, and diverticula of various forms grow out from the walls (Fig. 190). The principal outgrowths of the alimentary canal are the Malpighian tubules (*Mal*), which are attached to the anterior end of the proctodaeum, but various diverticula occur also on the mesenteron, and glands may open into the stomodaeum. The alimentary canal in all its parts is subject to many variations of form in different insects. Some of its principal types of structure are shown in Figs. 195, 196, 198, 199. During metamorphosis the entire digestive tract often undergoes much reconstructive alteration both in external form and in its histological structure, as is well illustrated in the Lepidoptera (Fig. 197), the changes being adaptive to the different feeding habits of the young and the adult of the same species.

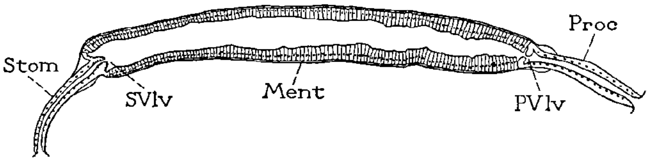

FIG. 189.—The alimentary canal of a collembolan, *Tomocerus niger*, showing in simple form the primary components of the food tract without secondary specializations. (*From Folsom and Welles*, 1906.) *Ment*, mesenteron; *Proc*, proctodaeum; *PVlv*, proctodaeal, or pyloric, valve; *Stom*, stomodaeum; *SVlv*, stomodaeal, or cardiac, valve.

3. THE STOMODAEUM

In its simplest condition the stomodaeum is little more than an inlet to the stomach or a short conduit to the latter from the mouth (Fig. 189, *Stom*). In most insects, however, the stomodaeum is a long tube of which the middle part is enlarged to form a storage chamber for reserve supplies of food; and this function assumed by the middle region was evidently the precursor of a specialization of the fore part of the tube into an organ of ingestion, and of the posterior part into a "stomach mouth" for regulating the passage of food into the ventriculus, or even in some cases for giving it a second chewing. Thus the stomodaeum, or primitive oesophagus, has become differentiated into three primary regions, namely, the *pharynx* (Fig. 190, *Phy*), the *crop* (*Cr*), and the *proventriculus* (*Pvent*). An undifferentiated part of the tube may remain as a definite *oesophagus* (*Oe*) between the pharynx and the crop, and, as we saw in the last chapter, the initial region just within the mouth is often distinguishable from the pharynx as a *buccal cavity* (*BuC*).

The primary functions of the stomodaeum thus appear to be mechanical; but there is little doubt that the organ in insects has secondarily come to be also a physiological adjunct to the stomach by increasing the space available for digestive purposes, since the food stored in the crop is subject to the action both of the salivary liquid mixed with the food during ingestion and of gastric juices that flow forward into the crop from the ventriculus.

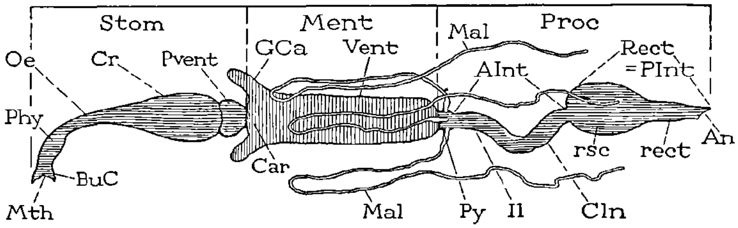

FIG. 190.—Diagram showing the usual subdivisions and outgrowths of the alimentary canal. *AInt*, anterior intestine; *An*, anus; *BuC*, buccal cavity; *Car*, cardia; *Cln*, colon; *Cr*, crop; *GCa*, gastric caecum; *Il*, ileum; *Mal*, Malpighian tubules; *Ment*, mesenteron (ventriculus); *Mth*, mouth; *Oe*, oesophagus; *Phy*, pharynx; *PInt*, posterior intestine (rectum); *Proc*, proctodaeum; *Pvent*, proventriculus; *Py*, pylorus; *Rect*, rectum (*rect*, rectum proper; *rsc*, rectal sac); *Stom*, stomodaeum; *Vent*, ventriculus.

Histology of the Stomodaeum.—The walls of the stomodaeum in general have a simple structure. The epithelium (Fig. 191 A, *Epth*) is usually flat, and the cell boundaries often indistinct. The intima (*In*) is relatively thick; its surface for the most part is sparsely covered with short hairs or spicules, though in the pharynx and the proventriculus there may be areas closely beset with long hairs or spines. In the proventriculus of some insects the intima is dense and produced into

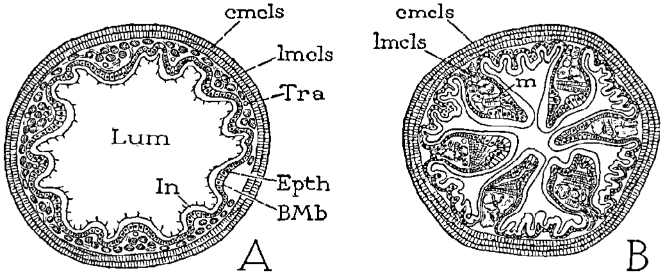

FIG. 191.—Sections of the stomodaeum of a grasshopper, *Dissosteira carolina*. A, the crop. B, the proventriculus. *BMb*, basement membrane; *cmcls*, circular muscles; *Epth*, epithelium; *In*, intima; *lmcls*, longitudinal muscles; *Lum*, lumen; *m*, muscles in folds; *Tra*, trachea.

lobes and teeth forming a special armature (Fig. 194). Both the epithelium and the intima are thrown into longitudinal folds which in most parts of the stomodaeum allow for expansion of the lumen as the latter becomes filled with food; but a certain number of the lobes are often definite structures, as shown by the increased thickness of the intima covering them and of the underlying epithelial cells (Fig. 191 B). These definite folds usually occur in multiples of two or three, there being commonly four, six, or eight major folds, with the same or a greater number of minor intermediate folds between them. The major folds are particularly developed in the pharyngeal and proventricular regions.

The muscular sheath is a very important part of the stomodaeum. It consists in general of an outer layer of circular fibers (Fig. 191 A, *cmcls*) and of an inner layer of longitudinal fibers (*lmcls*); but a detailed study of the stomodaeal muscularis shows that its fibers do not necessarily adhere strictly to the typical arrangement in all parts of the stomodaeum. The circular fibers generally run continuously around the tube without attachments to the latter. The longitudinal muscles, on the other hand, are sometimes inserted on the intima in the same manner as the somatic muscles are attached to the body wall, but in other cases they too appear to have no connections with the intima or the epithelium and arise as confluent branches of the circular muscles. The last condition is well shown in the crop of a caterpillar (Fig. 166, *Cr*) where the muscularis forms a veritable plexus of branching and uniting fibers constituting a sheath about the inner walls of the tube, but having no intimate connections with the latter. Where the folding of the stomodaeal walls is pronounced, the longitudinal muscles tend to become grouped in the spaces of the folds (Fig. 191 B).

The stomodaeum is generally well provided with dilator muscles (Figs. 166, 193). These muscles take their origins on the walls and apodemes of the head and on the walls of one or more of the thoracic segments. Their central ends usually penetrate between the fibers of the muscularis to be inserted either on the stomodaeal epithelium or on the intima, but in certain cases some of their fibers appear to unite with those of the muscularis.

The Buccal Cavity.—The true buccal cavity of the insect is the oral part of the stomodaeum (Figs. 155, 190, 192, 193, *BuC*) and should not be confused with the preoral cavity (Fig. 155, *PrC*), or external space enclosed between the mouth parts, which is often incorrectly called the "mouth cavity." As shown in the last chapter, the buccal cavity usually is not structurally differentiated from the pharynx (Fig. 192), but it may be defined as the initial part of the stomodaeum on which are inserted the second group of dilator muscles taking their origins on the clypeus, or the clypeal area of the head, and having their insertions anterior to the frontal ganglion and its connectives (Figs. 155, *dlbc*, 193, *34*).

The Pharynx.—The pharyngeal part of the stomodaeum follows the buccal cavity (Fig. 190, *Phy*), and, if not structurally differentiated from the latter, it is to be identified as that part of the stomodaeum whose dorsal dilator muscles take their origin on the frontal and dorsal areas of the head wall and are inserted posterior to the frontal ganglion and its connectives (Fig. 155, *Phy*). The pharynx typically lies before the nerve connectives between the brain and the suboesophageal ganglion, but in some insects there is a second pharyngeal chamber of the stomodaeum behind the connectives, the two parts being differentiated either by the contour of the stomodaeal tube or by their musculature or internal structure (Fig. 192). The precerebral and postcerebral pharyngeal regions are distinguished as the *anterior pharynx* (Figs. 192, 193, *APhy*) and *posterior pharynx* (*PPhy*), respectively. When there is no posterior pharyngeal development the postcerebral region of the stomodaeum becomes a part of the oesophagus. In general the distribution of the dilator muscles serves better to identify corresponding morphological parts of the cephalic stomodaeum than does the structure of the parts themselves. The principal modifications of the pharynx and its musculature have been sufficiently noted in connection with the feeding mechanism described in the last chapter.

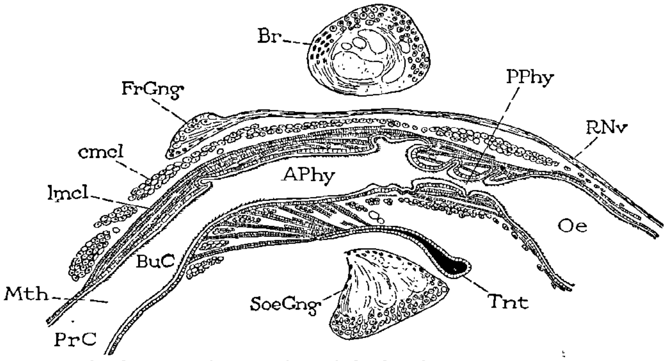

Fig. 192.—Longitudinal vertical section of the head part of the stomodaeum of a cockroach, *Blatta orientalis*, showing precerebral anterior pharynx (*APhy*) and postcerebral posterior pharynx (*PPhy*). (*From Eidmann*, 1924, *but relettered.*)

The Oesophagus.—The oesophagus has no definite morphological status; it is merely the narrow part of the stomodaeum following the pharynx that is not differentiated for purposes other than that of food conduction. Typically the oesophagus is a slender tube and may extend direct to the stomach, but more generally it is limited posteriorly by a proventricular or ingluvial section of the stomodaeum (Figs. 190, 198, 199, *Oe*). When the ingluvies, or crop, is a simple dilatation of the stomodaeal tube the oesophagus usually widens gradually into the crop (Fig. 190), and the latter may extend so far forward as practically to exclude the oesophagus (Figs. 193, 195).

The Crop, or Ingluvies.—The crop is ordinarily but an enlargement of the posterior part of the oesophagus (Figs. 190, 195, *Cr*). In some insects, however, it is a lateral diverticulum of the oesophagus having the form either of a simple sac (Fig. 197 B, C, *Cr*) or, as in some Diptera (Fig. 198), of a long, slender tube with a bladderlike swelling at the end (*Cr*). The intima of the crop is usually thick, the epithelium flat, and the walls of the entire organ, when not stretched by the food content, are thrown into numerous lengthwise folds and transverse wrinkles that allow of distention.

That the primary function of the crop is one of storage is amply attested by its size and structure. Most insects feed rapidly when food is available in abundance and accomplish more leisurely the digestive processes. Sanford (1918) found that cockroaches fed to repletion on a diet of oil and sugar could go for nearly two months before the crop content was exhausted. It seems equally clear, however, not merely that the crop is an antechamber of the ventriculus, or waiting room where the food is held in anticipation of its admission to the stomach, but that it is in itself the seat of a certain amount of food digestion, since it receives digestive liquids both from the salivary glands and from the ventriculus. Analyses have shown the presence of numerous digestive enzymes in the stomodaeum of various insects, but all enzymes reported from the stomodaeum occur also in the salivary glands or the ventriculus or in both, and it is probable that these organs are the sources of the enzymes discovered in the crop. A few writers have believed, however, that certain enzymes may be formed in the stomodaeal epithelium itself. Sanford (1918), for example, claimed that the fat-splitting enzyme lipase is a product of the crop walls in the cockroach, and Swingle (1925) thought it likely that maltase and invertase as well as lipase occurring in the crop must be produced there. On the other hand, both Abbott (1926) and Wigglesworth (1928) assert that lipase cannot be demonstrated in the crop walls of the cockroach, and Abbott says the presence of lipase in the crop is the result of regurgitation from the stomach. The production of enzymes in the stomodaeum of any insect has, therefore, not yet been established.

The question as to whether absorption takes place through the walls of the stomodaeum is one also that cannot be regarded as settled. Petrunkevitch (1900) and Sanford (1918) have contended not only that absorption takes place in the crop, but that in the cockroach the crop is the chief seat of absorption. This claim they base on histological studies of the crop epithelium of oil-fed roaches, the cells of which are found to be full of oil globules. Schlüter (1912), however, came to quite opposite conclusions from the same methods of study carried out on various orthopteroid species as well as on odonate larvae and on beetles. He asserts definitely that absorption does not take place in the crop, and that if fat appears in the ingluvial cells it gets there in some other way than by direct absorption from the crop lumen. Abbott (1926), again, agrees with Petrunkevitch and Sanford that the crop of the roach is an important organ for the absorption of fat, but he says that water and water-soluble substances are not absorbed in it.

The thickness of the stomodaeal intima would appear to be an effective barrier to more than a minimum of absorption taking place in any part of the stomodaeum, and the experiments of Eidmann (1922) on the relative permeability of the intima of the crop and intestine in *Blatta orientalis* give little support to the idea of absorption in the former. Eidmann found that both alkaline and acid substances diffuse very slowly, only in the course of hours, through the intima of the crop, which has a thickness of 5 to 8 microns, though they penetrate the relatively thin intima of the intestine in 10 or 15 minutes. In other Orthoptera the crop intima is often much thicker than that of the cockroach, and, in general, it would appear that, as Schlüter remarks, "an organ could scarcely be made less fitted for absorption."

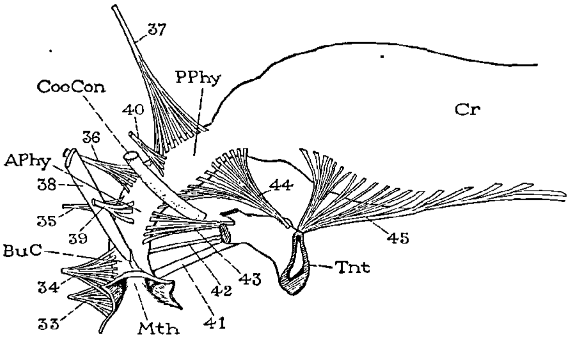

FIG. 193.—The cephalic dilator muscles of the stomodaeum of a grasshopper, *Dissosteira carolina.*

In the Diptera the bladderlike crop (Fig. 198, *Cr*) usually contains a clear liquid. That of *Tabanus*, according to Cragg (1920), does not serve as a food reservoir; its contents are apparently derived from the mesenteron and then again returned to the latter, a process that insures a thorough mixing of the gastric secretion with the ingested blood.

The Proventriculus.—This, the terminal region of the stomodaeum, is often structurally the most highly specialized part of the alimentary canal. In its simpler forms, however, as seen in the larvae of many insects and in some adults, it is merely the narrowed posterior end of the stomodaeum which is more or less invaginated into the anterior end of the mesenteron to form the cardiac valve (Fig. 189, *SVlv*).

In adult insects that feed on solid food the proventricular region usually becomes differentiated as a definite part of the alimentary tract between the crop and the ventriculus, and its inner walls develop a mechanism, often armed with strong cuticular plates or teeth (Fig. 194), that may serve several purposes. The armature of the proventriculus lies anterior to the funnel-shaped posterior part of the organ (*SVlv*) that enters the stomach, and for this reason it would appear to be a secondary addition to a more simple primitive structure; but since some modification of the mechanism at least is present in most of the chewing insects and also in the Hymenoptera, Eidmann (1924) suggests that the proventricular armature is a primitive equipment of the insect alimentary canal, which has been lost in most of the sucking orders.

The proventricular mechanism consists fundamentally of strong longitudinal folds of the walls of the organ projecting into the lumen. The folds are usually continuations of the less pronounced plications of the walls of the crop, and there are consequently four, six, or eight major proventricular folds and a varying number of minor intermediate ridges. A simple condition is found in the Acrididae, where the walls of the proventriculus are produced into six longitudinal elevations (Fig. 191 B), each deeply grooved anteriorly and tapering posteriorly to the margin of the short proventricular valve. The surfaces of the lobes are not strongly sclerotized in the grasshopper, and they are armed only with a few small marginal teeth and with areas of minute granulations on their distal halves. A layer of strong circular muscles runs continuously around the proventriculus (*cmcls*), but the longitudinal fibers are aggregated into six groups occupying the bases of the folds (*lmcls*). There appear to be also short inner transverse fibers in the crests of the folds (*m*) serving to compress the latter. By a contraction of the circular muscles the six major folds are evidently brought together and effectively block the entrance to the ventriculus. The channels between these folds, however, may permit the egress of ventricular liquids into the stomodaeum, and the brown liquid that grasshoppers sometimes eject from the mouth probably escapes from the stomach in this manner.

In the Blattidae (Fig. 194) the six major folds of the proventricular wall are densely sclerotized anteriorly forming an armature of six plates (*a*), each of which is produced centrally into a strong, sharp process with the point turned somewhat posteriorly. In the more tapering posterior half of the proventriculus behind the plates the folds are again thickened, forming here a circle of six soft, cushionlike lobes (*b*) covered with hairs or spines directed backward. The proventricular region is thus divided into a *proventriculus anterior* armed with the plates, and a *proventriculus posterior* containing the cushions. Beyond the cushions is the region of the stomodaeal valve (*SVlv*), which is a long, narrow tubular fold in the cockroach, on the inner walls of which the proventricular folds are continued as low ridges that taper gradually to the end of the valve. A more detailed account of the proventriculus of the cockroach is given by Sanford (1918) and by Eidmann (1925).

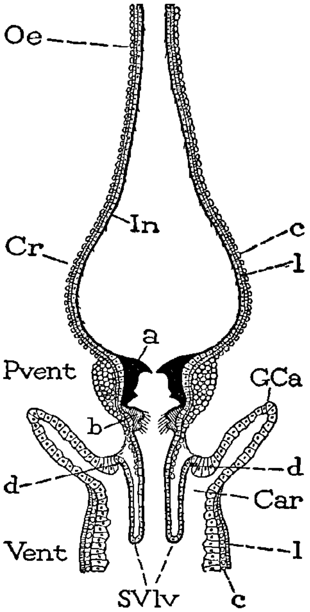

Fig. 194.—Section of the crop, proventriculus, stomodaeal valve, and cardiac end of the ventriculus of a cockroach, *Blatta orientalis*, diagrammatic. *a*, *b*, proventricular plates and pads; *c*, circular muscles; *d*, *d*, junction of proventriculus and ventriculus; *l*, longitudinal muscles.

The general structure of the proventriculus in the Gryllidae and Tettigoniidae is the same as the Blattidae, but the sclerotic plates are here longer and are broken up into series of transverse ridges ending in points that appear as six rows of overlapping teeth directed posteriorly. The proventriculus of *Gryllus* is described by DuPorte (1918), that of *Grylloblatta* by Sayce (1899), and that of *Stenopelmatus* by Davis (1927).

The sucking insects usually lack a proventriculus, other than the region of the cardiac valve, though the Siphonaptera are said to have a proventricular region armed with cuticular teeth. The flat, circular sac that intervenes between the oesophagus and the stomach in muscoid Diptera, which most writers refer to as the "proventriculus" (Fig. 198, *Car*), is the anterior part, or cardia, of the ventriculus (*Vent*), as will later be shown.

The function of the proventriculus unquestionably differs according to the structure of the organ and the nature of the food material in different insects. In its simpler forms, as we have seen, it acts merely as a sphincter between the crop and the stomach to regulate the passage of food material into the latter. With the development of folds and sclerotic armature on its inner walls, however, the organ acquires a more diversified function. In the first place, the folds projecting into the lumen serve to hold back the food in the crop without completely closing the ventricular entrance. Digestive liquids from the stomach may thus be permitted to flow *forward* into the crop through the channels between the folds and bring about a partial digestion of the crop food before the latter is transmitted to the stomach. This possible function of the proventriculus in Orthoptera and Coleoptera has been particularly stressed by Ramme (1913), who points out further that the movements of the proventricular lobes, brought about by the strong muscles surrounding the latter, must serve to mix the digestive fluids thoroughly into the food mass. Some insects accomplish an extraintestinal digestion of the food, supposedly by gastric juices ejected from the mouth.

The armature of the proventriculus often has the form of convergent lamellae, and this type of structure has suggested that the apparatus serves as a strainer to prevent larger pieces of hard indigestible matter in the food from entering the stomach, such material being later disposed of by regurgitation. The only definite evidence of normal regurgitation by insects, however, pertains to *Dytiscus*, which is said by Rungius (1911), Ramme (1913), Blunck (1916), and others to disgorge indigestible parts of the animals on which it feeds. According to Blunck, *Dytiscus* has no salivary glands, and digestion takes place in the crop by liquids from the stomach. The proventriculus, he says, grinds the food mass and pushes the larger fragments back into the crop, while at the same time it allows the liquefied residue to filter through into the stomach. A few hours after mealtime the beetle suddenly ejects several times from its mouth a turbid cloud of material, which, as it disperses in the water, is seen to contain undigested remnants of the food. Other insects, as far as observed, ordinarily pass all undigested refuse through the stomach and intestine. Sanford (1918) observed regurgitation by overfed cockroaches, but it is here evidently the result of too much feeding and not an example of a normal physiological process.

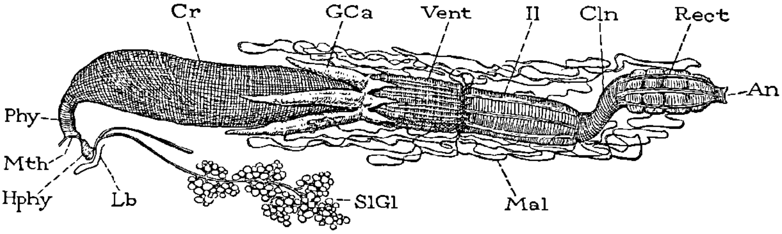

FIG. 195.—The alimentary canal, salivary glands, and Malpighian tubules of a grasshopper, *Dissosteira carolina*.

The movements of the stomodaeum of *Periplaneta fuliginosa* have been studied by Yeager (1931) who finds that peristalsis takes place in the crop in both a posterior and an anterior direction, and that the proventricular movements are contractile only. The activities of the proventriculus, he says, appear to be largely controlled by the first thoracic ganglion of the ventral nerve cord.

The earlier entomologists commonly regarded the proventriculus as a gizzard; judging from its structure in Orthoptera and Coleoptera they did not hesitate to name it the "chewing stomach" (*Kaumagen*). It was Plateau who first threw discredit on this idea, and later Ramme (1913) claimed to demonstrate that the proventriculus is in no case able to break up hard parts of the food. Much discussion has since ensued, and experimental evidence has seemed inconclusive. Recently, however, Eidmann (1924) has made observations that appear to be decisive. He finds that in cockroaches during moulting the post-cephalic part of the stomodaeal exuviae remains intact within the crop until the armature of the new proventricular cuticula is fully sclerotized; after this the old cuticula is broken up and the pieces discharged by way of the stomach and intestine. Furthermore, an examination of the food content of the crop and ventriculus, made at a certain time subsequent to feeding, shows that the food particles of the latter are smaller than those in the crop. From these observations Eidmann concludes that the proventriculus anterior of the cockroach is a chewing apparatus, and that after trituration the food is returned to the crop where it undergoes a preliminary digestion by the enzymes of the salivary secretion. The food is then passed into the stomach through the proventriculus posterior, which otherwise serves merely as a closing apparatus. Confirmatory evidence of the chewing function of the proventriculus is added by Davis (1927), who inserted small strands of wax into the proventriculus of live *Stenopelmatus* and found the wax indented by the proventricular teeth.

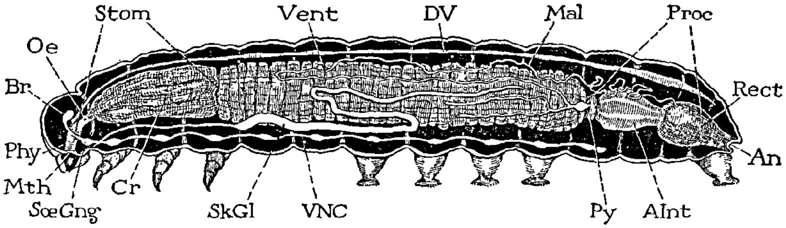

FIG. 196.—The alimentary canal, silk glands, dorsal blood vessel, and nerve cord of a caterpillar.

Finally, we may observe, the proventriculus serves in some cases as a stomach mouth (*Magenmund*), or pump (*Pumpmagen*, Emery, 1888). This function is particularly evident in the aculeate Hymenoptera. Here the four thick, inner lobes of the organ reach forward into the crop (honey stomach of bees), and the posterior part extends as a funnel-shaped tube into the ventriculus. The lobes open and close like a four-lipped mouth, and apparently it is by their activity that the food in the crop is transferred to the stomach.

The Cardiac Valve.—The cardiac, or stomodaeal, valve is essentially a circular fold of the stomodaeal wall projecting into the ventriculus from the posterior end of the stomodaeum (Fig. 194, *SVlv*). The valve is composed, therefore, of two cellular lamellae and is covered on each side by the stomodaeal intima. The basal ring of the outer lamella (*d, d*) marks the morphological terminus of the stomodaeum. In form the cardiac valve is generally cylindrical or funnel shaped, but it is not always symmetrically developed. The two lamellae are usually more or less free from each other and may include between them an extension of the stomodaeal muscles, but in some cases the two walls are adnate.

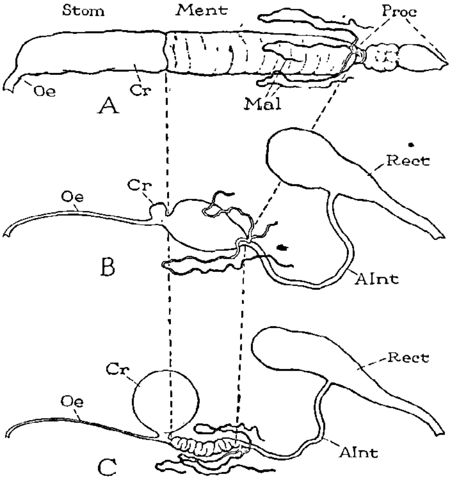

FIG. 197.—Transformation of the alimentary canal of a moth, *Malacosoma americana*, from the larva (A) through the pupa (B) to the imago (C).

The function of the cardiac valve is generally supposed to be that of preventing a return movement of the food from the stomach, but the fold does not entirely occlude the stomach entrance, since in some insects digestive juices flow forward from the latter into the crop. The projecting valvular tube conducts the food from the proventriculus well into the stomach lumen and partly shuts off a space around it in the cardiac end of the stomach, into which may open the gastric caeca, and in which may be situated special secretory cells of the ventricular wall that form the peritrophic membrane (Fig. 204 A, B).

4. THE MESENTERON

The middle section of the alimentary canal (Fig. 190, *Ment*) is the stomach of the adult insect and is therefore commonly called the *ventriculus*. Only the epithelial wall of the ventriculus is formed from the endodermal mesenteron of the embryo (Fig. 13 D, *Ment*), but usually the entire adult organ is termed the mesenteron, or mid-gut.

In the composite definitive alimentary canal the ventriculus begins morphologically at the base of the outer fold of the stomodaeal valve (Fig. 194, *d*), the line being marked by the termination of the stomodaeal intima. The walls of the ventriculus are distinguished from those of the stomodaeum by the larger size and more spongy appearance of the epithelial cells, by the absence of a permanent or uniform intima, and by a reversal in the arrangement of the fibers in the muscular sheath, the principal longitudinal muscles of the ventriculus (Fig. 201, *lmcl*) being external to the circular muscles (*cmcl*). The ventriculus ends posteriorly a short distance before the bases of the Malpighian tubules (Fig. 190, *Mal*), which, when present, define approximately the anterior end of the proctodaeum.

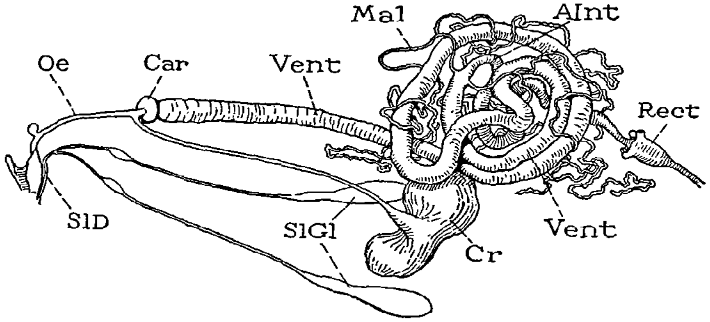

FIG. 198.—The alimentary canal and salivary glands of a fruit fly, *Rhagoletis pomonella*, showing the diverticular crop (*Cr*) and the cardiac sac (*Car*) of the ventriculus, characteristic of many Diptera.

General Form of the Ventriculus.—The ventriculus commonly has the form of a tube or elongate sac of approximately uniform diameter (Figs. 195, 196, *Vent*). Only occasionally does it show a differentiation into regions, though in some insects it is quite distinctly divided into two, three, or four parts.

The anterior end of the ventriculus surrounding the stomodaeal, or cardiac, valve is sometimes distinguished as the *cardia* (Figs. 190, 194 *Car*). In the muscoid Diptera the cardia becomes a small, flattened, circular sac containing the stomodaeal valve, separated from the rest of the ventriculus by a narrow constriction (Fig. 198, *Car*). Nearly all students of the alimentary canal of Diptera have called the cardia the "proventriculus," but its true nature is shown by the fact that the stomodaeal valve is invaginated into its anterior end (Fig. 204 B). In the mosquito (A) the cardia is less differentiated and is clearly the anterior part of the ventriculus.

In the horse fly *Tabanus*, as described by Cragg (1920), the ventriculus is differentiated into a slender anterior tubular region and into a posterior dilated region, the two differing both histologically and functionally as well as in form. The first part Cragg calls the "cardia," though this term should be restricted to the anterior end of the ventriculus; the second he says is functionally the true stomach of the horse fly, since all the blood swallowed at the time of feeding is passed into it.

The regional differentiation of the ventriculus is carried to its highest degree in the Hemiptera. In the more generalized Homoptera the organ is usually divided into three quite distinct parts (Fig. 209 A). The first part (1 *Vent*) is a sac lying within the filter chamber (*FC*); the second is a large croplike enlargement (2 *Vent*); and the third is a long slender tube (3 *Vent*), often called the "ascending intestine" since it turns forward to reenter the filter chamber. In the Heteroptera the ventriculus is commonly differentiated into four well-defined regions differing in length and diameter (Fig. 200 B), the fourth being provided in many families with numerous caecal diverticula (*GCa*). The principal modifications in the form of the heteropteran alimentary canal are shown by Glasgow (1914) in a long series of figures.

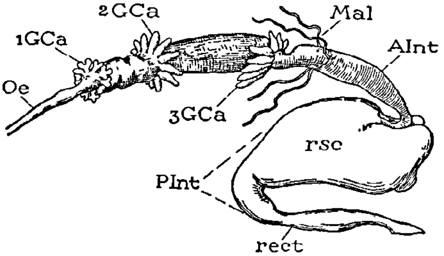

FIG. 199.—The alimentary canal of a scarabaeid larva, *Popillia japonica*, with three sets of gastric caeca (*1GCa, 2GCa, 3GCa*).

Caecal Diverticula of the Ventriculus.—Blind pouches varying in number and in length may be developed on different parts of the ventriculus. Most commonly they occur at the anterior end surrounding the stomodaeal valve. There are usually from two to six of these anterior gastric caeca (Fig. 190, *GCa*), though the number may be greater. In form they are generally simple blunt or tapering processes, but in the Acrididae each is divided at its base into an anterior branch and a posterior branch (Fig. 195, *GCa*). Caecal diverticula sometimes occur, however, on other parts of the ventriculus, as in the larvae of lamellicorn beetles, in which there may be three circles of them (Fig. 199, 1*GCa*, 2*GCa*, 3*GCa*), two near the anterior end of the stomach, the other near the posterior end. In the larva of the fly *Ptychoptera contaminata*, van Gehuchten (1890) describes a circle of eight small diverticula near the anterior end of the ventriculus (Fig. 200 A, *GCa*), and a pair of long glandular pouches (*gl*) arising from the extreme posterior end of the organ. In many Coleoptera a large part of the ventriculus is covered with small papilliform or sometimes elongate diverticula, but these structures in most cases are the crypts of epithelial regenerative cells (Fig. 206 C, *Cpt*) rather than true caeca.

A remarkable development of caecal appendages on the ventriculus occurs in the Heteroptera, where in many families a group of diverticula, varying greatly in number, size, and form, are given off from the fourth section of the stomach. An extensive study of the gastric caeca of the Heteroptera has been made by Glasgow (1914), who gives numerous illustrations of their various forms. In general there are two types of these organs: in one type the diverticula are short, of uniform size, and arranged in two or four rows along most of the extent of the fourth section of the stomach (Fig. 200 B, *GCa*); in the other type the caeca are fewer in number but are long tubes of varying length and often very unsymmetrically grouped (C). According to Glasgow the gastric caeca of the Heteroptera, wherever they occur, are invariably filled with bacteria, and the presence of the bacteria is hereditary, the organisms appearing early in the alimentary canal of the developing embryo. Glasgow says that "these normal bacteria appear not only to inhibit the development of foreign bacteria but to exclude them altogether." He suggests, therefore,

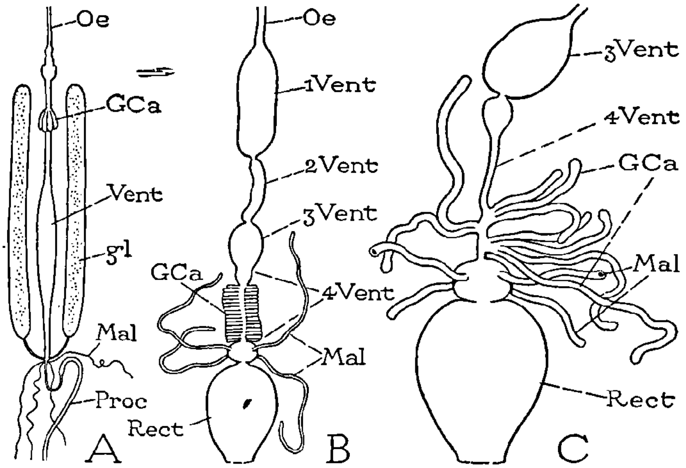

FIG. 200.—Examples of caecal diverticula on various parts of the ventriculus, and of subdivision of the ventriculus. A, larva of *Ptychoptera contaminata* (Diptera) with glandular diverticula (*gl*) from posterior end of ventriculus. (*From Van Gehuchten*, 1890.) B, C, *Peliopelta abbreviata* and *Blissus leucopterus* (Heteroptera) with four sections in the ventriculus, and gastric caeca arising from the fourth section. (*From Glasgow*, 1914.)

that the function of the caeca is merely to provide a safe place for the multiplication of the normal bacteria of the alimentary canal.

Histology of the Ventriculus.—The epithelial walls of the stomach are characteristically thicker than those of other parts of the alimentary canal, but the muscularis is usually more weakly developed than in the stomodaeal region. An intima is not always present, at least not in the form of a definite cuticular layer, and when it does occur as such it is continually or periodically shed into the lumen of the stomach. In most insects a thin *peritrophic membrane* surrounds the food contents of the ventriculus.

The Epithelium.—The appearance of the ventricular epithelium (Fig. 201, *Epth*) varies greatly according to the state of the digestive processes. Most of its cells are columnar, with irregular inner ends more or less projecting into the stomach lumen. The cytoplasm appears granular or spongy; the nuclei are large and generally occupy the middle or distal parts of the cell bodies, where, in sections, they form fairly even rows or lines following the inner contour of the epithelium. In addition to these larger, spongy cells that form most of the epithelial wall, there are usually to be seen other smaller cells (*rg*) of a denser texture occurring either singly or in groups between the bases of the larger cells (Fig. 202 B) or aggregated into definite clusters (*C*), sometimes contained in pockets, or *crypts*, of the epithelium (E). The larger cells, having their inner ends exposed or projecting into the stomach lumen, are the *digestive cells* (B, *dg*), that is, cells that take an active part in the processes of secretion or absorption; the smaller basal cells are the *regenerative cells* (*rg*), the function of which is to propagate cells to replace the digestive cells when the latter are exhausted by secretory activities or shed at the time of ecdysis.

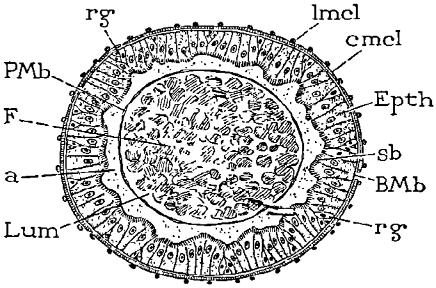

FIG. 201.—Diagrammatic cross section of the ventriculus. *BMb*, basement membrane; *cmcl*, circular muscles; *Epth*, epithelium; *F*, food material; *lMcl*, longitudinal muscles; *Lum*, lumen; *PMb*, peritrophic membrane surrounding the food and separated by space (*a*) from epithelium; *rg*, regenerative cells; *sb*, striated border.

The digestive cells constitute the functional epithelium of the stomach. Their central ends are often differentiated as a weakly staining, marginal layer of the epithelium, which, in sections, appears to be crossed by numerous fine lines perpendicular to the surface. This marginal zone of the stomach epithelium is known as the *striated border* (Figs. 201, 202 A, *sb*). The nature of the striated border has been the subject of much discussion. Earlier investigators believed it to be a coating of fine filaments covering the inner surface of the stomach, comparable with the ciliate lining of the mesenteron in Annelida. In the insects, however, the striated zone is a continuous layer in which the darker lines of the striae alternate with clear lines of a less dense material through which minute droplets of digestive liquids may be extruded from the inner parts of the cells. The surface of the striated border is generally observed to be defined by a delicate limiting membrane.

In most insects the digestive cells are of uniform structure throughout the ventriculus, except in that they may be of different sizes in different parts of the stomach or may be found in various stages of disintegration. In the larvae of Lepidoptera, however, there are two quite distinct types of digestive cells. Those of one type have the ordinary columnar or cylindrical form; those of the other, characterized as calyciform or goblet cells, have each a large ampulla in its mesal part opening by a narrow neck through a small aperture on the inner surface. The two types of digestive cells of the caterpillar have been studied particularly in *Galleria mellonella* by Yung-Tai (1929), who finds that they are differentiated even in the embryo, and that they are generated separately from the replacement cells. The cavities of the goblet cells are lined with a striated border like that of the columnar cells. Yung-Tai concludes that the goblet cells are exclusively secretory in function, while the ordinary cylindrical cells may be either secretory or absorptive, though the same individual cells do not function in both capacities. The goblet cells, he says, are not replaced after the moult to the pupa.

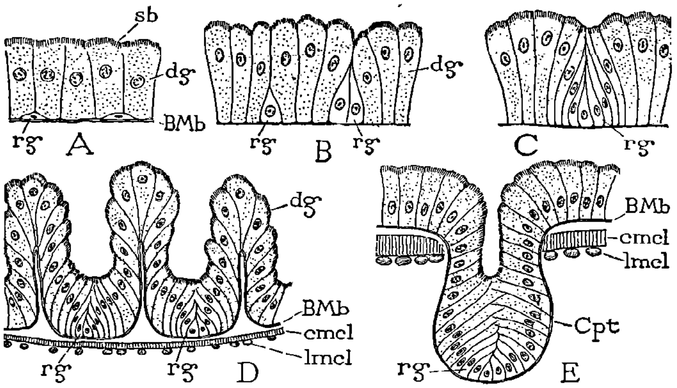

FIG. 202.—Diagrams showing various positions of the regenerative cells (*rg*) of the ventricular epithelium with relation to the digestive cells (*dg*).

From its very beginning the endoderm of insects appears to be an unstable tissue. As we saw in Chap. II, the formation of the mesenteron in the embryo is apparently a regenerative process following an earlier dissolution of the primitive archenteron. During postembryonic life of most insects the cells of the mesenteric epithelium are continually subject to various degrees of disintegration as a result of their secretory processes, or for the purpose of reconstructive growth in the ventriculus accompanying the moults. The replacement of the epithelium is either gradual and partial or rapid and complete, according to the nature of the disintegration processes. The new cells are formed from the special regenerative cells, which take no part in the other activities of the ventriculus. The processes of regeneration are in general the same regardless of the degree, time, or manner of cell replacement or the reason for its occurrence.

Both the digestive and the regenerative cells of the ventriculus are derived from the primitive endoderm, the digestive cells being so specialized for the functions of secretion and absorption that they have lost the power of reproduction, while the regenerative cells maintain unimpaired the property of mitotic division. The regenerative cells are usually of small size and lie beneath the others against the basement membrane (Fig. 202 B, *rg*). They are shown in a relatively simple condition in Collembola of all stages and in some dipterous larvae (Fig. 203, *rg*), where they occur singly or in small groups scattered throughout the length of the ventriculus.

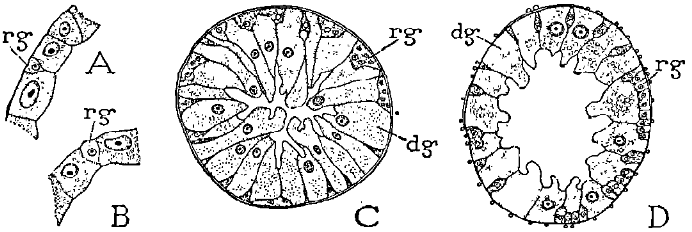

FIG. 203.—Sections of the ventriculus of a mosquito larva and pupa showing regenerative cells. (*From Samtleben*, 1929.) A, B, *Culex pipiens*, middle-aged larva. C, *Aëdes meigenanus*, newly forming pupa. D, *Culex pipiens*, larva just before pupation.

The regeneration cells of the ventricular epithelium generally form definite cell groups, or *nidi*, sharply distinguished from the surrounding digestive cells (Figs. 202 C, 205 B, 206 A, *rg*). From these specialized regeneration centers are propagated the new cells that replace the exhausted or discarded digestive cells. In the Hymenoptera the regeneration cells are contained in open pockets of the ventricular epithelium, but in other insects in which the regeneration cells are grouped in definite nidi, the pockets are generally closed by an overgrowth of the surrounding digestive cells (Figs. 202 C, 206 A), and the general contour of the inner surface of the epithelium gives no indication of the position of the nidi. The regeneration cells, however, may lie at the bottoms of deep folds or pockets of the epithelium. In some Coleoptera they are contained in evaginations of the stomach wall, forming pouchlike diverticula known as the *regenerative crypts* (Figs. 202 E, 206 C, *Cpt*), which may be so numerous as to give the entire external surface of the ventriculus a villous structure.

The Basement Membrane.—The epithelial cells of the ventriculus rest upon a membrane (Fig. 201, *BMb*) which appears to be a tunica propria, or product of the cell bases, differing in no respect from the basement membrane of the body wall or from that of the ectodermal parts of the alimentary canal. According to Deegener (1910) and Rungius (1911; Korschelt, 1924), however, the ventricular epithelium of *Dytiscus* is invested in a thick supporting layer (*Stützlamelle*) which is a nucleated connective tissue and is not to be identified with the tunica propria of the stomodaeum and proctodaeum.

The Peritrophic Membrane.—The food content of the stomach in many insects is separated from the ventricular epithelium by a thin membrane, which, though often in more or less intimate contact with the inner ends of the epithelial cells, typically surrounds the food mass as a cylindrical sheath for the most part free from the stomach walls. This food envelope is known as the *peritrophic membrane* (Fig. 201, *PMb*). It is not present in all insects, but it is known to occur in Collembola, Thysanura, Ephemerida, Odonata, Orthoptera, Neuroptera, Coleoptera, Hymenoptera, Diptera, and larval Lepidoptera, while it is said to be absent in Hemiptera and adult Lepidoptera, as well as in certain members of the orders in which it is usually present.

The peritrophic membrane is a product of the ventricular epithelium, being formed in most cases from the entire surface of the ventriculus, but in Diptera it appears to be produced by a band of specialized cells in the anterior end of the cardia encircling the base of the stomodaeal valve. In no case is it a continuation of the proventricular intima. Some writers have assumed that the peritrophic membrane is a nonchitinous structure because it is produced by endodermal cells; but several investigators, including Wester (1910), Campbell (1929), and von Dehn (1933), have found by chemical tests that the peritrophic membrane contains chitin, while Hövener (1930) says that it shows two characteristic properties of chitin, namely, double refraction and resistance to alkalies. There is no reason for supposing that chitin should not be produced from endodermal as well as from ectodermal derivatives of the blastoderm; the peritrophic membrane is evidently to be regarded as a chitinous intima of the ventriculus.

The component material of the peritrophic membrane is probably a secretion product of the matrix cells. Folsom and Welles (1906) claimed that the peritrophic membrane of Collembola is a direct transformation of the striated border of the ventricular epithelium, cast off from time to time, as a new striated border is formed beneath it, and Ertogroul (1929) described the peritrophic membrane in the silkworm as formed in the same manner. According to Yung-Tai (1929), however, the peritrophic membrane of the larva of *Galleria mellonella* consists of successive delaminations of a surface membrane of the ventricular epithelium, and that of the larva of *Vanessa urticae* is said by Henson (1931) to be a secretion product of the epithelial cells. Von Dehn (1933) contends that the peritrophic membrane is in no case identical with the striated border of the epithelium, since the membrane is chitinous and the striated border is cytoplasmic. The chitinous material of the peritrophic membrane, she says, appears in liquid droplets beneath the striated border, is extruded through the interstices of the latter, and runs together over the cell surfaces to form a continuous layer, which is then separated from the epithelium to become a peritrophic membrane. In the process of separation the striated border may be more or less disrupted and fragments may adhere to the membrane, but not as constituent parts of it.

In the larvae of most aculeate Hymenoptera the peritrophic membranes form a sac closed posteriorly about the food mass of the stomach, since the mesenteron does not open into the proctodaeum until the termination of larval life. The same is said to be true of the larvae of some Neuroptera. The food sac of a mature wasp larva (*Vespa*) appears as a bag filled with a black mass, the bag lying free in the ventriculus except for an attachment to the walls of the latter around the base of the stomodaeal valve. At the time of defecation the sac becomes detached and is ejected entire with its contents into the inner end of the cocoon, which the larva has already spun about itself, and here the dejectamenta dry to a hard black mass. The peritrophic membranes of the wasp larva are described by Rengel (1903), and those of ant larvae by Strindberg (1913), as being given off successively from the general surface of the ventricular epithelium. In the larva of the honey bee Nelson (1924) describes the peritrophic membrane as a thick homogeneous layer, apparently of gelatinous consistency, covering the inner surface of the epithelium, but at the anterior end of the ventriculus he says there is a ring of specialized cells from the surface of which streams of secretion issue and run caudad to join with the principal mass of the peritrophic membrane.

Since the peritrophic sac of hymenopterous larvae becomes entirely free from the walls of the ventriculus in the mature larva, except for its anterior attachment, it is clear that an examination of a larva at this stage would suggest that the membrane is a product only of the ring of specialized cells, noted by Nelson in the honey bee, surrounding the stomodaeal valve. The statement by Cuénot (1896) that the peritrophic membrane of Orthoptera is the product of secretion by cells occupying the anterior end of the mesenteron must, therefore, be taken with some reserve, especially since Davis (1927) finds the food envelopes of *Stenopelmatus* to be mostly a series of delaminations from the entire surface of the stomach epithelium, though possibly augmented from the secretion of special anterior cells. On the other hand, there appears to be reason to believe that in the Diptera, both larvae and adults, the peritrophic membrane may take its origin entirely from a band of specialized cells confined to the anterior end of the ventriculus.

In the adult honey bee the food material of the ventriculus is usually enclosed in a series of peritrophic membranes, which are given off successively from the inner surface of the epithelium. During periods of secretory activity the secretion products formed in the cells accumulate beneath a surface film, or border membrane, and the whole mass eventually separates from the cell layer, which then forms a new border membrane. Most of the discarded substances are dissolved, and the residue becomes a peritrophic membrane.

That the peritrophic membrane of Diptera is produced from cells in the anterior end of the mesenteron was first suggested by van Gehuchten (1890); but van Gehuchten called the cardiac enlargement of the mesenteron (Fig. 198, *Car*) the "proventriculus," and this terminology, adopted by many subsequent students of the alimentary canal of Diptera, has been a source of confusion to those who have not perceived that the organ in question is not the proventriculus of other insects (Fig. 190, *Pvent*) but is the cardiac section of the mesenteron. The cardia is best developed as an antechamber of the stomach in the muscoid Diptera, where it takes the form of a flattened, circular sac (Fig. 198, *Car*) with the stomodaeal valve invaginated into its anterior end (Fig. 204 B, *SVlv*). In the lower flies this region of the stomach is less differentiated, but it is recognized by Imms (1907) in the mosquito larva as the cardia (Fig. 204 A, *Car*). The anterior part of the wall of the cardia is formed by a band of specialized epithelial cells (*e*) surrounding the base of the stomodaeal valve (*SVlv*), and it is these cells apparently that secrete the substance which forms the peritrophic membrane (*PMb*).

The formation of the peritrophic membrane in Diptera as an apparent secretion from a ring of specialized cells in the anterior end of the mesenteron has been described by Haseman (1910) and Hövener (1930) in *Psychoda alternata*, and by Wigglesworth (1930) in *Glossina*. In *Psychoda*, according to Haseman, the glandular membrane-forming cells occupy a circular area 6 to 12 cells in length just beyond the base of the stomodaeal valve; the inner granular surface of the cells hardens to form the delicate peritrophic membrane, "which is continually fed back into the mid- and hind-intestine to envelop the food materials." In the description of the formation of the peritrophic membrane of the tsetse fly given by Wigglesworth the reader must understand that the term "proventriculus" refers to the cardia, or anterior end of the mesenteron. Figure 204 C, based on Wigglesworth's drawings of *Glossina,* shows a section through one side of the stomodaeal valve (*SVlv*) and the wall of the surrounding cardia (*Car*). As in most of the higher Diptera the lips of the valve are reflected forward, and in the circular space thus enclosed at the base of the valve is the ring of large secretory cells (*e*) of the anterior end of the mesenteric epithelium. The discharged products of these cells condense to form a cylindrical peritrophic membrane (*PMb*) fed back into the ventriculus from around the periphery of the reflected lips of the stomodaeal valve. In the mosquito larva, as shown by Imms (1907), the peritrophic membrane is formed in a similar manner (Fig. 204 A), but the generative cells here occupy most of the length of the cardia.

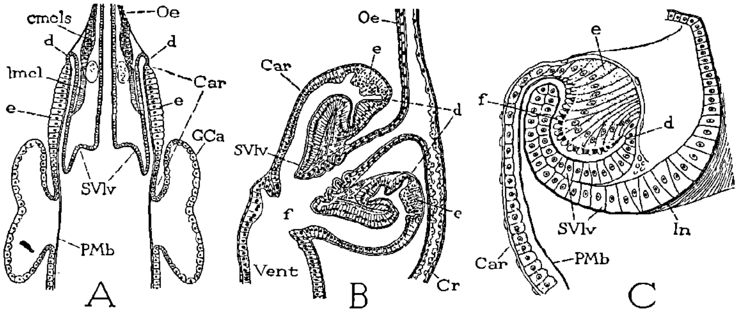

Fig. 204.—Sections of the stomodaeal valve, cardia, and peritrophic membrane of Diptera. A, *Anopheles maculipennis* larva. (*From Imms,* 1907.) B, *Calliphora erythrocephala,* stage almost adult. (*From Pérez,* 1910.) C, *Glossina* adult, one side of stomodaeal valve and wall of cardia. (*Diagrammatic from Wigglesworth,* 1929.)

Inasmuch as the peritrophic membrane, when present, usually completely surrounds the food content of the stomach (Fig. 201), the products both of epithelial secretion and of gastric digestion must penetrate the membranous envelope, the first to act upon the food, the second to be absorbed by the ventricular cells. The space between the epithelium and the peritrophic membrane (*a*) is generally filled with digestive liquid, granules, globules of secretion products, discharged epithelial cells, and presumably also with food material in solution that has passed outward through the peritrophic membrane. The permeability of the peritrophic membranes of the honey bee and the blow fly to various stains has been demonstrated by von Dehn (1933). At present no satisfactory explanation can be offered as to the general function of the membrane, which occurs also in other arthropods than insects.

The Muscularis.—The muscular sheath of the ventriculus is less strongly developed than that of the stomodaeum. The circular fibers (Fig. 201, *cmcl*) generally constitute the principal layer, the longitudinal fibers (*lmcl*), lying external to the circulars, being usually widely spaced, and sometimes groups of longitudinal fibers form special lengthwise muscle bands that look like cords stretched between the two ends of the stomach. Muscles of the latter type are particularly conspicuous in the caterpillars (Fig. 207 A, B, *Vent*). While in most insects all the longitudinal muscles of the ventriculus lie external to the circular muscles, a few lengthwise fibers are said by Rengel (1898) to lie within the circular fibers in *Hydrophilus*, and White (1918) claims that there is likewise in the honey bee an inner layer of very fine longitudinal fibers between the circular muscles and the basement membrane of the ventricular epithelium. A peritoneal covering of loose cellular tissue is said by some writers to surround the muscularis in certain insects, but usually the muscles of the alimentary canal have no very definite investiture.

Activities of the Ventricular Epithelium.—The activities of the epithelial cells of the ventriculus may be divided for descriptive purposes into four classes, as follows: (1) secretion and absorption, (2) excretion, (3) degeneration and regeneration of the digestive cells accompanying or following secretion, and (4) periodical delamination and replacement of the entire epithelium, mostly accompanying the moults.

Secretion and Absorption.—The primary functions of the cells of the ventricular epithelium are the production of liquids containing digestive enzymes, and the absorption and transmission to the blood of the products of digestion. Probably in most insects both these activities are properties of the same cells, but van Gehuchten (1890) has claimed that the two functions pertain to two sets of cells in the fly *Ptychoptera contaminata*, and Yung-Tai (1929) gives convincing evidence that the goblet cells in the larval epithelium of the moth *Galleria mellonella* are exclusively secretory, while the columnar cells may be either secretory or absorptive in function, though the two activities are not performed by the same cells of this group.

The discharge of the secretion products, in its simplest form, undoubtedly, is accomplished by the direct passage of the elaborated substances through the striated border of the secreting cells, and it is possible that the secretion discharge in all cases takes place by this method. With most insects, however, there is to be observed in the ventriculus a conspicuous process of budding from the inner ends of the epithelial cells. The extruded globules either disrupt and scatter their contents in the ventricular lumen or they become detached and are given off as free bodies which later disintegrate. Generally it has been supposed that these activities of the ventricular cells, which have been studied only as physical phenomena in histological preparations, are processes of holocrine secretion, but there is a recent tendency to regard them as disintegration processes following exhaustive periods of ordinary secretion. In any case they are anatomically degenerative changes and will be described in this category.

Excretion.—There is little doubt that the walls of the ventriculus play some part in excretion, in either an active or a passive role. The epithelial cells are often observed to contain large numbers of small crystalline bodies, which are found to be principally calcium salts, though some also are said to have the properties of uric acid concretions. Such deposits, together with bacterial inclusions, are at least eliminated with the shedding of the epithelium at the time of ecdysis.

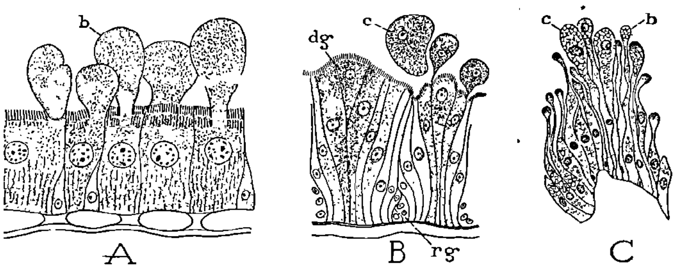

Fig. 205.—Examples of disintegration processes (supposedly holocrine secretion) in the stomach epithelium. A, *Ptychoptera contaminata* larva. (*From Van Gehuchten*, 1890.) B, *Gomphus descriptus* larva. (*From Needham*, 1897.) C, *Tabanus* adult. (*From Cragg*, 1920.)

Degeneration and Regeneration of the Digestive Cells.—Throughout the active life of most insects there takes place in the epithelium of the ventriculus a partial or complete disintegration of the digestive cells, followed by a replacement of the lost cells with new cells formed from the regeneration cells.

The simplest form of disintegration in the digestive cells consists of the accumulation of granular material in the inner ends of the cells, succeeded by a rupture of the cell wall and the discharge of the material into the ventricular lumen. The cell wall then closes, the striated border is reestablished, and the cell continues its digestive functions.

A second and more intensive form of disintegration involves a separation of the inner parts of the cells containing the granules and globules. The mesal border of the cell in this case swells out in the form of a bud, which becomes constricted at its base and finally separated as a free sphere from the body of the cell (Fig. 205 A). In Collembola, according to Folsom and Welles (1906), the bud is at first surrounded by a striated zone, which later is lost; but in most other insects the striated border disappears on the evaginating bud. The liberated sphere floats off into the stomach lumen and there undergoes a gradual dissolution which sets free its contents. This form of disintegration is the one generally observed in adult insects. The buds vary from rounded protuberances (A, *b*) to fingerlike processes or appear as small globules at the ends of long slender stalks (C, *b*). In most insects the buds are formed prior to feeding, and, as shown by Needham (1897) in odonate larvae, they may in such cases increase enormously in size and numbers in starved individuals. In the horse fly *Tabanus*, however, described by Cragg (1920), the buds are extended during the period of feeding, and after their discharge the epithelial cells go back at once to the normal resting condition. The horse fly, Cragg says, feeds at intervals of two or three days.

A third type of cell disintegration is similar to the last, except that the part of the cell given off contains a nucleus and is, therefore, an extruded cell. The cell, loaded with granular matter, degenerates and is dissolved in the stomach lumen. The liberation of nucleated cells, Needham says, is characteristic of dragonfly larvae (Fig. 205 B); in other insects it frequently accompanies the discharge of nonnucleated bodies, as in the horse fly (C, *c*) and in the honey bee. This form of disintegration, as well as the last or the two together, results in a rapid and extensive depletion of the digestive cells of the epithelium, necessitating their replacement by cells propagated from the regenerative cells.

All these forms of cell disintegration in the ventricular epithelium have generally been described as methods for the rapid discharge of secretion products. Only recently this interpretation is challenged by Yung-Tai (1929), who points out that secretions are always in the form of a diffusible liquid, and that the coarse granular contents of the buds and globules given off from the digestive cells have all the aspects of cytoplasmic degeneration products. He therefore contends that the processes ordinarily described as secretion discharge are really disintegration processes following active periods of secretion or absorption. This view is endorsed also by Henson (1930). The subject, however, must be studied from a physiological standpoint before conclusions can be justified.

Periodic Delamination and Replacement of the Ventricular Epithelium.—Reconstructive processes, varying in degree, usually occur in the stomach walls at the time of ecdysis, particularly at the moult of the larva to the pupa in holometabolous insects. In some insects the entire ventricular epithelium is shed and renewed at each moult, and in certain beetles a complete regeneration of the stomach wall is said to occur periodically throughout adult life.

A replacement of the entire ventricular epithelium accompanying each ecdysis has been described by Folsom and Welles (1906) and by Boelitz (1933) in Collembola, which moult throughout life, and a similar process accompanying the larval ecdyses has been observed in Dermestidae by Möbusz (1897) and Braun (1912), in the moth *Galleria melonella* by Yung-Tai (1929), and in the fly *Psychoda alternata* by Haseman (1910). The renewal of the ventricular epithelium in Collembola, according to Boelitz, is preceded by an evacuation of the stomach and starts with mitotic division in the regenerative cells, the activity of the latter beginning anteriorly and proceeding posteriorly. As the new cells multiply, the old epithelium is separated from the basement membrane, which remains intact, and is pushed toward the lumen of the stomach, finally to be thrown off into the latter, where it is digested and absorbed by the new epithelium. Folsom and Welles described the rejected epithelium of Collembola as formed by a longitudinal division of the primary epithelium, the outer layer remaining as the next functional epithelium; their account makes no mention of the regenerative cells later described by Boelitz.

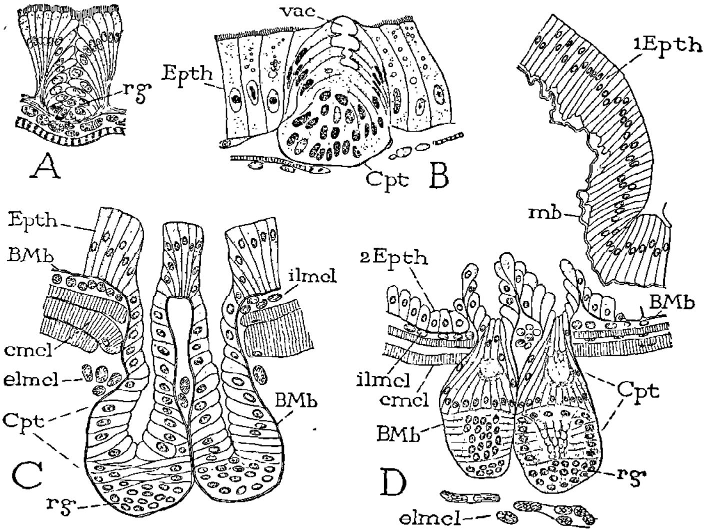

Fig. 206.—Regenerative cells of the ventricular epithelium. A, a nidus of regenerative cells of *Stenopelmatus*. (*From Davis*, 1927.) B, a crypt of regenerative cells of larva of *Dytiscus marginalis*. (*From Rungius*, 1911.) C, two crypts of adult *Hydrophilus piceus*. (*From Rengel*, 1898.) D, same during regeneration of new epithelium (*2Epth*), with old epithelium (*1Epth*) cast off.

In most holometabolous insects there is probably more or less of a renovation of the stomach epithelium accompanying each moult of the larva; but in the majority of cases observed the renovation does not involve a complete loss of the old cell wall. According to Braun (1912), in species of Lepidoptera, Coleoptera (except Dermestidae), Hymenoptera, and Diptera studied by him, active cell division and epithelial growth, in some cases accompanied by the loss of a few cells thrust out into the stomach lumen, take place during the periods of larval ecdysis. These activities of the mesenteron cells, however, he says are primarily for the purpose of growth in the alimentary canal following the moult, and only to a small degree do they have a regenerative significance.

At the penultimate moult of holometabolous insects, that is, with the change from the larva to the pupa, it is well known that the ventricular epithelium is cast off and replaced by a new cell layer that takes on more nearly the form of the ventriculus of the adult insect. Most investigators find that the pupal, or imaginal, epithelium is formed from the same regenerative centers that produce the new cells of the larval ventriculus. The statement by Mansour (1928), therefore, that the imaginal stomach of Rhynchophora is generated from the stomodaeum and not from the cells of the larval mesenteron, if true, would establish a most exceptional condition in these beetles, since it implies, as Mansour claims, that the imaginal stomach is of ectodermal origin.

A replacement of the stomach epithelium between the pupal and imaginal stages has not been generally observed, but Deegener (1904) says that the epithelium is renewed at the pupal moult in the beetle *Cybister*, and Russ (1907) describes a partial degeneration and replacement of the pupal epithelium in Trichoptera.

Finally, it appears that a complete renewal of the stomach epithelium may occur even in the imaginal instar of pterygote insects. Rengel (1898), for example, claims that a periodic shedding and regeneration of the entire ventricular epithelium take place in members of the Hydrophilidae throughout the lifetime of the adult beetles. He describes both processes in detail for *Hydrophilus* (Fig. 206 D). Though he says nothing of the physiological significance, it is to be supposed that the shedding of the old cell layer (1*Epth*) is a preliminary to the renewal of the epithelium (2*Epth*) following exhaustion from secretory activities. The old epithelium is entirely replaced by a new cell layer (C, *Epth*) formed from the regenerative cells (*rg*) of the ventricular crypts (*Cpt*).

5. THE PROCTODAEUM

The proctodaeum is the posterior ectodermal part of the alimentary canal. In its lesser degrees of development it is a simple tube (Fig. 189, *Proc*) constituting merely a conduit from the stomach to the anus; but, as the stomodaeum, the proctodaeum also is generally differentiated into several more or less distinct regions. The anterior end of the proctodaeum is approximately marked by the bases of the Malpighian tubules (Fig. 190, *Mal*), since these tubules are diverticula of the stomodaeal walls; but the true dividing line between mesenteron and proctodaeum is usually somewhat anterior to the bases of the tubules, and in some insects it lies a considerable distance before them. The entrance to the intestine from the stomach is generally more or less constricted, and the opening is guarded by a regulatory structure commonly known as the *pyloric valve* (Fig. 189, *PVlv*). The analogy with vertebrate anatomy implied in the term, however, is not exact, for the valvular apparatus in insects is usually, though not always, located behind the stomach in the anterior part of the proctodaeum.

The proctodaeum is furnished with extrinsic muscles that extend to its posterior parts from the wall of the abdomen. These muscles, often called the "suspensory" muscles of the proctodaeum, probably serve in part to maintain the position of the intestine, but they evidently have also a more active function. In some insects they are clearly dilators of the proctodaeum, since they spread in fan-shaped bundles from their origins to their insertions on the proctodaeal walls; in others, as in the caterpillars (Fig. 207 A), where they take a more longitudinal course, it would appear that they play some part in evacuation.

Subdivisions of the Proctodaeum.—The regions into which the proctodaeum is usually differentiated vary in different insects, and for this reason it is difficult to apply a consistent terminology to them. The names by which they are commonly designated are borrowed from human anatomy, and they have no excuse in entomology other than that of nomenclatural convenience.

The most general division of the proctodaeum is into an *anterior intestine* (Fig. 190, *AInt*) and a *posterior intestine* (*PInt*), the second being commonly termed the *rectum* (*Rect*). The two parts are usually separated externally by a sharp constriction, and internally by a *rectal valve*. In many insects, however, there is a short but distinct section of the proctodaeum that intervenes between the ventriculus and the true intestinal tube, which contains the sphincter valve that regulates the exit from the stomach. This section is the *pylorus* (*Py*). The Malpighian tubules (*Mal*) open into the anterior part of the proctodaeum, sometimes immediately behind the ventriculus; but when there is present a distinct pyloric region, they discharge into the latter.

The anterior intestine may be a simple tube, varying in length in different insects, but it is often subdivided into an anterior *ileum* (Fig. 190, *Il*) and a posterior *colon* (*Cln*). The posterior intestine is generally dilated anteriorly into a *rectal sac* (*rsc*) and narrowed posteriorly in a straight tubular part, or *rectum proper* (*rect*), that goes direct to the anus (*An*). Frequently the anterior intestine opens into the posterior intestine on the side of the rectal sac (Fig. 210 B), and in such cases the anterior end of the latter becomes a blind pouch, or *rectal caecum*. In some of the Heteroptera almost the entire proctodaeum consists of a large sac

(Figs. 200 B, C, *Rect,* 219 A, *r*). If this sac is the rectum, as it appears to be, a short tubular invagination of the intestinal wall behind the swollen bases of the Malpighian tubules is perhaps a remnant of the anterior intestine.

Histology of the Proctodaeum.—The walls of the proctodaeum resemble in structure those of the stomodaeum. The cells of the epithelium are flat or columnar, in most places showing little evidence of having a secretory function, and they are covered internally with a distinct cuticular intima. The muscle layer of the proctodaeum is less regular than that of the other sections of the alimentary canal and is frequently absent on some of the intestinal regions. In general the muscularis includes internal circular fibers and external longitudinal fibers, resembling thus the muscle sheath of the ventriculus rather than that of the stomodaeum; but the relative development of the two sets of fibers often varies greatly in different parts of the proctodaeum, and there may be additional muscles either outside or inside the usual layers. Special histological features of the proctodaeum will be described in treating of the several intestinal regions individually.

The Pylorus.—The anterior part of the proctodaeum is often differentiated as a well-defined region into which open the Malpighian tubules (Fig. 207 A, B, *Py*). Since the pyloric valve is usually situated here, this region is termed the pylorus ("gatekeeper") of the intestine (Deegener, 1904; Rungius, 1911, 1924; Weber, 1933), though the term in vertebrate anatomy applies to the posterior part of the stomach. Examples of a well-differentiated pyloric region are to be found in Coleoptera and in the larvae of Lepidoptera. In some insects, however, there is no pyloric valve other than a small epithelial fold between the mesenteron and proctodaeum, and in such cases there is consequently no differentiation in the external structure of the alimentary tube to distinguish a pyloric region from the rest of the intestine.

In the caterpillars the pylorus constitutes a distinct and highly specialized proctodaeal region (Figs. 196, 207 A, *Py*) between the ventriculus (*Vent*) and the enlarged middle chamber (*AInt*) of the intestine. The Malpighian tubules (*Mal*) open into its posterior part. The organ, when fully stretched out (Fig. 207 A, *Py*), presents a narrow posterior neck or stalk surrounded by a strong, external sphincter muscle (*sptr*) just behind the bases of the Malpighian tubules (*Mal*), and a widened anterior part continued forward as a calyxlike expansion continuous with the posterior end of the ventriculus (*Vent*). The line between the mesenteron and the pylorus is marked externally by a strong band of circular muscles (A, *g*), and internally by a corresponding fold (B, *g*). The proctodaeal intima up to this fold is covered with small spicules. Midway in the walls of the anterior part of the pylorus there is a second internal fold (A, B, *h*) which varies in height according to the contraction of the organ. The entire length of the pylorus is closely surrounded by a series of circular muscle fibers, outside of which there are widely spaced, branching longitudinal muscles (A, *lmcl*) that are free from the pyloric walls except at their ends. Posteriorly these muscles pass beneath the sphincter (*sptr*). In appearance the pylorus of the caterpillar varies much according to the state of contraction of the longitudinal muscles; in the same species it may be stretched out, as in Fig. 207 A, or again it may be contracted and thrown into strong circular folds as at B.

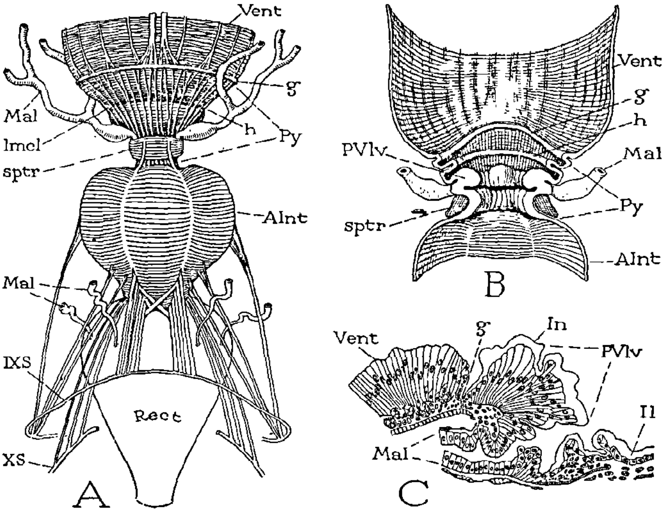

FIG. 207.—The proctodaeum, pylorus, and pyloric valve. A, proctodaeum of a noctuid caterpillar, showing highly developed pylorus (*Py*). B, internal view of pylorus of same in a contracted condition. C, section of proctodaeal pyloric valve (*PVlv*) of adult *Phyllophaga gracilis*. (*From Fletcher*, 1930.) *g*, junction of mesenteron and proctodaeum; *h*, fold of pyloric wall.

The Pyloric Valve.—Two different types of valvular structures are associated with the opening from the stomach into the intestine. In some insects a small, internal, circular fold, or ring of long cells, projects from the posterior margin of the mesenteric epithelium, forming a *ventricular valve;* in others an apparatus for closing the entrance into the intestine is developed in the pyloric region of the anterior end of the proctodaeum and constitutes a *proctodaeal valve.* The latter, when present, is clearly the more efficient occlusor mechanism and is the one generally found at this region.

A proctodaeal pyloric valve is typically developed in the Coleoptera, where it consists of one or two transverse folds or thick rings of epithelial cells in the pyloric region at the anterior end of the intestine (Fig. 207 C, *PVlv*) immediately before the openings of the Malpighian tubules (*Mal*). Usually the valvular rings are cut by the longitudinal folds of the pyloric wall into a series of opposing lobes. The sphincter muscle of the pyloric region serves to approximate the lobes, and short longitudinal muscles from the posterior end of the ventriculus inserted in the lobes of the valve apparently form the opening mechanism. A detailed description of the pyloric valve of *Dytiscus* is given by Rungius (1911; Korschelt, 1924).

The pyloric valve of caterpillars is situated in the narrow neck of the pyloric region of the proctodaeum (Fig. 207 A, *Py*). The inner walls of the latter are thrown into numerous longitudinal folds, four of which are particularly large (B, *PVlv*) and form opposing lobes that block the narrow entrance into the succeeding intestinal chamber. The large external sphincter muscle of the pylorus (A, B, *sptr*) surrounds the posterior ends of the valve folds posterior to the bases of the Malpighian tubules (*Mal*) and when contracted evidently shuts the lumen of the pylorus from that of the intestine. The external longitudinal muscles of the pylorus (A, *lmcl*), inserted beneath the sphincter, perhaps serve to relax the valve, but when they are contracted a deep transverse, internal groove cuts across the valve lobes, forming a circular channel into which the Malpighian tubules open (B). The lengthwise stretching of the pyloric region is perhaps accomplished by the muscles from the body wall inserted on the posterior parts of the intestine.

The Malpighian Tubules.—Excretory diverticula of the alimentary canal occur in Arachnida, Crustacea, Myriapoda, and Hexapoda. Those of Chilopoda and Hexapoda, known as the *Malpighian tubules,* are commonly observed to be attached to the anterior end of the proctodaeum, and embryologists generally assert that they take their origin as outgrowths from the proctodaeum. Tirelli (1929), however, quite circumstantially describes the tubules of *Cloeon dipterum* as opening into the mesenteron, and Henson (1932) claims that in the moth *Hepialus* the tubules arise from the mesenteron. Henson believes, therefore, that the functional parts of the tubules are of endodermal derivation in all Lepidoptera, and that only the terminal ducts opening into the intestine are of proctodaeal origin. In some caterpillars the pyloric region of the proctodaeum extends so far forward beyond the bases of the Malpighian tubules as to become virtually the posterior end of the stomach (Fig. 207 A, *Py*) and might be mistaken for a part of the mesenteron. In the Acrididae (Fig. 195) and other Orthoptera, however, the Malpighian tubules open so nearly on the line between the mesenteron and the proctodaeum that it might be questioned whether their epithelium is continuous with that of the ventriculus or with that of the intestine. Histologically the walls of the tubules more closely resemble the epithelium of the ventriculus than that of the proctodaeum. In the majority of insects, however, there is no doubt that the tubes arise from the proctodaeum, and in many cases they open into the latter well back from its anterior end.

The Malpighian organs of insects are typically long, slender, much convoluted tubules, frequently branched or arranged in clusters. In the Protura, however, according to Berlese (1910), they are represented by six small oval masses of cells projecting from the anterior end of the proctodaeum, each organ consisting of two large outer cells supported on a peduncle of slender cells extended from the intestinal epithelium. In the Japygidae the organs are small but tubular; as described by Silvestri (1905) and Tillyard (1930) they consist of six very short diverticula from the anterior end of the proctodaeum. Generally the Malpighian tubules lie entirely free in the body cavity, but in some insects their posterior ends penetrate beneath the outer tissues of the walls of the rectum. This latter condition is usual in the larvae of Lepidoptera (see Ishimori, 1924), and it occurs in some Neuroptera and many Coleoptera. Marcus (1930) says that in only a small proportion of the Coleoptera do the Malpighian tubules end freely in the body cavity. The terminal parts of the tubules are frequently united in various ways.

The number of Malpighian tubules is highly variable in different insects, and even within a single order. In the Myriapoda generally there are two tubules or not more than four; in the insects the number is usually greater, ranging from 1 to 150. A summary of the number of Malpighian tubules known to occur in the various orders of insects is given by Wheeler (1893*a*) and Veneziani (1905), and additional information on the number in Apterygota is given by Tillyard (1930).

From the foregoing sources and others it appears that the number of Malpighian tubules in Apterygota is usually 6, though only 4 are reported in some Lepismatidae, and the number may be as large as 16 in *Campodea* or 20 in *Machilis.* In Ephemerida the tubules are said to vary from 40 to more than 100, those of *Heptagenia* being arranged in 8 groups, according to Marshall (1927). Adult Odonata have 50 to 60 tubules, and a similar number is present in Plecoptera. In Orthoptera the number is generally large in adults, 20 to 100 or more, but the tubules are usually arranged in from 2 to 12 groups. The Gryllidae present an interesting exception in that only one short primary tube is present, but this one branches into a cluster of 100 to 120 long secondary tubules. According to Wheeler, only 6 tubules are present in embryos of *Blatta, Xiphidium,* and *Melanoplus.* In the Hemiptera, the Aphididae lack Malpighian tubules, the Coccidae have 2, and all others 4, the ends of which are sometimes united in pairs.

Among the holometabolous orders the number of Malpighian tubules is likewise variable. There are 6 to 8 in most Neuroptera, Wheeler reporting the odd number of 7 in a larva, probably *Chauliodes.* Mecoptera and Trichoptera have 6. In Coleoptera, most pentamerous forms have 4 tubules, and other groups have 6, but there are exceptions, as *Hydrophilus* with 6 and *Sitaris* with 4. The Lepidoptera, with rare exceptions, have always 6 tubules in both larvae and adults, but the 3 on each side branch from a common stalk. In *Galleria melonella*, however, there are numerous irregularly branched tubules from each stalk, and in certain Tineidae the 6 typical tubules of the larva are reduced to one pair in the adult. Among Hymenoptera there are 20 to 25 tubules in adult Tenthredinidae, only 6 in some ants, but in most forms a larger number is present, 12 to 150, generally arranged in 2, 3, or 4 groups. In larval Hymenoptera the number of tubules is generally 4, but there appear to be only 2 or 3 in chalcid larvae (Thomsen, 1927). The Diptera, both larvae and adults, generally have but 4 tubules. In some families all arise separately from the intestine; in others they are united in 2 groups of 2 each. *Culex* and *Psychoda* have 5 tubules.

It is difficult to form an opinion as to what may have been the primary number of Malpighian tubules in insects, but from the foregoing review it is evident that it was not large, since, when the tubules are numerous, they are usually arranged in a few groups. Wheeler concluded that the primitive insects probably had 6 excretory diverticula of the intestine, corresponding to the grooves between the usual 6 longitudinal folds of the proctodaeal wall.

A description of the histology and function of the Malpighian tubules will be given in the following chapter.

The Anterior Intestine.—The part of the intestine between the bases of the Malpighian tubules and the rectum is frequently a simple tube showing no differentiation into parts; it may be short and straight (Fig. 199, *AInt*), dilated into a saclike chamber (Fig. 196, 207 A), or greatly lengthened and variously looped and coiled (Fig. 198, 210 A). Very commonly, however, the anterior intestine is more or less distinctly divided into an anterior *ileum* (Fig. 195, *Il*) and a posterior *colon* (*Cln*), which may differ in histological characters and are usually separated by a constriction of the intestinal wall. The two parts are sometimes designated the "small intestine" and "large intestine," but their relative dimensions are not always in keeping with these terms.

The Posterior Intestine, or Rectum.—The opening from the anterior intestine into the posterior intestine is often guarded by a circular fold or group of lobes termed the *rectal valve.* In some cases a fold resembling the cardiac valve is formed by the invagination of the posterior end of the anterior intestine into the rectum; in others the walls of the rectum at the mouth of the opening are produced into opposing lobes forming an occlusor mechanism similar to the pyloric valve in the anterior end of the proctodaeum.

The muscular sheath of the posterior intestine, when fully developed, consists of internal circular fibers and external longitudinal fibers, but the strength of the muscularis varies much in different insects, and fibers of either set may be lacking. The longitudinal fibers are often collected into six external lengthwise bands. According to Davis (1927), there is in *Stenopelmatus* a layer of scattered internal longitudinal fibers inside the circular muscles of the rectum. In the region of the anus the circular muscles are usually well developed, forming here a group that functions as an anal sphincter. A peritoneal sheath is usually absent, but some investigators report the presence of a connective tissue membrane surrounding the muscularis.

An unusual condition exists in the larvae of most Lepidoptera, in which the rectum is provided with cellular membranes lying beneath the muscularis, which are penetrated by the Malpighian tubules. As described by Ishimori (1924) there are two of these rectal membranes, the outer one composed of a single layer of cells, the inner of two layers. The six Malpighian tubules enter beneath the outer membrane near the anterior end of the rectum (Fig. 207 A, *Mal*) and run posteriorly in the space between the two membranes; then they penetrate the inner double membrane and turn forward in the space between this membrane and the epithelium of the rectal wall. Here the tubules are either disposed in various convolutions and loops before they end, or they break up into a plexus of reuniting branches. Ishimori distinguishes five types of patterns formed by the terminal parts of the tubules, mostly characteristic of groups of families. In the Hepialidae alone the tubules end in the body cavity, and the rectum lacks the membranous sheaths.

The Rectal Organs.—In most insects the epithelium and intima of the rectal sac form structures commonly known as the "rectal glands." The organs in question take on two principal forms: In one they appear as oval, or elongate, padlike thickenings of the intestinal wall; in the other they are conical processes projecting from the wall into the lumen. Hence, to be noncommittal in the matter of function, we may describe the organs as *rectal pads* and *rectal papillae*.

The rectal pads are areas of the wall of the rectum on which the epithelium is composed of high, columnar cells forming elongate oval bodies elevated on the side toward the lumen (Fig. 208 A). The intima is usually thin over the surface of each pad but forms a thickened rim around its margin. Typically the rectal pads are six in number, equally spaced around the anterior part of the rectal sac, with their long axes longitudinal. In some cases, however, there are but three, as in the larvae of Odonata, while in others there may be a much greater number, as in Mecoptera, Trichoptera, and Lepidoptera. The organs are said to be absent in Ephemerida, Hemiptera, Coleoptera, and in most holometabolous larvae; but they are known to exist in representatives of Plecoptera, Odonata, Orthoptera, Neuroptera, Trichoptera, Lepidoptera, Mecoptera, and Hymenoptera, though in some members of these orders they are but little developed or are absent.

It is shown by Tonkov (1923, 1925) that two types of structure may be distinguished in the rectal pads of different insects. The first is a simple type, occurring in Plecoptera, Odonata, and Orthoptera, in which each organ consists of a single layer of cells (Fig. 208 A). In the second type there are two layers of cells, and organs of this variety may be either compact, as in the Mecoptera, Lepidoptera, and some Hymenoptera, or hollow, as in Neuroptera and certain Hymenoptera, owing to the presence of a lumen between the two cell layers (B). The origin of the two-layer structure of the rectal organs has been studied in *Vespa vulgaris* by Evenius (1933), who says that the inner layer represents the normal wall of the rectum, but that the outer layer is derived from cells lying originally in the body cavity around the proctodaeum, which gradually approach the rectum and become stratified upon it to form the outer walls of the rectal organs.

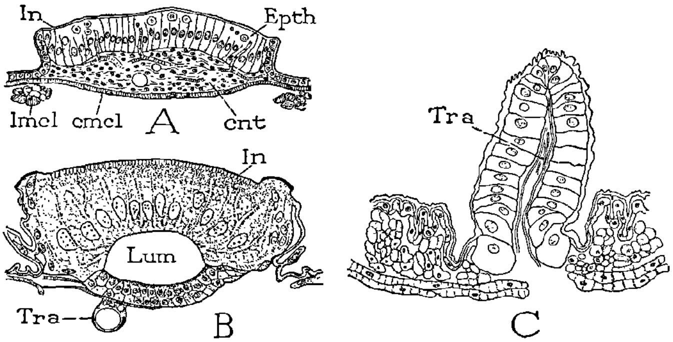

Fig. 208.—Examples of different types of rectal organs ("rectal glands"). A, section of simple padlike organ of *Eremobia*. (*From Faussek*, 1887.) B, hollow padlike organ of *Apis mellifica*. (*From Trappmann*, 1923.) C, papilla-like organ of the mydas fly. (*From Jahn*, 1930.)

Rectal organs of the papilliform type occur in the Diptera and Siphonaptera. The rectal papillae are hollow, conical invaginations of the intestinal wall (Fig. 208 C). The position of each is marked externally by a pit, which is penetrated by ramifying tracheal branches (*Tra*). According to Engel (1924), the usual number of rectal papillae in the Diptera is four or six, the larger number being confined to the Orthorrhapha; in *Culex pipiens* and in *Atherix ibis* there are four in the male and six in the female. The typical arrangement of the papillae is in a circle around the anterior end of the rectum, but in some species the position is irregular, and all the organs may fall into a single longitudinal row. In the Mydas fly *Mydas clavatus*, Jahn (1930) reports the presence of about 33 rectal papillae disposed approximately in three longitudinal rows.

The function of the rectal pads or papillae is not definitely known in any case. The supposed glandular nature of the organs has never been demonstrated, and some writers have suggested that the organs serve for breaking up the peritrophic membrane, others that they eliminate carbon dioxide from the blood, and still others that they absorb the food residue from the rectum. Wigglesworth (1932) has advanced the theory that the organs reabsorb water from the faecal matter in the rectum and thus play an important part in water conservation, but the structure of the organs does not in all cases appear to be particularly adapted to this role, since the covering cuticula is often more dense on the surface of the pads than elsewhere in the rectum (Fig. 208 B).

Various other types of rectal organs occur frequently in larval insects, some having the form of simple eversible lobes, and others a more complicated structure, such as the well-known rectal gills of anisopteran dragonfly larvae.

Anal Glands.—In some insects, especially in the Coleoptera, there are ectodermal glands opening in such close proximity to the posterior end of the rectum that they are known as *anal glands*. These glands serve principally as organs of defense by discharging substances having strong and repulsive odors, or even explosive properties, as in the case of the bombardier beetle.

6. THE FILTER CHAMBER

In most of the Homoptera an unusual modification of the alimentary canal produces an organ known as the *filter chamber*, in which two ordinarily distant parts of the digestive tube are closely applied to each other and bound together by a connective tissue sheath (Fig. 209 A, *FC*). The parts involved in the filter chamber are usually the two extremities of the mesenteron and the anterior end of the proctodaeum. The organ thus formed is supposed to be a device for allowing some of the excess water and soluble carbohydrates of the food to be eliminated by diffusing directly from the anterior part of the stomach into the intestine, while the protein and fatty materials are retained to be digested and absorbed in the stomach.

The ventriculus of a typical homopterous alimentary canal consists of three parts. The first (Fig. 209 A, 1*Vent*) is an anterior enlargement lying immediately posterior to the stomodaeal valve (*SVlv*) and is enclosed in the filter chamber; the second is a large, croplike sac (2*Vent*) serving as a storage reservoir; the third is a long, tubular section (3*Vent*), the functional stomach of the insect, which turns anteriorly to reenter the filter chamber (*FC*) and opens into the proctodaeal intestine (*AInt*) at the point where the Malpighian tubules (*Mal*) are given off from the latter within the chamber. Most writers apparently have not understood the morphological relationships of the various parts in the complicated homopterous alimentary canal, since the two ventricular sacs are usually regarded as parts of the crop. Cecil (1930), however, in a paper on *Philaenus*, states that the "mid-intestine or stomach is that part of the alimentary canal posterior to the oesophageal valve and anterior to the Malpighian tubules." The histology of the digestive tube, as shown by Cecil in *Philaenus* and by Hickernell (1920) in the cicada, leaves little doubt that the ventriculus begins and ends in the filter chamber, though Hickernell calls the anterior part in the filter chamber the "anterior crop," and the second stomach sac the "posterior crop."

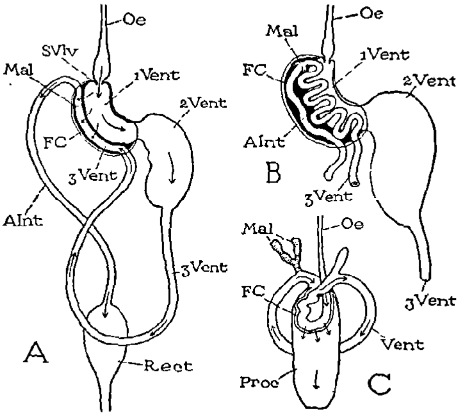

Fig. 209.—The filter chamber of Homoptera. A, diagram of a simple type of filter chamber in which the two extremities of the ventriculus and the anterior end of the intestine are bound together in a common sheath. B, the ventriculus convoluted in the filter chamber and the intestine issuing from its posterior end. C, the filter chamber of *Lecanium*, diagrammatic. (*From Weber*, 1930.)

In most of the Homoptera the intestine, instead of issuing from the anterior end of the filter chamber, as shown at A of the diagram (Fig. 209), makes a loop within the chamber and emerges at the posterior end (B). By this complication the chamber evidently becomes more efficient as a filter, and its effectiveness is usually again increased by a zigzag course assumed by the ventricular and intestinal tubes within the chamber, and by their enclosure in deep folds of the epithelium of the first ventricular sac (Figs. 209 B, 210 D).

A more primitive type of filter chamber is described by Knowlton (1925) in the aphid *Longistima caryae*. The digestive tract of this insect is for the most part simple, but, Knowlton says, "for a short distance the tube is complicated by the anterior end of the mid-intestine doubling back and forming a loop through the muscular wall of the posterior end of the mid-intestine and the anterior end of the hind-intestine" (Fig. 210 A). An even simpler form of the organ occurs in some of the Coccidae, as in *Lecanium* (Fig. 209 C), where the anterior end of the ventriculus (*Vent*) forms a loop imbedded in the anterior end of the short, wide proctodaeum (*Proc*). Here the Malpighian tubules arise outside the region of the filter chamber. If this structure in the Coccidae is the prototype of the filter chamber in other Homoptera, it suggests that the muscular and peritoneal coverings of the organ are derived from the proctodaeum rather than from the mesenteron.

An extreme type of modification in the alimentary canal occurs in the diaspine Coccidae, in which the middle part of the tube is all but obliterated. The oesophagus ends in a stomach sac, which, according to Berlese (1909), has no connection with the intestine except for two ligaments. Childs (1914), however, believes that there is a very delicate membranous union between the stomach and the intestine in *Epidiaspis piricola*, which is so easily destroyed in specimens prepared for histological study that it is usually lost. In any case it seems probable that most of the food material passes through the walls of the stomach into the blood, and that superfluous as well as waste substances are excreted from the blood through the walls of the intestine and the two huge Malpighian vessels.

The usual structure of the filter chamber is well shown in its more simple form of development in the Cicadidae. The alimentary canal of the cicada (Fig. 210 B) is extremely long relative to the length of the body; for most of its extent it is a slender tube thrown into many transverse loops against the dorsal wall of the abdomen above the great air chamber that usurps a major part of the abdominal cavity. The oesophagus (*Oe*) opens through a stomodaeal valve into a large S-shaped stomach region composed of two elongate sacs (*FC*, 2*Vent*), the anterior of which is the filter chamber and contains the first section of the ventriculus (Fig. 209 A, 1*Vent*). From the second stomach sac the tubular third section of the ventriculus (Fig. 210 B, 3*Vent*) goes first posteriorly and then turns forward to reenter the filter chamber, within which it continues anteriorly in many loops buried in the epithelial wall of the first part of the ventriculus, until it ends at its junction with the proctodaeum. The latter emerges from the anterior end of the filter chamber as a narrow intestinal tube (*AInt*), which turns posteriorly and after many crosswise loops finds its way to the rectum (*Rect*). The four Malpighian tubules (*Mal*), arising from two short basal trunks within the filter chamber, go posteriorly and emerge from the posterior end of the chamber. An interesting account of the histology of the alimentary canal of *Magicicada septendecim* is given by Hickernell (1920), who shows that the third tubular section of the mesenteron (3*Vent*) is the part of the stomach in which the secretory processes are most active.

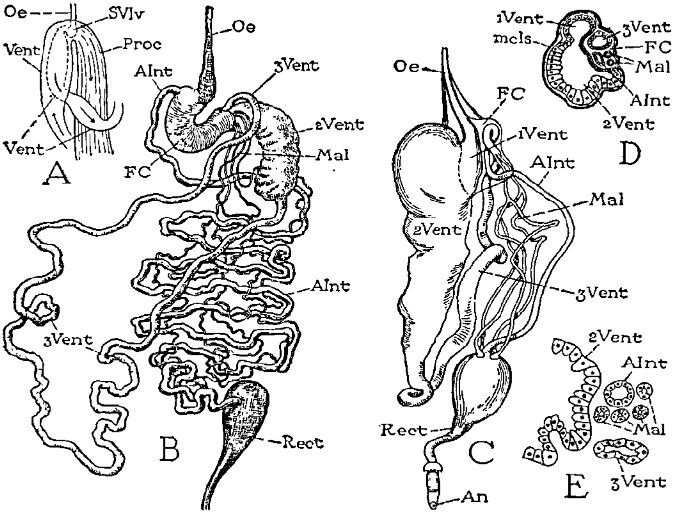

Fig. 210.—The alimentary canal and filter chamber of Homoptera. A, *Longistigma caryae*, the two extremities of the ventriculus and the upper end of the proctodaeum. (*From Knowlton*, 1925.) B, *Magicicada septendecim*, entire alimentary canal. C, *Tricentrus albomaculatus*, entire alimentary canal. D, same, section of filter chamber. E, same, section behind the filter chamber through two parts of ventriculus, anterior intestine, and Malpighian tubules. (C, D, E *from Kershaw*, 1913.)

The croplike second part (2*Vent*) serves as a food reservoir and is often found distended with liquid.

In the more typical structure of the filter chamber, as already noted, the anterior end of the intestine forms a loop within the chamber and emerges from the posterior end of the latter (Fig. 209 B). This type of structure is shown in a simple form in the membracid *Tricentrus albomaculatus* (Fig. 210 C) described by Kershaw (1913). A cross section of a filter chamber of this form taken below the origin of the Malpighian tubules (D) cuts through the first ventricular chamber (1*Vent*) at its junction with the large second ventricular sac (2*Vent*), through the posterior end of the ascending third part of the ventriculus (3*Vent*), and the descending intestinal tube (*AInt*), as well as through the Malpighian tubules (*Mal*), the two basal stalks of which in *Tricentrus* do not divide until after they emerge from the filter chamber (C, E, *Mal*).

GLOSSARY OF TERMS APPLIED TO THE ALIMENTARY CANAL

Alimentary Canal.—The food tube traversing the body; in insects consisting of an endodermal *mesenteron*, an ectodermal *stomodaeum*, and an ectodermal *proctodaeum*. (*Darmkanal.*)

Anal Glands.—Ectodermal glands opening close to the anus.

Anterior Intestine (*AInt*).—The part of the proctodaeum between the ventriculus and the rectum, or between the pylorus and the rectum when a proctodaeal pyloric region is distinct. (*Small intestine, Dünndarm.*)

Anterior Pharynx (*APhy*).—The precerebral part of the pharynx in insects having also a pharyngeal section of the stomodaeum behind the brain.

Anus (*An*).—The posterior opening of the alimentary canal.

Buccal Cavity (*BuC*).—The first part of the stomodaeum, lying just within the mouth; its dilator muscles arising on the clypeus, and inserted before the frontal ganglion and its connectives.

Cardia (*Car*).—The anterior part of the ventriculus; in many Diptera taking the form of a small spherical sac, often mistaken for a proventriculus.

Cardiac Valve (*SVlv*).—See *stomodaeal valve.*

Colon (*Cln*).—The posterior part of the anterior intestine, between the ileum and the rectum. (*Large intestine, Dickdarm.*)

Crop, or Ingluvies (*Cr*).—An enlargement of the oesophageal region of the stomodaeum. (*Kropf, jabot.*)

Digestive Cells (*dg*).—The secretory and absorptive cells of the ventricular epithelium as distinguished from the regenerative cells.

Dilator Muscles.—Muscles extending from the body wall to the alimentary canal; called also *suspensory muscles.*

Filter Chamber (*FC*).—A part of the alimentary canal in Homoptera in which the two ends of the ventriculus and the beginning of the intestine are bound together in a membranous and muscular sheath.

Ileum (*Il*).—The anterior part of the anterior intestine, between the ventriculus or pylorus and the colon. (*Small intestine, Dünndarm.*)

Ingluvies.—See *crop.*

Intestine (*Int*).—The proctodaeum, or the part of the proctodaeum beyond the pylorus. (The term applied also to the entire alimentary canal.)

Mesenteron (*Ment*).—The endodermal stomach, or *ventriculus*, of the insect. (*Mid-gut, midintestine, Mitteldarm, Chylusdarm, Magen.*)

Mouth (*Mth*).—The anterior opening of the stomodaeum; primarily located in the ventral wall of the head, but in most sucking insects retracted into the head with the transformation of the cibarium into a sucking pump, in which case the *functional mouth* (*mth*) is the entrance to the pump chamber.

Nidus.—A group of regenerative cells in the ventricular epithelium. (*Regenerationsherde.*)

Oesophagus (*Oe*).—A tubular part of the stomodaeum between the pharynx and crop, or sometimes extending to the stomach. (*Speiseröhre.*)

Peritrophic Membrane (*PMb*).—A cylindrical membranous envelope surrounding the food in the ventriculus, and sometimes extending into the proctodaeum; generated from the ventricular epithelium, either from all or a part of the length of the latter or from a ring of specialized cells at its anterior end.

Pharynx (*Phy*).—The part of the stomodaeum between the mouth or buccal cavity and the oesophagus, the dorsal dilator muscles of which arise on the frons and the dorsal part of the cranium and are inserted posterior to the frontal ganglion and its connectives; usually not extending beyond the nerve ring of the head, but in some insects there is a *posterior pharynx* behind the brain.

Posterior Intestine (*PInt*), **or Rectum** (*Rect*).—The terminal section of the proctodaeum commonly termed the "rectum," but usually divided into an anterior *rectal sac* (*rsc*), and a posterior *rectum proper* (*rect*). (*Mastdarm.*)

Posterior Pharynx (*PPhy*).—A pharyngeal chamber of the stomodaeum behind the brain, present in Orthoptera, Coleoptera, and some other insects.

Proctodaeum (*Proc*).—The posterior ectodermal part of the alimentary canal. (*Hind gut, hind intestine, Hinterdarm, Enddarm.*)

Proventriculus (*Pvent*).—A specialized part of the stomodaeum immediately anterior to the ventriculus. (*Gizzard, gésier, chewing stomach, Kaumagen.*)

Pyloric Valve (*PVlv*).—A valvular fold usually situated in the pyloric region of the proctodaeum, but sometimes formed by the posterior end of the ventriculus.

Pylorus (*Py*).—An anterior part of the proctodaeum usually containing the pyloric valve, sometimes distinctly differentiated from the true intestinal region and forming anatomically the rear end of the stomach.

Rectal "Glands."—Padlike or papilliform structures on the inner wall of the rectal sac (not demonstrated to be glands).

Rectal Sac (*rsc*).—The enlarged anterior part of the rectum, sometimes produced into a large *rectal caecum.*

Rectal Valve.—A circular or lobate fold of the proctodaeal wall between the anterior intestine and the rectum.

Rectum (*Rect*).—The posterior intestine, including the *rectal sac* and the posterior, narrow *rectum proper* opening at the anus.

Regenerative Cells (*rg*).—The cells that generate the replacement cells of the ventricular epithelium.

Regenerative Crypt (*Cpt*).—A pocket of the ventricular epithelium containing a group (nidus) of regenerative cells.

Stomach.—The ventriculus, or mesenteron.

Stomach Mouth.—A term sometimes given to the proventricular apparatus forming a mouthlike entrance to the ventriculus. (*Magenmund, Pumpmagen.*)

Stomodaeal Valve (*SVlv*).—The cylindrical or funnel-shaped invagination of the posterior end of the stomodaeum into the cardiac part of the ventriculus. (*Cardiac valve.*)

Stomodaeum (*Stom*).—The anterior ectodermal part of the alimentary canal. (*Fore-gut, fore intestine, Vorderdarm.*)

Striated Border (*sb*).—The inner cytoplasmic layer of the ventricular epithelial cells with fine lines perpendicular to the surface. (*Stäbchensaum, Härchensaum, plateau strié, bordure en brosse.*)

Suspensory Muscles.—See *dilator muscles.*

Ventriculus (*Vent*).—The endodermal stomach of the insect. (See *mesenteron.*)

CHAPTER XIV

THE ORGANS OF DISTRIBUTION, CONSERVATION, AND ELIMINATION

The organs and tissues to be described in this chapter have no morphological relation to one another, but they have this in common that they are all closely associated with the blood, or circulating medium of the body cavity.

The products of digestion, on being passed through the walls of the alimentary canal, are discharged directly into the blood and must be carried by the latter to the body tissues. The mechanism of food distribution in insects includes the blood as the carrier, and the organs that keep the blood in circulation, namely, the heart, the diaphragms, and other pulsating structures. Conservation and elaboration of reserve food materials are functions of the fat body. The elimination of waste products is accomplished by various organs, including the body wall, the alimentary canal, the tracheal tubes, and special organs of excretion.

1. THE BLOOD

The body liquid of insects, known as the *blood*, in common with that of most other animals, consists of a fluid part, the *blood plasma*, or *haemolymph*, and of free floating cells, the *blood corpuscles*, or *haemocytes*.

During the development of the arthropod various free spaces appear in the body of the embryo between the principal germ layers. These spaces, which are remnants of the primitive blastocoele, become filled with a clear liquid and constitute the *haemocoele*, or primary blood cavity of the animal. The principal haemocoele cavities of the insect embryo are a ventral *epineural sinus* (Fig. 19 B, *EpnS*) lying below the yolk, and a dorsal *cardiac sinus* (Fig. 21, *CdS*) extending along the midline of the back above the yolk. Most of the cardiac sinus eventually becomes enclosed in a mesodermal tube, which is the dorsal blood vessel. The epineural sinus remains open; it expands laterally and unites with the cavities of the rudimentary coelomic sacs (Fig. 19 B, *Coel*), or with the coelomic spaces between the mesoderm layers (Fig. 21), to become a part of the definitive body cavity (*BC*). The clear lymphlike liquid of the embryonic haemocoele thus comes to fill all the spaces of the body and appendages not occupied by cellular tissues and, together with other substances later added to it, forms the plasmatic haemolymph of the definitive body cavity.

Almost from the beginning the embryonic haemolymph contains free floating cells (Fig. 21, *BCls*), which become the definitive blood cells, or haemocytes. The blood cells of the embryo are described as being formed by proliferation from the ventral part of the mesoderm (Fig. 19 B, *BCls*); but the phagocytic and digestive properties which they later develop suggest an affinity with the endoderm. It may be possible, therefore, that the blood cells are really derived from the intermediate strand of the endoderm, and that they are genetically related to the vitellophags and the cells of the mesenteron. The blood cells multiply by mitotic and amitotic division, and it is probable that their numbers are kept up during postembryonic stages entirely by division, though various writers have claimed that new haemocytes are produced in the adult from cell masses lying near the heart, from the fat tissue, from the epidermis, or from unknown sources.

The Haemolymph.—The plasma of insect blood is a somewhat viscid liquid. Usually it is transparent, but, owing to contained pigments, it is commonly tinted with amber, yellow, brown, or green, or, especially in larval insects, more strongly and often brightly colored with these same hues and sometimes with orange and red. The blood color is characteristic of species or of different stages of the same species, but not of families or orders. It has no correlation with the nature or color of the food, all shades of blood tints being found in both herbivorous and carnivorous insects. Often the blood is darker or more brightly colored in the larvae of holometabolous insects than in the adults, in which pale tints are more generally prevalent. In lepidopterous larvae and pupae, according to Geyer (1913), there is in many species a difference of blood color between the sexes. As a rule the blood of female caterpillars is green, and that of male caterpillars pale yellow or colorless. The green color of the female blood, Geyer says, is due to chlorophyll dissolved in the plasma, that of the male to xanthophyll.

Composition of the Haemolymph.—Numerous substances are contained in the blood plasma; some are component parts of it, but most of them are associated bodies or the products of digestion, oxidation, and metabolism. Cuénot (1891) distinguished in the blood of the larva of *Saturnia pyri* four principal groups of ingredients. First, an albuminoid, *haemoxanthin*, primarily yellow but becoming blackish brown by the absorption of oxygen from the air; second, *fibrin*, which he says is very abundant; third, *lutein*, a yellow substance extracted by alcohol; and, fourth, *uranidin*, normally dissolved in the plasma, but precipitated in extracted blood as blackish-green granules. All these substances, however, Cuénot says, are not present in the blood of all insects. The blood albumins he believed to be nutritive materials derived from the food; the lutein, which is particularly abundant in caterpillars, he attributed to the luteins of plants (chlorophyll and xanthophyll).

A summary of later studies on the composition of insect blood plasma given by Muttkowski (1923) enumerates a long list of substances of several physiological groups. The haemolymph, Muttkowski says, contains serum, gelatin, fibrinogen, and various substances in solution, including water, gases, salts, food materials, pigments, respiratory proteins, waste products, enzymes, and special substances. Water constitutes fully three-fourths of the plasma. The gases oxygen, nitrogen, and carbon dioxide are always present, the last being a waste product. In ashed blood, Muttkowski reports the finding of iron, copper, sodium, potassium, calcium, magnesium, and probably ammonia, present mostly in the form of chlorides, sulphates, nitrates, phosphates, and carbonates. During feeding, nitrites are present in abundance, but only nitrates are found in the blood of starved specimens. The organic content of the haemolymph includes albumin, globulin, fibrinogen, haemoxanthin, gelatin, nucleoprotein, and during feeding various hydrolyzed proteins. Fat globules are always present but are said to be more abundant during feeding. Other groups of substances in the blood include waste products, pigments of various kinds, enzymes, and certain special substances, such as cantharidin characteristic of the blood of blister beetles (*Meloe*). Little is known specifically of the blood enzymes of insects, but the presence of enzymes is indicated by the histolysis of tissue fragments in the blood such as takes place particularly during the pupal metamorphosis. Analyses of the gas content of the blood of *Dytiscus* and *Hydrophilus* given by Barratt and Arnold (1911) show the presence of carbon dioxide and nitrogen, but no oxygen. These writers contend, therefore, that the insect blood serves as a nutritive medium but not as an oxygen carrier.

Hydrogen-ion Concentration in the Blood.—The blood of insects usually has an alkaline reaction. Studies made on the hydrogen-ion content show a considerable range of pH values, but it is likely that some of the differences recorded are the result of different methods of measurement. Thus Glaser (1925), from tests made on several species of Orthoptera, Diptera, and Lepidoptera, found a variation in the blood pH from 6.4 to 8.0, while Bodine (1926), studying the blood of various species of Acrididae, reports a range of pH values from 6.4 to 7.05. Both investigators agree that there is no correlation between the hydrogen-ion concentration of the blood and the age or sex of the insect. Glaser found no constant pH differences between larval, pupal, and imaginal stages of *Bombyx mori*, *Malacosoma americana*, and *Musca domestica;* and Bodine observes that fluctuations of pH values are not produced by differences of food. Making due allowance for errors of technique, it is evident that the hydrogen-ion concentration of insect blood ranges close to neutrality, but that it varies normally within rather wide limits as compared with that of human blood.

Respiratory Proteins of the Blood.—The principal oxygen-fixing proteins found in the blood of animals are haemoglobin and haemocyanin. The first is an iron compound having a bright-red color, which makes its presence easily detected. The second is a colorless compound of copper, which becomes blue on oxidation; but because it generally occurs in very small quantities in the blood, it usually does not make its presence visibly apparent.

The red respiratory protein haemoglobin, so characteristic of the blood of vertebrates, is present also in some invertebrate animals, including many Annelida, certain Mollusca, and some of the Arthropoda. Among insects it is notably present in the "bloodworms," which are the larvae of certain species of the dipterous genus *Chironomus.* These larvae are mostly aquatic and live either in tubes attached to the surface of submerged objects or in burrows in soft mud at the bottom of the water. They are conspicuous by reason of their bright-red color. A *Chironomus* larva, according to Leitch (1916), is by weight 50 per cent blood, and the blood has an oxygen capacity of 0.06 cubic centimeter per larva. The haemoglobin of the bloodworms, Leitch shows, is not a storer of oxygen, as had been supposed, but is a medium for oxygen transportation. "There is," she says, "a constant binding of oxygen at the surface of the body and the constant giving up of it on the interior," resulting in "a continuous mixing and interchange of oxidized and reduced blood kept in motion by the beating of the heart." The haemoglobin is carried in solution by the blood, and its quantity, Leitch observes, is just that amount which will enable the larva to utilize the small quantity of oxygen in its medium within the confinement of its tube or burrow. The *Chironomus* larvae have but a rudimentary tracheal system and the spiracles are closed. Their bodies are provided with external blood-containing filaments known as "blood gills," and yet it is claimed by Fox (1921) that these filaments have no respiratory function, the interchange of gases taking place through the general body integument.

Copper is known to be present in considerable quantity in the blood of many invertebrates. In some of the decapod crustaceans, in scorpions, and in the horseshoe crab, an organic copper compound, haemocyanin, is held in solution in the blood and is said to act as a respiratory oxygen-fixing medium.

The presence of haemocyanin in the blood of insects has not been definitely proved; but it has been shown by Muttkowski (1921, 1921*a*), from tests made on the ash of entire incinerated insects, that copper is of general occurrence in insects of all the principal orders and is present in nymphs, larvae, and adults. The amount of copper in insects he says is entirely comparable with that found in crayfish blood. Muttkowski infers, therefore, that the role of copper in insects is the same as that of copper in the decapods, "namely, that it serves as the nucleus of a respiratory protein—haemocyanin." It has not been found, however, that oxygen is present in the blood of insects lacking haemoglobin in amounts greater than that which would be normally dissolved in the plasma; though the quantity thus held in solution appears to be sufficient for the needs of many internal parasitic larvae.

The presence of copper in insects has been verified by Melvin (1931), who finds that, while measurable quantities of copper are present in newly hatched nymphs and in larvae, pupae, and adults, there is found a larger percentage of it in certain products given off by insects, such as cast skins, empty egg cases, and cocoon linings, than in the insects themselves.

The Haemocytes.—The cellular elements of insect blood occur in such variety of forms that it is impossible to give a satisfactory general description of them. The fact that they frequently take amoeboid shapes shows that they are cells of a primitive nature; and, as far as known, all the true blood corpuscles are descendants by division from the embryonic blood cells formed in the embryo (Fig. 19 B, *BCls*).

Attempts have been made by several writers to classify the blood cells of insects. Hollande (1911) differentiates four groups of them, distinguished as *proleucocytes, phagocytes, granular leucocytes,* and *oenocytoids,* which are present in insects generally, except that the last are absent in Orthoptera. The proleucocytes are young leucocytes, the cytoplasm of which is basophile, and which reproduce actively by mitotic division. From them are derived the other more specialized forms of haemocytes. The phagocytes are distinguished by their larger size, their hyaline cytoplasm, and their phagocytic activities. The granular leucocytes are characterized by a granular structure of their cytoplasm, and they also are sometimes phagocytic. The oenocytoids, so named from their resemblance to oenocytes, are large cells with rounded or spherical forms, incapable of phagocytosis, having a homogeneous cytoplasm strongly acidophile.

In addition to these more common forms of haemocytes, Hollande (1909, 1911) describes in certain Coleoptera and in the larvae of Lepidoptera other blood cells having oval or spherical forms in which the cytoplasm is filled with spherules, sometimes colorless, and sometimes tinted with yellow. These bodies he calls *cellules à sphérules.* They are particularly abundant in Coccinellidae, Chrysomelidae, and Cantharidae and give an opacity to the blood characteristic of these beetles. The spherules, Hollande says, are elaborated within the cell cytoplasm, and he believes they are enzyme-containing bodies. Eventually they are given off into the blood by the rupture or disintegration of the cell. The spherule cells of caterpillars differ in many ways from those of Coleoptera, but they appear to be cells of the same type. Still another form of haemocyte Hollande (1911) distinguishes as *adipoleucocytes,* these being blood cells in which the cytoplasm has become charged with small oily fat droplets.

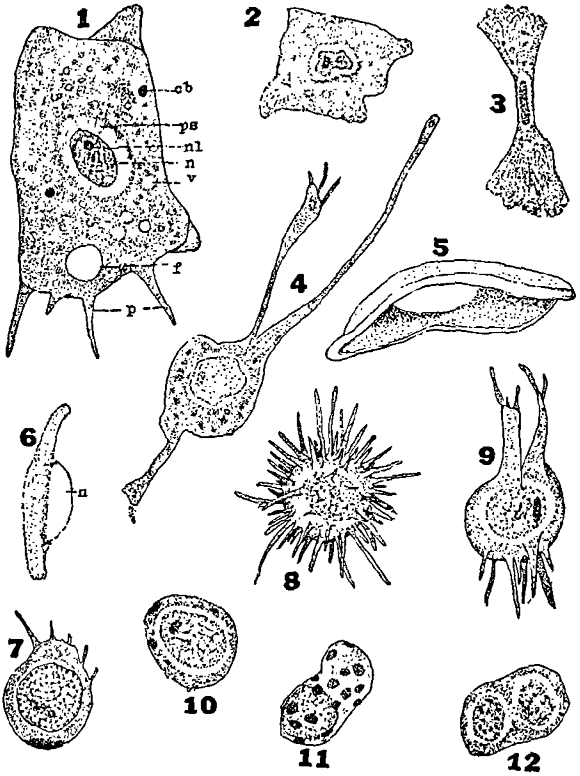

Fig. 211.—Examples of haemocytes of various insects. (*From Muttkowski,* 1924.) 1, *Dytiscus* larva. 2, 3, 4, 7, 9, *Leptinotarsa.* 5, *Aeschna.* 6, *Dytiscus.* 8, *Pieris rapae.* 10, *Enallagma.* 11, *Dytiscus* imago. 12, *Hydrophilus.*

In a more recent study of the blood cells of insects, Muttkowski (1924) recognizes two principal types of cells distinguished by differences in size, form, and staining reactions. The cells of one kind he calls *chromophile leucocytes,* because of the strong affinity of their cytoplasm for aniline dyes; those of the other, which are larger and color but faintly in aniline stains, he calls *amebocytes.* The chromophile leucocytes Muttkowski describes as rounded and slightly flattened bodies, which take on various forms (Fig. 211, 7 to 12). They may extend pseudopodia in varying numbers (7, 8), but the processes are always short. Some of these leucocytes are phagocytic, the phagocytic forms being particularly abundant during metamorphosis. The chromophile leucocytes are the more primitive blood cells, their nuclei are large, and they divide by mitosis. The simple forms of these cells are evidently the proleucocytes of Hollande.

The amoebocytes (Fig. 211, 1 to 6), as described by Muttkowski, are generally larger than the chromophile leucocytes and are more variable in size and shape. When active they resemble free amoebae (1), but they take on various forms when contracted or floating (5, 6). The nucleus is generally oval but is frequently irregular (2, 4) and is surrounded by a clear perinuclear area (1, *ps*). The cytoplasm is differentiated into a thin film of ectoplasm and a granular endoplasm, the latter containing numerous small vacuoles (*v*), occasionally cytoplasmic bodies (*cb*), and generally a few small fat globules (*f*). The pseudopodia (*p*) are usually slender but vary greatly in length and numbers (4); during coagulation of the blood they become enormously long, and in clotting they form a pseudopodial meshwork.

For a more complete review of the study of blood corpuscles in insects the student is referred to the work of Paillot (1933). In the blood of caterpillars Paillot distinguishes four principal types of cells, which he calls *micronucleocytes*, *macronucleocytes*, *micronucleocytes with spherules* (that is, having the cytoplasm filled with refringent granules), and *oenocytoids*. All forms are capable of mitotic division, each cell producing daughter cells of its own kind. Only the micronucleocytes are phagocytic. Blood cells similar to those of caterpillars, Paillot says, are found in the larva of *Neurotoma* (Hymenoptera), but in coleopterous larvae (*Hydrophilus* and Elateridae) the haemocytes are quite different and appear principally in two forms.

The Blood during Metamorphosis.—During the period of transformation from the larva to the imago in holometabolous insects, the blood becomes so charged with the debris of disintegrating tissues that the pupa appears to be filled with a thick, creamy pulp. At the beginning of metamorphosis the cells of the fat body detach themselves from one another and float free in the body liquid (Fig. 218, *FtCl*). Very soon they undergo a dissolution (*FtCl'*, *FtCl''*) by which their contents, consisting now principally of fat globules (*f*) and great numbers of small proteid granules (*a*), are set free in the blood. Among this mass of liberated material there may still be seen a few normal haemocytes (*BCl*).

With many insects, during the time of metamorphosis, the prevailing type of blood cells are the phagocytes, which are often distended with particles of degenerating tissues, especially muscle fragments. In the pupa of Diptera spherical bodies filled with muscle fragments (*sarcolytes*) are particularly abundant and are known as *spherules of granules*, or *Körnchenkugeln*. Most investigators have regarded these spherules as blood phagocytes gorged with ingested sarcolytes. It cannot always be demonstrated, however, that such bodies are of a cellular nature, and the writer (1924) has found that sarcolyte spherules, occurring in great abundance in the larva of the apple fruit fly *Rhagoletis pomonella* are almost certainly mere masses of sarcolytes given off directly from muscles undergoing histolysis. These sarcolyte spherules eventually break up and add their contents to the accumulation of material already in the blood. Included in the latter, besides the bodies already mentioned, are also numerous small nucleated masses of protoplasm (*caryolytes*) probably derived from the muscles, and great numbers of minute grains and other unidentifiable fragments of disintegrating tissues. Toward the end of the pupal period these temporary inclusions of the blood begin to disappear, probably going into solution by complete histolysis, and, shortly after the transformation to the adult, the blood again becomes clear and regains its normal condition.

Clotting of the Blood.—With most insects when the blood issues from a small wound it thickens and forms a viscous plug closing the aperture in the integument. This "clotting" of the insect blood has been studied by Muttkowski (1924*a*), by Yeager, Shull, and Farrar (1932), and by Yeager and Knight (1933). The last writers, after investigating the blood of 47 species, found that insects can be divided into three groups according to the clotting properties of the blood, as follows: (1) species in which clotting does not take place, (2) species in which clotting is produced mainly by an agglutination of the haemocytes, and (3) species in which clotting is principally a coagulation of the plasma. The grouping of species according to blood clotting has no relation to taxonomic classification. Insects having no clotting of the blood occur among Homoptera, Coleoptera, Lepidoptera, and Hymenoptera. The honey bee larva furnishes a typical example in this class, the nonclotting properties of its blood having been shown by Bishop, Briggs, and Ronsoni (1925). Insects forming a cellular coagulum include Orthoptera, Homoptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera; those in which the blood clot is principally a plasmatic coagulum occur in Heteroptera, Orthoptera, Coleoptera, and Lepidoptera.

Where clotting consists essentially of a coagulum formed by the blood cells, as in the cockroach, described by Yeager, Shull, and Farrar, the haemocytes throw out fine threadlike pseudopodia and become agglutinated into clumps, which spread out and appear to disintegrate. The plasma undergoes little change visible under the microscope and exhibits no fibrin formation, but there appears in it a granular precipitate. When the haemocytes take no part in the clotting, a fibrous coagulum is formed in the plasma. An intermediate type of clotting involving both the plasma and the haemocytes is described by Muttkowski (1924*a*). In this case the gelatin of the blood coagulates and the haemocytes become agglutinated, while those of the amoebiform type throw out pseudopodia and form a meshwork which contracts tightly and draws the lips of the wound together. In addition, however, a fibrous net is formed among the haemocytes, which, by contraction, brings about a still better closure of the wound and a complete stoppage of the blood flow. Muttkowski was able to demonstrate the effectiveness of the haemolymph alone to produce a clot by killing the haemocytes with cyanide fumes.

2. THE ORGANS OF CIRCULATION

The primary blood cavity of an animal is the embryonic haemocoele, or body space between the ectoderm and endoderm, which is the remnant of the earlier blastocoele left after the invasion of the latter by the gastric endoderm. The haemocoele in triploblastic animals is then again invaded by the mesoderm and in most cases is finally reduced to tracts enclosed in mesodermal walls, which constitute the blood vessels.

The cardiac sinus of the young insect embryo is the dorsal part of the haemocoele lying above the yolk or the alimentary canal between the upper ends of the lateral sheets of mesoderm (Fig. 21, *CdS*). As development proceeds, the mesoderm layers approach each other from opposite sides in the cardiac sinus; their opposing surfaces become hollowed lengthwise, and, when the two layers meet, the lips of their furrows unite to form a median dorsal tube. This mesodermal tube is the *dorsal blood vessel* (Figs. 22, 212, 214, *DV*). Its lumen is merely a restricted part of the cardiac sinus and is filled with blood liquid containing blood cells (Fig. 213 A, *BCls*). The dorsal vessel is the only part of the haemocoele of insects that is closed by definite walls; elsewhere the blood is contained in the body cavity because of the embryonic union of the ventral part of the haemocoele with the cavities of the coelomic sacs. In some of the other arthropods, however, as in the larger Crustacea and Arachnida, there may be present an elaborate system of blood vessels branching from the dorsal organ.

The parts of the dorsal mesoderm not included in the cardiac rudiments extend laterad in the upper part of the body from the walls of the dorsal vessel (Fig. 22, *DDph*) and are drawn out into thin sheets of cells. These cells give rise to the transverse dorsal muscles of the body and to connective tissue membranes more or less uniting the muscle fibers. The two wings thus formed extending laterad from the dorsal vessel constitute the *dorsal diaphragm* (Figs. 212, 213 A, *DDph*). The muscles become attached to the body wall along the lateral parts of the dorsum;

the membranes become continuous with the delicate peritoneal covering of the somatic muscles. The dorsal diaphragm shuts off a space in the upper part of the body cavity containing the dorsal blood vessel, which is known as the *pericardial cavity,* or *dorsal sinus* (Fig. 212, *DS*). In some insects the ventral transverse body muscles, stretched between the lateral margins of the sternal region of the body wall, form a continuous series of fine fibers often held in a delicate membrane. This structure, when present, constitutes a *ventral diaphragm* (Fig. 212, *VDph*). Beneath the ventral diaphragm is a free space enclosing the nerve cord (*VNC*) and the ventral longitudinal muscles; it represents a part of the embryonic epineural sinus and is known as the *ventral sinus* (*VS*) in the adult anatomy. The body cavity between the dorsal diaphragm and the ventral diaphragm, when the latter is present, containing the principal visceral organs is the *perivisceral sinus* (Fig. 212, *PvS*).

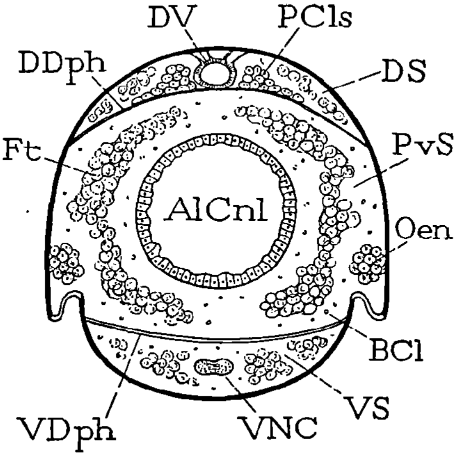

Fig. 212.—Diagrammatic cross section showing subdivisions of the body cavity. *AlCnl,* alimentary canal; *BCl,* blood cell; *DDph,* dorsal diaphragm; *DS,* dorsal sinus; *DV,* dorsal blood vessel; *Ft,* fat tissue; *Oen,* oenocytes; *PCls,* pericardial nephrocytes; *PvS,* perivisceral sinus; *VDph,* ventral diaphragm; *VNC,* ventral nerve cord; *VS,* ventral sinus.

The dorsal vessel is regularly pulsatile and is the principal organ by which the blood is kept in motion. The dorsal and ventral diaphragms, however, are rhythmically contractile and function as important adjuncts to the dorsal vessel in the circulation of the blood. Finally, there are present in many insects other pulsating organs located in various parts of the body and in the appendages, which apparently serve to drive the blood into the extremities.

The Dorsal Vessel.—The dorsal blood vessel when fully developed extends from the posterior end of the abdomen into the head. The organ is differentiated into an anterior part known as the *aorta,* and a posterior part called the *heart,* but, while the two sections are anatomically different, their distinguishing features are difficult to define. The heart is in general the pulsating part of the tube, though the aorta frequently is provided with pulsating vesicular diverticula, and, according to Wettinger (1927), the dorsal vessel of the larva of *Tipula selene* pulsates throughout its length. The cardiac section is usually confined to the abdomen, but it may extend into the thorax. The heart is characteristically chambered, that is, slightly dilated in each body segment, but the pulsating vesicles of the aorta also are segmental dilatations that may be regarded as of the same nature as the cardiac chambers. The heart is provided with openings (ostia) for the admission of the blood, and the aorta likewise may have apertures for the same purpose.

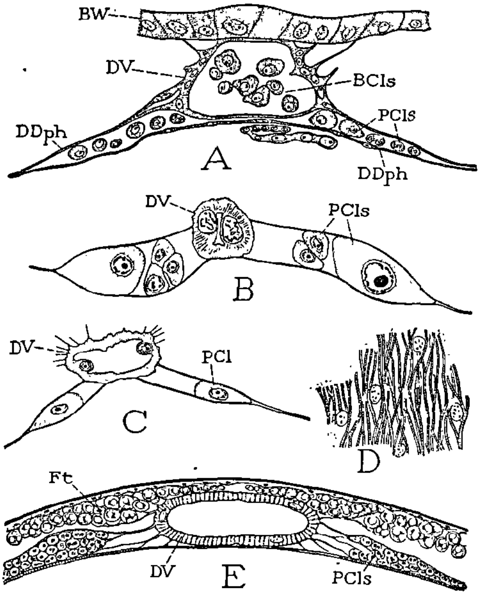

FIG. 213.—Structure of the dorsal blood vessel and associated tissues as seen in sections. A, heart of proctotrypid larva, *Phaenoserphus viator.* (*From Eastham,* 1929.) B, middle part of dorsal vessel of a sarcophagid larva, *Miltogramma punctatum.* (*From W. R. Thompson,* 1921.) C, posterior part of same. D, tangential section of heart wall of *Aeschna* larva. (*From Zawarzin,* 1911.) E, heart of adult *Apis mellifica* and neighboring parts of dorsal sinus.

The Heart.—The cardiac part of the dorsal vessel is usually marked by the presence of more or less distinct symmetrical segmental swellings of the tube (Fig. 215 A, *Ht*). These dilatations are known as the *chambers* of the heart. Typically, each heart chamber has a pair of vertical or oblique slitlike openings, the *ostia* (*Ost*), in its lateral walls, one ostium on each side, placed generally behind the middle of the chamber, and sometimes close to the posterior end. In some insects the cardiac chambers are separated by well-marked constrictions; in others they are apparent only as slightly widened parts of the vessel. In general there are no internal valves between the heart chambers except the ostial flaps, to be described presently, but Wettinger (1927) reports the presence of well-developed valvular structures in the heart walls of the larva of *Tipula selene* in addition to the ostial flaps, and Popovici-Baznosanu (1905) describes a pair of valves in the heart of certain chironomid larvae lying just before the last cardiac chamber, which evidently prevent the backward flow of the blood into the latter. In some other chironomid larvae the same writer finds swellings of the heart wall between the consecutive pairs of ostia, but these structures he says are protruding heart cells and not valves. Valve-like folds of the heart wall in some cases may be the lips of closed and otherwise functionless ostia.

The chambered part of the dorsal vessel is usually limited to the abdominal region of the body and commonly begins in the second abdominal segment (Fig. 215 B). In Blattidae, however, according to Brocher (1922), and in *Japyx* (Fig. 214), as shown by Grassi (1887), there is a typical cardiac chamber not only in the first abdominal segment but also in the third and the second segments of the thorax, each provided with a pair of lateral ostia. In the larvae of Ephemerida, according to Popovici-Baznosanu (1905), a pair of ostia is present in the metathorax. Ampulla-like enlargements of the aorta occur in the two wing-bearing segments and in the first abdominal segment of various insects, sometimes provided with ostial openings, but these aortic swellings or diverticula do not have the usual structure of the cardiac chambers.

The number of chambers in the abdominal section of the dorsal vessel may coincide with the number of segments occupied here by the tube, the maximum being nine. But generally there is not a distinct chamber in the first segment, and the number of chambers may be variously reduced to a minimum of one, as in Mallophaga and Anoplura, though the single large terminal swelling of the heart in these insects is probably a compound chamber, since it contains two or three pairs of ostia (Fulmek, 1906). The heart of larval Odonata has a single large posterior chamber (Zawarzin, 1911; Brocher, 1917*a*) provided with two pairs of ostia in Aeschnidae and one pair in Agrionidae, and having two pairs of alary muscles. In the hemipteron *Nezara* the heart, as described by Malouf (1933), consists likewise of a single large swelling of the dorsal vessel, provided with three pairs of ostia.

Though reduction in the number of chambers in the heart usually results from a suppression of the cardiac swellings in the anterior abdominal segments, the heart may be shortened also at the posterior end. The last chamber of the heart commonly ends either abruptly or in a narrowed tapering process that may extend posteriorly through the tenth abdominal segment. The ~~end of the~~ vessel in either case is generally closed; in certain dipterous larvae (*Tipula*, *Chironomus*) the heart is said to have a dorsal terminal opening, but it is possible that this median ostium represents the last pair of ostia united dorsally in a common aperture. In the larvae of Ephemerida the heart terminates in three slender branches which open into the bases of the cerci and the median caudal filament.

The typical cardiac ostia have usually the form of vertical or oblique slits in the sides of the segmental chambers of the heart. Frequently the openings lie in deep lateral inflections of the heart walls, and these ostial pouches, projecting inward and forward within the lumen of the heart, form a series of paired valve-like flaps having the true ostia at their free inner ends. The flaps virtually mark the division of the cardiac tube into chambers. The ostial valves evidently are so constructed as to admit the blood into the heart when the wave of diastole runs forward through the tube, and to prevent its escape during systole; they possibly serve also to obstruct a rearward flow of blood within the vessel; and yet the heart of certain insects is known at times to reverse the direction of its beat, and to cause a backward flow of blood when the systolic waves run caudad.

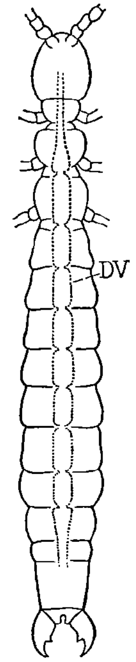

FIG. 214.—Dorsal blood vessel of *Japyx*. (*From* Grassi, 1887.)

The walls of the heart consist of muscle tissue immediately derived from the cardioblasts, or heart-forming cells of the embryonic mesoderm, which are converted into semicircular or circular striated muscle fibers that compose the heart tube (Fig. 213). In larval insects the striations of the cardiac fibers are sometimes indistinct or not evident. The ostial valves are also muscular, and therefore probably contractile. The lining of the heart is simply the normal muscle surface, consisting usually of a thin layer of hyaline sarcoplasm beneath a delicate limiting membrane. Outside the heart there may be a sheath of adventitious connective tissue. The vessel is usually suspended from the dorsal wall of the abdomen by fine radiating strands attached to the epidermis (Fig. 212), which appear to be filamentous processes of the heart walls (Fig. 213 A).

The mechanism of the heart is not fully understood. The contractions of the organ are produced undoubtedly by the muscles of the heart walls. Diastole, it is often assumed, is effected by the muscles of the diaphragm, but these muscles are attached to the ventral wall of the heart, and it has been observed in some cases that the heart continues to beat when the diaphragm muscles are cut. Since the systolic waves run through the tube, it would seem that the successive chambers may be expanded by the blood forced into them. While ordinarily the succession of contractions in the dorsal vessel is in a forward direction, a temporary reversal of the heart beat has been observed in various insects. This appears to be a normal process and recently has been carefully studied by Gerould (1929, and other papers). A periodic reversal of the heart beat, Gerould finds, occurs particularly in Lepidoptera at the end of the larval period and may continue through the pupal and imaginal periods. In the silkworm, phases of antiperistalsis begin about 48 hours before pupation, alternating with phases of forward beating. Pupation is accompanied by a vigorous backward pulsation, and during the pupal and imaginal periods the heart beats regularly with alternating forward and backward series of pulsations, the time of each phase being greatly shortened in the adult. A reversed flow of the blood during antiperistalsis, Gerould says, can be shown by injections of india ink.

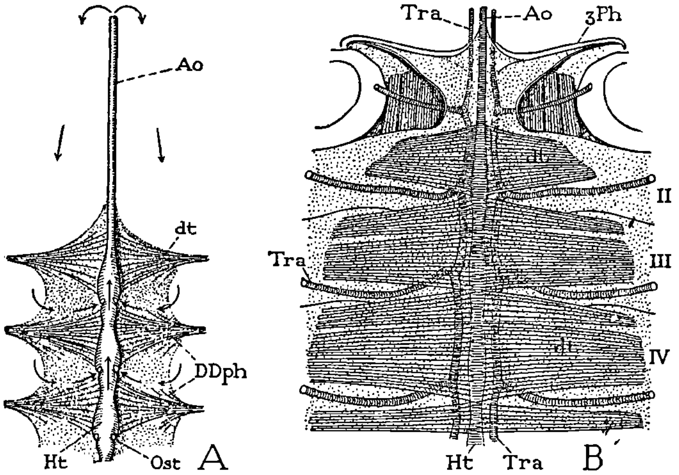

FIG. 215.—The dorsal blood vessel and the dorsal diaphragm. A, diagram of aorta and three chambers of the heart with corresponding part of the dorsal diaphragm, dorsal view, arrows suggesting the course of blood circulation. B, dorsal vessel and dorsal diaphragm of *Dissosteira carolina* from metathorax to fifth abdominal segment, ventral view.

The dorsal vessel is innervated both from the occipital ganglion of the stomodaeal nervous system and from ganglia of the ventral nerve cord.

The Aorta.—The aorta is the slender part of the dorsal vessel continued forward from the first chamber of the heart into the head (Fig. 215 A, *Ao*). Usually it begins in the first segment of the abdomen; but if the cardiac region of the vessel extends into the first abdominal segment or into the thorax, the aorta is correspondingly shortened (Fig. 214). The aorta is not always a simple tube; in the honey bee, as it enters the thorax, it is thrown into a series of short loops closely bound together in a sheath of connective tissue; in the Lepidoptera it makes a large bend upward in the mesothorax (Fig. 216). Dorsal diverticula of the aorta occur in Odonata, Orthoptera, Coleoptera, and Lepidoptera. Within the head the aorta opens into the head cavity behind or beneath the brain, and its lateral and ventral walls, continued before the brain, end in delicate attachments to various tissues of the head.

The ampullalike swellings or diverticula of the aorta are of particular interest since by their structure they suggest that they are modified segmental chambers of the dorsal vessel anterior to the true cardiac region. In the acridid *Dissosteira* the aorta begins in the first abdominal segment (Fig. 215 B), but it has here a large dorsal dilatation (not visible from below), which lies in the posterior part of the concavity of the strongly elevated tergal plate of this segment. Again, in the metathorax and the mesothorax the aorta gives off dorsal diverticula forming two sacs lodged in the scutellar cavities of the metatergum and mesotergum, respectively. A weakly developed extension of the diaphragm is present in each of these segments attached to the dorsal vessel in the usual manner. The aortic sacs of *Dissosteira* are covered by thick spongy masses of compactly aggregated cells closely attached to the walls of the sacs, and throughout its length the aorta is accompanied by strands of similar cells, which are probably pericardial nephrocytes (see page 416).

The larvae of Odonata, as described by Brocher (1917*a*), have a dorsal tubular diverticulum of the aorta in the mesothorax and in the metathorax. In each segment a delicate membrane containing transverse muscle fibers is stretched above the diverticulum between the bases of the wings. Each membrane is perforated by two apertures having valvular lips opening into the aortic diverticulum beneath it. These membranes, Brocher claims, are pulsating organs that draw the blood into the dorsal sinuses above them and discharge it into the aorta.

In *Dytiscus* likewise the aorta gives off dorsal diverticula in the mesothorax and the metathorax, and each diverticulum is covered by a sheet of muscle tissue attached laterally on the wall of the tergum, above which is a blood-filled sinus. The aortic diverticula have the form of stalked ampullae widened above into flattened chambers. The first is lodged in the cavity of the mesotergal scutellum, the second lies beneath the median tongue of the metascutellum. The aortic ampullae and associated structures of *Dytiscus* are described by Korschelt (1924) from the work of Oberle and Kuhl. These authors believe that the muscular membranes serve to compress the ampullae, and that the latter thus act as accessory pulsating organs to drive the blood forward through the aorta. Brocher (1916), however, claims that there is a pair of openings into each aortic ampulla from the sinus above it, and he explains the structures as organs for creating a circulation of the blood through the wings, the blood returning to the sinus being then sent into the aorta.

A pulsating organ connected with the aorta occurs also, according to Brocher (1919), in the mesothorax of Lepidoptera. A muscular membrane is stretched across the anterior half of the cavity of the scutellum (Fig. 216, *p*) above a tracheal air sac lodged in the median scutellar lobe and encloses a small sinus (*i*) in the dorsal part of the thorax. The aorta entering the thorax dips ventrally beneath the second phragma (*2Ph*) and then makes a large loop dorsally (*j*, *l*) in the mesothorax. From the dorsal part of the loop a diverticulum (*k*) goes straight upward to the back and terminates in a small bilobed vesicle in the anterior end of the sinus above the pulsating membrane. The posterior wall of the vesicle is perforated by two small ostia (*Ost*), each having its ventral lip prolonged into the lumen of the vesicle in the form of a valvular flap. Brocher gives experimental evidence showing that the pulsations of the membrane (*p*) draw the blood into the sinus (*i*) above it from the thorax and from the wings and discharge it through the ostia into the aortic vesicle, whence it is carried forward in the aorta to the head.

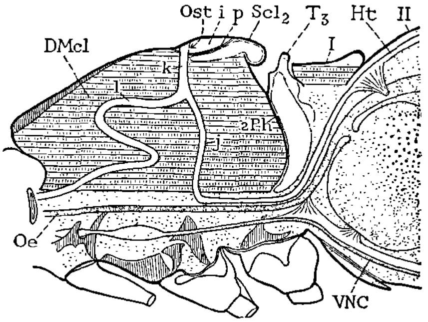

Fig. 216.—Vertical section of thorax and base of abdomen of *Sphinx convolvuli*, showing aortic diverticulum (*k*) and pulsating membrane (*p*) in mesothorax. (*From Brocher*, 1919.)

The Dorsal Diaphragm.—The dorsal diaphragm, when typically developed, consists of two delicate connective tissue membranes enclosing between them the dorsal transverse body muscles, which are inserted medially on the ventral wall of the heart. The degree of development in both the membranous and the muscular elements of the diaphragm, however, varies much in different insects. Usually the dorsal diaphragm is well developed only in the abdomen, though it may extend in a much reduced condition into the thorax.

The diaphragm muscles are commonly known as the "wing muscles" of the heart (alary muscles) because typically they occur in fan-shaped groups of fibers spreading from their points of origin on the tergal plates to their insertions on the heart (Fig. 215 A, *dt*). In some insects, however, the diaphragm fibers are all approximately transversely parallel and arise serially along the laterodorsal parts of the body wall (B). The median ends of the muscles terminate in fine branching, tendonlike fibrils either attached to the lateroventral parts of the heart wall or continuous across the ventral wall with fibrils from the opposite side. In general the diaphragm muscles are present only in the body segments containing a chamber of the heart (Fig. 215 B, *II*, *III*, *IV*) and are therefore usually limited to the abdomen. In the Blattidae, however, in which the heart and dorsal diaphragm are continued into the metathorax and mesothorax, there are, according to Brocher (1922), groups of muscle fibers in each of these thoracic segments.

The diaphragm membranes in some cases are almost entirely absent or form but a scant binding between the muscle fibers, consisting of a weblike tissue full of large and small fenestrae. On the other hand, the membranes may form a continuous and fairly tough septum entirely separating the dorsal sinus from the perivisceral space of the body cavity. In *Dissosteira* (Fig. 215 B) the membrane of the diaphragm behind the first abdominal segment appears to leave no openings into the dorsal sinus, and, laterad of the diaphragm muscles, it is continuous with a connective tissue covering over the muscles of the body wall. When the diaphragm muscles are arranged in groups, the lateral edges of the diaphragm usually form free folds between the points where the muscles are attached on the tergal walls (Fig. 215 A), thus leaving openings from the perivisceral sinus into the dorsal sinus. The membranous diaphragm usually extends anterior to the first heart muscles in the abdomen and may be continued a varying distance into the thorax as membranous fringes along the sides of the aorta.

The Dorsal Sinus.—The dorsal, or pericardial, sinus is coincident in extent with the dorsal diaphragm, and, according to the development of the diaphragm, it is more or less shut off by the latter from the perivisceral sinus. The dorsal sinus contains, besides the dorsal vessel, some of the median longitudinal muscles of the body wall, the dorsal longitudinal tracheal trunks when the latter are present, masses of fat cells, and usually sheets or masses of special "pericardial cells" resting on the diaphragm along each side of the heart (Fig. 212, *PCls*). The pericardial cells are in most cases nephrocytes (see page 416). Segmental tracheal trunks enter the dorsal sinus laterally, either above the lateral margins of the diaphragm or between the groups of muscle fibers (Fig. 215 B), and unite here with the dorsal longitudinal tracheal trunks if the latter are present; otherwise the transverse trunks from opposite sides may become continuous in dorsal commissures above the heart. The dorsal diaphragm is sometimes penetrated by parts of the Malpighian tubules, which make convoluted loops within the sinus.

The Ventral Diaphragm.—A ventral diaphragm is not a constant feature of insect anatomy. When well developed, as in Acrididae and

Hymenoptera, the ventral diaphragm forms a continuous ventral sheet of tissue composed mostly of the ventral transverse muscles of the abdomen. In *Dissosteira* the ventral diaphragm extends through the length of the body from the head into the seventh abdominal segment. In the anterior part of the thorax it is a very delicate membrane without muscles and appears to be attached laterally to the salivary glands and sheets of fat tissue. Between the spreading bases of the sternal apophyses in the metathorax, however, there appears in the diaphragm a series of fine transverse muscle fibers attached laterally on the apophyses. The fibers continue throughout the length of the abdominal part of the diaphragm as its principal tissue. In the abdomen the muscles have their attachments on the sterna at the bases of the anterior and lateral sternal apodemes. The anterior and posterior fibers in each segment spread somewhat forward and rearward to bridge the spaces intervening between the consecutive segments. By this arrangement there is left a series of intersegmental notches along the lateral margins of the diaphragm where the latter has no connection with the body wall, and the openings thus formed appear to be the only connection between the ventral sinus and the perivisceral cavity of the abdomen, except for the wide space below the free posterior margin of the diaphragm.

In some insects the ventral transverse muscles consist of compact bundles of fibers in each segment, and in such cases there is no ventral diaphragm.

Other Pulsating Organs.—Muscular pulsating membranes similar to those associated with the aortic vesicles or ampullae are present in the dorsal part of the thorax in some insects where there are no modifications of the aorta and no openings into the latter. Janet (1906) first called attention to a pulsating organ of this kind in the cavity of the mesoscutellum of ants, and Brocher (1919) says that a very delicate pulsating membrane is present in the back of the metathorax in the sphinx moth, though the aorta makes no connections with it in this segment (Fig. 216). Freudenstein (1928) describes pulsating membranes in both the mesothorax and the metathorax of the honey bee, that of the mesothorax containing muscle fibers and having perforations to allow the blood to escape from the sinus above it into the thoracic cavity. A similar pulsating membrane, according to Brocher (1921), occurs in the mesothorax of *Vespa* and also in Tabanidae. Both Freudenstein and Brocher regard these structures as organs for maintaining a circulation of blood through the wings, the returning channels from the latter being the posterior parts of the basal wing membranes.

Small pulsating membranes have been observed in various other parts of the body in a few insects. In the head a pulsating vesicle situated between the bases of the antennae, which apparently drives the blood into these appendages, is described in Blattidae by Pawlowa (1895) and by Brocher (1922), and a similar structure has been found in the honey bee by Janet (1911) and Freudenstein (1928). Pulsating membranes in the legs of certain Hemiptera are described by Brocher (1909) and others (see Weber, 1930).

Course of the Blood in Circulation.—The heart ordinarily pulsates in a forward direction; but, as we have seen, it may reverse the direction of its beat, and in some insects its action appears to alternate regularly between phases of anterior and posterior pulsation. The blood in the dorsal sinus is drawn into the heart through the ostia with the expansions of the heart chambers, and, when the systolic waves run forward, it is expelled into the head from the open anterior end of the aorta. Here it percolates laterally and posteriorly (Fig. 215 A). If pulsating organs are present in the antennal region, as in the cockroach and the honey bee, an active circulation takes place through the antennae. In the thorax the blood collects in the ventral sinus, from which it circulates through the legs. From the dorsal part of the thorax in the alar segments it enters the anterior parts of the wing bases and returns by way of channels in the posterior parts, the centripetal stream being expedited by the pulsating membranes of the thorax, where such membranes are present, and is then discharged into the aorta, if there are openings into the latter, or otherwise sent back into the thoracic cavity. From the thorax a large part of the blood must be drawn into the ventral sinus of the abdomen, especially in insects in which the ventral diaphragm is well developed and actively pulsates in a posterior direction. Leaving the ventral sinus by the openings along the sides and at the posterior end of the ventral diaphragm, the blood goes upward through the perivisceral spaces and is drawn into the dorsal sinus by the movements of the dorsal diaphragm, which pulsates rhythmically in an anterior direction. Here it reenters the dorsal vessel through the ostia and is again driven forward into the head by the beating of the heart.

For a more detailed account of the course of the blood in circulation the student should consult the various papers by Brocher (1909–1922). The subject of blood circulation in the wings of insects is reviewed in a recent paper by Yeager and Hendrickson (1934) in connection with a special study of the circulation in the tegmina and wings of the cockroach.

3. THE FAT BODY

The majority of insects feed most intensely during the immature stages of their lives. Many insects take but little food, and some none at all, during the imaginal period, and yet it is usually in the early part of the adult stage that the reproductive elements are brought to maturity. The physiological economy of the insect, therefore, must include a system of food conservation to guarantee a consummation of the reproductive function, or to compensate for the inequality of ingestion between the immature and adult stages. In the Holometabola, moreover, the constructive metabolism that takes place in the pupa is partly dependent on food reserves stored in the body during the larval period.

The principal tissue that serves for the deposit of nutritive and energy-forming substances is that which constitutes the so-called *fat body*, a derivative of the mesoderm, formed in the embryo. In normally fed insects this adipose tissue consists of loosely aggregated or compact masses of cells (Fig. 212, *Ft*), usually opaquely white, but sometimes brightly colored, irregularly distributed in the perivisceral spaces of the abdomen and thorax, in the dorsal and ventral sinuses, in the head, and in the appendages. The fat body can scarcely be termed an organ since it has no definite organization, and its cells apparently have little interdependence or interrelation. The fat cells, however, are usually closely adherent, except at the time of metamorphosis, and are so densely packed that they assume polygonal shapes (Fig. 217 A). The external surfaces of the cell masses are often smooth and regular, and in such cases they appear to be covered by a delicate membranous sheath (B). Numerous finely branching tracheae ending in clusters of tracheoles penetrate to all parts of the fat body.

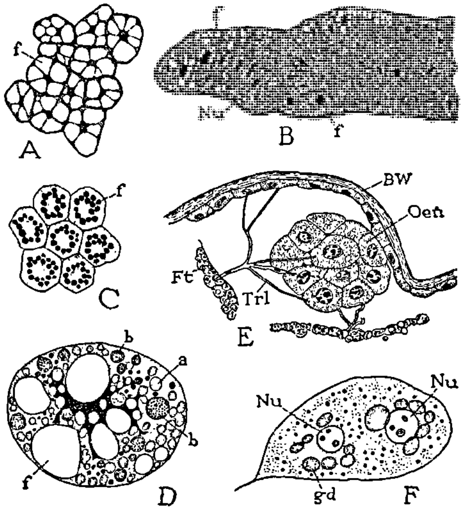

Fig. 217.—Fat tissue, oenocytes, and nephrocytes. A, group of unstained fat cells of young male moth of *Malacosoma americana*. B, part of larval fat body, with nuclear stain, of *Hyphantria cunea*. C, larval fat cells of *Malacosoma* treated with osmic acid. D, fat cell of braconid pupa, *Macrocentrus ancylivora*. (*From Schmieder*, 1928.) E, oenocytes of dipterous larva, *Cryptochaetum iceryae*. (*From Thorpe*, 1930.) F, nephrocyte of *Pediculus humanus*. (*From Nuttall and Keilin*, 1921.)

A differentiation occurs in the cells of the fat body of most insects that results in the appearance of two types of cells, the differences becoming more marked with the age of the individual. The cells of one type, which always constitute the bulk of the fat body, are characterized by a strong vacuolization of their cytoplasm with globules of oil-like fat; those of the other type have little fat, but their cytoplasm contains many small, refringent granules, which are found to be uric acid products. The fat-containing cells, because of their functional relation to nutrition, are *trophocytes;* the others are known as *urate cells.* The two types of cells, however, are not distinct in their origin, both being derived from the primitive undifferentiated cells of the young fat tissue.

The Trophocytes of the Fat Body.—During postembryonic periods of feeding, the trophic cells of the adipose tissue increase in size until they become usually the largest cells in the body, except for the nephrocytes and the oenocytes. From an early period, with some insects in the embryo, these fat-body trophocytes store up fatty materials within their cytoplasm in the form of oil-like globules (Fig. 217 C, *f*). In the mature cells the fat globules become so large that they may occupy most of the perinuclear parts of the cells (A), and the nuclei are often distorted in shape by their pressure. The fat of insects occurs mostly in the form of an oily liquid. For a discussion of the nature of insect fat the student is referred to the work of Timon-David (1930).

Though the fat-forming and fat-storing activities of the adipose trophocytes give the latter their characteristic appearance of "fat cells," the same cells have also other important functions. In some insects the fat cells store up glycogen in their cytoplasm; according to de Boissezon (1932) glycogen is to be found in the mosquito only in the trophocytes of the fat body. In the Holometabola, as the time of metamorphosis approaches, the fat cells elaborate large quantities of albuminoid bodies in the form of small granules held in the cytoplasm between the globules of fat (Fig. 217 D, *a, b*). These proteid inclusions are formed in the fat cells apparently by the action of nuclear enzymes on nutritive materials taken in from the blood.

During the period of metamorphosis in holometabolous insects, the fat body disintegrates, and its cells, now released from pressure, become large spheres floating free in the blood (Fig. 218, *FtCl*). Soon, however, most of the cells themselves begin a process of gradual dissolution (*FtCl′, FtCl″*); their nutritive contents are thus dispersed in the blood (*a, f*), where they become available to the growing tissues of the pupa. The fat body of the adult is regenerated toward the end of the pupal period apparently from larval fat cells that do not suffer complete histolysis, and these pupal cells may go over into the imaginal stage fully charged with fatty inclusions for the use of the adult (Fig. 217 A).

The Urate Cells.—It was formerly held that the urate cells of the fat body are ductless excretory organs, which extract waste products from the blood and retain them in their cytoplasm. Berlese suggested that they act as substitutes for the Malpighian tubules during the period of metamorphosis when the excretory tubules are undergoing reconstruction. Hollande (1914), however, in a study of the urate cells of *Vanessa*, claims that the urate granules are produced within the cells of the fat body itself, and that they are waste products of the final transformations of the albuminoid inclusions of the active trophocytes. Certain cells of the fat body, absorbing these products from contiguous cells, become thus differentiated as the urate cells. Hollande asserts that the urate granules are first formed around the nuclei of the trophocytes and are later dispersed in the cytoplasm. The granules remain in the urate cells through the pupal stage and for a long time during the life of the imago. In the mosquito, according to de Boissezon (1930*a*), crystalline deposits are never seen in cells of the fat body during the first stage of the larva but appear after the first moult and increase with the age of the larva. During metamorphosis, he says, they become still more abundant, especially in the peripheral cells, and in the adult stage they are present in greatest numbers in hibernating females.

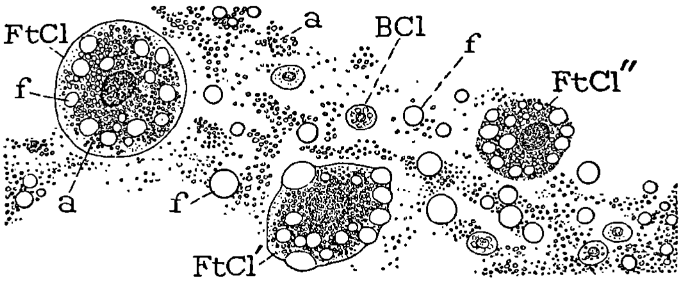

FIG. 218.—Disintegrating fat cells in the pupal blood of *Malacosoma americana*. *a7* albuminoid granules; *f*, fat globules.

The histochemical studies of de Boissezon (1930*b*) on the urinary cells of *Culex* indicate that the crystalline deposits are probably purine bodies. They are always situated in the cytoplasm near the nucleus, and microscopic examination shows that they are formed by the nucleolus. It is probable, therefore, that they are disintegration products of nucleinic acid, which, by further reduction, forms purine bases. In so far as these products are retained in the cells, de Boissezon points out, the urate cells may be said to be "kidneys of accumulation."

4. THE OENOCYTES

The oenocytes are large cells found in the body cavity of most insects, either arranged in groups (Fig. 217 E) or scattered individually among the tissues of the abdomen, where they are usually associated with the fat cells. They occur apparently in all the pterygote orders but are said to be absent in the Apterygota. Investigators agree that the oenocytes originate in the embryo from the ectoderm along the sides of the abdomen, arising here from points just posterior to the spiracles in the first eight segments. According to Wheeler (1892), the oenocyte cells remain imbedded in the epidermis at their points of origin in Ephemerida, Odonata, Plecoptera, and Isoptera, but in Corrodentia and Thysanoptera, though still attached to the epidermis, they form segmental clusters of cells projecting into the body cavity. In Trichoptera and Lepidoptera the oenocytes are free from the body wall and occur in groups connected with tracheae in the neighborhood of the spiracles, the cells being held together by finely branching tracheal tubes. In the Coleoptera they form loose clusters or bands of cells along the sides of the abdomen lying against the visceral organs. In most adult Hemiptera and Hymenoptera the oenocytes are generally distributed as free cells among the cells of the fat tissue, but in some larval Hymenoptera they are said to be arranged in paired segmental groups lying mostly in contact with the epidermis of the first eight abdominal segments (Eastham, 1929), and in the hemipteron *Rhodnius,* according to Wigglesworth (1933*b*), they are imbedded in the epidermis. Oenocytes are not known to occur in adult Diptera, though they are present in dipterous larvae as metameric cell clusters attached to the body wall (Fig. 217 E).

Though much attention has been given to the histology of the oenocytes and their growth and changes from the larva to the imago, no consensus of opinion has yet been reached concerning the function of the cells. Some of the earlier writers regarded the oenocytes as excretory organs that retain waste products in their cytoplasm, while others have favored the view that they are glands of internal secretion. Glaser (1912), studying the oenocytes of the larva of the leopard moth *Zeuzera pyrina,* concluded that the cells are the seat of production of oxydases in insects. Hollande (1914*a*), however, claims that the oenocytes are in a sense complementary to the fat cells in that they form and conserve in their cytoplasm deposits of wax. The wax, he says, disappears from the cells during metamorphosis, and also after fasting or after egg laying, just as the fat disappears from the fat cells. Hollande, therefore, would rename the oenocytes *cerodecytes.* The term "oenocyte" refers to the usual pale amber color of the cells, but the latter are in some insects brown, yellow, green, or red, and sometimes colorless.

5. THE CORPORA ALLATA

The corpora allata are small, compact, cellular bodies, generally oval, elliptical, or spherical in form, lying at the sides of the stomodaeum behind the brain in the back of the head or in the neck, and sometimes in the prothorax, where they are closely associated with the stomodaeal nervous system (Fig. 249, *CA*). They are said to be present in all orders of insects. Formerly the bodies were assumed to be nerve ganglia; they were described by Hofer (1887) as "paired posterior visceral ganglia." Heymons (1895) later discovered that they take their origin from the ectoderm of the lateral walls of the head, and he, therefore, termed them "ganglia allata" in reference to their transposed definitive position. More recent investigations by Heymons (1899*a*), Nabert (1913), Ito (1918), and others have shown, however, that the organs do not have the structure of nerve tissue and cannot, therefore, be regarded as ganglia. Their origin from the ectoderm suggests an anatomical analogy at least with the oenocytes.

The origin of the corpora allata from the ectoderm has been observed by Heymons (1895), Carrière and Bürger (1897), Strindberg (1913), Nelson (1915), and Ito (1918). The first three writers assert that the bodies are proliferated from the wall of the first maxillary segment. Nelson, however, describes the bodies in the honey bee as arising from invaginations between the bases of the rudiments of the mandibles and first maxillae, associated with the invaginations that form the adductor apodemes of the mandibles; according to Ito, those of the silkworm are formed as cellular ingrowths from the mesal surfaces of the adductor apodemal invaginations. Subsequently the rudiments of the corpora allata become solid masses of cells; they lose their connections with the ectoderm, migrate mesally and dorsally, and finally become attached to the ventrolateral angles of the coelomic sacs of the antennal segment. Those of *Forficula* are said by Heymons to unite with each other in a single median body. In their definitive position the corpora allata are innervated from the occipital ganglion (or ganglia) of the stomodaeal nervous system, and each is invested in a sheath continuous with the neurilemma of the nerve; the latter, according to Nabert, goes in some cases to the surface of the corpus allatum, and in others branches within it.

The comparative structure of the corpora allata has been minutely described by Nabert (1913). In some insects, Nabert says, the component cells of the bodies are distinct, but generally each body consists of a more or less uniform, reticulated, multinucleate granular mass, coloring strongly in stains, containing numerous vacuoles, with the nuclei rich in chromatin. In Phasmidae there is a central core of secretion products. During metamorphosis of the silkworm, according to Ito (1918), "the corpora allata become conspicuously enlarged and altered in shape. The structure of the cells undergoes a gradual change, and the nuclei become greatly ramified and contain a great many chromatin granules." In the imago, Ito says, the bodies increase to four or five times the larval size; the nuclei are irregular in shape and undergo chromatolysis; the cytoplasm is alveolated with vacuoles containing granular secretion products. Both Nabert and Ito conclude that the corpora allata are glands of internal secretion; Wigglesworth (1934, 1934*a*) has produced evidence suggesting that they are the source of hormones that induce moulting.

6. THE ORGANS OF ELIMINATION

The term *elimination*, in an unrestricted sense, refers to the physiological discharge of any useless or waste substances from the body tissues; by a more limited definition, *excretion* is the elimination of waste products of metabolism. Many substances discharged through the excretory tissues or organs, and therefore classed as excreta, are simply materials, such as salts, unavoidably taken into the body in excess of the need for such matter. On the other hand, waste products of metabolism that are truly excretory substances are not necessarily removed from the body; they may be merely separated from certain tissues where their presence would be detrimental and stored in others where they become harmless. Finally, excretory substances, whether stored or eliminated, may serve some useful purpose in the economy of the animal. Unused or indigestible parts of the food material ejected from the alimentary canal are not excreta, though much excretory matter may be voided with the food refuse in the faeces.

Eliminated substances are solid, liquid, or gaseous in form. The principal gas expelled as a waste is carbon dioxide, and the principal liquid is water. Solid excreta are given off mostly in crystalline masses or in aqueous solution. They include nitrogenous and nonnitrogenous organic compounds and inorganic salts.

Almost any epithelial tissue of the body may assume an excretory function, but special organs of excretion are developed generally from the ectoderm or the mesoderm or from both these germ layers. Most of the arthropods have no excretory organs corresponding morphologically to the nephridia of Annelida and Onychophora, their excretory functions being accomplished by the integument and the walls of the alimentary canal. Exceptions are found perhaps in the head glands of Crustacea, which are generally regarded as modified nephridial organs.

The organs or tissues of insects that serve to eliminate substances that cannot be physiologically utilized in the body include (1) the general body integument; (2) certain specialized parts of the integument, such as the surfaces of gills and of integumentary glands; (3) the capillary end tubes of the tracheal system; (4) the walls of the alimentary canal; (5) specific excretory tubes opening into the proctodaeum, known as the *Malpighian tubules.* In addition, there are the masses of pericardial cells, and groups of similar cells in other parts of the body, generally called "nephrocytes," which have been supposed to eliminate foreign and waste substances from the blood and to store them in their cytoplasm, but which perhaps function in a manner preliminary to excretion by changing colloidal substances to crystalloids that can be eliminated through the Malpighian tubules and excreting tissues in other parts of the body.

Though we define excretory substances as the end products of metabolism and excess matter that cannot be put to any physiological use, this is not to say that such substances may not be made to serve some practical purpose in the biological economy of the animal. Numerous instances might be cited in which insects make use of their excreted matter. Excretory substances discharged from glands often have offensive odors which become a part of the insect's means of defense. The products of the Malpighian tubules may be employed in the construction of larval cases or injected into the fabric of the cocoon. Other excretory substances held within the body may be deposited within the integument, where they serve as pigments giving surface color markings, and it is possible even that the nitrogenous component of the cuticula, a most important part of the physical organization of insects, is to be regarded as an excretory product eliminated with the moults.

The Integument as an Excretory Tissue.—The body wall of many animals serves as an excretory organ in the elimination of waste substances from the body, including inorganic salts and nitrogenous compounds. The arthropod integument has, as its outer layer, a cuticula in which the nitrogenous substance chitin is a prevailing if not the predominant element, and in which there usually occur calcium salts or other incrustations in varying amounts. The cuticula is periodically cast off and renewed. In this way the arthropod loses with each moult a large amount of nitrogen and whatever calcium or other substances may be contained in the exuviae.

It has been suggested, therefore, that moulting in the arthropods is primarily a process of excretion, particularly of nitrogen excretion. Chitin constitutes probably 30 to 40 per cent of the insect cuticula, but, as Uvarov (1928) points out, there are other substances associated with it which are also nitrogenous. These substances include pigments, such as those in the scales of Lepidoptera, which, Uvarov says, "are clearly the final products of metabolism transferred to certain parts of the integument, and deposited there instead of being excreted." In this connection it is interesting to recall the suggestion of N. Holmgren (1902) that the cuticular covering of the integument has originated as a hardening of secretions thrown off from the epidermis between filaments on the outer surface of the latter.

The products of most of the integumentary glands of insects serve some specific purpose in the biology of each species, but, as already mentioned, it is probable that some of them are primarily excretory substances.

Respiration in insects, no matter what mechanical devices are developed to facilitate it, always takes place through some part of the ectoderm, and, in this way, the ectoderm serves as an excretory tissue for the elimination of carbon dioxide and water. Insects, such as most of the Collembola, lacking tracheae or certain larvae having closed or rudimentary tracheal systems respire directly through the integument, and it is known that many insects having well-developed tracheae discharge at least a part of their carbon dioxide directly through the body wall. But the tracheal tubes themselves are merely invaginations of the body wall, and the ultimate tracheoles are developed in cells of the ectodermal tracheal epithelium. Both external gills and internal rectal gills are also parts of the ectoderm specially modified for respiratory purposes.

Excretion through the Walls of the Alimentary Canal.—Many investigators have observed the accumulation of crystalline bodies in the walls of the mesenteron of various insects. Most of these bodies are salts of calcium, but some also are said to react to tests for uric acid salts. In either case the bodies are probably excretory products or excess substances that cannot be utilized. The insect, making little use of calcium in its body structures, must necessarily eliminate most of the calcium absorbed from its food, and analyses of the faeces always show a high percentage of calcium in the latter. It seems probable that excretory matter may be eliminated also directly through the walls of the proctodaeum, but most of the intestinal excretion takes place through the Malpighian tubules. The function of the rectal glands, as we have seen (page 383), has not been exactly determined.

The Nephrocytes.—In nearly all the Arthropoda and in the Onychophora, variously distributed throughout the body and even in the appendages, there are groups of special cells having the common property of absorbing ammonia carmine injected into the blood, and of retaining a precipitate of carmine in their cytoplasm. Because of their action on carmine, these cells have been supposed to have a similar action on other substances naturally present in the blood, such as waste products of metabolism or other injurious bodies, and for this reason they have been termed "storage kidneys" (*reins d'accumulation*), or *nephrocytes*. The structure and distribution of the carmine-absorbing cells in the Arthropoda have been elaborately studied by Kowalevsky (1892), Metalnikoff (1896), and Bruntz (1904).

The carmine-absorbing cells of insects occur particularly in the pericardial sinus, where they form masses or long strands of cells on each side of the heart, known as the *pericardial cells* (Figs. 212, 213, *PCls*). Cells of this kind, however, are often to be found in other parts of the body, generally as single cells or small irregular cell groups, though sometimes in clusters of definite shapes, which in certain cases have been taken for glands. The general distribution in the body of insects of cells having the properties of the pericardial cells has been described by Keilin (1917, 1924) and by Nuttall and Keilin (1921).

The pericardial cells of insects are generally large and are often binucleate (Fig. 217 F). They are always found to have an acid reaction. They are of mesodermal origin and are derived, according to Heymons (1895), from the same parts of the mesodermal layers that form the heart and the dorsal diaphragm. Hollande (1922) says that the cells of the larva generally persist during metamorphosis and become the pericardial cells of the imago. Functionally, Hollande finds that the pericardial cells have preponderantly the power of absorbing colloids, such as albumins and globulins, or their derivatives, and he claims that their well-known property of absorbing certain pigments results from their affinity for colloids in general. For the most part the cells take up only coloring matter of a colloidal nature. Rarely they contain crystalloids. At the approach of the pupal metamorphosis, Hollande observes, the cytoplasm of the pericardial cells in some insects, particularly in Coleoptera, Trichoptera, and Lepidoptera, becomes charged with albuminoid inclusions, but these inclusions usually disappear by the end of the transformation period.

The studies of Hollande (1922) on the physiology of the pericardial cells of insects sustains the view that these cells play an important role in excretion, but they discredit the idea that the cells have a storage function. Hollande claims that, when the cells absorb ammonia carmine, they precipitate the carmine, and that the latter remains in the cytoplasm because it is but little soluble in the cell juices. Normally, he finds, the pericardial cells are agents for breaking down complex colloids, which are transformed by ferments produced in the cells into crystalloids. The latter are then given off into the blood, from which they are removed by the Malpighian tubules. This view is in accord with that earlier expressed by Cuénot (1896). Hollande summarizes his findings on the function of the pericardial cells as follows: Each cell is a ductless glandular body with a merocrine type of secretion, possessing the property of neutralizing alkaline substances present in excess in the blood, and also that of absorbing certain colloid substances; by means of its diastases, functioning in an acid medium produced by the cell itself, it splits the complex colloidal molecules, transforming them into simpler crystalloid compounds that are rejected into the blood, from which they are finally eliminated by the Malpighian tubules.

The pericardial cells, therefore, Hollande points out, may be likened in some respects to the liver of a vertebrate animal and might be called *hepatic cells* more appropriately than "renal" cells, or "nephrocytes," though they differ physiologically from a vertebrate liver in that no glycogen function has been detected in connection with them. In any case, however, the pericardial cells and presumably also the similar cells in other parts of the body play an important part in the physiology of the insect.

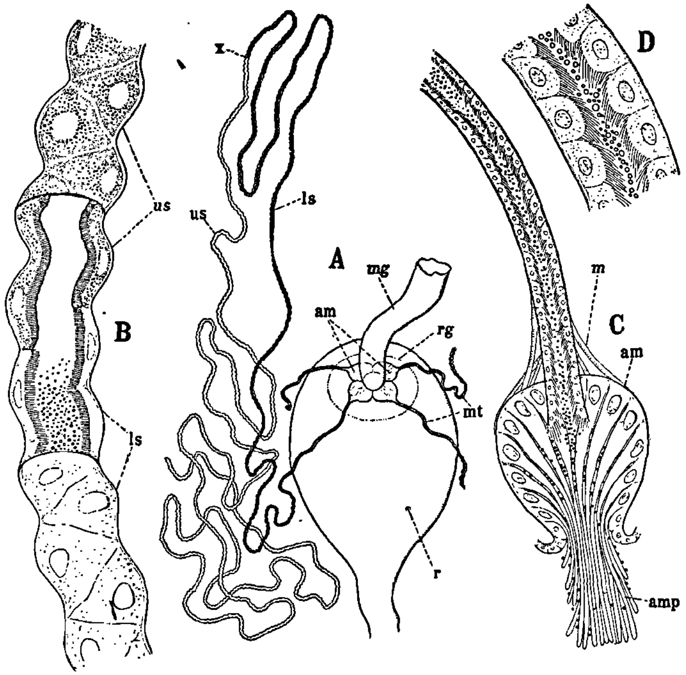

FIG. 219.—Structure of the Malpighian tubules of a hemipteron, *Rhodnius prolixus*. (*From Wigglesworth*, 1931*a*.) A, origin of Malpighian tubules (*mt*) from intestine, with one tubule shown in full. B, part of tubule at junction of distal (*us*) and proximal (*ls*) parts shown in optical section. C, basal ampulla (*am*) of a tubule with elongate cell processes (*amp*) projecting into intestine. D, structural details of proximal part of tubule.

The Malpighian Tubules.—The specific excretory organs of insects that correspond functionally to the nephridia of Annelida and Onychophora and with the kidneys of Vertebrata are the Malpighian tubules, the general morphology of which was discussed in the last chapter.

Histologically the walls of the Malpighian tubules resemble in some respects the wall of the mesenteron rather than that of the proctodaeum, with which they are anatomically continuous. Each vessel is a long, narrow epithelial tube composed of large cells limited externally by a basement membrane (Fig. 219 B, D). The inner ends of the cells usually project into the lumen of the tube and often almost occlude the passage. The cytoplasm of the cells sometimes shows a fine striation in its outer part perpendicular to the basement membrane. Generally there is no evidence of a cuticular lining to the Malpighian tubules such as that of the proctodaeum, but the cells of the epithelium may have a distinct "striated border" closely resembling the striated border of the mesenteron. Fine cilialike strands have been described by some writers as projecting from the inner ends of the cells in certain insects. A thick coating of such processes is said by Noël and Tahir (1929) to be present in the tubules of *Bombyx mori*, almost filling the lumina, but the filaments appear to be simply fine cytoplasmic prolongations of the cells.

Each Malpighian tubule in some insects is differentiated into two or three parts. Very frequently there is a vesicular enlargement, or ampulla, at the base of each tube (Fig. 219 A, *am*), but in some cases also the distal part of the tube is distinctly differentiated into two sections by histological differences and by differences in the contents of the lumen. In the reduviid *Rhodnius prolixus*, as described by Wigglesworth (1931*b*), each tubule abruptly changes in its structure and contents at a point between its proximal third and distal two-thirds (Fig. 219 B). The ampulla at the base of each tubule has the cells of its outer wall prolonged into slender processes that project down into the lumen of the proctodaeum (C, *amp*).

The outer surfaces of the Malpighian tubules are richly supplied with fine branching tracheae, and some writers have described an investing tunic of connective tissue, which is said in some cases to contain elastic strands and even true muscle fibers. Thus, according to Léger and Duboscq (1899), in the tunic of the Malpighian tubules of Gryllidae there are small superficial bundles of elastic fibers, and deeper striated muscle fibers forming a spiral about the entire length of each tubule. In certain Tettigoniidae the same writers describe a single long muscle taking a spiral or almost axial course along each tubule. Trappmann (1923) likewise reports the presence of muscle fibers in the Malpighian tubules of the honey bee, each tubule having six or eight fibrillae forming flat bands arranged in wide spirals almost parallel with the axis of the tubule. Veneziani (1905) finds elastic fibers in the tubules of the larva of *Cerambyx*, and true muscles in the larval tubes of *Melolontha*. In *Dytiscus*, Rungius (1911; Korschelt, 1924) says there are fine fibrillae in the tunic of the Malpighian tubules, which are evidently contractile elements, but that no true muscle fibers having a cross striation are present. All these investigators assert that the tubules of freshly narcotized specimens exhibit waving movements and also pulsations of their walls which expel the products of excretion. According to Eastham (1925), only the basal stalks of the Malpighian tubules of *Drosophila* and *Calliphora* are provided with muscle fibers, but the fibers here are arranged circularly and longitudinally and are continuous with the muscular sheath of the intestine. Peristalsis, he says, occurs in the musculated parts of the tubules, and the entire tubes exhibit a waving movement as a result of the contraction of the muscles in their basal stalks. Wigglesworth (1931*b*) reports the presence of a few muscle fibers on the ampullae and lower ends of the Malpighian tubules of *Rhodnius* that run out from the wall of the mesenteron, but otherwise he says the tubules in this insect have no muscles.

The discharge of excretory products from the walls of the Malpighian tubules has been described by various writers as taking place by the usual method of liquid diffusion through the cell walls, by the expulsion of small masses through the striated border, and by the extrusion of cytoplasmic globules charged with excretory matter, which are constricted off and set free in the lumen. There is reason to believe that the first is the normal method of excretion, and that the formation of globules on the ends of the cells is an artifact resulting from the technique of fixation.

Substances reported to be eliminated by the Malpighian tubules of insects include urea, uric acid, urates of sodium, of calcium and ammonia, leucin, and various salts of calcium and potassium, such as oxylates, carbonates, and phosphates. Guanin, the characteristic excretory product of Arachnida, is unknown in insects. Most of the nitrogen excreted is in the form of uric acid. Calcium salts often constitute a large part of the Malpighian output, but they are not to be regarded as true excretory products. In analyses of excretory matter from the rectum, especially in carnivorous species, as pointed out by Wigglesworth (1931*a*), there must be distinguished substances derived directly from the food in the stomach, and substances that are products of metabolism excreted through the Malpighian tubules.

In addition to their excretory function, the Malpighian tubules of certain insects are known to produce just before the time of pupation a substance which is spun out of the anus in the form of silk threads, with which the cocoon is woven. This silk-forming function of the larval Malpighian tubules has been described in the neuropterous species *Mermeleon formicarius* and *Chrysopa perla* (Lozinski, 1911), in the curculionid *Phytonomus arator* (Lebedew, 1914), and in the chalcid *Euplectrus bicolor* (Thomsen, 1927). It was claimed by von Gorka (1914) that the Malpighian tubules produce digestive enzymes, but a study of the enzymes of cockroaches and caterpillars made by Dirks (1922) shows an entire absence of ferments in the Malpighian tubules.

GLOSSARY OF TERMS USED IN THIS CHAPTER

Alary Muscles.—The dorsal transverse muscles of the body, attached medially on the heart, usually arranged in fan-shaped groups of fibers. (*Wing muscles of the heart.*)

Aorta (*Ao*).—The anterior nonchambered part of the dorsal blood vessel.

Blood.—The body-cavity liquid and its contents.

Blood Cells (*BCls*).—The cellular elements of the blood. (*Haemocytes, leucocytes.*)

Cardiac Sinus.—The dorsal part of the embryonic haemocoele, a part of which becomes the lumen of the dorsal blood vessel.

Cardioblasts (*Cdbl*).—The cells of the upper edges of the embryonic mesoderm that form the dorsal blood vessel.

Cerodecytes.—See *oenocytes.*

Corpora allata (*CA*).—A pair of small cellular bodies of ectodermal origin associated with the stomodaeal ganglia behind the brain. (*Ganglia allata, corpora incerta.*)

Diaphragm (*Dph*).—One of the horizontal partitions of the body cavity. (See *dorsal diaphragm,* and *ventral diaphragm.*)

Dorsal Diaphragm (*DDph*).—The membranous and muscular sheets of tissue extending from the dorsal blood vessel to the laterodorsal parts of the body wall, separating the dorsal sinus from the perivisceral sinus.

Dorsal Sinus (*DS*).—The space of the definitive body cavity above the dorsal diaphragm and the heart. (*Pericardial sinus.*)

Dorsal Vessel (*DV*).—The dorsal blood vessel, consisting of the pulsatile *heart* and the nonpulsating *aorta.*

Epineural Sinus.—The ventral part of the embryonic haemocoele between the yolk and the ventral nerve cord.

Fat Body.—The masses of fat-containing cells usually distributed throughout the body cavity.

Fat Cell.—One of the component cells of the fat body.

Haemocoele.—The blood spaces of the embryo, or remnants of the blastocoele after invasion of the latter by the mesoderm.

Haemocytes (*BCls*).—The cells of the blood. (*Leucocytes.*)

Haemolymph.—The blood plasma, or liquid part of the blood.

Heart (*Ht*).—The chambered part of the dorsal blood vessel.

Heart Chamber.—One of the segmental swellings of the heart.

Hepatic Cells.—See *nephrocytes.*

Leucocytes.—See *haemocytes.*

Malpighian Tubules (*Mal*).—The excretory tubules opening into the anterior end of the proctodaeum.

Nephrocytes.—Special cells scattered in groups in various parts of the body, but especially abundant in the dorsal sinus, where they are known as *pericardial cells;* probably have some function in connection with excretion and have been termed "hepatic cells."

Oenocytes.—Large ectodermal cells occurring in the abdomen of most insects, sometimes within the epidermis, but generally free in lateral segmental groups, or scattered through the fat body. (*Cerodecytes.*)

Ostial Valves.—Valve-like pouches of the heart wall containing the ostia at their inner ends.

Ostium (*Ost*).—One of the paired and usually lateral openings (ostia) of the heart.

Pericardial Cells (*PCls*).—Strands of special cells along the sides of the heart, probably in most cases nephrocytes.

Pericardial Sinus (*DS*).—See *dorsal sinus.*

Perivisceral Sinus (*PvS*).—The principal part of the body cavity, between the dorsal diaphragm and the ventral diaphragm if the latter is present.

Phagocytes.—Haemocytes having active ingestive and digestive properties.

Pulsating Membranes.—Small muscular membranes found in the thorax, head, and appendages of various insects, the rhythmic contractions of which probably contribute to the circulation of the blood.

Trophocytes.—Cells that elaborate nutritive materials; the cells of the fat body having a trophic function in distinction from the urate cells.

Urate Cells.—Cells of the fat body that become charged with urate crystals.

Valves of the Heart.—Internal valve-like lobes of the heart walls between the chambers, said to be present in certain dipterous larvae.

Ventral Diaphragm (*VDph*).—A membranous and muscular sheet present in some insects stretched between the lateral edges of the abdominal sterna, sometimes extending into the thorax, separating the ventral sinus from the perivisceral sinus.

Ventral Sinus (*VS*).—The space of the definitive body cavity below the ventral diaphragm, containing the nerve cord.

Wing Muscles of the Heart.—See *alary muscles.*

CHAPTER XV

THE RESPIRATORY SYSTEM

Respiration includes chemical and physical processes. The chemical phase of respiration is the oxidation accompaniment of metabolism in the body tissues, which results in the formation of carbon dioxide and water. Physical respiration has to do with the transportation of oxygen to the tissues and the removal of carbon dioxide. In the many-celled animals, in which the vital tissues are surrounded by an integument, the consumption of oxygen and the production of carbon dioxide are mostly internal processes. The respiratory gases, therefore, must penetrate the body wall and must be transported within the body to and from the cells of all the tissues. Hence respiration in the Metazoa includes *external respiration*, *gas transportation*, and *internal respiration*. Internal respiration is essentially the process of oxidation; it therefore belongs to the realm of physiology. External respiration and the internal transportation of the respiratory gases are physical processes, and a study of the anatomical structures concerned with these processes is properly a part of the subject of morphology. The special mechanical devices that may be developed to facilitate the interchange of gases between the environment and the blood or the cellular tissues of the animal constitute the *respiratory system.*

Physical respiration, in its simplest form, is probably nothing more than ordinary gas diffusion through permeable membranes, and the dispersal of the respiratory gases within the body by diffusion in the blood. In its higher development, the physical phase of respiration is expedited by the development of special organs for bringing air into the body, and by the presence of chemical substances in the blood that act as carriers of the respiratory gases.

In some of the smaller, soft-skinned insects, external respiration is accomplished by gas diffusion through the general body integument, and the transportation of the respiratory gases depends upon the diffusion of the latter in the blood. In all insects, external respiration takes place through some part of the ectoderm, but generally at places where the ectoderm, by reason of the delicacy of its external cuticular layer, is specially adapted to the transmission of gases. Such respiratory areas of the ectoderm occur both in the integument and in the proctodaeal section of the alimentary canal. In some cases these areas may be flat surfaces where the cuticula is sufficiently thin to allow of gas diffusion. Usually, however, they take the form of evaginations, known as *blood gills*, or of invaginations, termed *tracheae*, including the terminal tracheoles. The predominant mode of external respiration in insects is by means of tracheae.

Gas transportation within the body cavity is reduced to a minimum in insects provided with a well-developed tracheal system, since the tracheal invaginations branch so profusely and penetrate so thoroughly to the tissues that oxygen must be carried directly to almost every cell of the body. And yet it is probable that some of it escapes into the blood to supply the needs of the blood tissues, and, as shown in the last chapter, it is not certain that there may not be present in the insect blood a small amount of an oxygen-carrying protein. Carbon dioxide, on the other hand, being given off from all exposed cell surfaces, evidently, cannot be taken up entirely by the tracheae; investigations have shown that at least a part of the carbon dioxide produced in tracheated insects is diffused into the blood and eliminated through the integument.

1. THE INTEGUMENT AS A RESPIRATORY ORGAN

Insects that do not have tracheae, or that have an imperfect or a secondarily closed tracheal system and are not provided with other devices for respiration, must effect the outer exchange of gases directly through the integument. The best known examples of insects lacking tracheae are the Collembola, the majority of which have no breathing mechanism of any kind, and certain species of aquatic Chironomidae, in which tracheae, if present, are very imperfectly developed. Many parasitic insect larvae, living entirely submerged in the liquids or tissues of the host, also must respire through the soft body wall, though they may be provided with a well-developed tracheal system. Seurat (1899) observes that some internal parasitic hymenopterous larvae have a system of finely branching tracheal tubes covering the inner surface of the body wall, into which air is absorbed from that dissolved in the blood of the host. Certain parasitic larvae are provided with filamentous processes of the body wall that appear to be gills.

Though with the majority of free-living insects having a normally open tracheal system inspiration takes place largely through the tracheae, there is evidence to suggest that the expiration of carbon dioxide takes place at least in part by way of the integument. Thus Krogh (1913), finding that the carbon dioxide deficit in the tracheae of the hind leg of a grasshopper after expiration is always considerably lower than the oxygen deficit, concluded that a large part of the carbon dioxide formed in the tissues of the leg must be carried away by other means than the tracheae. The same idea has been expressed by other investigators and appears to be demonstrated experimentally for certain insects. Von Buddenbrock and von Rohr (1923), for example, claim that in *Dixippus morosus* one-fourth of the carbon dioxide produced is given off through the body wall, and Demoll (1927) reports finding no carbon dioxide in the tracheae of *Melolontha*. On the other hand, Wrede (1926) found little evidence of carbon dioxide expiration through the skin of ordinary caterpillars. In aquatic caterpillars, however, such as certain species of *Bellura*, *Nymphula*, and *Pyrausta* that lack gills, respiration under water, Welch (1922) has pointed out, must take place through the general body integument.

It has not been shown that any particular part of the integument, when gills are absent, serves for the elimination of carbon dioxide, but we may suppose that diffusion would be most likely to take place through the less dense areas, such as the conjunctive membranes and other parts where sclerotization is weak or absent. In the Acrididae there are fenestralike, unpigmented areas of the body wall along the midline of the back above the heart chambers in the abdomen, and above the aortic pouches in the thorax, which suggest that they may be permeable to gases and perhaps serve for the elimination of carbon dioxide. In soft-skinned aquatic dipterous larvae carbon dioxide is usually found to be given off over the entire body surface.

2. BLOOD GILLS

Various aquatic larval insects are provided with thin-walled, hollow diverticula of the integument or of the proctodaeum, which, in the absence of definite knowledge concerning their function, are usually termed "blood gills." External processes of this kind, variously distributed on the body, occur on the aquatic larva of the beetle *Hygrobia* (*Pelobius*) *tarda*, on the aquatic larvae of certain species of *Chironomus*, and on the aquatic caterpillar of *Cataclysta fulicalis*. The tapering fleshy processes arising near the anus of many tipulid larvae are sometimes cited also as examples of blood gills, and it is said that streams of blood may be seen to circulate through them (Brown, 1910; Gerbig, 1913), but each of these processes is penetrated by a trachea, and Gerbig suggests, therefore, that the organs serve in a double capacity of blood gills and tracheal gills. The "gills" of the *Hygrobia* larva, however, which consist of clusters of delicate filaments arising behind the bases of each pair of thoracic legs, contain no tracheae; and the same is true of the group of slender processes arising at the posterior end of the abdomen of *Chironomus* larvae, and of the filamentous appendages distributed over the body of the larva of *Cataclysta fulicalis*. These organs, therefore, may be supposed to be blood gills. The characteristic tail of certain parasitic hymenopterous larvae has been supposed to be a gill. A respiratory function has not been demonstrated in connection with this organ, but Wigglesworth

(1931) points out that, when it has the form of a fluid-filled vesicle, its surface offers a respiratory possibility.

Proctodaeal evaginations occur in some trichopterous larvae, and in the larvae of certain Simuliidae, which are protractile from the anus and are generally regarded as organs for aquatic respiration. The structure of the slender proctodaeal evaginations of a trichopterous larva is described by Branch (1922), who finds that the organs are hollow tubular diverticula produced from the posterior ends of the six folds in the wall of the prerectal part of the intestine. They are capable of being extended from the anus, apparently by pressure exerted by the abdominal walls, and each is retractile by a branched muscle inserted within it, which arises on the body wall. The similar processes of *Simulium* larvae, as described by Headlee (1906), consist of three simple or branched, soft, translucent filaments protractile through the anus from the ventral wall of the rectum, into which they may be retracted by a pair of muscles arising on the dorsum of the abdomen and inserted by branches on their bases. Since each of these processes contains masses of fine tracheal tubes filled with air, Headlee suggests that the organs perhaps function both as blood gills and as tracheal gills.

Most of the supposed "blood gills" of insects have not been subjected to physiological tests for a respiratory function. Experiments on *Chironomus* larvae made by Fox (1921), using the infusorian *Bodo sulcatus* as an indicator, which is positively chemotactic to certain concentrations of dissolved oxygen, appear to show that oxygen consumption takes place through the general body wall and not through the so-called gill filaments. Similar results were obtained from microspectroscopic tests. Carbon dioxide, according to Fox, is given off likewise through the general integument of the *Chironomus* larva. The structure and function of the gill-like anal lobes of mosquito larvae have been studied by Wigglesworth (1933, 1933*a*), who concludes that the organs serve for the absorption of water, since respiratory tests show that oxygen is absorbed on all parts of the body, though most actively at the bases of the anal lobes, and that carbon dioxide is given off equally from the entire body surface.

3. THE TRACHEAL SYSTEM

Invaginations of the integument for respiratory purposes occur in the Onychophora and in some terrestrial forms at least of all the major groups of Arthropoda. The organs probably, as claimed by Ripper (1931), are formed independently in most of the several groups in which they are developed. Some of the Arachnida, a few isopod crustaceans, most of the Chilopoda, and the majority of insects have branched tracheae. Most of the Diplopoda are provided with segmental clusters of unbranched respiratory tubules, and one family of the Protura has unbranched tracheae arising only on the thorax. The Arachnida have tracheae and respiratory pouches known as "lung books," so named because their walls are produced into parallel lamellate folds. In the Onychophora the respiratory invaginations take the form of groups of small tubules irregularly scattered over the inner surface of the body wall.

Development of the Tracheae.—The respiratory tubes of insects are formed in the embryo as simple invaginations of the ectoderm along the sides of the body (Fig. 220). The external orifices of the depressions become the *spiracles* (*Sp*); the internal tubular parts are the rudiments of the tracheae (*Tra*). The tracheal pits extend inward and branch into ramifying tubes that eventually extend to all parts of the body in insects having a fully developed tracheal system. Judging from the position of the abdominal spiracles in adult insects, it would seem that the primitive position of the tracheal invaginations is in the lateral parts of the dorsum of the body segments just above the limb bases. In embryos the spiracular rudiments commonly are thus located (Fig. 221).

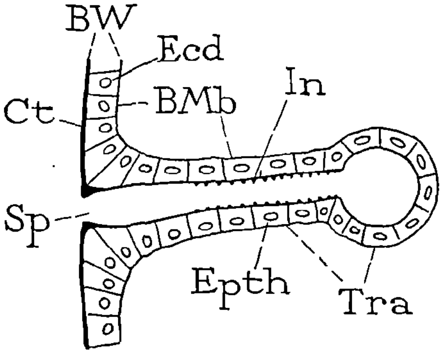

FIG. 220.—Diagram showing the relations of the layers of a tracheal invagination to the layers of the body wall. *BMb*, basement membrane; *BW*, body wall; *Ct*, cuticula; *Ecd*, epidermis; *Epth*, tracheal epithelium; *In*, intima (tracheal cuticula); *Sp*, spiracle; *Tra*, trachea.

Number of Spiracles.—It is possible that the primitive insects had a pair of tracheal invaginations in each of the 17 somites of the gnathal, thoracic, and abdominal regions of the body; but there is no suggestion of tracheae ever having been formed in the protocephalon. Direct proof of the existence of tracheal invaginations, however, has been found only on 14 segments, which are the second maxillary segment, the 3 thoracic segments, and the first 10 abdominal segments.

Tracheal invaginations of the second maxillary segment are said by Nelson (1915) to be formed in the embryo of the honey bee, where they appear on the anterior part of the segment above the bases of the labial rudiments. These tracheal pits of the second maxillary segment, Nelson says, give rise to the tracheal system of the head but are soon closed and leave no trace of their existence in the head of the adult bee. In some of the Sminthuridae (Collembola) a pair of spiracles is situated on the sides of the neck close behind the head (Fig. 222 B). Davies (1927) believes that these apparent cervical spiracles belong to the prothorax because of their position relative to the muscle attachments on the posterior margin of the head capsule. When we consider, however, that the submarginal ridge of the head on which these muscles are inserted marks the intersegmental line between the two maxillary segments (Fig. 54 A, *pos*), and that the membranous neck is derived in part from the segment of the labium, it becomes evident that the neck spiracles of *Sminthurus* lie in the region of the second maxillary segment.

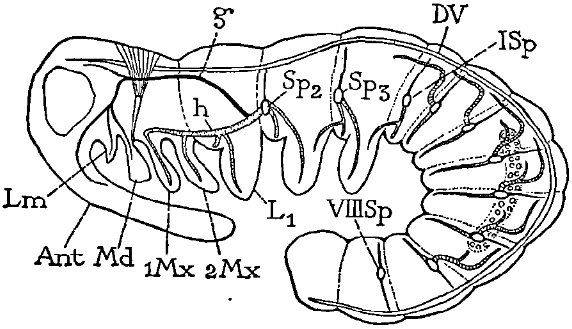

FIG. 221.—Diagram of the tracheation and position of the spiracles in the embryo of *Dixippus morosus*. (*From Lehmann*, 1925.)

These spiracles, therefore, may be persisting examples of the second maxillary spiracles, known otherwise only as temporary tracheal openings in the embryo of the honey bee.

Prothoracic spiracles are present in the embryonic stage of some insects, but these spiracles are completely obliterated before hatching. The embryonic prothoracic spiracles have been described by Cholodkowsky (1891) in *Blattella*, and by Wheeler (1889) in *Leptinotarsa.*

The thorax of postembryonic stages of all insects, except Diplura, never has more than two pairs of spiracles, and these two pairs are formed in the embryo on the anterior part of the mesothorax and the metathorax, respectively (Fig. 221, Sp_2, Sp_3). In many insects, however, the thoracic spiracles migrate forward during development and come thus to have a definitive position in the secondary intersegmental membranes or in the posterior parts of the segments preceding. The mesothoracic spiracles particularly are subject to this anterior migration and hence often occur in larval or adult insects on the sides of the prothorax, for which reason they are frequently called the "prothoracic" spiracles. The anterior (mesothoracic) spiracles are usually the larger of the thoracic spiracles, those of the metathorax being generally small, and sometimes rudimentary, as in certain larvae. In adult Pterygota the thoracic spiracles have a "pleural" position, but it is probable that their definitive location between the pleural sclerites is a result of the secondary upward extension of the subcoxal plates of the leg bases on each side of the spiracles.

The Diplura differ from other insects in that some species have three and others four pairs of spiracles on the thorax. The greater number occurs in certain species of Japygidae (Fig. 222 A). The first spiracle (Sp_2) lies in the extreme posterior part of the prothorax; the second (Sp_2') is situated on the side of the mesothorax above and behind the leg base; the third (Sp_3) is in the anterior part of the metathorax before the leg base; and the fourth (Sp_3') corresponds in position to the mesothoracic spiracle (Sp_2'). The first spiracle of the series (Sp_2) is very evidently the usual mesothoracic spiracle of other insects displaced into the prothorax; the third (Sp_3), likewise, would appear to represent the usual metathoracic spiracle. The two posterior spiracles (Sp_2', Sp_3'), therefore, are not represented in Thysanura and Pterygota, but it is most interesting to observe that their positions on the segments correspond exactly to the usual position of the spiracles in Chilopoda (Fig. 52 A). Moreover, these posterior thoracic spiracles of Diplura fall in line with the series of abdominal spiracles (*Isp*). Hence we might conclude that the anterior thoracic spiracles of Diplura represent the two thoracic spiracles present

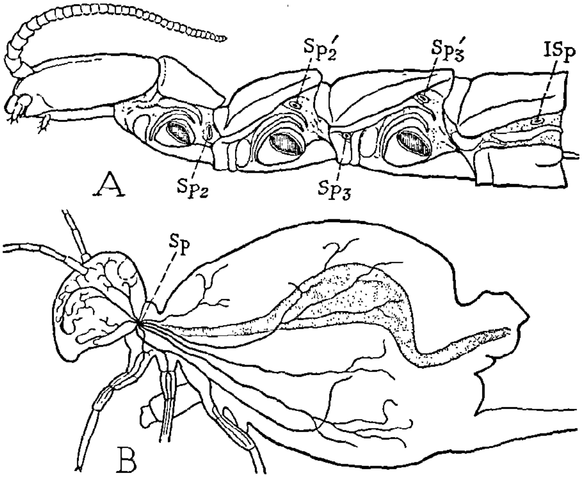

Fig. 222.—Unusual position of spiracles in certain apterygote insects. A, *Heterojapyx gallardi*, with two mesothoracic and two metathoracic spiracles on each side. B, *Sminthurus viridis*, with a spiracle on each side of the neck. (*From Davies*, 1927.)

in other insects, and that the posterior spiracles, belonging morphologically to the same series as the abdominal spiracles, have been eliminated from the thorax of other insects. If, then, the anterior thoracic spiracles have had an independent origin, we have here an explanation of the curious fact that the structure of these spiracles in pterygote insects is almost always different from that of the abdominal spiracles. In *Campodea*, according to Grassi (1886), the anterior metathoracic spiracles are absent, but the same spiracles are frequently rudimentary or absent in Pterygota.

On the abdomen there are usually eight pairs of spiracles, and this is the maximum number of abdominal spiracles in postembryonic stages of all insects, but the number may be variously reduced. Cholodkowsky (1891) reports the existence of a pair of tracheal invaginations on each of the first nine abdominal segments in the embryo of *Blattella* (*Phyllodromia*); and Heymons (1897) finds in the *Lepisma* embryo, in addition to nine distinct pairs of abdominal spiracles, masses of ectodermal cells on the tenth segment at points corresponding to the spiracular invaginations on the preceding segments, which he takes to be rudiments of a tenth pair of abdominal spiracles. The first abdominal spiracles are often situated close to the thorax, but their abdominal relation is shown by the fact that they always lie posterior to a line through the base of the third phragma, which is an intersegmental fold between the metathorax and the first abdominal segment.

Organization of the Tracheal System.—As the primary tracheal invaginations grow into the body of the insect, they divide a short distance from their origins into major and minor branches, and the latter eventually ramify to all the tissues. In insects having a well-developed tracheal system some of the branches from consecutive and opposite spiracles unite to form longitudinal trunks and transverse commissures. In general, the mature tracheal system attains an organization having a pretty definite fundamental pattern.

General Plan of the Body Tracheation.—It is probable that in a primitive stage each somite of the body was independently tracheated from its own pair of spiracles, and that the connection of the segmental systems by longitudinal trunks is a secondary condition evolved to give more efficient aeration. In general it is found that in each half of each segment there are three principal tracheae given off from the longitudinal trunk (Fig. 223 B, *LTra*) in the neighborhood of the connection of the latter with the spiracle. Hence we may suppose that primarily a short *spiracular trachea* (Fig. 223 A, *a*) extended inward from the spiracle and gave off three main branches. Of the latter, one is a *dorsal trachea* (*b*) going to the dorsal musculature of the body wall and to the dorsal blood vessel; another is a *ventral trachea* (*c*) supplying the ventral musculature and the ventral nerve cord, and sending a branch into the leg in the leg-bearing segments; the third is a median *visceral trachea* (*d*) having its principal ramifications on the walls of the alimentary canal, with branches to the fat body and, in the appropriate segments, to the gonads and the genital ducts.

The plurisegmental longitudinal trunks are formed by the union of anterior and posterior branches from the spiracular tracheae of consecutive segments. The lengthwise trunks most generally present are a pair of *lateral longitudinal trunks* (Fig. 223 B, *LTra*), one on each side of the body, connecting all the spiracular tracheae from the first thoracic spiracle to the last abdominal spiracle. But there is often present also a pair of *dorsal longitudinal trunks* (C, *DTra*), connecting the dorsal tracheae of successive segments, and sometimes a pair of *ventral longitudinal trunks* (E, *VTra*) uniting the ventral tracheae. In some insects, finally, there are *visceral longitudinal trunks* on the sides of the alimentary canal (E, *VsTra*).

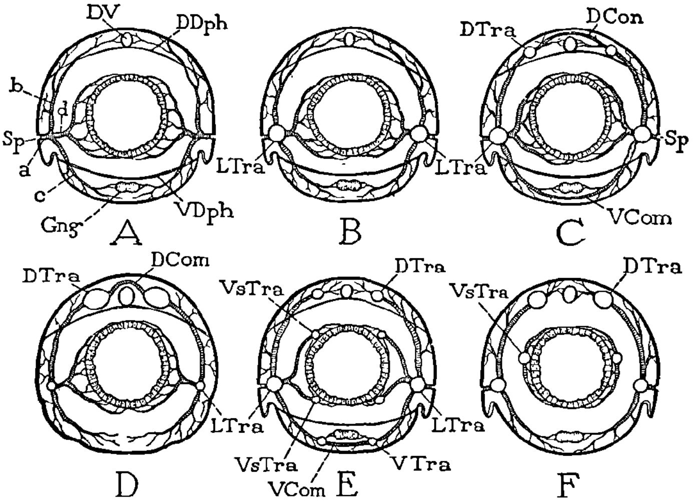

FIG. 223.—Diagrammatic cross section of the abdomen showing the principal tracheae and tracheal trunks. *a*, spiracular trachea; *b*, *c*, *d*, dorsal, ventral, and visceral segmental tracheae; *DCom*, dorsal commissure; *DDph*, dorsal diaphragm; *DTra*, dorsal plurisegmental tracheal trunk; *DV*, dorsal blood vessel; *LTra*, lateral plurisegmental tracheal trunk; *Sp*, spiracle; *VCom*, ventral commissure; *VDph*, ventral diaphragm; *VsTra*, visceral plurisegmental tracheal trunk; *VTra*, ventral plurisegmental tracheal trunk.

By anastomosis of the dorsal or the ventral tracheae in each segment there are frequently formed *commissural trunks* continuous from one side of the body to the other. Thus there may be present a *dorsal tracheal commissure* (D, *DCom*) crossing above the dorsal blood vessel, or a *ventral tracheal commissure* below the ventral nerve cord (E*VCom*).

The lateral longitudinal trunks are usually the largest tracheae in the insect. Because of their size and their immediate connection with the spiracles, these trunks become generally the chief avenues of air circulation in the body. In dipterous larvae and pupae, however, in which the lateral spiracles are suppressed and functionally replaced by dorsal spiracles connected with the ends of dorsal trunks, it is the dorsal trunks that become the major respiratory passages (Figs. 223 D, 228, 229, *DTra*). The lateral trunks (*LTra*) in such cases are reduced and appear as a series of small connectives between the transverse tracheae. Ventral longitudinal trunks are not often developed, but they are present in the abdomen of some Orthoptera. In the Odonata a visceral trunk arises from each of the dorsal trunks in the anterior end of the abdomen, crosses above the crop to the opposite side of the body, where it goes posteriorly along the lateral wall of the mesenteron, and finally unites with the lateral trunk of the same side in the eighth abdominal segment (see Tillyard, 1917).

Kennedy (1922*a*) and Steiner (1929) have attempted, from a study of the Zygoptera, to deduce a more detailed concept than that given above of the primitive tracheation springing from each primary tracheal invagination, from which might be evolved the basic pattern of the tracheal system in each of the insect orders. Kennedy observes, however, that the "readiness of the tracheal system to develop new branches has been one of the things which has made homologization of the branches seem a hopeless task." We may add that the same condition still prevails to such an extent that it would be useless to present here any attempt at a comparative study of the tracheal system. A review of the facts known concerning the fundamental plan of the tracheal system in the principal orders of insects is given by Lehmann (1925).

Tracheation of the Head.—The tracheation proceeding from the first thoracic spiracles is necessarily different from that of the other spiracles, because from these primarily mesothoracic spiracles originates the tracheal supply not only of the prothorax and mesothorax but also of the head.

The tracheae of the head usually arise from two principal pairs of head trunks given off from the first spiracles. One of these on each side is a *dorsal head trunk*, the other a *ventral head trunk*. The actual number of tracheae entering the back of the head from the thorax, however, may be increased by an immediate branching of the two primary trunks, and it is not clear that the principal trunks themselves are in all cases strictly homologous branches.

A relatively simple condition of the head tracheation is described by Lehmann (1925) in *Dixippus morosus*. The dorsal head trunk (Fig. 221, *g*) sends branches to the antennae, the compound eyes, the mandibles, the brain, and the adductor muscles of the mandibles. The ventral trunk (*h*) branches to the first and second maxillae and to the mandibular adductors and forms an anastomosis with the dorsal trunk. A similar distribution of the head tracheae, Lehmann says, occurs in *Machilis* and in Ephemerida. In *Lepisma,* according to Šulc (1927), a short cephalic trunk springs from the dorsal branch of the first (mesothoracic) spiracle and soon divides into a *trachea cephalica dorsalis* and a *trachea cephalica ventralis.* The first branches to the prothoracic tergum, the dorsum of the head, the brain, the optic lobes, the upper parts of the eyes, and the antennae. The second branches to the prosternum and neighboring organs, the posterior part of the head, the salivary glands, the inner region of the eyes, and the gnathal appendages. From this it would appear that in general the procephalic part of the head is tracheated from the dorsal head trunk, and the gnathal region from the ventral trunk, though Lehmann finds that the mandibles receive their tracheae from the dorsal trunk. The ventral trunk, Lehmann says, is the first head trachea formed in the embryo of *Dixippus,* the dorsal trunk being an outgrowth from it.

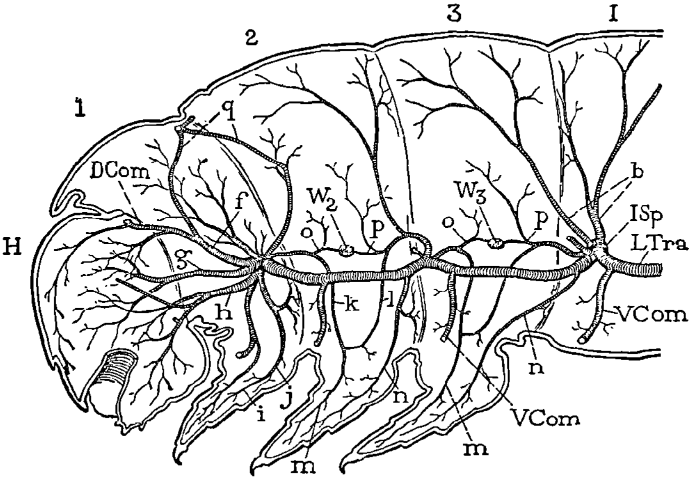

FIG. 224.—Tracheation of the head and thorax of a noctuid caterpillar, inner view of right side.

Studies on the head tracheation of other insects show a considerable diversity in the distribution of the branches from the principal trunks. Thus, according to Alt (1912; Korschelt, 1924), the ventral head trunks of *Dytiscus* supply almost all the tracheation of the head muscles and give branches to all the appendages, including the antennae and mandibles, as well as to the first and second maxillae.

In the caterpillar (Figs. 224, 225) three large tracheal trunks enter the head from each anterior spiracle, one (*f*) being dorsal, another (*h*) ventral, and the third (*g*) having a middle position between the other two. The dorsal and middle trunks, however, branch from a common base on each side. The dorsal trunks (*f*) go upward and unite to form a commissure (*DCom*) in the posterior dorsal part of the head. Each gives off posteriorly an anterior arm of the dorsal X-shaped commissure of the prothorax (*q*) and anteriorly several small branches to the mandibular muscles. From the apex of the head commissure a pair of long tracheae diverge anteriorly along the arms of the V-shaped epistomal ridge of the facial wall of the cranium, giving off branches to the dorsal muscles of the pharynx, and finally ending in the labrum. The middle trunks (*g*) enter the sides of the head and break up into large branches distributed to the lateral parts of the mandibular muscles. The ventral trunks (*h*) divide each into two main branches as they enter the head. One branch turns upward into the ventral parts of the mandibular adductors; the other proceeds forward beneath the oesophagus, giving off first a dorsal trachea, of which a branch penetrates the brain, while the rest of the main branch is distributed to the oesophagus, pharynx, muscles of the maxilla and labium, and the ventral parts of the head generally.

The head of the honey bee larva, as described by Nelson (1924), is supplied with three pairs of tracheae from a transverse commissure uniting the first spiracles. Of these the mesal pair goes to the brain. The second pair gives off branches in the upper part of the head to the aorta and the brain, but the main trunks go ventrally and ramify to the maxillae, the mandibles, the antennal rudiments, and the labrum. The lateral third pair goes to the salivary glands. In the embryo of the bee, Nelson (1915) says, the invaginations from the temporary second maxillary spiracles give off each four primary tracheal branches, one going posteriorly, one dorsally, and the other two anteriorly. The posterior branches connect with the tracheal system of the thorax, the dorsal branches from opposite sides unite to form the anterior commissure, and the anterior branches on each side become the two principal pairs of head tracheae.

Tracheation of the Thorax.—The tracheal system of the thorax is often complex and differs much in different insects. In its simpler forms, however, it departs little from the more generalized plan of segmental tracheation in the abdomen, except for the supply of tracheae to both the prothorax and the mesothorax from the mesothoracic spiracles, and in the frequent reduction or obliteration of the metathoracic spiracles.

A good example of generalized tracheation in the thorax is seen in a caterpillar (Fig. 225). The large lateral trunks (*LTra*) are continuous from the abdomen to the mesothoracic spiracles (Sp_2), which are situated on the sides of the dorsum of the prothorax. The metathoracic spiracles (Sp_3) are rudimentary, but the site of each is connected with the lateral trunk by a small tracheal strand. The principal somatic and visceral branches are given off from the lateral trunk in the neighborhood of the spiracles, and in each segment there is a well-developed ventral commissure (*VCom*) crossing the anterior part of the sternal region.

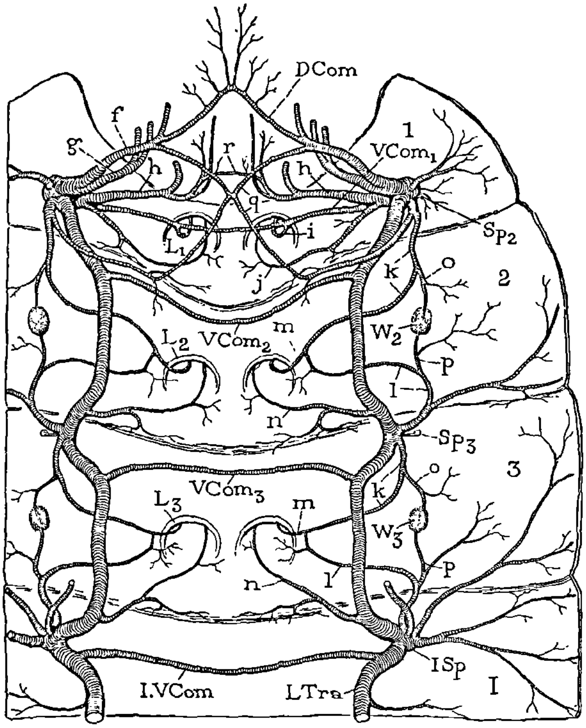

FIG. 225.—Tracheation of the thorax and first abdominal segment of a noctuid caterpillar, dorsal view.

The tracheation of the thoracic legs of the caterpillar is of particular interest because in some respects it illustrates the leg tracheation typical of most insects. Each leg has two tracheae, one lateral, the other median. In the prothorax the lateral trachea of the leg (*i*) is derived from the ventral commissure; the median one (*j*) comes directly from the branches of the first, or mesothoracic, spiracle. In the mesothorax and the metathorax, the lateral leg trachea (*m*) is a branch from a tracheal loop (*k*, *l*) formed apparently by the union of tracheae from the spiracles preceding and following, that is, from the mesothoracic and metathoracic spiracles in the case of the mesothoracic legs (L_2), and from the metathoracic and first abdominal spiracles in the case of the metathoracic legs (L_3). Each lateral leg trachea of the wing-bearing segments, therefore, in its entirety has the form of a Y, the arms of which (*k*, *l*) proceed from successive spiracles, while the stem (*m*) enters the leg. The median leg trachea (*n*) in these segments springs from the lateral trunk in the neighborhood of the spiracle following.

Tracheation of the Wings.—In the caterpillar it is to be seen that each internal wing rudiment (Figs. 224, 225, W_2, W_3) is penetrated from opposite ends by two tracheae (*o*, *p*) given off from the arms of the lateral Y-shaped leg trachea (*k*, *l*) of the same segment. The two basal wing tracheae appear to become continuous through the wing rudiment in older larvae. It has been shown by Chapman (1918), from a comparative study of the basal connections of the wing tracheae, that the wing tracheation here exemplified in the caterpillar represents the primary tracheation of the wing in all insects. There are, of course, many deviations from the typical condition and many developments along different lines of specialization; but all such modifications, Chapman shows, may be derived from the fundamental simple plan in which two tracheae proceed from the convergent arms of the lateral leg trachea and enter the wing base. According to Kennedy (1922*a*), the anterior branch is the original wing trachea. There is probably no morphological significance in the origin of the wing tracheae from the Y-shaped leg tracheae, since this particular tracheation of the legs occurs only in the wing-bearing segments. The spiracles and the wings belong to the lateral areas of the dorsum, while the legs arise from the pleural areas.

The wing rudiments of holometabolous larvae are at first penetrated by bundles of tracheoles given off from the basal trachea, but the tracheoles are later replaced by the definitive tracheae, which enter the veins of the mature wings and persist throughout the life of the insect to aerate the living tissues within the veins. According to Comstock (1918), the anterior basal trachea of each wing gives off the tracheae of the costal, subcostal, radial, and medial veins; the posterior one gives off the cubital and anal tracheae. When the connective through the wing base, or *transverse basal trachea*, is developed, however, "the medial trachea," Comstock says, "tends to migrate along the transverse basal trachea toward the cubito-anal group of tracheae" and thus becomes more closely associated with the posterior wing tracheae in the wings of more specialized insects.

Tracheation of the Abdomen.—With insects having a fully developed tracheal system, the lateral tracheal trunks extend posteriorly to the last pair of spiracles, which are usually those of the eighth abdominal segment. In the caterpillar (Fig. 226) the principal abdominal branches are given off from the longitudinal trunks in the neighborhood of the spiracles. Transverse ventral commissures (*VCom*) uniting the lateral trunks occur in each of the first seven segments, and in the eighth segment there is a dorsal commissure (*DCom*). The ganglia of the ventral nerve cord, except the last, are tracheated by branches springing from the ventral commissures of their proper segments, regardless of the positions of the ganglia (Figs. 226, *VIIs*, 227, *s*). The composite last ganglion,

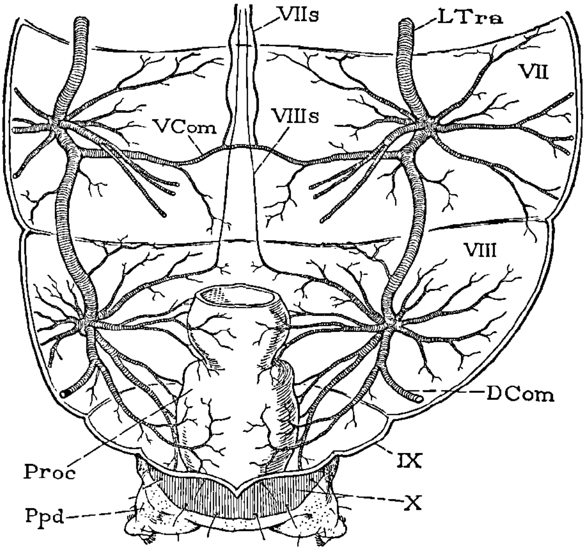

FIG. 226.—Tracheation of the posterior abdominal segments of a noctuid caterpillar, dorsal view.

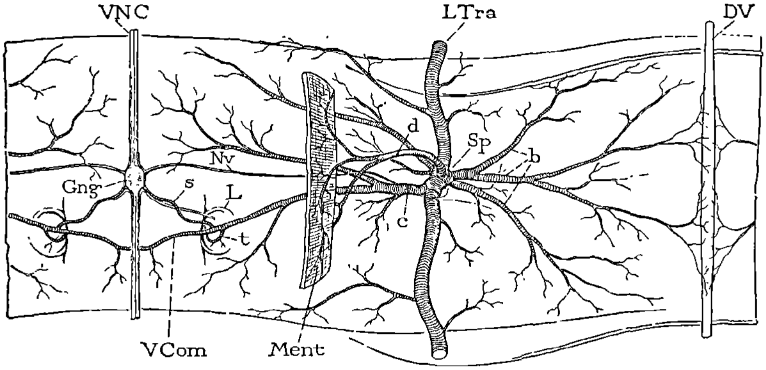

FIG. 227.—Tracheation of the ventral region and the right half of the third abdominal segment of a noctuid caterpillar.

lying in the sixth segment, for which there is no ventral commissure, receives its tracheae (Fig. 226, *VIIIs*) directly from the lateral trunks opposite the eighth spiracles. The abdominal legs of the caterpillar, except the last pair, also are tracheated from the ventral commissures (Fig. 227, *t*). The leg tracheae of the abdomen, therefore, correspond to the lateral tracheae of the prothoracic legs (Fig. 225, *i*), which have no counterparts in the mesothorax and metathorax. The visceral tracheae of the abdomen (Fig. 227, *d*), going principally to the walls of the alimentary canal, arise from the lateral trunks near the spiracles. The heart (*DV*) is tracheated by terminal branches of the dorsal tracheae (*b*).

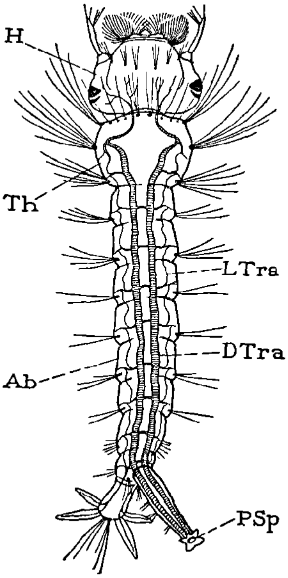

Fig. 228.—A mosquito larva, dorsal view, showing dorsal tracheal trunks opening through posterior spiracles only (*PSp*), and lateral trunks along the line of the closed adult spiracles.

Modifications of the Tracheal System.—All insects do not have a fully developed equipment of respiratory tubes. In various holometabolous larvae, especially aquatic and parasitic species, the tracheal system is more or less reduced or rudimentary, and the spiracles may be closed. This condition in such insects is clearly the result of a secondary degeneration of the tracheae. In *Machilis*, groups of segmental tracheae arise from the spiracles, but there are no longitudinal trunks. *Campodea* and Protura (Eosentomidae) have thoracic tracheae only, which in the second group are said to be unbranched. Most of the Collembola have no tracheae at all, and in tracheated forms, such as *Sminthurus* (Fig. 222 B), the tracheae arise from a single pair of spiracles located at the back of the head. It may be questioned, however, even in the Apterygota, whether the imperfect state or absence of the tracheal system represents a primitive condition or is the result of a degeneration of the tracheae in forms whose small size makes cutaneous respiration sufficient. The presence of a fully developed tracheal system with complete longitudinal trunks in Japygidae suggests that the insect tracheal system in its usual form is an inheritance from common ancestors older than modern Apterygota.

An interesting example of specialization in the tracheal system is seen in the larvae and pupae of most Diptera, in which the dorsal longitudinal trunks become the principal respiratory passages (Figs. 228, 229, *Dtra*). The dorsal trunks of all dipterous larvae open to the exterior through spiracles situated at one end or at both ends of the body (*ASp*, *PSp*). These dorsal spiracles appear to be secondary respiratory orifices, since in some cases there are present also the usual lateral spiracles, though the latter are closed and remain rudimentary during the larval and pupal stages and are not functionally restored until the imaginal stage. All dipterous larvae have a pair of posterior dorsal spiracles, and some have in addition an anterior pair on the prothorax. The pupae have only the anterior dorsal spiracles. In a tipulid larva the lateral and dorsal tracheal trunks are equally developed; but in most other dipterous larvae, as is well shown in a mosquito larva or a muscoid maggot (Figs. 228, 229), the dorsal trunks (*DTra*) are proportionately greatly enlarged, while the lateral trunks (*LTra*) are reduced to inconspicuous connectives between the roots of the transverse tracheae along the line of the closed and rudimentary lateral spiracles.

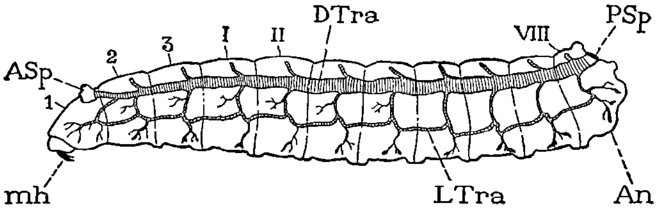

Fig. 229.—Larva of a muscoid fly with anterior and posterior dorsal spiracles (*ASp*, *PSp*) at ends of dorsal tracheal trunk; lateral spiracles absent.

According to the distribution of the functional spiracles, several types of respiratory conditions may be distinguished. The *holopneustic* type is the generalized one in which the insect is provided with the usual bilateral series of 10 pairs of open spiracles; if there are only anterior and posterior functional spiracles, the insect is said to be *amphipneustic;* if it has anterior spiracles only, it is *propneustic;* if it breathes by posterior spiracles only, it is *metapneustic;* if all the spiracles are closed, it is *apneustic.* These terms and others referring to the distribution of the functional spiracles are more precisely defined in the Glossary at the end of this chapter.

Structure of the Spiracles.—In their simplest form the spiracles are merely the openings from the integument into the tracheae (Fig. 230 A, *t*) representing the primitive apertures of the tracheal invaginations (Fig. 220, *Sp*). Such spiracles have no provision for regulating the size of the tracheal aperture. Spiracles of this kind occur in some of the Apterygota, and it is probable that some of the spiracles of lower Pterygota, such as the thoracic spiracles of Plecoptera, are of the same type of structure.

In general, however, the primary tracheal apertures are more or less sunken into secondary depressions of the integument (Fig. 230 B). The external part of each spiracle thus becomes a pitlike or tubular chamber, which is the *spiracular atrium* (*Atr*). The atrium opens, on the one hand, to the exterior by the secondary *atrial orifice* (*a*) and, on the other, into the trachea by the primitive *tracheal orifice* (*t*). The walls of the atrium are often rugose and may be strengthened by transverse circular ridges, but such structures are not true taenidia, which pertain to the walls of the tracheae only. The atrial walls are also commonly clothed with hairs or other cuticular processes, such as occur on the external body wall. In some cases the atrium is subdivided into an outer and an inner chamber, which differ in diameter or in the structure of their walls, but in general the atrium is quite distinct from the spiracular trachea. The lips of the atrial orifice may be flush with the surface of the integument, raised in a marginal flange or short tube, or produced into a pair of valve-like plates, which are sometimes movable by special muscles. The opening is often contained in a small sclerotic plate of the body wall forming a distinct spiracular sclerite, or *peritreme* (B, *Ptr*).

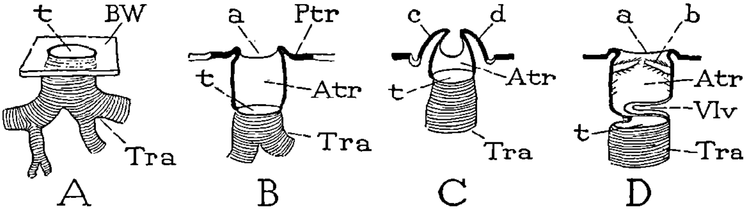

FIG. 230.—Structure of spiracles, and two principal types of spiracular closing apparatus. A, simple spiracle without an atrium. B, an atriate spiracle. C, atriate spiracle with lip type of closing apparatus. D, atriate spiracle with closing valve at inner end of atrium. *a*, atrial orifice; *Atr*, atrium; *b*, filter apparatus; *BW*, body wall; *c*, *d*, anterior and posterior lips of atrium; *Ptr*, peritreme; *t*, tracheal orifice; *Tra*, trachea; *Vlv*, valve.

Atriate spiracles are usually provided with a mechanism for regulating the passage of air to and from the spiracular trachea. This mechanism is generally called the *closing apparatus*, though it serves both to open and to close the spiracle. The structure of the closing apparatus differs much in different insects, and it is often quite different between the thoracic and the abdominal spiracles of the same species. Two principal types of occlusor mechanism, however, may be distinguished, with numerous modifications under each. The first type is a device of one kind or another for closing the outer lips of the atrium (Fig. 230 C). The second is a mechanism for regulating the size of the tracheal aperture at the inner end of the atrium (D).

Accessory structures are often present in the outer part of the atrium in spiracles of the second type, which simply guard the atrial orifice (Fig. 230 D, *b*). Such structures commonly have the form of opposing rows of tapering processes of the atrial wall thickly clothed with interlacing hairs, the whole mass of which forms a *filter apparatus* that freely permits the passage of air, but which prevents the entrance of foreign particles or water into the atrium (Fig. 233, *b*).

A closing apparatus of the spiracles is absent in some of the higher insects, but the lack of the mechanism in such cases is probably a secondary condition. The thoracic spiracles are more variable in structure than are the abdominal spiracles, and in general the lip type of closing apparatus is characteristic of them; the abdominal spiracles more consistently have the inner type of closing mechanism. Unusual modifications of the spiracular structure occur in certain holometabolous larvae, as in the so-called "biforous" spiracles of coleopterous larvae and the dorsal spiracles of dipterous larvae. It will be possible to give here only a brief description of the principal varieties of spiracular structure, illustrated by a few typical examples.

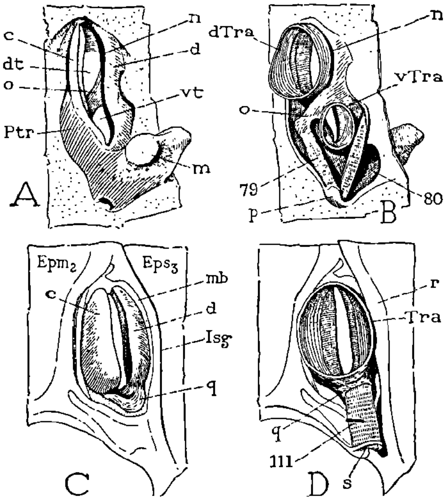

FIG. 231.—Thoracic spiracles of a grasshopper, *Dissosteira carolina;* examples of spiracles of the lip-closing type. A, first spiracle, outer view. B, same, inner view, with closing and opening muscles (*79, 80*). C, second spiracle, outer view. D, same, inner view, with closing muscle (*111*).

Spiracles with an External Closing Apparatus.—The type of spiracular structure in which the closing apparatus is formed by the lips of the atrial aperture is well illustrated in the thoracic spiracles of Acrididae. In *Dissosteira carolina* the first, or mesothoracic, spiracle, lying in the membrane between the prothorax and the mesothorax, is an obliquely vertical slit in the peritremal sclerite (Fig. 231 A) with strongly protruding anterior and posterior lips. The anterior lip (*c*) is a rigid elevation of the anterior edge of the atrial aperture; its inner face, however, is soft and deeply grooved parallel with the outer margin. The posterior lip (*d*) is a weaker and freely movable flap, but it has a sharp, strongly sclerotized marginal band (*n*), which, when the spiracle is closed, fits into the groove of the anterior lip. The atrium of this spiracle is the shallow cavity between the lips. From it there are given off two tracheae, a large dorsal one (B, *dTra*) and a smaller ventral one (*vTra*). In the septum between the two tracheal openings is a strong bar (*o*) projecting anteriorly and ventrally from the posterior lip. Upon the free end of this process is inserted a short muscle (*79*), which has its origin ventrally on the peritreme. A second muscle (*80*) arises close to the first and is inserted on the base of the posterior lip of the spiracle. The first muscle (*79*) is the occlusor of the spiracle; the second (*80*) is its antagonist. The different action of the two muscles results from the opposition of their points of insertion relative to the long axis of the posterior movable lip.

The second, or metathoracic, spiracle of *Dissosteira* (Fig. 231 C, D) is even more simple than the first. Externally it presents two thick, elongate, oval, valve-like lips (C, *c*, *d*) separated by a vertical cleft. Both lips of this spiracle are movable, though they are united ventrally in a small sclerotic lobe (*q*). On the inner surface of the spiracle (D) it is seen that a small muscle (*111*) is inserted on this lobe, which takes its origin on a process (*s*) of the margin of the mesocoxal cavity. This muscle is the occlusor of the spiracle. Its contraction revolves the spiracular lips toward each other and closes the aperture between them. The lips open automatically by the elasticity of their basal connections.

Spiracles having the lip type of closing mechanism are of common occurrence on the thorax in most groups of insects. In the Blattidae the thoracic spiracles differ from those of Acrididae, but each is a simple structure closed by the external atrial lips. The metathoracic spiracle of an adult *Dytiscus*, as described by Alt (1909; Korschelt, 1924) is very similar to that of *Dissosteira*. The thoracic spiracles of Hemiptera (see Mammen, 1912) are of the lip-closing type. In the honey bee the large first thoracic spiracle is closed by an operculum, which is the large, flattened, lidlike anterior lip of the atrium.

Spiracles with an Internal Closing Apparatus.—Spiracles in which the closing apparatus lies at the inner end of the atrium and regulates the tracheal opening comprise the majority of insect spiracles, but this type of spiracular structure is particularly characteristic of abdominal spiracles. With spiracles of this kind, the atrium is usually a well-defined open cavity of the integument (Fig. 230 D, *Atr*) and may be long and tubular. The entrance, however, is often guarded by a filter apparatus, usually in the form of two rows of matted brushes projecting from opposite walls of the atrium (*b*). The lips of the atrial aperture have various forms, but they are never movable and they take no active part in the closing of the spiracle. The size of the atrial orifice varies much regardless of the size of the atrium; sometimes it is contracted to a small pore opening into a relatively large atrial chamber, and in special cases it is closed.

Two common subtypes of structure are found among spiracles of the inner closing type. In one subtype the occlusor mechanism is a simple pinchcock apparatus (Fig. 232 A), consisting of two sclerotic bars (*e*, *f*) in opposite walls of the atrium just before the mouth of the trachea (*t*), with a muscle (*osp*) stretched between their projecting ends. The contraction of the muscle brings the bars together and thus closes the tracheal entrance (B). Usually a second muscle arising on the body wall is inserted on the end of the anterior bar opposite the attachment of the occlusor muscle and acts as a dilator of the spiracle (C, D, *dlsp*). The abdominal spiracles of Blattidae have a closing apparatus of this kind (C), but the free end of the anterior bar is prolonged as a manubrium (*g*) to give stronger effect to the muscles. The dilator muscle (*dlsp*) in Blattidae arises anteriorly on the deflected lateral lobe of the tergum that contains the spiracle. In the Acrididae (D) the closing mechanism of the abdominal spiracles is a modification of the blattid type, in which the posterior bar is absent, and the anterior bar is represented by the entire anterior wall of the atrium (*e*), which is movable and produced ventrally in the manubrium (*g*). The occlusor muscle arises on the tergal wall immediately behind the spiracle, and the long dilator muscle (*dlsp*) arises on the lateral edge of the sternum.

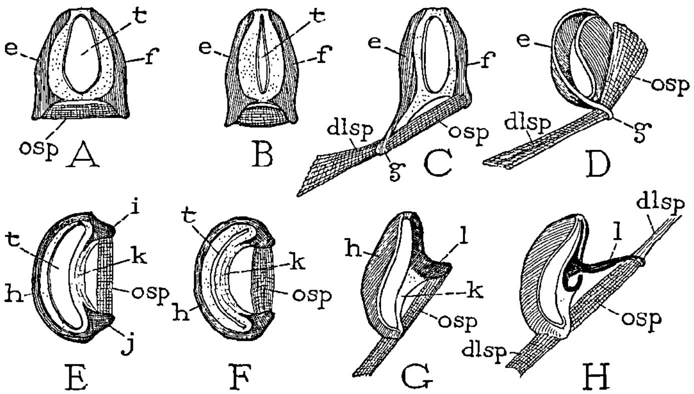

Fig. 232.—Examples of spiracles with an inner closing apparatus, diagrammatic. A, B, the pinchcock, or double-valve, type of closing apparatus, open and closed. C, an abdominal spiracle of *Blatta*. D, same of *Dissosteira*. E–H, varieties of the single-valve type of closing apparatus. *dlsp*, dilator muscle; *e*, anterior bar; *f*, posterior bar; *g*, manubrium of anterior bar; *h*, bow; *i*, *j*, dorsal and ventral muscle processes; *k*, closing valve; *l*, lever of valve; *osp*, occlusor muscle.

In the second subtype of occlusor apparatus in spiracles of the inner closing type the effective organ is a valve. The valve consists of a fold of the inner end of one wall of the atrium (Fig. 230 D, *Vlv*), and of a mechanism for inflecting the fold over the tracheal mouth (Fig. 232 E). An occlusor apparatus of this kind is the common form of closing apparatus in the abdominal spiracles of holometabolous insects. The essential elements of the closing structure (Fig. 232 E) include, first, a crescentic or semicircular elastic bar (*h*), the so-called *closing bow* (*Verschlussbügel* of Landois and Thelin, 1867), the ends of which (*i, j*) are produced outside the atrial walls as two thick conical processes (*Verschlusskegeln*); second, a soft, convex fold (*k*), the *closing band* (*Verschlussband*), projecting into the atrial lumen from the wall opposite the bow; and, third, a closing muscle (*osp*) stretched like a bowstring between the ends of the bow. The closing band, or valve, is usually on the posterior wall of the atrium and is located just before the mouth of the trachea (Fig. 230 D). The contraction of the occlusor muscle (Fig. 232 E, *osp*) pulls on the two ends of the bow and forces the valve (*k*) inward until it entirely closes the tracheal orifice (F, *t*). In some spiracles the closed valve overlaps externally the bow on the opposite margin of the aperture (Fig. 230 D). The opening of the spiracle may be caused entirely by the elasticity of the bow, but usually a dilator muscle, arising ventrally on the body wall, is inserted on the lower process of the bow opposite the attachment of the occlusor muscle.

A simple closing apparatus of the form just described occurs in the abdominal spiracles of many insects, but numerous departures from the typical structure are found in the holometabolous orders. A common modification results from the suppression of the ventral process of the bow (Fig. 232 G), and the development of a point of flexure between the dorsal process (*l*) and the upper end of the bow. The pull of the closing muscle on the dorsal process then brings the base of the latter and the closing band (*k*) against the inner edge of the bow to close the tracheal aperture. This type of structure, found with variations in the Coleoptera, might also be supposed to be a derivative of the pinchcock type of mechanism (A, B, C), but its effective element is a valve, as in a typical valvular spiracle (E). The valve mechanism is highly developed in Lepidoptera by the extension of the dorsal muscle process into a long lever (H). A dorsal dilator muscle or strand of elastic tissue (*dlsp*), arising on the body wall and inserted on the lever, is present in caterpillars, in addition to a ventral muscle, which is here inserted on the atrial wall.

The structural details and action of the closing apparatus of a caterpillar spiracle are shown in Fig. 233, representing the first thoracic spiracle, in which the structure is the same as that of the abdominal spiracles, except that the position of the parts is reversed, the lever and the valve being anterior in the thoracic spiracles and the bow posterior. The lever (*l*) is supported on a looped bar in the membranous valve (B, *Vlv*), and the latter, when closed, is received into a deep concavity of the posterior atrial wall. Distal to the valve the atrial aperture is protected by a filter apparatus composed of two opposing mats of thick, brushlike processes (*b*) projecting from the anterior and posterior walls of the atrium.

Biforous Spiracles.—In the larvae of various families of Coleoptera there occur spiracles of a type known as "biforous." The term originally implied that each spiracle had two external openings, but it is now commonly extended to other spiracles similar in appearance, but having only one opening or probably, in some cases, none at all.

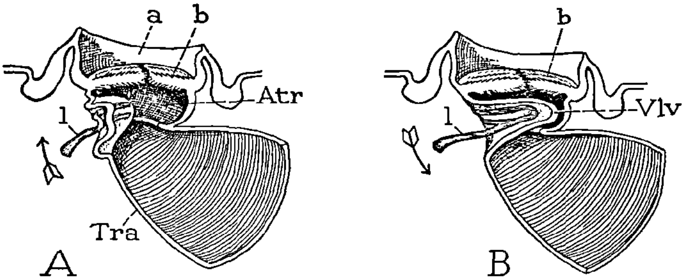

Fig. 233.—Horizontal section of left first spiracle of a noctuid caterpillar, showing ventral view of dorsal half. A, atrial valve open. B, atrial valve closed.

Good examples of true biforous spiracles are found in the larvae of Elateridae. The functional openings of these spiracles are secondary formations, since the primary atrial orifice is closed except during ecdyses. A larval spiracle of *Alaus oculatus* presents externally an ovate peritremal area (Fig. 234 A) having anteriorly a dark sclerotic thickening (*m*) and posteriorly two elongate convergent plates (*n*). The thickening marks the site of the closed atrial orifice (*a*). The convergent plates have each a clear median area traversed by an axial line (*a'*). Internally, the spiracle consists of a closed atrial chamber (E, *Atr*), which gives off posteriorly a wide membranous pouch (*p*), the external wall of which consists of a thin doubly convex membrane strengthened by branching and interjoining trabeculae (B, E, *q*). External to the pouch, and projecting beyond it posteriorly, are two shallow cuticle-lined chambers (*r*) beneath the convergent external plates of the spiracle (A, *n*). A manipulation of the spiracles of *Alaus oculatus* demonstrates beyond question that these chambers can be widely opened along the axial lines of their outer walls and gives every reason to believe that the openings are natural clefts, though in the usual condition their lips are closely appressed (D, *a'*). Roberts (1921) has shown that in sections the spiracles of *Agriotes* are cleft along the median lines of the posterior chambers. It has often been claimed, however, that the chambers are closed cavities, and that observed openings are artifacts.

The spiracles of *Alaus oculatus* thus appear to consist of a closed atrial chamber (Fig. 234 C, *Atr*) provided with a broad posterior diverticulum (*p*), and of two open, secondary posterior chambers (*r*), the inner walls of which are adnate with the outer wall of the atrial pouch, forming a thin, doubly arched, trabeculated septum (*q*) between the posterior chambers and the pouch of the atrial chamber. Air entering the posterior chambers evidently must diffuse through the trabeculated septum in order to enter the atrium and the associated tracheae. At each ecdysis the primary atrial aperture is opened (B, *a*) to permit the withdrawal of the tracheal exuviae, and the entire spiracular structure is renewed.

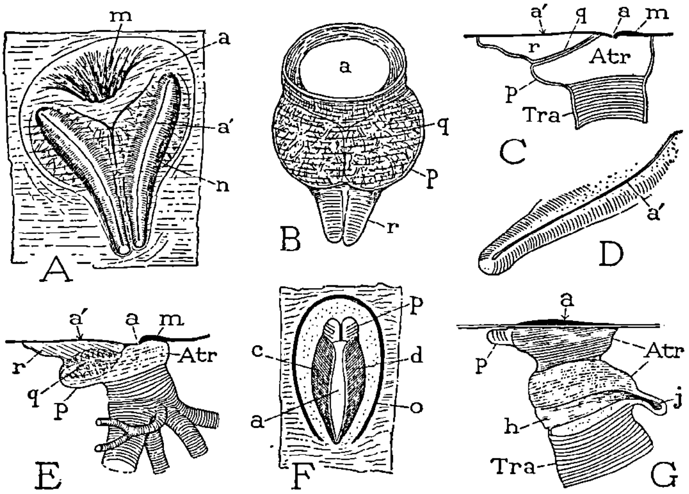

FIG. 234.—Types of "biforus" spiracles of coleopterous larvae. A, *Alaus oculatus*, functional spiracle. B, same spiracle during moulting. C, sectional diagram of *Alaus* type of spiracle. D, one of the openings (*a'*) of posterior chamber of *Alaus* spiracle. E, inner structure of *Alaus* spiracle and end of trachea. F, *Cactophagus validus*, abdominal spiracle. G, same, inner structure. *a*, primary atrial orifice; *a'*, orifice of secondary atrial chamber (*r*); *Atr*, atrium; *c*, *d*, anterior and posterior atrial lips; *h*, bow of closing apparatus; *j*, muscle process; *m*, cuticular thickening; *n*, outer wall of secondary atrial chamber (*r*); *o*, peritreme; *p*, atrial pouch; *q*, inner wall of secondary chamber; *r*, secondary atrial chamber; *Tra*, trachea.

Other so-called "biforous" spiracles of coleopterous larvae have a more simple structure. In many of these the primary atrial aperture is widely open (Fig. 234 F, *a*), but from one end of the atrium there project two pouches (*p*) beneath the body wall and entirely free from the latter (G, *p*). With such spiracles there is no question of separate external openings into the pouches. On the other hand, there are doubly pouched spiracles having the atrial orifice practically closed, as in

Histeridae, in which the pouches are not separated from the integument and have very thin outer walls. In such cases the exterior wall of each pouch much resembles that of the posterior chambers of *Alaus* and may even be marked by a faint median line. Much discussion has centered around the question as to whether these pouches are open to the exterior or are closed. Steinke (1919) seems to concede that they may be open in some cases, but he rightly says it is a very difficult thing to prove. If they are closed, as they appear to be, the exchange of respiratory gases must take place by diffusion through their very delicate outer walls.

In the larvae of *Donacia* the dorsally situated spiracles of the eighth abdominal segment have each a pair of slender tubular pouches extended into a long free spine-like process of the peritreme. The respiratory spines of these posterior spiracles are used to penetrate the vascular tissues of water plants for obtaining air. According to Böving (1910), the spines are inspiratory in function and are imperforate; expiration takes place through the open lateral spiracles and through the atrial apertures of the posterior spine-bearing spiracles. It is evident that there is needed a thorough comparative study of biforous spiracles in Coleoptera. From the foregoing discussion it appears that there may be two types of closed spiracles here included, one in which the atrium gives off a pair of imperforate diverticula, into which air diffuses through the external integument, the other (Elateridae) in which the diffusion surfaces are concealed in secondary open invaginations of the body wall.

Dorsal Spiracles of Dipterous Larvae.—Spiracles of a unique type of structure occur in the larvae and pupae of Diptera directly connected with the ends of the dorsal tracheal trunks. The position, structure, development, tracheal connections, and the temporary nature of these dorsal spiracles suggest that they are secondary respiratory structures having no relation to the lateral spiracles, which are closed or suppressed during immature stages and functionally restored in the adult.

The anterior larval or pupal spiracles take the form of perforated lobes or tubes (Fig. 229, *ASp*) or of trumpetlike horns arising from the posterior part of the prothorax. The posterior larval spiracles (*PSp*) are usually contained in a pair of prominent plates situated on the eighth segment or the composite terminal segment of the abdomen, where they are generally exposed, though they may be concealed in a shallow cavity or elevated on a respiratory tube (Fig. 228). The posterior spiracles typically have one, two, or three openings. In tipulid larvae the posterior spiracular plates were formerly supposed to consist of a mesh of fine rods branching from a central disc, admitting air through the interstices, but Gerbig (1913) has shown that the peripheral area of the spiracle is imperforate, and that the functional opening is a median slit in the entral disc obscured by its overlapping lips. In first-instar larvae the piracular apertures are plainly open.

The external part of each prothoracic dorsal spiracle of cyclorrhaphous arvae has the form of a small lobe, usually branched or digitate, with umerous pores communicating with the atrium (Fig. 235 A). The osterior spiracles present each two openings in the first instar of the arva and usually three in the second and third instars (B). The spiraular apertures open into a large atrial chamber (*Atr*) connected with the nd of the corresponding dorsal tracheal trunk. At the first and the econd moult the entire spiracular structure is formed anew and takes n a different form characteristic of the ensuing instar. Investigators o not agree as to whether the new atrial chamber is an outgrowth of the ne preceding or an ingrowth from the integument, but in either case the ld chamber serves for the discharge of the tracheal intima and is then losed, while the new formation becomes the functional breathing orifice r the succeeding instar. The site of the earlier spiracle is marked by scar on the surface of the integument (A, *u*), which remains connected ith the base of the new atrial cavity (*w*) by a strand of cuticular tissue *v*). At the third moult of the larva the dorsal spiracles are not renewed. he lateral imaginal spiracles of these flies appear first on the fourth nstar of the larva (formed within the puparium) just before the transrmation to the pupa.

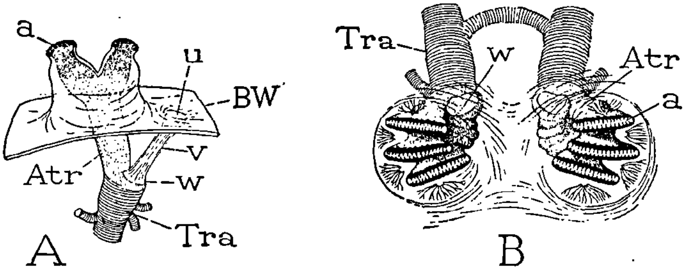

FIG. 235.—Spiracles of a trypetid fly pupa and maggot, *Rhagoletis pomonella*. A, nterior spiracle of pupa. B, posterior spiracles of a third instar larva. *a*, spiracular penings; *u*, outer scar of preceding spiracle; *v*, remnant of preceding spiracle; *w*, inner scar.

Structure of the Tracheae.—Since the tracheal tubes are invaginaons of the body wall, their own walls contain the same structural yers as does the body wall, only in reverse order (Fig. 220). The atrix layer of a trachea is an epithelium of flat polygonal cells (Fig. 236, *pth*) continuous with the epidermis around the spiracle. On the outde is a basement membrane, and on the inside a strong cuticular intima *In*). The characteristic feature of an insect trachea is its closely ringed ppearance resulting from the presence of folds or thickenings of the ntima in the form of minute circular or spiral ridges, the *taenidia* (*tn*), which project on the inner surface. In some insects the inner walls of the tracheae are covered by short spicules or clothed with simple or branched hairs arising from the taenidial ridges.

The taenidia are generally not continuous through any considerable length of the trachea but form a succession of ridges, each of which makes a few turns around the tracheal wall and then terminates. When a trachea is broken, the torn edge usually pulls out in a long spiral band (Fig. 236 A), which, it will be observed in most cases, is not a single taenidium but a strip of the tracheal wall containing several taenidia. The taenidia of the large dorsal trunks of some dipterous larvae, however, appear to be simple, uninterrupted rings, since a single taenidial "thread" may be easily removed from the broken end of a trunk. While in general the taenidia are continuous around the walls of a trachea and serve to keep the tube open, those of the dorsal trunks of a tabanid larva, and presumably in other dipterous larvae, are all jointed, or broken by points of flexibility, in a definite line along each side of the trachea. A trachea having this structure, when devoid of air, collapses to a flat band. Dunavan (1929) has observed that a collapsing and also a shortening take place in the dorsal tracheal trunks of a living *Eristalis* larva during respiration. In insects having a mechanical respiration, Krogh (1920*a*) distinguishes *respiration tracheae* (that is, *ventilation tracheae*), which are oval in cross section and easily compressible, from *diffusion* tracheae, which are rigid and cylindrical.

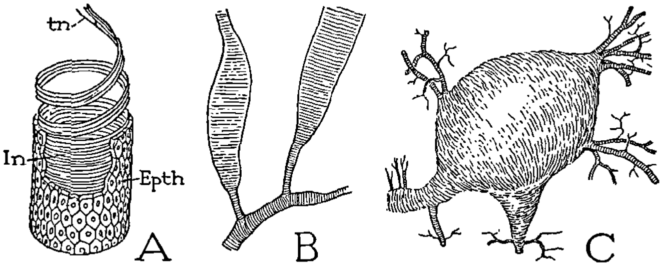

FIG. 236.—Structure of a tracheal tube, and examples of tracheal air sacs. *Epth*, epithelium; *In*, intima; *tn*, taenidium in spiral band of cuticular intima artificially separated.

The Tracheal Air Sacs.—The tracheal tubes are seldom of a uniform or an evenly tapering diameter; generally they are widened in some places and narrowed at others. If a widened part of a trachea forms a conspicuous enlargement in the course of the tube, the dilatation is called a *tracheal air sac* (Fig. 236 B, C). Air sacs are present in certain members of most of the pterygote orders and reach their greatest development in some of the cyclorrhaphous Diptera, and in the Apidae among the Hymenoptera, but they are absent in Apterygota and in holometabolous larvae. They vary greatly in size from minute vesicles to large bags and may be widely distributed in the body, in the head, and in the appendages. In the honey bee the lateral tracheal trunks of the abdomen are transformed into voluminous air sacs, and smaller sacs occur abundantly throughout the rest of the body and in the legs. The cicadas are remarkable for the great air space that occupies most of the abdominal cavity (Fig. 237). This air-filled sac has been claimed to be a diverticulum of the alimentary canal, but it can readily be demonstrated in various cicada species that the abdominal air chamber opens directly to the exterior through the first abdominal spiracles, and that tracheal tubes issue from its walls.

The air sacs respond in a greater degree than do the tracheal trunks to increased and decreased pressure in the body resulting from the movements of respiration and thus give a more efficient ventilation to the tracheal system during breathing. The air sacs in some insects are particularly responsive to the respiratory movements because their walls lack the taenidial ridges characteristic of the tracheae. It is generally assumed that the intima of the air sacs as well as that of the tracheae is a chitinous membrane. Tests made by van Wisselingh (1898) on the air sacs and tracheae of the house fly, and by Campbell (1929) on the air sacs and attached tracheae of both the house fly and the honey bee failed to show the presence of chitin; but Koch (1932) claims that with more delicate methods of technique the presence of chitin can be demonstrated in the tracheal intima of both these insects.

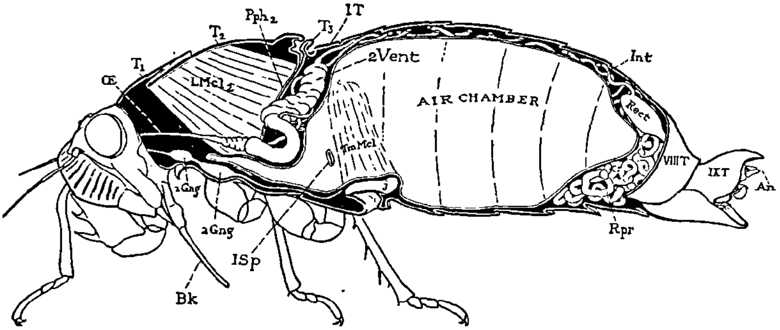

Fig. 237.—Longitudinal section of *Magicicada septendecim*, showing the great air chamber occupying most of the abdomen and opening to the exterior through the first abdominal spiracles (*ISp*).

The Tracheoles.—The final link between the end branches of the tracheae and the cells of the body tissues is formed by minute tubules called *tracheoles*. The tracheoles are said to differ from the tracheae in that they are contained within single cells. They are cuticular canals, generally less than a micron in diameter, lacking taenidial ridges, formed in elongate and usually branched cells of the tracheal epithelium.

When the tracheoles are first developed they have no opening into the lumen of the trachea, but with the removal of the tracheal intima at the succeeding moult the lumina of the tracheoles becomes continuous with the cavity of the trachea. In other words, a tracheole, apparently, is a tubular outgrowth of the newly forming tracheal intima formed within a single cell of the tracheal epithelium. A tracheole, therefore, is probably not a truly intracellular structure but resembles the duct of a unicellular gland, which penetrates the cell body as an invagination of the cell wall. During the formative stage the tracheole becomes coiled within its cell, but as the cell elongates the tracheole straightens out, until finally it extends a long distance from its point of origin, and the attenuated cell matrix around the tube becomes scarcely perceptible.

The tracheoles are usually given off in clusters from the tracheae. In some cases they appear to be simple tubules, but generally they are dichotomously branched. The terminations of the tracheoles have not been studied in many insects, but their final branches have been found to anastomose in a fine capillary network over the tissue cells, in which there may be united groups of tracheoles from several different tracheal sources. Von Wistinghausen (1890) has described the tracheole capillary net of the silk glands of caterpillars, and E. Holmgren (1896) finds a similar network of anastomosing tracheoles not only on the silk glands but also on the fat cells, the Malpighian tubules, and the walls of the mesenteron in caterpillars. According to Holmgren (1896*a*), the canaliculi of the tracheole net are formed in a different set of cells from those in which the primary tracheoles are generated.

The tracheole endings usually lie on the surfaces of the cells, but they are said in some cases to dip beneath the cell surface and thus appear to lie within the body of the cell. It is probable, however, that the tracheoles do not ordinarily penetrate the cell cytoplasm. Where they are seen to lie within the circumference of an epithelial cell, Holmgren says, they are contained in a pouch or sheath of the basement membrane. The tracheole net of most muscles is also superficial. In the wing muscles, however, according to Athanasiu and Dragoiu (1913, 1915), the tracheae branch profusely between the fibers, and the tracheoles penetrate into the fibers, where they ramify abundantly among the sarcostyles and anastomose to form an intricate network about the latter.

Tracheal Gills.—Organs known as *tracheal gills* are hollow, thin-walled evaginations of the integument or of the intestinal wall containing finely branched tracheae and usually an abundance of tracheoles. They are present on many aquatic larvae and on some pupae, and in a few cases they are retained in the adult stage. In form, tracheal gills vary from fine filaments to broad plates or dilated sacs. They may be situated on any external part of the body, including the head, the thorax, and the abdomen, or in the rectal part of the proctodaeum, but they are usually confined to the exterior of the abdomen.

Typical filamentous tracheal gills occur on the larvae of Plecoptera, some Ephemerida, most Trichoptera, the neuropteron *Corydalus cornutus,* on several species of aquatic lepidopterous larvae of the genus *Nymphula,* and on the pupa of the dipterous genus *Simulium.* The slender tapering appendicular processes borne on the sides of the abdominal segments of sialid larvae and of gyrinid and certain other coleopterous larvae are usually regarded also as having a respiratory function because each is penetrated by a tracheal branch from the lateral tracheal trunk. Familiar examples of plate-like tracheal gills are those that occur along the sides of the abdomen of many ephemerid larvae and at the end of the abdomen of larvae of zygopterous Odonata.

An interesting description of the filamentous gills of lepidopterous larvae is given by Welch (1922), who finds that each gill filament contains a tracheal branch from the main lateral trunk of the tracheal system, and that the inner surface of the gill is covered by innumerable tracheoles lying parallel with one another. Nearly five hundred gill filaments may be present on a single individual of *Nymphula obscuralis.* The three terminal gills of zygopterous larvae are borne by the epiproct and the paraprocts. Usually they have the form of elongate plates, but in certain species they are vesicular. An account of their various forms and their structure is given by Tillyard in his Biology of the Dragonflies (1917). Most highly developed of all tracheal gill structures are the rectal gills of the larvae of anisopterous Odonata. These gills consist of six sets of invaginations of various shapes projecting in longitudinal rows from the inner wall of the anterior part of the rectum, together forming the so-called "branchial basket." The respiratory lobes are richly tracheated from the dorsal and visceral longitudinal trunks of the tracheal system. A detailed account of the form and structure of these organs is given by Tillyard in the work above cited.

Though parasitic larvae generally have no special respiratory equipment for breathing the oxygen dissolved in the blood of the host, gill-like structures have been observed in a few cases. Thorpe (1930) has shown that a pair of long, well-tracheated terminal lobes of the parasitic fly larva *Cryptochaetum iceryae* take up oxygen more actively than does the general integument of the insect. Certain parasitic chalcid larvae have groups of branched trachealike filaments arising externally from the body wall in the neighborhood of the anterior and posterior spiracles, which have been regarded as gill structures. According to Clausen (1932), however, these filaments are tracheae, but they are given off from trunks of the host tracheal system that have become fused with the body wall of the parasite and thus serve for the respiration of the latter. The connecting trunks, Clausen points out, are usually broken in dissections, and hence the branching tracheae penetrating the host tissues appear to be outgrowths from the integument of the larva.

4. GENERAL MECHANISM OF TRACHEAL RESPIRATION

Respiration through tracheae branching to all parts of the body may be accomplished entirely by the diffusion of gases within the tracheae; but probably the majority of adult insects produce a partial ventilation of the tracheal system by means of movements of the body wall. In the second case, tracheal breathing has many features in common with lung breathing and involves the presence of a mechanism for producing and controlling the respiratory movements.

Respiration by Gas Diffusion in the Tracheae.—Since many insects, especially larval forms, do not make any perceptible breathing movements, it is evident that respiration in such cases must be accomplished largely or entirely by the diffusion of gases through the tracheae. It is possible, however, that with some larvae the movements of the body or particularly the successive contraction of the lateral body muscles overlying the longitudinal tracheal trunks may cause an irregular passage of air through these trunks. Likewise it may be supposed that in the larvae of Diptera the pulsations of the heart might effect a compression of the large dorsal trunks lying to each side of the heart. As already mentioned, it has been observed by Dunavan (1929) that the dorsal trunks of an *Eristalis* larva both shorten and collapse during respiration, though Dunavan was not able to discover the means by which the activity of the tracheae is produced. In general, however, there can be no doubt that diffusion accounts for the major part of gas transfer through the tracheae of insects that make no specific respiratory movements, and, even in insects that actively breathe, it is only the larger tracheae that are ventilated; the peripheral respiration is always by means of gas diffusion.

The part played by diffusion in the respiration of insects has been conclusively shown by Krogh (1920, 1920*a*). Using tenebrionid larvae and the larva of *Cossus* as subjects having an open tracheal system, and aeschnid larvae as examples of aquatic insects with a closed tracheal system and breathing by means of gills, Krogh demonstrated experimentally the interchange of gases in the tracheae by means of gas diffusion entirely. Though he points out that respiration by diffusion is practicable only for small animals, since the rate of diffusion varies directly with the diameter of the tracheae and inversely to their mean length, there are many insects much smaller than the forms on which he worked that are active breathers. The production of respiratory movements is dependent on the body structure, and it would be quite impossible for a soft-skinned larva to make rhythmic respiratory movements such as those made by adult insects. A *Dytiscus* larva, constructed on the plan of an adult insect, however, breathes by active pulsations of the abdomen, as Krogh has shown in a later paper. We may conclude, therefore, that it is practical for all insects to breathe by gas diffusion, but that active respiration gives a more efficient gas exchange and is practiced by many insects structurally capable of making rhythmic expansions and contractions of the abdomen.

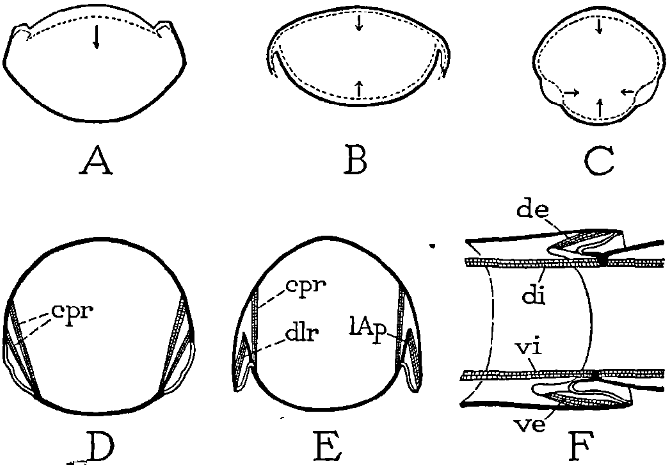

Fig. 238.—*Diagrams of respiratory mechanisms.* A, B, C, *three types of abdominal expiratory movements made by insects.* (*From Plateau,* 1884). D, section of segment with compressor muscles only. E, section of segment with compressor and dilator muscles. F, lengthwise section showing protractor (*de, ve*) and contractor (*di, vi*) muscles.

Respiration by Tracheal Ventilation.—The mechanical elements necessary for the production of breathing movements by the body are present in the fundamental relations between the segmental plates of the body wall and the somatic muscles. The possibility of breathing, therefore, is possessed by all insects with sclerotic plates in the body wall, and, after the acquisition of tracheae, mechanical respiration needed only the development of control centers in the nervous system.

The Respiratory Movements.—The movements of respiration affect principally the abdomen. They are produced by the somatic muscles and by the elasticity of the body wall. Expiration results from a dorsoventral compression of the abdomen or, in some cases, also from a longitudinal contraction of the abdomen. The effectors in the first case are the lateral tergosternal muscles (Fig. 238 D, *cpr*); in the second they are the intersegmental longitudinal muscles (F, *di, vi*). Both movements may occur together in the same insect. Expiration may be accomplished entirely by the elasticity of the body wall; but, in insects that breathe strongly, some of the vertical and longitudinal muscles are generally converted into dilators and protractors of the abdomen by a change in their mechanical relations to the plates on which they are attached. Thus, with insects in which the abdominal terga overlap the edges of the sterna (E), some of the external lateral muscles become dilators (*dlr*) if their tergal attachments are ventral to their sternal attachments, and in such cases the effectiveness of the dilators is usually increased by the dorsal extension of their sternal attachments on lateral apodemal arms of the sternum (*lAp*). Similarly, a protractor apparatus is formed by a transposition of the anterior ends of the external dorsal and ventral muscles to the posterior margins of the terga and sterna, respectively (F, *de*, *ve*), so that these muscles become antagonistic to the internal longitudinals (*di*, *vi*). The effectiveness of the protractors likewise may be increased by the forward extension of their points of insertion on anterior tergal and sternal apodemes.

A comprehensive study of the breathing movements of insects has not been made in recent years, and our best source of information on the subject is still the work of Plateau (1884). By means of lantern projections of the shadows of living insects, Plateau made observations on the respiratory movements of insects representing the principal orders. From his results he distinguished three principal types of respiratory mechanism, based on the structure of the abdomen and the manner of breathing. In the *first type* (Fig. 238 A), the sterna are usually firm and strongly convex and move but little in respiration; the terga, on the other hand, are mobile and noticeably rise and fall with each inspiration and expiration. Insects that breathe in this manner include Heteroptera and Coleoptera. In the *second type* (B), the terga are large and overlap the sterna laterally, usually concealing the membranous lateral zones of the segments. Both the terga and the sterna approach and separate in this type of structure, but the movements of the sterna are the more pronounced. Here Plateau includes the Odonata, Acrididae, aculeate Hymenoptera, and Diptera. He observes, however, that in Phryganiidae and Hymenoptera the dorsoventral movements of the abdomen are accompanied by more pronounced movements in a longitudinal direction. The *third type* of respiratory mechanism (C) is found in insects having the terga and sterna separated on the sides of the abdomen by ample membranous areas. During breathing the terga and sterna approach and separate, while the lateral membranes correspondingly bulge outward or are drawn inward. Insects having this type of structure include Tettigoniidae, Neuroptera, Trichoptera, and Lepidoptera.

The rate and amplitude of the breathing movements are characteristically different in different insects and vary also in each individual according to the strength of external stimuli and according to the activity of the insect. Lee (1925), for example, records the average rate of breathing for females of *Melanoplus femur-rubrum* as being 5.8 a minute at 49°F., and increasing to 26.6 at 80°. Herber and Slifer (1928), however, find much variation in the breathing of quiescent grasshoppers when observations are continued for a considerable length of time, the variations affecting not only the rate of breathing but also the depth of the abdominal pulsations. Thus they report for a male of *Melanoplus femur-rubrum,* observed for an hour, a fluctuation from 21.5 to 67.5 seconds in the time occupied by 10 respiratory movements. The Tettigoniidae appear to be more active breathers than the Acrididae, and during stridulation the breathing of the males is especially pronounced. The Phasmidae, on the other hand, are very slow breathers. According to Stahn (1928), the European walkingstick *Dixippus morosus* when at rest makes only 1.4 to 2.3 expirations a minute, though all stimulating influences cause an increase in the respiratory rate. The breathing movements of *Dixippus* are said to affect both the abdomen and the thorax.

Course of the Air in the Tracheae.—During recent years there has been much discussion on the question of a differential function of the spiracles as inspiratory and expiratory orifices, and on that of the direction of the air currents in the longitudinal tracheal trunks.

Experiments made by Lee (1925) on the respiration of grasshoppers (Acrididae) and observation that the thoracic and first two abdominal spiracles open during the expansion of the abdomen and close during contraction, while the last six abdominal spiracles open and close with the reverse movements, seemed to show that in normal breathing by grasshoppers inhalation takes place through the anterior spiracles, and exhalation through the posterior spiracles. Lee's results were disputed by MacKay (1927); and McArthur (1929), after making similar experiments on several species of Acrididae, arrived at the following conclusions: The first four spiracles of the grasshopper are usually inspiratory and the last six expiratory, but the action of the spiracles is variable under both normal and abnormal conditions; the mechanism of the spiracular valves is capable of reversing the times of opening and closing of the spiracles relative to the respiratory movements of the abdomen; the direction of air currents through the tracheae can thus be reversed, or the air can be forced into any one of several possible paths by the internal control of the spiracular valves.

Subsequent investigations have confirmed in general Lee's original claim that the air stream goes posteriorly through the body of Acrididae. With a more efficient apparatus than that used by the preceding writers, McGovran (1931), experimenting on *Chortophaga viridifasciatus,* reports that the respiratory movements produce a pulsatory movement of air through the tracheal trunks, and that inspiration is principally into the thorax, while expiration is principally by way of the abdomen. An adult female, at 28°C., passed an average of 0.222 cubic centimeter of air through the body per minute per gram body weight. Finally, the work of Fraenkel (1932) gives essentially the same results on Orthoptera. The thoracic and first two pairs of abdominal spiracles, Fraenkel says, open during inspiration and close during expiration, while the other six pairs of abdominal spiracles show a reverse action relative to the respiratory movements of the body. Furthermore, Fraenkel demonstrated experimentally in *Schistocerca gregaria* a movement of the respiratory air posteriorly in the tracheae. Quantitative measurements showed from 5 to 20 cubic millimeters transported per second, or from 7.5 to 24.4 cubic millimeters with each expiratory movement.

The work of von Buddenbrock and von Rohr (1923) on the respiration of *Dixippus morosus* led these investigators to the conclusion that the tracheal air stream goes *forward* in the walkingstick, the thoracic spiracles being expiratory and the abdominal spiracles inspiratory, except that a small quantity of air may sometimes issue from the next to the last pair of abdominal spiracles. Stahn (1928) obtained the same results in experiments on *Dixippus*, but he observes that the expiratory stream appears often to be interrupted by expiration through the abdomen during passive breathing. According to Du Buisson (1926), the action of the spiracular valves in *Dixippus* is variable. During ordinary breathing, he claims, inspiration takes place through all the spiracles, but the reverse may occur, or, again, the movements are disordered and have no rhythm. In earlier studies on *Stenobothrus* and *Locusta*, Du Buisson (1924, 1924*a*) claimed that in these insects also inspiration usually takes place through all the spiracles, but that expiration is ordinarily by way of the thoracic spiracles only. Under unusual conditions, however, he says, *Stenobothrus* may keep the thoracic spiracles continuously closed, and expiration then takes place through the abdominal apertures.

That insects have no definitely fixed direction of breathing is also the conclusion of Demoll (1927), deduced from experiments on *Melolontha*. By subjecting either the thorax or the abdomen of an intact beetle to nascent chlorine, he found that the insect was quickly killed. If the wings were cut off, however, and the thorax protected from the gas while the abdomen was exposed to it, the insect was unaffected, since the open tracheae of the wing stumps, together with the spiracles of the thorax, afforded a sufficient means of respiration and allowed the insect to keep the abdominal spiracles closed.

From the diversity of the results obtained by different investigators we may conclude that there is no law governing inhalation and exhalation through special sets of spiracles applicable alike to all insects, and that the direction of the respiratory currents may alternate even in the same individual; but it appears that respiration has a usual though not a fixed course in each species, which presumably is characteristic also of the family, and probably of the order in most cases.

The Function of the Air Sacs.—The greater diameter of the air sacs as compared with that of the tracheae makes the walls of the sacs relatively weaker, and the air sacs are, therefore, more responsive than the tracheae to variations of pressure in the surrounding blood or other tissues, created by the alternating respiratory movements of the body wall. Particularly is this true of air sacs, such as those of the honey bee, which have no taenidia in their walls. In their response to pressure changes the air sacs resemble lungs; but inasmuch as peripheral tracheae are given off from them, their action is more accurately stated by Betts (1923), who says, "the function of the air sacs is that of the bag of a bellows," or, as Demoll (1927) puts it, they guarantee an intensive ventilation of the tracheae during breathing. By a device for making direct observations on the action of the tracheal sacs under varying pressures, Demoll demonstrated that the sacs are compressed with increasing pressure around them, a part of their air content being thus driven into the pressure-resisting tracheal tubes, and that, with decreasing pressure, they are inflated. There is no direct evidence that the air sacs function as storage chambers for air. In special cases they serve to give atmospheric pressure against the inner surfaces of tympanal organs or, in certain aquatic species, to maintain buoyancy in the water.

The Respiratory Stimuli.—Most studies on the respiratory stimuli of insects appear to be based on the assumption that carbon dioxide is not carried by the blood, and that, therefore, the respiratory movements must be regulated by the relative amounts of carbon dioxide and oxygen in the tracheal air, and experiments have shown, in fact, that such is the case. Temperature also influences the rate of breathing, but its primary effect is presumably on the processes of metabolism. The mechanism of breathing response to increased or decreased activity on the part of the insect has received little attention experimentally; but inasmuch as it has been shown that a part of the carbon dioxide produced by metabolism may be eliminated by other means than the tracheae, it is probable that most of it is thrown off from the tissues into the blood. If so, it then becomes possible that the ordinary respiratory regulation in insects, as in vertebrates, is brought about by fluctuations of the hydrogen-ion concentration of the circulating medium. The stimulus for the fundamental rhythmic movements of respiration, Fraenkel

(1932*a*) concludes, arises within the controlling nerve centers and has no peripheral source.

The first attempts at determining the regulatory value of gases on the respiratory movements of insects are those of Babák and Foustka (1907). From experiments on the breathing reactions of libellulid larvae to alterations in the carbon dioxide and oxygen pressure of the water medium, these investigators concluded that the rate and amplitude of breathing are dependent on the oxygen supply that reaches the nervous system through the tracheae, but that carbon dioxide or carbonic acid can scarcely be a regulatory stimulus for respiration, since it is effective only in excessive amounts. Stahn (1928), however, claims that the experimental methods of Babák and Foustka were not reliable for determining the effects of small quantities of carbon dioxide. Experimenting with *Dixippus morosus*, Stahn found that small increases in the carbon dioxide content of the inspired air are reflected in the rate of the breathing movements, and that the effects of an excess of carbon dioxide are remarkably parallel with the effects of deficiency of oxygen. In brief, Stahn concludes that the primary stimulating agent for increased breathing activity is carbon dioxide in small excess over the amount in ordinary air, the lower threshold being 0.2 per cent of carbon dioxide in the inspired air, and the effective maximum about 0.3 to 3 per cent. A slight decrease in the oxygen content, however, has the same effect as an increase of carbon dioxide, the maximum effectiveness of oxygen as a control stimulus being from 20 to 15 per cent. A strong and apparently toxic acceleration of breathing occurs when the oxygen content falls below 8 per cent, or when the carbon dioxide content exceeds 12 or 15 per cent.

The respiratory effects of temperature have been studied by Walling (1906), who found that normal grasshoppers (Acrididae) making on the average 40 contractions of the abdomen a minute at 14°C. increase the rate of breathing to 110 contractions a minute as the temperature, during a period of 4 hours, is increased to 54°C.; at still higher temperatures the rate declines, and respiration ceases at 59°C. Lowered temperature has an opposite effect. At 5°C. grasshoppers breathe faintly, if at all, from five to six times a minute, though breathing by normal individuals may not cease until the temperature falls to 0°C. It will be noticed that the breathing rate of grasshoppers at ordinary temperatures given by Walling is considerably higher than the figures of Lee (1925) quoted above.

Nothing is known definitely as to how the varying carbon dioxide and oxygen pressure in the tracheal air makes itself effective as a respiratory stimulus. It has been supposed that there may be sensory nerves connecting the tracheae with the respiratory nerve centers; but a sensory innervation of the tracheae has not been observed, and Stahn suggests that the respiratory centers may be stimulated directly by the condition of the air that diffuses from the tracheoles into the nerve ganglia.

The Respiratory Nerve Centers.—There is no specific respiratory center in the nervous system of insects for the production and regulation of the breathing movements. Each ganglion of the ventral nerve cord of the abdomen contains an independent respiratory center controlling the movements of its segment, but it appears that the thoracic ganglia also play a part in the production or control of the respiratory movements. Experimental results in some cases are possibly somewhat confused by the fact that the ganglion proper to a segment may lie in some other segment, and that the thorax often contains one or more of the abdominal ganglia. Though Matula (1911) claimed that in *Aeschna* larvae the activity of the ventral ganglia is under the control of a cerebral breathing center, his conclusion was disproved by Wallengren (1913), who showed that headless larvae are still sensitive to the oxygen tension of the water. On the other hand, Wallengren found that dragonfly larvae having the prothorax removed give no response to external respiratory stimuli, from which observation he concluded that the prothoracic ganglion plays an important role in the respiratory regulation. At an earlier date H. Z. Ewing (1904) had shown that in grasshoppers each ganglion of the ventral nerve cord contains a respiratory center and will activate the breathing movements of its segment when the latter is removed from the rest of the body.

The more recent work of Stahn (1928) on the respiration of *Dixippus morosus* and *Aeschna* larvae and of Fraenkel (1932*a*) on *Schistocerca* confirm the view that the head contains no respiratory nerve center; but Stahn concludes that there must be distinguished in the body ganglia primary and secondary respiratory centers. The first lie in the abdominal, the metathoracic, and the mesothoracic ganglia, and possibly also in the prothoracic ganglion; the second is contained in the prothoracic ganglion. The primary centers of *Dixippus*, as shown in insects with both head and prothorax removed, are responsive only to large dosages of carbon dioxide (12 to 15 per cent) in the inspired air or to large decreases in the oxygen content (10 to 8 per cent or less). The secondary center of the prothoracic ganglion, on the other hand, is a center for finer adjustments, since insects from which the prothorax has not been removed are responsive to much smaller increases of carbon dioxide (up to 12 or 15 per cent), and to much smaller decreases in the oxygen content of the inspired air (down to 10 or 8 per cent). In *Aeschna* larvae, Stahn says, the respiratory control is almost entirely taken over by the secondary centers of the prothorax.

Mechanism of Respiration in the Tracheoles.—In living insects the tracheoles are filled to a varying extent from their distal ends with a liquid. The composition of this liquid is unknown, but it is of such a nature that it can be absorbed through the walls of the tracheoles. It has been shown by Wigglesworth (1930*a*, 1931) in mosquito larvae and in certain other insects that the amount of liquid in the tracheole branches distributed to a muscle is inversely affected by the activity of the muscle (Fig. 239). From various experiments Wigglesworth concludes that the absorption of the liquid from the tracheoles is a direct result of increased pressure resulting from the formation of metabolites surrounding the ends of the tracheoles, to which the tracheole walls are impermeable.

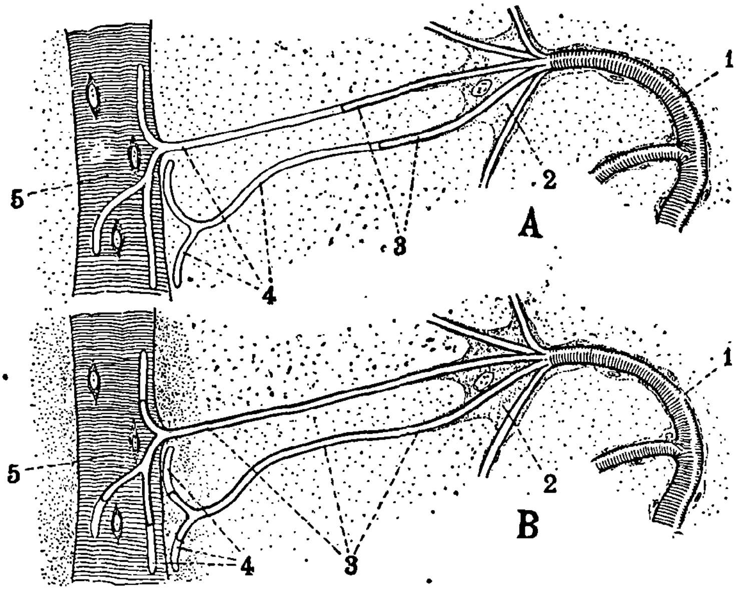

FIG. 239.—Diagrams of movement of liquid in the tracheoles. (*From Wigglesworth, 1930a.*) *1*, trachea; *2*, tracheole cell; *3*, parts of tracheoles containing air; *4*, parts containing liquid; *5*, muscle.

Following metabolic activity in the muscles, or supposedly in any other tissue, therefore, the liquid is absorbed from the tracheoles, and air extends toward their extremities, where it comes into closer proximity to the cells requiring oxidation (B).

By several experiments Wigglesworth sought to demonstrate his theory. In the first place, it was found that asphyxiation of mosquito larvae causes at first a violent muscular reaction, which is followed by penetration of air from the tracheae into the tracheoles going to the muscles. Lactic acid, Wigglesworth showed, is produced by the mosquito larva during asphyxiation. In a second set of experiments the liquid was absorbed from the tracheoles following infiltrations into the body of 10 and 5 per cent solutions of sodium chloride, and of lactic acid and potassium lactate at different strengths, the last being effective down to 2 per cent. Again, it was found that the same effect was produced by allowing the body liquid from one larva to diffuse into a second. Finally, testing the effect of gases, Wigglesworth showed that carbon dioxide and hydrogen cause muscular contraction followed by extension of air in the tracheoles, until the insect is narcotized. Treatment with oxygen then restores activity, with a consequent further penetration of the air, followed again by a rise of the liquid in the tubules. Poisonous gases have the same effect as nonpoisonous gases, but "the extent to which air moves down the tracheoles depends upon the degree of muscular activity which precedes the death of the insect." Soon after death the liquid rises in the tracheoles. From these experiments it seems clear, as Wigglesworth contends, that the absorption of the oxygenated liquid, and conversely the penetration of air into the tracheoles going to muscles, is caused by the metabolic activity in the muscles.

The respiratory effect of the movement of the liquid in the tracheoles is that the air of the tracheae is quickly brought into closer relation with the cells of a tissue as metabolism in the latter creates a need for it (Fig. 239 B). Presumably, under normal conditions, oxygen is continually dissolved in the tracheole liquid and with the latter is taken into the cells. It is possible that the entire oxygen supply of the tissues enters the latter by way of the tracheoles; but it does not seem possible that all the carbon dioxide produced can be absorbed into the tracheoles, no matter how intimately the latter may cover the cell surfaces or penetrate the cell bodies.

GLOSSARY OF TERMS APPLIED TO THE RESPIRATORY SYSTEM

Air Sac.—An enlargement of a tracheal tube, usually without taenidia in its walls.

Amphipneustic.—With only the first pair and one or two pairs of posterior spiracles open.

Apneustic.—Without specific external breathing organs, either spiracles or gills; the tracheal system usually absent or rudimentary.

Atrial Orifice.—The external opening of the spiracular atrium. (*Porta atrii.*)

Atrium (*Atr*).—The spiracular chamber formed by a secondary invagination of the body wall external to the primary tracheal orifice.

Biforous Spiracles.—Spiracles of coleopterous larvae having two pouches of the atrium originally supposed to open separately to the exterior.

Blood Gills.—Hollow, nontracheated, usually filamentous respiratory evaginations of the body wall or the proctodaeum.

Branchia.—A gill, either a tracheal or a blood gill.

Branchiopneustic.—The spiracles functionally supplanted by gills.

Closing Apparatus of a Spiracle.—The closing mechanism and opening, formed either of the lips of the atrium or by a valve at the inner end of the atrium. (*Verschlussapparat.*)

Closing Band.—The movable valvular fold of the inner closing mechanism of a spiracle. (*Verschlussband.*)

Closing Bow.—The rigid but elastic lip of the inner closing mechanism of a spiracle opposite the valve. (*Verschlussbügel.*)

Diffusion Tracheae.—Cylindrical tracheae having noncollapsible walls (see *ventilation tracheae*).

Dilator Muscle of a Spiracle (*dlsp*).—A muscle serving to open either the external or the internal closing apparatus of the spiracular atrium.

Dorsal Trachea.—The dorsal segmental trachea originating at a spiracle.

Dorsal Tracheal Trunk (*DTra*).—A longitudinal dorsal trunk uniting the series of dorsal tracheae.

External Respiration.—The process of transferring the respiratory gases through the body wall; taking place in insects through thin areas of the ectoderm, either at the body surface or in the walls of evaginations (gills) or invaginations (tracheae).

Filter Apparatus.—Finely branching processes of the atrial wall of some spiracles, forming often two thick but air-pervious mats just within the atrial orifice. (*Reusenapparat.*)

Gills.—Respiratory evaginations of the body wall or the proctodaeum (see *blood gills,* and *tracheal gills*).

Hemipneustic, or Hypopneustic.—With some of the spiracles functionally suppressed.

Holopneustic.—Having the usual (generally 10) pairs of open spiracles.

Hyperpneustic.—With supernumerary spiracles; as in the thorax of some Diplura.

Internal Respiration.—The process of oxidation accompanying metabolism in the cells of the body tissues.

Lateral Tracheal Trunk (*LTra*).—The usual longitudinal tracheal trunk on each side of the body closely connected with the lateral spiracles.

Metapneustic.—With only the last pair of spiracles open.

Occlusor Muscle of a Spiracle (*osp*).—A muscle serving to close either an outer or an inner closing apparatus of the spiracular atrium.

Peripneustic.—With none or only a few spiracles closed in each lateral series.

Peritreme (*Ptr*).—A sclerite of the body wall containing the spiracular opening.

Propneustic.—With only the first pair of spiracles open.

Respiration.—The entire series of physical and chemical processes accomplishing oxidation and the removal of carbon dioxide.

Respiratory System.—The anatomical adaptations of the animal that facilitate external respiration.

Spiracle (*Sp*).—A primary tracheal orifice, or the secondary atrial orifice and structures (peritreme, atrium, closing apparatus) usually associated with the latter. (*Stigma.*)

Spiracular Trachea.—The short, usually unbranched trachea arising directly from the spiracle.

Taenidia (*tn*).—The circular or spiral thickenings of the inner cuticular walls of the tracheae.

Tracheae (*Tra*).—The breathing tubes formed as multicellular invaginations of the ectoderm.

Tracheal Commissures.—Transverse tracheal trunks continuous from one side of the body to the other.

Tracheal Gills.—Gills containing tracheae and tracheoles.

Tracheal Orifice.—The primary opening at the point of formation of a trachea, whether exposed externally or concealed in a secondary atrial depression of the body wall.

Tracheal System.—The part of the respiratory system composed of the tracheae and tracheoles.

Tracheoles.—The minute end tubes of the tracheal system, formed within single cells of the tracheal epithelium, and usually branched in digitate extensions of the matrix cells.

Ventilation Tracheae.—Tracheae with collapsible walls, responding to varying surrounding pressure.

Ventral Trachea.—The ventral segmental trachea originating at a spiracle.

Ventral Tracheal Trunk (*VTra*).—A longitudinal ventral tracheal trunk uniting the series of ventral tracheae.

Visceral Trachea.—The median segmental trachea originating at a spiracle, branching to the alimentary canal, the fat tissue, and the reproductive organs.

Visceral Tracheal Trunk (*VsTra*).—A longitudinal tracheal trunk closely associated with the walls of the alimentary canal.

CHAPTER XVI

THE NERVOUS SYSTEM

An animal is a highly organized mass of matter charged with the potentiality of chemical and physical activity, but its latent energy tends always to remain in a state of equilibrium with surrounding conditions. There must be, therefore, some *stimulus* for the release of energy to activate the motor tissues, and stimuli must be in all cases changes in the forces opposed to the energy of living matter. In the lower animals it seems probable that effective stimuli consist only of changes in the impinging energy of the environment or of physical or chemical changes within the body of the animal. The reason for animal activity is the necessity of the animal's making advantageous adjustments to changes in its immediate surroundings. If an individual is to live successfully, therefore, it must be provided with a responsive mechanism by which its behavior will be brought into harmony with changes in its environment.

An animal is formed of chemical compounds of many different kinds, but most of its component substances may be classed in two groups. Those of one group are stable compounds, the alteration of which results only in damage to the organism. These substances form the integument, the skeleton, the connective tissue, and the supporting framework of muscles, glands, and cells. Substances of the other group are labile compounds, highly unstable in their molecular structure, and some of them liable to sudden disruption on sufficient increase of stimulus. It is these substances that cause the activities of the animal. They occur principally in the secreting cells of glandular tissues, in the contractile tissue of muscles, and in the receptive and conductive parts of nerve tissue.

Since the stimuli for action in the labile tissues of the animal come primarily from the environment, there must be some provision for transmitting their effect from the stable periphery of the animal to the internal tissues in which is stored the latent energy that makes action possible. Moreover, since the normal activities of a living creature are advantageous to the organism, there must be also some provision for controlling and directing the results of the liberated energy. Both of these requirements are furnished by the nervous system, though directive movement is partly the result of the mechanical construction of the motor mechanism.

The environmental stimuli include electromagnetic changes, chemical changes, changes in the rate or kind of molecular motion, and changes in the degree of pressure exerted by material masses touching upon the animal's body. The external stimuli, however, are not transmitted in kind to the interior of the body; all forms of energy in nature probably have one effect on the peripheral receptive cells of the nervous system, which is an alteration in the rate of metabolic activity in the latter. This induced change in the rate of metabolism is then propagated through the nerve fibers to the tissues at their inner terminals. What the animal "feels" or "does" in response depends upon the organization of the central nervous system and the motor mechanism.

The concept of environment must be broadly understood. Not only does the animal as a whole have its environment, but each internal tissue and every individual cell of the body has its own environment created by the conditions immediately surrounding it. Stimuli, therefore, arise both in the external environment and in the internal environment. The distribution of internal stimuli may be accomplished either by an inner elaboration of the nervous system or by the production of substances, known as *hormones*, which are broadcast in the circulating medium, and which initiate activities in certain tissues or organs remote from their source. Little is known of the presence or effect of hormones in insects. The insect nervous system, on the other hand, is highly developed, and its structure is now well understood in many respects.

1. GENERAL STRUCTURE, ORGANIZATION, AND FUNCTION OF THE NERVOUS SYSTEM

Anything that produces a change in the metabolic activity of the labile constituents of living matter is called a *stimulus*. The quality of living matter that makes it responsive to stimuli is termed *sensitivity*. The effect of the stimulus on the tissue, however, does not end with the first impact; it is transmitted from molecule to molecule, and this property of progressive reaction to stimuli is known as *conductivity*. Since it appears that reaction to a stimulus in all cases involves a destructive chemical action in the labile constituents of the tissue involved, a period of *recovery* is necessary for the restoration of the discomposed substances to their original form. *Fatigue* arises when stimuli follow in too rapid succession to allow of complete recovery.

The properties of sensitivity and conductivity are presumably common to all protoplasm in some degree. They are highly developed in the protoplasm of nerve tissue; they constitute, in fact, the fundamental qualities of nerve tissue upon which the functions of the nervous system depend. Since both are automatic processes, however, they must be controlled. The ends of nerves exposed to stimuli, therefore, are usually guarded by special receptive end organs, the structure of which exerts a selective limitation on the effective stimuli. Conductivity is effective also only within certain limits. When the stimulus received from an end organ reaches a certain intensity, reaction in the nerve takes place at maximum strength. On the other hand, when the stimulus becomes too strong, the reaction again may cease.

Development and Organization of the Nervous System.—It is a most interesting fact that the entire nervous system, as we learned in Chap. II, is derived from the ectoderm (Fig. 17). We can imagine that the primitive longitudinal nerve cords of annelids and arthropods were highly sensitive ventrolateral tracts of the body wall from which nerves were given off to the internal organs (Figs. 15 A, 240 A). In this case stimulation was direct from the exterior to the interior.

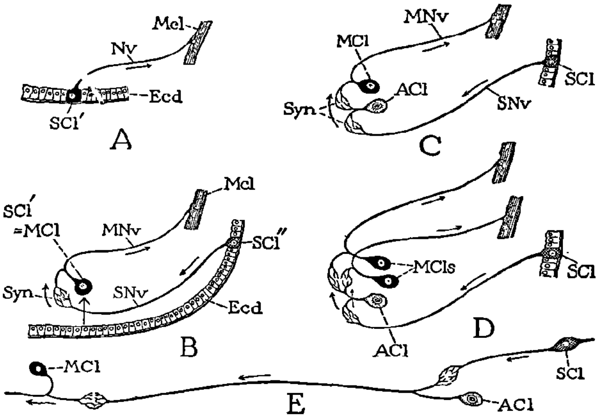

FIG. 240.—Evolution of motor and sensory neurones and the nerve synapse, diagrammatic. A, a primitive sense cell (*SCl′*) in the ectoderm transmitting stimuli directly to a muscle (*Mcl*). B, the primitive sense cell separated from the body wall becomes a motor cell (*MCl*) and must now be stimulated from a second sensory cell (*SCl″*) in the ectoderm, thus differentiating the motor neurone from the sensory neurone, which communicate through a synapse (*Syn*). C, a third, or association, neurone (*ACl*) interposed in the synapse, allows more than one motor neurone (D) to be stimulated through a single sensory neurone, and facilitates long distance transmission (E).

Differentiation of Motor and Sensory Nerves.—With progressive development, the primitive sensory cells of the ectoderm became detached internally from the integumentary cells and finally came to lie within the body cavity where they form free strands of nerve tissue. The primary nerve cells (Fig. 240 A, *SCl′*), thus cut off from direct contact with external stimuli (B, *SCl′*), must now be stimulated indirectly through a second set of sensory cells (*SCl″*), which, on the one hand, retain connections with the exterior and, on the other, establish communication by means of nerve fibers with the cells of the first order. Thus a more highly organized nervous system is evolved, consisting of *afferent, sensory nerves* (*SNv*) proceeding inward from sensory cells on the body wall (*SCl''*) to the buried cells (*SCl'*) of the first set, and of *efferent*, so-called *motor nerves* (*MNv*), going from the latter to the working tissues of the body. The localized parts of the nervous tracts where the sensory and motor nerves communicate is the *central nervous system.* The incoming sensory nerves and the outgoing motor nerves constitute the *peripheral nervous system.*

The Neurone.—A nerve fiber is simply a prolongation of a nerve cell, or *neurocyte* (Fig. 241, *NCl*). The neurocyte and all its branches constitute a *neurone.* Usually there is one principal branch, the *neurite*, or *axon* (*Axn*), which is the nerve fiber of the neurone. A lateral branch of the axon, generally given off near the neurocyte, is termed a *collateral* (*Col*). Both the axon and the collateral end in *terminal arborizations* of fine branching fibrils (*b, c*). Similar branching fibrils springing directly from the neurocyte are distinguished as *dendrons,* or *dendrites* (*a*). If a nerve cell has but one main nerve proceeding from it, it is said to be unipolar; if two, it is bipolar; and if it has more than two nerve processes, it is multipolar. The motor nerve cells are typically unipolar (Fig. 242 A). Sensory cells are either bipolar (B), or multipolar (C), according as they have one *distal process* (*d*) or several.

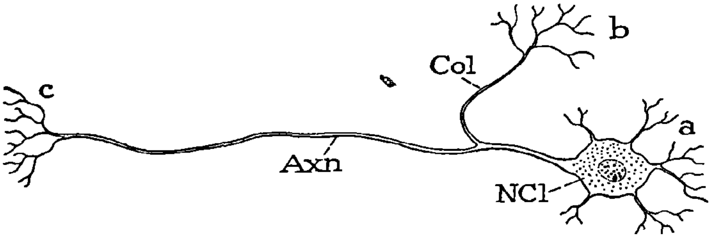

Fig. 241.—Diagram of a neurone. *a*, dendrites of the cell body; *Axn*, axon, or neurite; *b*, *c*, terminal arborizations; *Col*, collateral branch of the axon; *NCl*, the cell body, or neurocyte.

Nerve Trunks.—The ordinary nerves of the body are usually bundles of nerve fibers. Some nerve trunks contain only motor fibers, and some contain only sensory fibers, but in most cases the two kinds of fibers are contained in the same bundle. The main branches of a nerve are smaller bundles of fibers separated off from the main trunk, but the terminal branches consist of single fibers. A nerve trunk and its branches, including the terminal fibers, are surrounded by a nucleated sheath, termed the *neurilemma.*

Ganglia.—An aggregation of neurocytes constitutes a ganglion; but a ganglion usually contains also the collaterals of the motor nerves, the terminal arborizations of the sensory axons, and generally another group of cells the branches of which make connections between the sensory and motor neurones. The ganglion cells are mostly situated at the periphery of the ganglion (Fig. 259 A, *GngCls*). The central part of the ganglion is occupied by a dense mass of nerve fibrils, which constitutes the *neuropile* (*Npl*), or *medullary tissue.* Clusters of terminal fibrils forming small bodies in the neuropile are termed *glomeruli.* In addition to the true nerve cells, a ganglion usually contains also other cells of ectodermal origin which form a supporting tissue. These cells, distinguished as *glia* cells, have irregular shapes and are generally profusely branched among the elements of the true nerve tissue. The ganglion is surrounded by a nucleated neurilemma (*Nlm*) continuous with that of the nerves that issue from it.

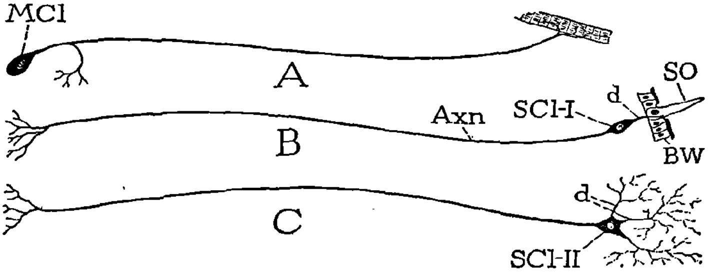

FIG. 242.—Types of neurones, diagrammatic. A, motor neurone with muscle terminals. B, sensory neurone of Type I, with unbranched terminal process (*d*) going to a sense organ. C, sensory neurone of Type II, with branched distal processes distributed on various tissues.

The Synapse.—The central mechanism by which a motor neurone receives an impulse from a sensory neurone is not a direct connection between the two systems. The motor and sensory neurones are separate in their origin, and they never unite. Communication is established between the terminal arborizations of the sensory axon and arborizations of a collateral branch of the motor axon, either by a direct association of the fibrils (Fig. 240 B) or through an intermediate, or *association,* neurone (C, D, *ACl*). The interlocking of the terminal fibrils from the communicating neurones is called a *synapse* (*Syn*).

The Association, or Internuncial, Neurones.—Ordinarily, in the more highly organized animals, the nerve synapses are not established directly between sensory neurones and motor neurones but, as just noted, by way of a third element in the nervous system known as an *association,* or *internuncial, neurone* (Fig. 240 C, D, E, *ACl*). The axon and collateral of an association neurone make a two-way connection between neurones of the sensory and the motor systems. The association neurones may thus give communication between neighboring (C, D) or far distant neurones (E). Moreover, the introduction of the association neurone into the synaptic mechanism makes possible also a multiple internuncial system, inasmuch as arborizations of several or many different nerves may be intermingled (D); and, finally, there may be a series of association neurones interposed between the receptive neurone and the motor mechanism. Thus the stimulus from a single receptor may have a widespread effect on the motor system. The association neurones are contained entirely within the ganglia and the ganglionic commissures and connectives, but some of them extend long distances in the central nervous system.

The neurocytes of the association neurones of insects are mostly large, plasmatic cells with large nuclei containing but a small amount of chromatin. Among them, however, there are certain cells, occurring principally in the brain, which are sharply differentiated from the general type of association cells by their small size and round nuclei rich in chromatin. Association cells of this type are distinguished as *globuli cells.* The axons of globuli cells are confined within definitely limited regions.

The Central Nervous System.—The central stations of the nervous system are functionally the parts of the nervous tracts containing the synapses between the sensory nerves and the motor nerves. In the higher animals, as we have seen, they are located in the ganglia, which contain also the cell bodies of the motor and association neurones. Anatomically the nerve centers of insects may be classed as somatic and visceral. The somatic central system includes the complex nervous mass called the *brain* (Fig. 246, *Br*), lying in the head above the stomodaeum, and a chain of connected ventral segmental ganglia forming the *ventral nerve cord* (*VNC*), lying beneath the alimentary canal, extending from the mouth to the posterior part of the body. This is the principal central system of all arthropods and is generally termed *the central nervous system.* The visceral ganglia are located on the dorsal wall of the stomodaeum and, together with their peripheral nerves, constitute the *stomodaeal nervous system,* often called the "stomatogastric," or "sympathetic," system. The distribution of the nerves from the two central systems, however, does not correspond entirely with the location of the ganglia; some of the nerves of the alimentary canal have their centers in the ganglia of the ventral nerve cord, and some of the somatic muscles may be innervated from the stomodaeal ganglia.

The Peripheral Nervous System.—The peripheral nervous system consists of the axons of the motor neurones, the cell bodies of which are contained in the central ganglia, and of the axons, cell bodies, and terminal processes of the sensory neurones. The motor axons go outward to muscles and glands. The sensory axons proceed inward from peripherally located neurocytes, which are always bipolar or multipolar cells that maintain a connection by means of their distal processes with surfaces from which sensory stimuli are received.

In the Arthropoda there are two distinct sets of sensory neurocytes, distinguished as *sensory cells of Type I,* and *sensory cells of Type II.* Those of the first type (Fig. 242 B, *SCl-I*) are always bipolar cells lying either within or just beneath the epidermis of the body wall (*BW*) or the epithelium of the ectodermal parts of the alimentary canal, and their distal processes (*d*) are usually connected with specific ectodermal sense organs (*SO*). The cells of the second type (C, *SCl-II*) are either bipolar or multipolar. They lie on the inner surface of the body wall and on the wall of the alimentary canal, and their distal processes (*d*) go to the epidermis, the connective tissue, the somatic and splanchnic muscles, and the alimentary epithelium.

The Sense Organs.—A sense organ is a structure designed for the reception of a specific kind of stimulus and for the transmission of the effect of the stimulus to a sensory nerve. Sense organs are located either externally or internally and accordingly are termed *exteroceptors* or *interoceptors.* The interoceptors, however, include organs that are morphologically external since some of them may be situated in the alimentary canal. True internal sense organs that lie within the body cavity and respond to internal conditions of the organism are distinguished, therefore, as *proprioceptors.* No specific proprioceptors are known to occur in insects, the distal processes of sensory cells of Type II having always free endings on the tissues they innervate. Exteroceptors, on the other hand, are abundant on many parts of the body and appendages, and in the ectodermal sections of the alimentary canal. The sense organs are usually complex structures (Fig. 266) in which there are associated with a sensory cell of Type I (*SCl*), or a group of such cells, one or more accessory ectodermal cells, and usually a special modification or development of the covering cuticula. The specific structure of the external part of a sense organ is presumably in each case such as to exclude all but a certain kind of stimulus.

Animal Behavior.—Whatever an animal does in a state of nature, or the way it acts under experimental conditions, zoologists call its *behavior.* There appear to be two types of behavior. In one, the actions of the animal are direct responses to stimuli received from the outside or to the stimuli of physiological conditions or hormones within it; in the other, consciousness seems to be an activating force not directly dependent on external conditions. Whether conscious control of nervous activity is real or only apparent need not be discussed in a work on morphology; but mechanistic action evidently depends on anatomical structure.

The Mechanistic Theory of Behavior.—Since the activities of the motor mechanism of an animal depend entirely upon stimuli received from a nerve, it is clear that the animal cannot make any action for which there is no nervous mechanism. The immediate source of all activity, therefore, is at the receptive ends of the motor nerves. The problem to be solved, then, is how the motor nerves are stimulated in such a way as to produce coordinated and apparently purposeful action. The answer is that, if there is no internal source of motor stimulation, the stimulation must be received from the sensory nerves, and that it is the organization of the sensory and association nerve tracts that determines the specific activity of the motor tracts. Here it must be understood that inhibition as well as increment of activity plays an important part. Hence the reactions of an animal to an external stimulus or set of stimuli may depend entirely on the organization of its nervous and motor mechanism. Simple reactions of this kind are *reflexes;* more complicated performances that result in specific orientation to external conditions are called *tropisms.* Some *instincts* are mere tropisms, but in many cases they involve sequences of reactions and stimuli that must follow in regular order. The operation of an instinct may thus take on a mysterious aspect, but sequence of action is now highly developed by inventors of electrical and other mechanical apparatus, and it is entirely conceivable that the result of one physiological reaction may give the stimulus that allows the next to be operative. While it is not known what part physiological conditions and hormones may play in initiating instinctive acts in insects, it would seem that such influences also must be present.

If an animal exhibits an ability to "learn," that is, to give a certain reaction to a given set of stimuli more readily after a number of repetitions, it is supposed that some primary resistance in the synapse has been broken down, and that the conduction of the stimulus over the same tract in the central system becomes smoother and finally automatic. "Learning" is usually connected with the association of an unaccustomed stimulus with a common stimulus to which there is an established reaction, as in the association of a color, a sound, or some mechanical contrivance with the normal food of an animal. The newly acquired habit of reacting to the secondary or circumstantial stimulus is called *associative memory,* and its corresponding action in the nervous system is termed a *conditioned reflex.* It seems certain that such reflexes must be conditioned through the association neurones of the central nervous mechanism, for it is the intervention of these neurones between several sensory tracts, on the one hand, and the motor tracts, on the other, that gives the possibility of combining two or more sensory impulses in a common motor reaction.

Consciousness.—The property of awareness is, of course, positively known to exist only in ourselves. In its simplest manifestation consciousness is a translation of the forms of energy existing in the environment into psychic equivalents. Red, for example, is a form of consciousness corresponding to electromagnetic "waves" of a certain length; sound is another form of consciousness produced by molecular vibration, and so on for everything else that is consciously perceived. Whether insects possess consciousness or not is a subject not worth discussing, since the fact cannot be known. The reactions of insects to stimuli that generate specific forms of consciousness in us may be, and in most cases probably are, entirely automatic and unaccompanied by any psychic equivalent of the stimulus. However, some insects are capable of developing conditioned reflexes, and the conditioned reflex would seem to be the closest physiological approach to reason. The student of insect behavior, however, must be content to record the observed reactions of his subjects to stimuli, without attributing to them the sensations aroused in himself by the same stimuli.

2. THE CENTRAL NERVOUS SYSTEM

In the evolution of the annelid-arthropod nervous system it would appear that the first centralized group of nerve cells had its origin in the ectoderm at the anterior pole of the body, forming here a small ganglion associated with a sensory *apical plate.* Later there appeared several paired groups of sensory cells at the bases of tentacular or other sensory organs behind the apical plate. Then these various primary nerve centers united in a single ganglionic mass, which is the so-called *archicerebrum* of the annelid worms (Fig. 16 A, *Arc*). This primitive "brain" lies above the anterior end of the alimentary tract, where, in some of the Annelida, it is still not detached from the ectoderm (Fig. 243 A). Finally, two lateroventral nerve strands, consisting of nerve cells and fibers, are developed from the ectoderm along the entire length of the body (*VC*) and are connected anteriorly with the archicerebrum. Thus is established the definitive nervous system, consisting in its simplest form of a suprastomodaeal brain, which originates in the prostomium, though subsequently it may be displaced posteriorly, and of paired ventral nerve strands formed in the postoral part of the trunk.

Following segmentation of the body, the neurocytes of the nerve strands become aggregated in the segments, producing segmentally arranged ganglia. In this stage (Fig. 16 B), therefore, the central nervous system consists of an anterior median brain (archicerebrum) located in the head above the alimentary tract, and of two long, ganglionated nerve cords situated laterally in the ventral part of the body, in which the ganglia (*Gng*) are united lengthwise by interganglionic *connectives* of nerve fibers (*Con*), and crosswise by transverse fibrous *commissures* (*Com*). Finally, in most of the Annelida and all Arthropoda, the lateral cords have approached each other (C), and the pair of ganglia in each segment have united to form a compound median ganglion, though the connectives in most cases remain double.

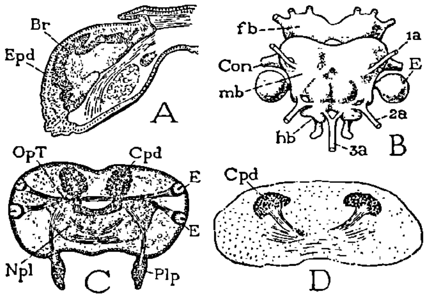

FIG. 243.—Examples of brain structure in Annelida. A, vertical section of prostomium of *Eunice punctata*, showing continuity of brain and epidermis. B, brain of *Eunice punctata*, dorsal view. C, transverse section of brain of *Podarke obscura*. D, same of *Nereis pelagica*, showing position of corpora pedunculata. (A, B *from Heider*, 1925; C *from Hanström*, 1927; D *from microphotograph by Hanström*, 1928.)

Various stages in the evolution of the ventral nervous system, from a condition in which the lateral strands are widely separated to one in which they are united in a median cord, are well shown in the Annelida. In some primitive forms, moreover, the nerve tissue is not entirely detached from the ectoderm. In the Onychophora the nerve strands are widely separated, lying above the bases of the legs, and they show scarcely more than a beginning of ganglionic differentiation.

GENERAL STRUCTURE OF THE CENTRAL NERVOUS SYSTEM OF INSECTS

The central nervous system of insects consists of a mass of nerve tissue, called the *brain*, lying above the anterior end of the stomodaeum, and of a *ventral nerve cord*, composed of median segmental ganglia and paired connectives, lying beneath the alimentary canal. The two parts are joined by connectives embracing the stomodaeum.

The brain is a composite structure, but there is a difference of opinion as to how many primary segmental ganglia enter into its composition. A distinct prostomial ganglion is not evident in the ontogeny of the arthropod nervous system, but the internal structure of the adult brain demonstrates, as will later be shown, that a large part of the cerebral mass, from which the optic lobes of the compound eyes take their origin, is identical with a corresponding part of the brain in the annelid worms. This first part of the definitive arthropod brain is known as the *protocerebrum* (Fig. 245 C, 1*Br*). If the primitive arthropods had preantennal appendages (Fig. 70, *Prnt*), the nerve centers of these appendages lay immediately behind the optic centers and are included in the protocerebrum. The nerve centers of the first antennae constitute a distinct second section of the brain called the *deutocerebrum* (Fig. 245 C, 2*Br*). In all insects and in most crustaceans the nerve centers of the second antennae form a third part of the brain, or *tritocerebrum* (3*Br*). The tritocerebral lobes, however, are united by a commissure (*ComI*) that always lies beneath the stomodaeum, and in some Crustacea the second antennal ganglia themselves are not contained in the suprastomodaeal brain. The ganglia of the second antennal segment, therefore, are without question the first ganglia of the primitive ventral nerve cord (Fig. 244 A, B, 2*AntGng*), and the primitive arthropod brain included only the ganglia contained in the protocerebrum and deutocerebrum.

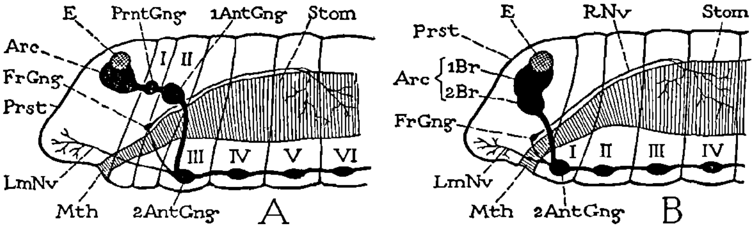

FIG. 244.—Diagrams illustrating two theories of the segmentation of the arthropod head and the composition of the brain. A, the primitive head region as commonly supposed to include the prostomium (*Prst*) and six somites (*I–VI*); the brain formed of the prostomial archicerebrum (*Arc*) and preantennal and first antennal ganglia, with the second antennal ganglia added later. B, the head region supposed to include the prostomium and only four postoral somites; the brain formed from the archicerebrum differentiated into protocerebrum (*1Br*) and deutocerebrum (*2Br*), with the first postoral, or second antennal, ganglia finally added to form the tritocerebrum.

If the preantennal and first antennal appendages represent true somites of the body, then the suprastomodaeal brain mass includes the highly developed archicerebrum (Fig. 244 A, *Arc*) of the prostomium, rudimentary preantennal ganglia (*PrntGng*) of the first somite (*I*), and antennal ganglia (1*AntGng*) of the second somite (*II*). It seems somewhat incongruous that two pairs of segmental ganglia should lie above the stomodaeum and have no substomodaeal connectives.

A more simple concept of the brain structure, and incidentally of the procephalic segmentation, is presented by N. Holmgren (1916) and by Hanström (1927, 1928*a*, 1930), according to which the entire suprastomodaeal part of the brain is derived from the prostomial archicerebrum (Fig. 244 B, *Arc*), while the second antennal centers are assumed to be the ganglia (2*AntGng*) of the first true somite (*I*). As a corollary to this view the preantennae and first antennae become appendicular structures analogous to the prostomial tentacles of the Annelida, and the protocerebral and deutocerebral divisions of the brain (1*Br*, 2*Br*) are specializations of the ocular and antennal centers of the archicerebrum. The theory disregards the evidence of metamerism in the postocular region of the procephalon based on the presence of paired cavities in the mesoderm, which are usually regarded as coelomic sacs of preantennal and first antennal somites (Wiesmann, 1926). According to the other interpretation, these apparent somites are "secondary segments."

The foregoing theory, especially as elaborated by Hanström, has much to commend it. The annelid brain is often highly evolved and may be differentiated into several distinct parts (Fig. 243 B, *fb, mb, hb*) corresponding to the centers of its principal sensory nerves; it contains well-developed corpora pedunculata (C, D, *Cpd*). The primary arthropod brain, therefore, may be supposed likewise to have been secondarily differentiated into protocerebral and deutocerebral regions as a result of the specialization of the ocular and antennal centers. The protocerebrum contains corpora pedunculata identical in structure with those of the annelids. The procephalic part of the arthropod head (Fig. 245 A, *Prc*) is formed in the embryo of the externally unsegmented cephalic lobes, which evidently represent principally the prostomium (*Prst*), but it usually includes also the reduced tritocerebral segment (*I*). The tritocerebral, or second antennal, nerve centers, however, are actually the first ganglia of the ventral nerve cord (A, *GngI*), though in most arthropods they are secondarily added to the primary cerebrum (C, 3*Br*). They innervate the second antennae, the region of the mouth, and the preoral part of the prostomium and are united by connectives with both the brain and the stomodaeal nervous system (Fig. 244 B, 2*AntGng*). With the addition of the tritocerebral ganglia to the arthropod brain, the primitive brain connectives (Fig. 245 A, *CoeCon'*) are shortened (B) and finally suppressed (C). The definitive connectives (C, *CoeCon''*) are those between the tritocerebral ganglia and the first ganglia of the gnathal region.

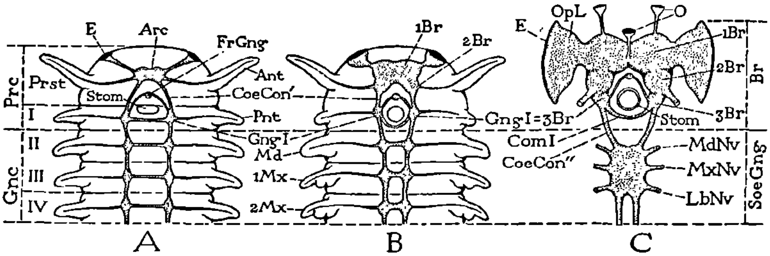

Fig. 245.—Diagrams illustrating the theoretical evolution of the insect brain from the archicerebrum and the first postoral ganglia, and the formation of the suboesophageal ganglion from the ganglia of the gnathal segments. *Ant*, antenna; *Arc*, archicerebrum; *Br*, definitive brain; *1Br*, protocerebrum; *2Br*, deutocerebrum; *3Br*, tritocerebrum; *CoeCon'*, *CoeCon''*, primitive and definitive circumoesophageal connectives; *ComI*, commissure of ganglia of first somite; *FrGng*, frontal ganglion; *Gnc*, gnathocephalon; *GngI*, ganglion of first somite; *OpL*, optic lobe; *Pnt*, postantenna (second antenna); *Prc*, procephalon; *Prst*, prostomium; *SoeGng*, suboesophageal ganglion; *Stom*, stomodaeum.

The next three ganglia of the ventral nerve cord are those of the segments that become the gnathal region of the insect head (Fig. 245 A, *Gnc*). These ganglia are always united with one another in the mature insect (C) to form a second composite nerve mass of the head, known as the *suboesophageal ganglion* (*SoeGng*) because it lies in the ventral part of the head beneath the stomodaeum (Fig. 249). The principal nerves of this ganglion are those of the mandibular, maxillary, and labial appendages.

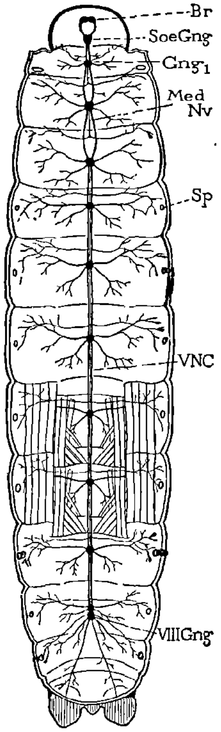

FIG. 246.—Ventral nervous system and brain of a caterpillar, *Malacosoma americana.*

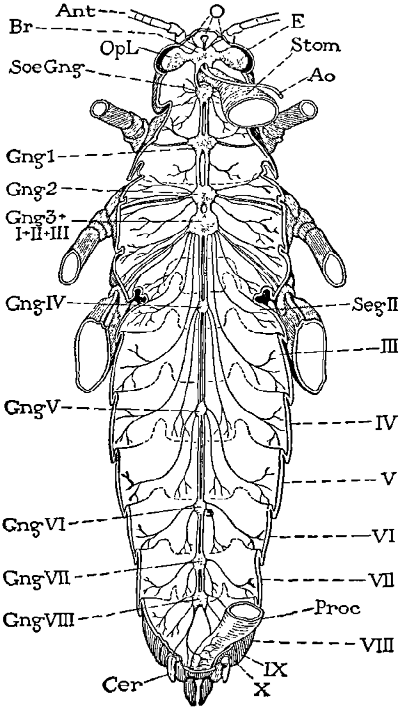

FIG. 247.—Ventral nervous system and brain of a grasshopper, *Dissosteira carolina.*

The thoracic region of the insect body contains three primitive median ganglia corresponding to the three thoracic segments. Usually these ganglia remain distinct (Fig. 246), but frequently the mesothoracic and metathoracic ganglia are united, and the definitive ganglion of the metathorax may include one or more primitive abdominal ganglia (Fig. 247, *Gng*3 + *I* + *II* + *III*).

In the insect abdomen there are at most eight definitive segmental ganglia, corresponding to the first eight abdominal somites (Fig. 246); but the last is always a composite ganglion, since it innervates the eighth and succeeding segments. The nerve cord of the abdomen, however, is often variously shortened by the union of two or more of the posterior ganglia, and the ganglia are subject to a displacement anteriorly, so that a ganglion belonging to some particular segment may actually lie in a more anterior segment (Fig. 247, *GnglV, GngV*). The nerves from each ganglion, however, consistently go to the segment in which the ganglion had its origin. Hence, morphologically, a ganglion should be numbered according to the segment it innervates, and the distribution of the nerves from a composite ganglion is usually the best index of the composition of such a ganglion.

All the ganglia of the ventral nerve cord have a tendency to unite with each other in various combinations in different insects. An extreme condensation is attained in the larvae of cyclorrhaphous Diptera, in which the entire ventral nerve cord, including the suboesophageal ganglion, is consolidated into an elongate mass of nerve tissue, from which the entire body is innervated.

The Brain and Its Nerves

The insect brain is principally a center of association between the major sense organs located on the head and the motor neurones of the gnathal, thoracic, and abdominal regions of the body. Most of its bulk consists of a mass of neuropile tissue; but within this mass are contained, on the one hand, the roots of the nerves from the compound eyes, the ocelli, and the various sense organs of the antennae and the preoral cavity, and, on the other, the anterior terminals of nerve tracts from the suboesophageal ganglion and the ganglia of the ventral nerve cord in the thorax and abdomen. The brain, therefore, is necessary for the initiation of all activities that are normally stimulated through the cephalic sense organs. It takes no part in the regulation of such activities, which are directly controlled from the centers of the suboesophageal and body ganglia. Hence a decapitated insect may be said to be incapable of "voluntary" action; but its vital functions continue in operation as long as its body tissues remain alive, and, if artificially stimulated through somatic receptors, many of the motor mechanisms can be set into normal activity. The insect brain contains but few motor neurones.

General Structure of the Brain.—In external form the brain varies much in different insects, but it always shows a differentiation into three successive parts, which are distinct at least in its internal organization and are usually more or less apparent in the external contour of the adult brain as three pairs of lateral swellings, or lobes (Fig. 248). The first and largest part is the forebrain, or *protocerebrum* (1*Br*), the second is the midbrain, or *deutocerebrum* (2*Br*), the third is the hindbrain, or *tritocerebrum* (3*Br*). The lateral lobes of the protocerebrum and the deutocerebrum are united with each other by internal commissural tracts (Fig. 251, 1*Com*, 2*Com*); the tritocerebral lobes are connected generally by a free nerve trunk, the *suboesophageal commissure* (Figs. 249, 250, 251, 3*Com*), that passes below the stomodaeum. From the tritocerebral lobes there proceed posteriorly and ventrally the *circumoesophageal connectives* (*CoeCon*) to the suboesophageal ganglion (Figs. 248, 249, *SoeGng*) in the lower part of the head. The lobes of the forebrain bear laterally the large *optic lobes* (*OpL*), which contain the complex visual centers of the compound eyes (Figs. 256, 257). The optic lobes are generally narrowed at their bases, and in some insects they are greatly elongate (Fig. 252, *OpL*). The facial ocelli are connected with the anterior or dorsal aspect of the protocerebrum by long slender stalks, the *ocellar pedicels* (Fig. 249, *OPdcl*), at the ends of which are conical enlargements containing the centers of the short ocellar nerves. The true nerve trunks of the brain arise principally from the deutocerebrum and tritocerebrum.

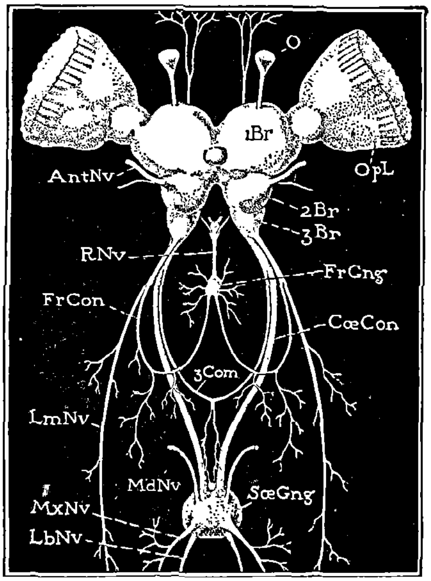

FIG. 248.—Head nervous system of *Dissosteira carolina*, anterior view. (For lettering see Fig. 249.)

The substance of the brain consists largely of a neuropile mass of intricately entangled arborizations of association neurones, the cell bodies of which are located for the most part in the cortical region of the brain. The only motor centers of the insect brain are situated in the deutocerebral and tritocerebral lobes, from which are innervated the antennal muscles, and probably the muscles of the labrum and some of the stomodaeal muscles. In the decapod crustaceans the centers of the oculomotor muscles of the eye stalks are located in the protocerebrum. The principal features to be distinguished within the brain (Fig. 251) are special groups of cells, fiber tracts, and compact bodies formed of dense aggregations of association neurities and of glomeruli of their terminal arborizations.

The Nerves of the Brain.—The principal nerves of the insect brain are the nerves of the compound or simple lateral eyes, the dorsal ocelli, the antennae, the labrum, and the frontal ganglion connectives. In addition there may be present a dorsal tegumentary nerve, connectives with the occipital ganglia of the stomodaeal system, and sometimes other nerves.

Nervus opticus.—The true nerves of the compound or simple lateral eyes are the groups of retinal neurites received in the outer ends of the optic lobes (Fig. 251, *OpNv*), in which are located the optic centers (*I, II, III*). The optic nerves, therefore, are generally very short; but in insects having rudimentary optic centers, the optic nerves may be long trunks, as in the termites and in caterpillars (Fig. 250 A, *OpNv*). The lateral ocelli of coleopterous larvae, however, are developed in close proximity with the outer ends of the long optic lobes of the brain containing the centers of the future compound eyes (Fig. 252).

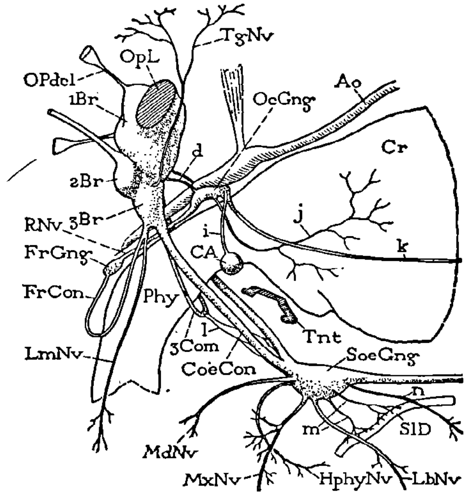

Fig. 249.—Head nervous system of *Dissosteira carolina*, lateral view. *Ao*, aorta; *1Br*, protocerebrum; *2Br*, deutocerebrum; *3Br*, tritocerebrum; *CA*, corpus allatum; *CoeCon*, circumoesophageal connective; *3Com*, tritocerebral commissure; *Cr*, crop; *FrCon*, frontal ganglion connective; *FrGng*, frontal ganglion; *HphyNv*, hypopharyngeal nerve; *LbNv*, labial nerve; *LmNv*, labral nerve; *MdNv*, mandibular nerve; *n*, cervical nerve; *OcGng*, occipital ganglion; *OPdcl*, ocellar pedicel; *OpL*, optic lobe; *Phy*, pharynx; *RNv*, recurrent nerve; *SlD*, salivary duct; *SoeGng*, suboesophageal ganglion; *TgNv*, dorsal tegumentary nerve.

Nervi ocellarii.—The slender ocellar pedicels uniting the facial ocelli with the brain (Fig. 249, *OPdcl*) are commonly called the ocellar "nerves," but it has been shown by Cajal (1918) that the primary ocellar centers lie in the enlarged outer ends of the pedicels (Fig. 258 A, *OC*), since it is here that the inner ends of the retinal fibers (B, *b*) are associated with the terminals (*c*) of nerves from the brain that traverse the stalks. The true ocellar nerves, therefore, are the groups of retinal fibers (*b*) that terminate in the outer ends of the ocellar stalks. The ocellar pedicels are comparable with the optic lobes of the compound eyes.

Nervus ganglii occipitalis.—This is a short, slender nerve connective on each side (Figs. 249, 250 B, *d*) proceeding from the back of the brain to the occipital ganglion of the stomodaeal nervous system (*OcGng*). The fibers of the occipital ganglion connectives, as shown by Holste (1923) in *Dytiscus*, originate from small groups of cells lying in the dorsal part of the protocerebrum, from which they traverse the calyx glomeruli of the corpora pedunculata to make their exit from the posterior wall of the brain.

Nervus antennalis.—The antennal nerves (Figs. 248, 250, 251, *AntNv*) have their roots in the deutocerebrum (Fig. 251) and are the only nerves given off from this part of the brain in insects. Each nerve consists of both sensory and motor fibers, which are sometimes contained in a single trunk, and sometimes separated in sensory and motor branches. The sensory fibers come from the various sense organs of the antenna; the motor fibers go to the antennal muscles within the head and to those located in the scape of the appendage.

Nervus tegumentalis.—A dorsal tegumentary nerve arises from the posterior or lateral surface of the brain in some insects and goes to the dorsal part of the head. The roots of this nerve in *Dytiscus*, according to Holste (1923), can be traced as far as the fibrous mass of the deutocerebrum close to the exit of the motor nerve of the antenna; but Hanström (1928) thinks that the dorsal tegumentary nerve must arise in the tritocerebrum, and that it belongs to the same system as the tegumentary labral nerve. In Acrididae a large tegumentary nerve arises clearly from the base of the tritocerebrum (Fig. 249, *TgNv*). It goes dorsally close behind the brain and forks before the mandibular muscles into two branches distributed to the epidermis of the fastigial area between the compound eyes but apparently gives no branches to the muscles.

Nervus lateralis.—This is a slender nerve present in lepidopterous larvae. It arises from the side of the brain just above the root of the circumoesophageal connective (Fig. 250 A, B, *a*) and divides into two branches. One branch (*b*) goes forward and ventrally to the facial region of the head laterad of the clypeal triangle, where it appears to innervate the mandibular muscles; the other branch (*c*) turns posteriorly and unites with the lateral occipital ganglion (B, *OcGng*) of the stomodaeal nervous system. Nothing is known of the central connections of this nerve or of the origin of its fibers.

Nervus labrofrontalis.—The labrofrontal nerve is a short trunk arising anteriorly from the tritocerebrum. It soon divides into a *frontal ganglion connective* (Figs. 248, 249, 250 A, *FrCon*) and a *labral nerve* (*LmNv*). The frontal connective goes anteriorly and medially to the frontal ganglion (*FrGng*) of the stomodaeal system, sometimes making a long anteroventral loop, as in *Dissosteira* (Fig. 248), from which are given off nerves to the labral muscles and the retractors of the mouth angles. The labral nerve (*LmNv*) proceeds to the labrum and probably contains both motor and sensory fibers.

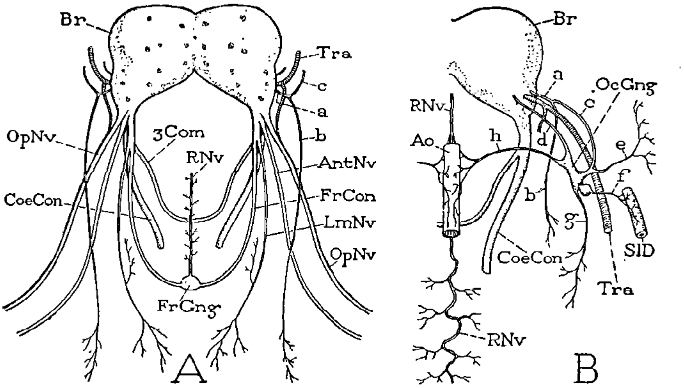

Fig. 250.—Brain, cerebral nerves, and stomodaeal nervous system of a noctuid caterpillar. A, anterior view of brain and frontal ganglion. B, posterior view of right half of brain and postcerebral parts of stomodaeal nervous system.

The preoral distribution of the labral nerve, given off from the postoral tritocerebrum, has led some entomologists to conclude either that the labrum belongs to the tritocerebral head somite or that the roots of the labral nerve have their origins in the protocerebrum. Neither alternative seems to be supported by facts. In the decapod crustaceans a tegumentary nerve, arising posterior to the antennal nerve, gives off a posterior branch which is said to innervate the epidermis of the entire cephalothorax, and also the nephridial sacs (Keim, 1915). Evidently, therefore, tegumentary nerves of the brain have no segmental limitations, and their distribution is of no morphological significance. If it is assumed, however, that the tritocerebral brain lobes represent the first postoral ganglia of the primitive ventral nerve cord, there is nothing incongruous in the fact that they innervate the preoral part of the prostomium, since there is no provision for the innervation of this region from the prostomial part of the brain (Fig. 244 B).

Nervus subpharyngealis.—In some insects a pair of small nerves is given off from the suboesophageal tritocerebral commissure, which are said to innervate the ventral dilator muscles of the stomodaeum.

The tritocerebral commissure, however, is sometimes included in the circumoesophageal connectives and the suboesophageal ganglion, and in such cases the subpharyngeal nerves spring from the anterior end of the latter ganglion. In the acridid *Dissosteira* two median ventral nerves arise from the tritocerebral commissure (Fig. 249, *l*), but they appear to innervate the neurilemma of the circumoesophageal connectives and the suboesophageal ganglion.

Nervus postantennalis.—Nerves of the postantennal appendages are entirely absent in insects, since these appendages are represented only by embryonic rudiments in the Hexapoda; but in the Crustacea they constitute the principal nerves (second antennal nerves) of the tritocerebral ganglia.

The Protocerebrum.—The forebrain, or protocerebrum, is the dorsal and largest part of the cerebral mass (Fig. 248, *1Br*). It includes the lateral *protocerebral lobes* (Fig. 251, *PcrL*), the median *pars intercerebralis* (*Picr*), and sometimes ventral *accessory lobes* (*AcL*), or *Nebenlappen.* Within the neuropile mass of the forebrain are to be distinguished groups of globuli cells, dense clusters of fibers and glomeruli forming the so-called "bodies" of the brain, and various fibrous tracts.

The globuli cells of the brain are specialized association cells characterized by their small size, compact arrangement, and richly chromatic nuclei. Hanström (1930) distinguishes in the arthropod brain generally three primary paired groups of globuli cells, namely, on each side, a *median* dorsal group (Fig. 251, *GbI*), a posterior *lateral* group (*GbII*), and a ventrolateral *ventral* group (*GbIII*). The several globuli groups are subject to much variation in the extent of their development. In the insects the dorsal and ventral groups are reduced or usually absent, while the lateral groups (*GbII*) become prominent elements in the brain of most Pterygota. The neurites of the globuli cells form some of the most important fibrous bodies of the brain.

The fibrous and glomerulous masses of the protocerebrum include the dorsal *corpora pedunculata* (Fig. 251, *Cpd*), the median dorsal *pons cerebralis* (*Pncr*), the *corpus centrale* (*Cc*), the ventrolateral *corpora ventralia* (*Cv*), and sometimes dorsal *corpora optica.* In addition to these bodies of the protocerebrum proper, however, there are connected with the protocerebrum the *optic centers* of the compound eyes (*I*, *II*, *III*) situated in the optic lobes, and the *ocellar centers* located in the outer ends of the ocellar pedicels.

Pons cerebralis.—The protocerebral bridge (Figs. 251, 252, *Pncr*), lying in the dorsal and posterior part of the pars intercerebralis, is a transversely elongate body, usually horseshoe shaped with the concavity forward or downward. The substance of the pons is mostly glomerulous; but according to Bertschneider (1921), the pons glomeruli of *Deilephila* forms two lateral swellings of the body with a fibrous commissure between them. The pons cerebralis is the "posterior dorsal commissure" of C. B. Thompson (1913), but it is evident from its structure that the body is an association center, since fibers enter it from many parts of the brain. In most arthropods there are associated dorsally with the pons the two cell masses of the dorsal globuli cells (Fig. 251, *GbI*), and in such cases the neurites of these cells form the body of the pons. Dorsal globuli cells associated with the pons, however, are said by Hanström to occur among insects only in Apterygota and Ephemerida.

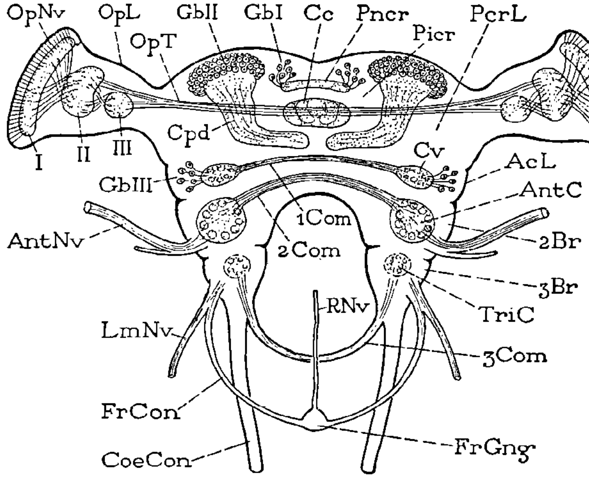

Fig. 251.—Diagram of the internal fibrous bodies and fiber tracts of the insect brain. *AcL*, accessory lobe; *AntC*, antennal center; *2Br*, deutocerebrum, *3Br*, tritocerebrum; *Cc*, corpus centrale; *1Com*, protocerebral commissural tract; *2Com*, deutocerebral commissural tract; *3Com*, tritocerebral commissure; *Cpd*, corpus pedunculatum; *Cv*, corpus ventrale; *GbI*, *II*, *III*, three groups of globuli cells; *I*, lamina ganglionaris; *II*, medulla externa; *III*, medulla interna; *OpL*, optic lobe; *OpNv*, optic nerves; *OpT*, optic tract; *PcrL*, protocerebral lobe; *Picr*, pars intercerebralis; *Pncr*, pons cerebralis; *TriC*, tritocerebral center.

Corpus centrale.—The central body of the brain (Figs. 251, 252, *Cc*) lies anterior or ventral to the pons. In the insects it consists of several distinct groups of glomeruli, which together form an oval or flattened mass with the long axis transverse. The subdivision of the central body constitutes the chief difference in internal structure between the brain of insects and that of Crustacea, in which the central body consists of a single mass of glomeruli. The central body has no nerve cells directly connected with it, but it is a most important center of association between the terminals of fibers from all other parts of the brain.

Corpora pedunculata.—The pedunculate bodies (mushroom bodies, *pilzförmigen Körper*) are situated in the dorsal part of the brain between the protocerebral lobes and the pars intercerebralis (Figs. 251, 252, *Cpd*).

In their typical form these bodies are mushroom shaped, as their name implies. Each consists of an expanded cap in the upper or posterior part of the brain covered with a mass of globuli cells, and of a large, thick fibrous stalk, or *pedunculus,* extending forward. The corpora pedunculata constitute the largest and most highly developed association centers in the brain of pterygote insects and are the most conspicuous features of the internal cerebral structure.

The cellular caps of the pedunculate bodies are the lateral groups of protocerebral globuli cells (Fig. 251, *GbII*), but in most insects and in many other arthropods each primitive cell group becomes subdivided into two or three distinct secondary groups of cells (Fig. 253 A). The pedunculus of each body is formed of the axons of the globuli cells (B, *f*). When the globuli cells are separated into groups, therefore, each pedunculus contains as many confluent bundles of fibers as there are cell groups in the cap. Immediately beneath the cell cap, the axons of the globuli cells give off short arborizing collaterals, which form synaptic associations (*h*) with the terminals of incoming fibers (*g*) from other parts of the brain. There is thus formed, corresponding to each cell group at the upper end of the pedunculus, a cup-shaped mass of fibrils and glomeruli (A, B, *a*), which is known as a *calyx.* According to the number of cell groups, each pedunculus may be surmounted by a single calyx or by two or three calyces.

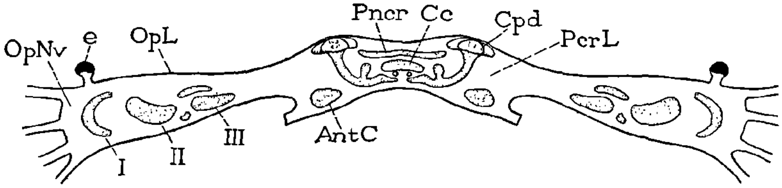

Fig. 252.—Section of the brain of *Dytiscus marginalis.* (*From Holste,* 1923.)

The pedunculi extend forward in the dorsal part of the brain and terminate in two large root branches (Figs. 252, 253 A). One branch (Fig. 253 A, *c*), the *median root* (Balken), goes inward from the main stalk of the pedunculus, and the two median roots from opposite sides usually end in proximity to each other (Figs. 251, 252), though in the Isoptera each again turns posteriorly and is extended toward the back of the brain beneath the central body and the pons. The other branch (Fig. 253, *d*), or *posterior root* (cauliculus, *rücklaufige Wurzel*), goes posteriorly and dorsally anterior to the central body and the pons. In *Lepisma* each root of the pedunculus ends in a cluster of swellings (*Trauben*).

The axons of the calyx cells entering the pedunculus proceed to the distal end of the latter, where each appears to divide, one branch entering the median root, the other the posterior root. Within the roots the fibers are said to end in arborizations that form intercommunicating associations with one another, but to have few if any connections here with nerves from other parts of the brain. In some cases fibers have been observed extending between the inner ends of the median roots of the two pedunculate bodies. The principal association centers of the corpora pedunculata, where nerves intermingle from all parts of the brain, are the glomeruli of the calyces (Fig. 253 B, *h*).

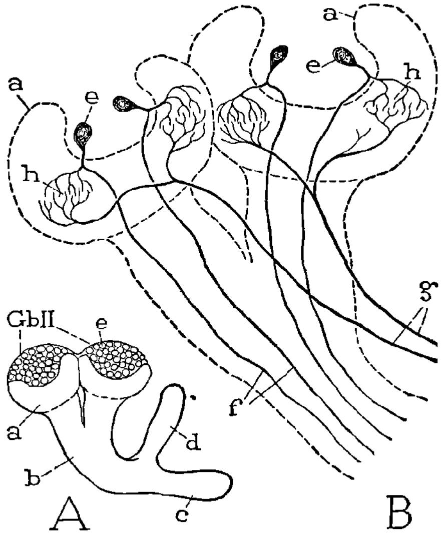

FIG. 253.—Structure of a corpus pedunculatum, diagrammatic. A, pedunculate body with two calyces (*a*) containing the globuli cells (*e*) of group II; stalk (*b*) ending in two roots (*c*, *d*). B, showing synapses (*h*) in the calyces between incoming nerves (*g*) and collaterals of the calyx cells (*e*), the axons of which (*f*) form the stalk and roots of the pedunculate body.

The lateral globuli cells, the axons of which compose the stalks of the pedunculate bodies, occur in all arthropods and in the annelid worms; and in both these groups the cell axons form variously developed bundles of fibers. The latter reach their highest complexity in the pterygote insects. Corpora pedunculata, Hanström (1928) says, are first met with in the annelid family Hesionidae, in which the neurites of two groups of globuli cells form a pair of stalks, which bend mesally at their inner ends and are united by a transverse fibrous commissure (Fig. 243 C). With these bodies are associated the roots of the palpal nerves. In the higher annelids, as in Aphroditidae and Nereidae (D), the corpora pedunculata are well-developed bodies (Fig. 254), each composed of a large cap formed of two or three groups of globuli cells (*Gb*), and of a thick stalk containing the neurites (*f*) of these cells, in which are the principal associations (*j*) of the fibers (*i*) from the sensory root of the palpus nerve.

In the Arthropoda the size and complexity of the corpora pedunculata appear in general to be correlated with the development of the compound eyes, which are the principal sense organs directly associated with the protocerebrum; but, on the other hand, as in the Isoptera, the pedunculate bodies may be highly developed, though the eyes are small or absent. Many comparative studies of the pedunculate bodies in insects show that the relative size of the organs gives a pretty fair index of the development of instincts and "intelligence"; and yet complex instincts may be operative in larval forms, though, as Hanström (1925) has shown in the caterpillar, the brain centers are in a rudimentary stage of development.

The presence of distinct corpora pedunculata in the brain of annelid worms, as demonstrated by Hanström, can lead only to the conclusion that the major part at least of the arthropod protocerebrum has been evolved directly from a prostomial nerve mass corresponding to the archicerebrum of Annelida.

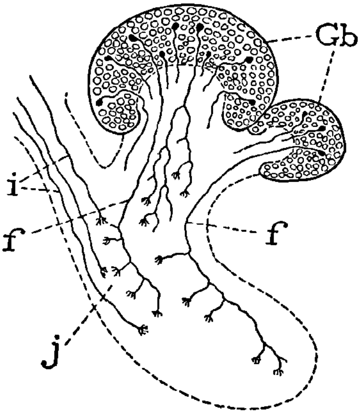

FIG. 254.—Corpus pedunculatum of an annelid, *Nereis virens*. (*From Hanström*, 1927.)

Corpora ventralia.—The ventral bodies (lateral bodies, *Nebenlappen, parosmatische Massen*) lie in the ventrolateral parts of the brain just above the antennal glomeruli of the deutocerebrum (Fig. 251, *Cv*). Some writers (Holste, 1923; Beier, 1927) regard the ventral bodies as belonging to the deutocerebrum; but generally they are included in the protocerebrum, and they are united with each other by a transverse commissural tract (1*Com*) that passes beneath the central body and the median roots of the corpora pedunculata. The ventral bodies, according to Hanström, are formed primitively of the association neurites of the ventral globuli cells (*GbIII*), but these cells persist in only a few arthropods, and generally the ventral bodies consist only of masses of glomeruli. They are association centers having fibrous connections with the central body, the corpora pedunculata, the pons, the optic lobes, the antennal glomeruli, and other parts of the brain.

The ventral bodies are usually not well developed in the higher insects, though they appear to be of large size in both adult and larval Coleoptera, and, according to Bretschneider (1921), they are particularly large and highly elaborated in the Lepidoptera, the region containing them forming accessory lobes (*Nebenlappen*) of the protocerebrum. On the outer surface of each of these lobes on the back of the brain, Bretschneider says, there is a mass of cells (evidently the ventral globuli cells) from which fibers stream into the ventral bodies as do those of the lateral globuli into the stalks of the corpora pedunculata. The relatively large size of the ventral bodies in the Lepidoptera Bretschneider regards as a primitive character in this order, since the bodies in *Deilephila* are very similar to those of *Forficula,* and in both these insects they are the best connected parts of the brain. The size and complexity of the ventral bodies in insects generally, however, have an inverse relation to the development of the corpora pedunculata, the latter, Bretschneider believes, supplanting the ventral bodies in importance in most insects.

Corpora optica.—Optic bodies are not generally present in the insect brain. In some of the Apterygota, however, according to Hanström (1928), there is in the dorsal part of the brain a pair of small bodies lying above the pons cerebralis, which in *Machilis* are connected with the glomeruli of the ocellar nerves and with the medullae externae of the optic lobes. These optic bodies, therefore, are association centers of both the ocelli and the compound eyes. Similar optic centers occur also in the Branchiopoda among the Crustacea.

The Optic Centers.—The ganglionic centers of the lateral eyes, contained within the optic lobes, are so intimately associated with the protocerebral lobes of the fully formed brain that they may be regarded as a part of the protocerebrum, though they are distinct from the latter in their origin. As described by Wheeler (1891) in the Orthoptera, the optic lobes are formed from sporadic clusters of cells delaminated at an early embryonic stage from the outer edges of the procephalic ectoderm. Soon the scattered cells arrange themselves on each side of the primitive head region in four longitudinal rows similar to the eight median rows of neuroblasts that are to form the median part of the brain, and which are continuous with the eight rows of neuroblasts in the neural ridges of the postoral region. The cells generated from the neuroblasts of the optic lobes, however, Wheeler says, do not resemble those produced from the neuroblasts of the central strands and appear to multiply irregularly.

The optic centers of all arthropods, regardless of the nature of the lateral eyes connected with them, have evidently had a common origin, the prototype of which, or an analogous structure, is to be found in some of the annelid worms. In the polychaete family Eunicidae, Hanström (1926) describes a very simple optic center, located in an optic lobe of the brain, intervening between the eye and the cerebrum proper (Fig. 255 A). The optic nerves (*OpNv*) consist of the short retinal fibers from the eye (*E*) to the optic lobe (*OpL*). Within the latter the fibers break up into terminal arborizations that form associations with terminals from nerves of the optic tract (*OpT*), some of which arise from cells located within the optic lobe, while others have their origins in the brain itself and send their neurites into the optic center (*I*). The optic tract traverses the brain between the two optic lobes and probably has connections with other parts of the cerebrum.

From this primitive optic center of the Eunicidae it is but a step to the more complicated but still very simple structure of the optic center in the branchiopod Crustacea (Fig. 255 B). Here, as shown by Hanström (1926), there are in each optic lobe two ganglionic bodies, a distal *lamina ganglionaris* (*I*) and a proximal *medulla* (*II*), surrounded by ganglion cells. The postretinal fibers (*OpNv*) from the eye penetrate into the lamina, where their thickened terminal parts are associated with terminals from two groups of neurones. The neurocytes of one group lie distal to the lamina, and their axons (*a*) extend proximally into the medulla, giving off arborizations in both optic masses; the cells of the other group (*b*) are associated with the medulla and send their axons distally into the lamina, where they end in fine terminal branches. It is to be observed that there is here no crossing of the fibers between the two optic masses. Cells of another set belonging to the medulla (*c*) have short fibers that end within the latter. The optic center, finally, is connected with the brain by neurones whose cell bodies (*d*) lie proximal to the medulla and give off branching collaterals into the latter, while their axons form the optic tract (*OpT*) extending proximally into the brain. Some of the optic fibers end in the lateral part of the brain, but others go into the optic commissures situated above and behind the central body.

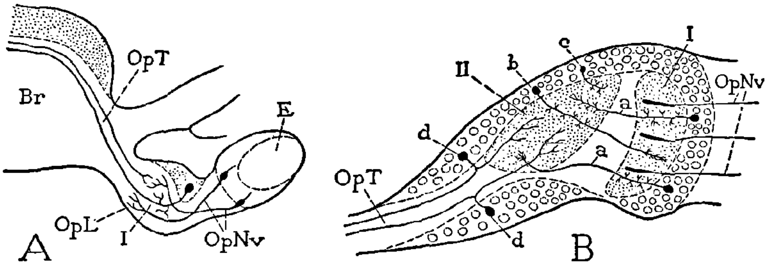

FIG. 255.—Optic lobe of an annelid worm and a branchiopod crustacean. (*From Hanström*, 1926, 1928.) A, section of brain, optic lobe, and eye of *Leodice norwegica*, with a single synaptic junction (*I*) between the optic nerves and the fibers of the optic tract. B, optic lobe of *Artemia*, with two synaptic regions (*I*, *II*).

The optic lobes of Diplopoda and Chilopoda contain likewise two optic masses; but in most Crustacea and in all Insecta there are characteristically three principal association centers in each optic lobe (Fig. 251), namely, a distal *periopticon*, or *lamina ganglionaris* (*I*), a median *epiopticon*, or *medulla externa* (*II*), and a proximal *opticon* or *medulla interna* (*III*). The connection between the eye and the periopticon remains essentially the same in all forms; but the number and variety of the optic neurones, the structure and connections of the fibrous masses, and the associations of the fibers in the optic tract with other parts of the brain, all become increasingly complex with the progressive evolution of the compound eye and the function of "vision."

The optic centers of insects are probably the most intricate nervous mechanisms developed among the arthropods. Space cannot here be devoted to a minute description of their details, and the student should consult particularly the work of Zawarzin (1914) on the optic lobes of the larva of *Aeschna*, that of Bretschneider (1921) on Lepidoptera (*Deilephila*), and that of Cajal and Sánchez (1915), in which are elaborately described the optic centers of the honey bee (*Apis mellifica*) and of the blow fly (*Calliphora vomitoria*).

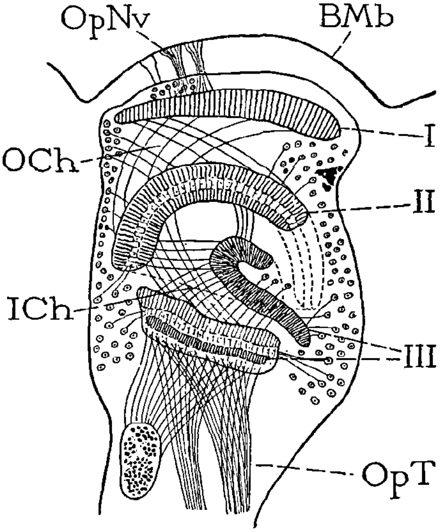

FIG. 256.—Optic lobe of a moth, *Deilephila euphorbiae*, showing the three synaptic regions (*I*, *II*, *III*) with intervening chiasmata (*OCh*, *ICh*) characteristic of insects. (*From Bretschneider*, 1921.)

The grosser structure of the optic centers will be more easily understood from Bretschneider's figure of the optic lobe of *Deilephila* (Fig. 256). Here it is seen that the postretinal fibers (*OpNv*) penetrate the basement membrane of the eye (*BMb*) in bundles that enter the lamina ganglionaris (*I*). The lamina and the medulla externa (*II*) are connected by crossing fibers that form the *outer chiasma* (*OCh*). Peripheral cells in the outer part of the optic lobe send their axons into the medulla externa, which has a distinctly laminated structure owing to the stratified arrangement of the terminals of the penetrating axons. The medulla interna (*III*) is subdivided into two fibrous masses, which are connected by fibers that cross with those from the external medulla to form the *inner chiasma* (*ICh*). The medulla interna shows four layers of stratified fibrils within its substance, and it has elaborate fiber connections through the optic tract (*OpT*) with various parts of the brain. One bundle of fibers goes to the corpus ventrale, another to the central body and the pons, a third forms a union with the bridge and the corpus pedunculatum, a fourth crosses beneath the central body in a commissural tract to the opposite eye, giving terminals into the central body, and a fifth rather large bundle traverses the ventral part of the brain going directly to the suboesophageal ganglion. Still other fibers end in the neuropile mass of the protocerebral lobe.

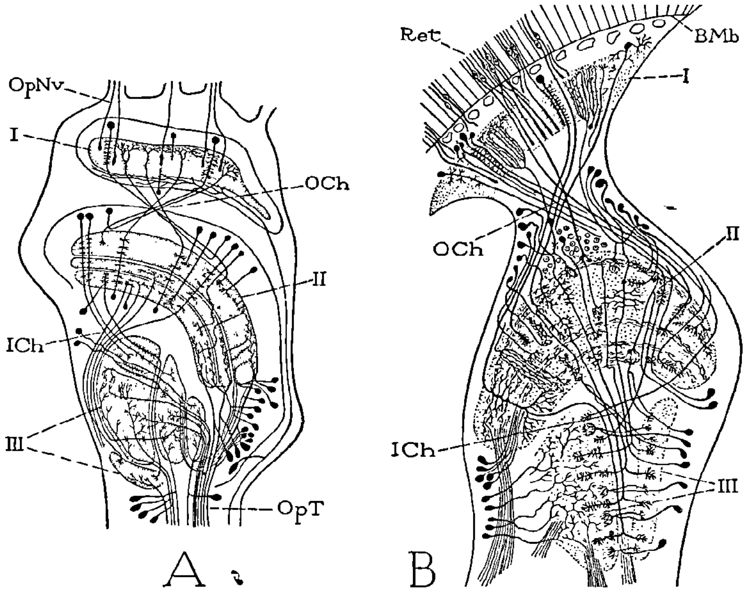

FIG. 257.—Examples of structural details in the optic lobes of insects, diagrammatic. A, *Aeschna* larva. (*From Zawarzin*, 1914.) B, *Calliphora vomitoria*. (*From Cajal and Sánchez*, 1915.)

The figure by Zawarzin (Fig. 257 A), showing diagrammatically the relations of the nervous elements in the optic lobes of the larva of *Aeschna*, will give a clearer idea of the nature of the associations of the optic neurons within the several optic masses. The medulla interna (*III*) of the *Aeschna* larva is subdivided into four secondary parts. It will be seen here that the laminated structure of the fibrous bodies, especially of the medulla externa (*II*), results from the alignment of successive groups of fibrils given off from the neurites traversing them. The fibers connecting the lamina with the medulla externa form a distinct outer chiasma (*OCh*), and those between the medulla externa and the medulla interna form a second inner chiasma (*ICh*). In addition to the interrupted fiber tracts extending from the eye to the brain through the three ganglionic centers, the proximal elements of which have their roots in the four parts of the medulla interna, there are also continuous fibers connecting the lamina ganglionaris and the medulla externa individually with the brain.

The optic centers of the blow fly, as depicted by Cajal and Sánchez (Fig. 257 B), differ considerably in detail from those of the dragonfly larva and in some respects are more complex. Most of the postretinal fibers end in the lamina ganglionaris (*I*), but some of them go through the outer chiasma (*OCh*) and terminate in the medulla externa (*II*). The medulla interna (*III*) is subdivided into two parts, within which are symmetrically distributed the dichotomously branched terminals of the neurones of the lamina externa. The optic tract is composed of fibers that connect with the medulla interna and with the medulla externa, but not with the distal lamina.

For a full description of the actual structure of the optic ganglia the student must have recourse to the papers above cited; the figures given here are but diagrams. After following the wonderful maze of intricate detail in the nerve centers of the compound eyes, however, we are still at a loss to understand how the effect of light on the receptor organ is transformed by the optic apparatus into specific reflexes in the motor mechanism or into a perception of variations in light intensity, color, form, and motion. This, fortunately, lies outside the subject matter of morphology.

The lateral ocelli of endopterygote larvae are connected with the optic centers of the compound eyes, the latter being first developed in the pupa. The lateral ocelli, therefore, appear to be temporary larval organs, as are most of the other special structures of the larva. The compound eyes are not evolved from the larval ocelli but are newly formed in the epidermis of the pupa, or in some cases in that of the larva. The retinal parts of the ocelli, at the time of metamorphosis, are withdrawn from the surface and degenerate, but in some insects (see Günther, 1912; Marshall, 1928) remnants of them persist at the side of the optic nerve of the adult (Fig. 252, *e*). With exopterygote insects, in which the compound eyes are formed in the embryo, the imaginal eye is often relatively larger than or of different shape from that of the nymph or larva. The enlargement of the eye involves an increase in the size of the lamina ganglionaris lying below it, and the increment in the lamina, as shown by Zawarzin (1914) in the dragonfly, is formed from a part of the latter that remains in an undeveloped embryonic condition during the larval stage.

The Ocellar Centers.—The ganglionic centers of the facial ocelli lie in the distal parts of the ocellar pedicels (Fig. 258 A, *OC*). It has been shown by Cajal (1918) that the inner ends of the short retinal fibers (B, *b*) are here associated with the distal terminals of long fibers (*c*) that traverse the ocellar pedicels from the brain; these fibers were mistaken by earlier writers for the ocellar nerves. The fibers from the ocellar centers, according to Cajal, go to the lower part of the brain where they are associated with the terminals of branches from the optic tracts of the compound eyes. Hanström (1928) believes that the neurocytes of the neurones of the ocellar tracts are large association cells lying mediodorsally in the pars intercerebralis. This appears to be the site of the primitive optic center of the brain, and in *Machilis* the ocellar tracts end here in lateral glomeruli. The median facial ocellus is said to have two strands of fibers in its pedicel, which in the Odonata make a chiasmatic crossing in the brain. Blackman (1912) records the occurrence in *Melanoplus femur-rubrum* of two distinct median ocelli, each complete in every respect, innervated through a bifurcate median pedicel, with a conical swelling at the end of each branch beneath the corresponding ocellus.

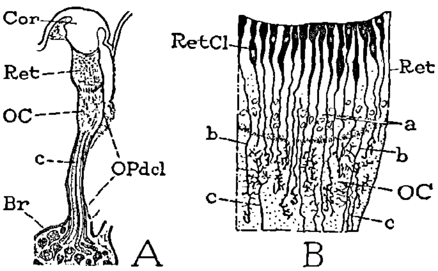

Fig. 258.—Innervation of an ocellus. (*From Cajal,* 1918.) A, median ocellus of a dragonfly, *Libellula,* and its cerebral pedicel (*OPdcl*). B, section of ocellar retina (*Ret*), and ocellar center (*OC*) in distal part of pedicel containing the synapses between the retinal nerves (*b*) and fibers (*c*) traversing the pedicel from the brain.

The Deutocerebrum.—The deutocerebrum is the part of the brain containing the centers of the antennal nerves. Its lateral parts generally form a pair of distinct lobes in the adult brain (Figs. 248, 249, *2Br*), from which the antennal nerves arise. The sensory fibers of the antennal nerve trunks terminate in numerous glomeruli distributed principally in the periphery of the deutocerebral neuropile (Fig. 251, *AntC*). The ganglion cells of the motor fibers going to the antennal muscles lie in the lateral parts of the deutocerebral lobes. The antennal glomeruli of opposite sides are connected by a fibrous *deutocerebral commissure* (*2Com*) which traverses the lower part of the brain.

The Tritocerebrum.—The tritocerebral part of the brain is relatively small in insects, owing to the absence of postantennal appendages and the consequent lack of nerves to these organs. The region of the tritocerebrum is usually evident as a pair of swellings or distinct lobes (Figs. 248, 249, *3Br*) beneath the deutocerebral lobes, from which the circumoesophageal connectives (*CoeCon*) proceed ventrally and posteriorly around the sides of the stomodaeum to the ventral head ganglion. The tritocerebral lobes are connected with each other by a *substomodaeal commissure* (*3Com*). The commissure is often more or less united with the circumoesophageal connectives, and, when it is not evident as a free trunk, it is probably submerged in the connectives and in the anterior part of the suboesophageal ganglion. The principal nerves of the tritocerebrum in insects are the frontal ganglion connectives (Figs. 248, 249, 250 A) and the labral nerves (*LmNv*), but small nerves arising from the commissure must also have their roots in the tritocerebral ganglia.

Morphologically, as we have seen, the tritocerebral lobes of the brain represent the first paired ganglia of the primitive ventral nerve cord and are primarily postoral in position (Fig. 245 A, B, *GngI*), their union with the brain being secondary (C, *3Br*). The unique feature of the tritocerebral ganglia is their connection with both suprastomodaeal parts of the nervous system, namely, with the protodeutocerebral brain mass, and with the stomodaeal system (Fig. 244).

The Fiber Tracts of the Brain.—All the internal parts of the brain are intricately connected with one another by fibrous tracts formed of the axons of association neurons. Three of these tracts lying within the brain may be termed commissures, because some of their fibers at least go continuously across the brain between corresponding parts of opposite sides. A fourth tract of the same nature forms a free nerve trunk. The first commissure consists of fibers of the optic tract (Fig. 251, *OpT*) that connect the medullary bodies of the optic lobes with each other; the second (*1Com*) unites the corpora ventralia beneath the roots of the pedunculate bodies; the third is the deutocerebral commissure (*2Com*) traversing the ventral part of the brain between the antennal centers; the fourth is the tritocerebral commissure (*3Com*), called the suboesophageal commissure because it is usually a free nerve trunk passing beneath the stomodaeum (Fig. 249). The other tracts run in all directions and connect the cerebral bodies with one another. The optic centers, as we have seen, are connected by fibers from the optic tract with the corpora pedunculata, the central body, the ventral bodies, and the antennal centers. The corpora pedunculata receive fibers from all parts of the brain as well as from the suboesophageal ganglion; and the central body has connections almost as extensive. The ventral bodies are more important centers in some insects than in others; when well developed they too have widely distributed connections. The largest tracts of the brain, however, go from the antennal centers to the calyces of the corpora peduculata and here put the antennal sense organs in communication with fibers from all the other cerebral centers and from the ventral nerve cord.

A study of the nerve associations in the brain suggests that the principal centers through which the sense organs of the head exert an influence on the motor mechanism of the rest of the body are the corpora pedunculata and the corpus centrale. As yet, however, neurologists have given much less attention to the connections between the cerebral centers and the centers of the ventral nerve cord than they have given to local associations within the brain itself.

The Ventral Nerve Cord

The ventral nervous system, as distinguished from the suprastomodaeal part of the brain and the stomodaeal system, consists of the postoral series of segmental ganglia and their connectives, constituting the so-called *ventral nerve cord.* Morphologically, as we have seen, the ventral nerve cord begins with the tritocerebral ganglia of the brain and includes the primitive ganglia of the gnathal region of the head, as well as the ganglia of the thorax and abdomen. Since the general structure of the ventral nerve cord and the structure of the tritocerebral ganglia have already been described, we shall give attention here only to the composite suboesophageal ganglion of the head, the internal organization of a body ganglion, and the median nerves of the thoracic and abdominal ganglia.

The Suboesophageal Ganglion.—The ventral nerve mass of the head is composed of the united ganglia of the primitive gnathal segments. The histology of this composite ganglion has been but little studied by precise neurological methods, which is unfortunate because of the long-standing dispute as to the number of ganglia that are contained in it. The suboesophageal ganglion innervates the mandibles (Fig. 249, *MdNv*), the hypopharynx (*HphyNv*), the maxillae (*MxNv*), the labium (*LbNv*), the salivary ducts (*m*), and at least some of the muscles of the neck (*n*). The nerve trunks contain both motor and sensory fibers. The longitudinal nerve tracts that enter or traverse the suboesophageal ganglion are of great importance, since they contain the connective fibers between the sensory centers of the head and the motor centers of the body, but we have little detailed information concerning them. In addition to being the central organ of the gnathal and cervical nerves, the suboesophageal ganglion is also an inhibitory center of the body ganglia, since, with its removal, the somatic reflexes are found to become more readily excited by artificial stimuli.

General Structure of a Body Ganglion.—For a full account of the internal structure of the ganglia of the ventral nerve cord the student must consult the detailed work of Zawarzin (1924*a*) on the *Bauchmark* of the larva of *Aeschna.* We can here give only a brief résumé of Zawarzin's descriptions.

A segmental ganglion of the thorax or abdomen is usually an oval or polygonal mass of nerve tissue, continuous anteriorly and posteriorly with the interganglionic connectives (Fig. 259 A). From its sides proceed two or three principal *lateral nerves* (1*Nv*, 2*Nv*, 3*Nv*); and in some insects a *median nerve* (*MedNv*) arises posteriorly, or also anteriorly, between the bases of the connectives. The ganglion is invested in a nucleated sheath, the neurilemma (*Nlm*), which is continuous over the connectives and the nerves. The principal cellular elements of the ganglion (*GngCls*) are arranged peripherally, mostly in the lateral and dorsal parts. The central and ventral parts are occupied by a neuropile mass (*Npl*). The lateral nerves of the ganglion that contain both motor and sensory fibers arise each from dorsal and ventral fibrous roots within the ganglion, the dorsal root containing the motor fibers (Fig. 260, *MF*), the ventral root the sensory fibers (*SF*).

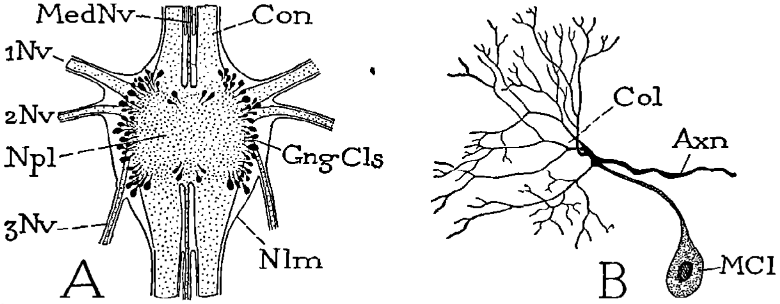

Fig. 259.—A typical ganglion of the ventral nerve cord, and a ganglion motor cell. (*From Zawarzin,* 1924*a*.) A, an abdominal ganglion and its nerve trunks, showing position of the nerve cells in the ganglion. B, a motor neurone of an abdominal ganglion of an *Aeschna* larva.

Within the neuropile there may be distinguished five regions (Fig. 260). Dorsally is the region of the dorsal interganglionic connective fibers (*a*, *b*). Beneath this is the motor center (*c*), or region of the dorsal nerve roots. Ventrally is situated the region of the ventral connective fibers (*f*, *g*, *h*), and immediately above it the sensory center (*e*), or region of the sensory ventral roots of the lateral nerves. The central part of the ganglion (*d*) contains the principal neuropile mass. At the ends of the ganglion only the dorsal and ventral fiber tracts are continued into the connectives.

In each ganglion there are six principal groups of nerve elements: (1) the cell bodies and roots of the motor fibers of the lateral nerves; (2) the roots of the sensory fibers of the lateral nerves; (3) the cell bodies and fibers of the intraganglionic association neurones; (4) the cell bodies and collaterals of the interganglionic association neurones; (5) the cell bodies and roots of the motor fibers of the median nerve; and (6) the roots of the sensory fibers of the median nerve.

The cell bodies of the motor neurones of the lateral nerves lie in the dorsolateral parts of the ganglion (Fig. 260, *j, k*). Each is a large unipolar cell (Fig. 259 B, *MCl*) with a slender mediodorsal process, from which are given off finely branching collaterals (*Col*) into the dorsal motor center of the ganglion, while the main shaft of the fiber, or axon (*Axn*), turns outward to enter the dorsal part of a lateral nerve.

The sensory fibers entering the ganglion from the lateral nerve trunks (Fig. 260, *SF*) go to the region of the sensory neuropile (*e*) in the lower part of the ganglion, where some of them (*s*) end in terminal arborizations, while others (*t, u*) give off branching collaterals and then turn forward and proceed through the connectives to some more anterior ganglion. The sensory neuropile, therefore, contains fiber endings both of the lateral sensory nerves of the ganglion and of sensory fibers from the more posterior ganglia. The collaterals of some of the sensory nerves end in the side of the ganglion on which the nerve enters (*u*); others cross to the opposite side (*t*).

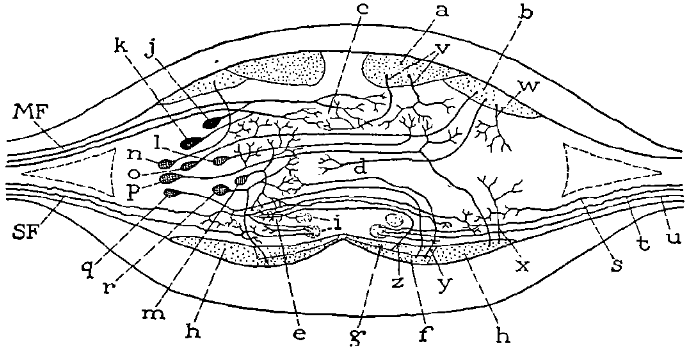

Fig. 260.—Diagrammatic cross section of an abdominal ganglion of an *Aeschna* larva. (From Zawarzin, 1924*a*.) *a, b,* dorsal fiber tracts of longitudinal commissures; *c,* motor neuropile; *d,* central neuropile; *e,* sensory neuropile; *f, g, h, i,* ventral fiber tracts of connectives; *j, k,* motor neurocytes; *l, m, n, o, p, q, r,* neurocytes of association neurones; *s, t, u,* sensory fibers; *v, w, x, y, z,* fibers entering ganglion from connectives.

The association neurones of the ventral nerve cord include local neurones of each ganglion and neurones whose axons form the principal fibers of the interganglionic connectives. The cell bodies of these neurones are situated in the lateral parts of the ganglion (Fig. 260, *l, m, n, o, p, q*). The local, or intraganglionic, association neurones are of two types. In one type (*m*) the nerve process is T-shaped, and the two branches lie in the same side of the ganglion as the cell body, one branch going dorsally, the other ventrally, to intermediate between the dorsal motor neuropile and the ventral sensory neuropile. In the other type (*l*) the neurone connects the two halves of the ganglion, a collateral being given off in one side, while the axon crosses to the other side, where it ends in terminal arborizations.

The fibers of the interganglionic connectives originate from cells lying laterad of the intraganglionic neurones. The axons give off collaterals in the ganglion of their origin, some of which branch in the motor neuropile (Fig. 260, *n, o, p*), others in the median or sensory neuropile (*q, r*), but the main neurites proceed either anteriorly or posteriorly through the connective tracts to other ganglia of the ventral nerve cord. Zawarzin describes three types of connective fibers in an abdominal ganglion of the dragonfly larva: *tautomere* fibers (*n, r*), which leave the ganglion through the connective on the side of their origin after giving off a collateral in this side; *heteromere* fibers (*o, q*), which give off one collateral and then cross the ganglion to enter the connective of the opposite side; and *hekateromere* fibers (*p*) which cross the ganglion but give off a collateral in each side. Some of the connective fibers unite successive ganglia, others go long distances through the ventral nerve cord. The connective tracts pass superficially through the dorsal and ventral parts of the ganglia. In the dragonfly larva Zawarzin distinguishes in each dorsal tract a median division (*a*), which contains fibers that go long distances through the nerve chain, and a lateral division (*b*) containing shorter fibers; and in each ventral tract he finds an external median group (*f*) of long fibers, an internal median group (*g*) of short fibers, and a lateral group (*h*) of short fibers. Besides these tracts of association connective fibers, there are two internal ventral tracts on each side (*i*) which contain the sensory fibers that traverse the connectives.

The motor and sensory roots of the median nerves lie in the posterior parts of the ventral ganglia, but they will be described under a separate heading treating of the median nerves.

The structure of a thoracic ganglion in the dragonfly larva is essentially the same as that of an abdominal ganglion, except that it is more complicated in all its details, owing to the presence of appendages on the thorax. Since no exact study has been made on the histology of the thoracic ganglia of an adult winged insect, it is not known to what extent the nervous equipment is increased in the imago to serve the mechanism of flight.

The distribution of the motor and sensory fibers from the lateral nerves in an abdominal segment of the larva of *Aeschna* is described by Rogosina (1928). The majority of the motor fibers in any one segment are derived from cells lying within the ganglion of that segment, but some of them come from the ganglion of the preceding segment, the muscles of each segment thus having a plurisegmental innervation. In the second thoracic segment of the dragonfly larva, Zawarzin says, there are only six pairs of motor nerve cells that supply fibers to the muscles of this segment. Since the number of muscles in the segment and its appendages greatly exceeds the number of motor cells innervating them, a single fiber must branch to several muscles. It is interesting to observe that Rogosina finds in an abdominal segment of the same insect a corresponding number of peripheral sensory nerve cells of Type II innervating the muscles, the connective tissue, and the epidermis.

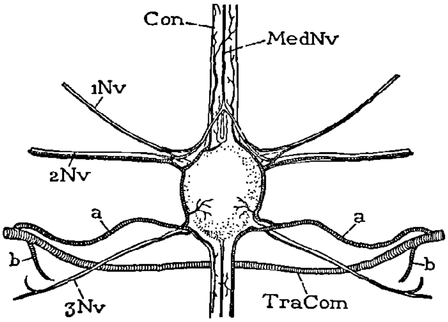

FIG. 261.—Tracheation of an abdominal ganglion of a noctuid caterpillar, dorsal view.

The ganglia and nerves of the ventral nerve cord are abundantly supplied with trachea. In a caterpillar each ganglion (Fig. 261) receives a trachea on each side (*a, a*) from the ventral tracheal commissure of its segment (*TraCom*). Each ganglionic trachea divides at the root of the posterior nerve into anterior and posterior branches distributed to the ganglion, the lateral nerves, and the connectives.

The Median Nerves.—The ventral nerve cord of some insects, as we have seen, includes a longitudinal *median nerve* lying between each pair of interganglionic connectives. The median nerve takes its origin from the posterior part of the ganglion lying before it and gives off a pair of lateral branches that extend outward to the neighborhood of the spiracles. In some cases the median nerve terminates at the bifurcation into the lateral branches; in others it continues beyond the branches to the ganglion following. The occurrence of median nerves in different groups of insects has not been well studied, but the nerves are commonly present in larval forms, and it is probable that where they are not present as independent trunks their fibers are buried in the interganglionic connectives and issue from the following ganglia in the anterior nerve trunks of the latter.

The typical arrangement and distribution of the median nerves are well shown in a caterpillar (Fig. 262), in which there is a median nerve for each of the 11 ganglia of the ventral nerve cord posterior to the head (Fig. 246). In the thorax each median nerve appears to end at its bifurcation into the lateral branches (Fig. 262, $MedNv_2$), which are given off from a small triangular swelling; but in the abdomen a slender median filament continues to the next ganglion. The exact terminations of the fibers of the median nerves have not been determined, though the endings of the lateral nerves are usually found to be distributed to the tracheae and the spiracles. In the caterpillar each lateral branch (*l*) goes outward over the inner face of the ventral muscles in the anterior end of the segment *behind* the one containing the ganglion in which the main trunk of the median nerve takes its origin. Along its course the lateral nerve gives off small branches and breaks up finally into terminal fibers distributed to the tracheal trunks in the neighborhood of the spiracle, one of which innervates the occlusor muscle of the spiracle. The nerve center of each segmental pair of spiracles is thus located in the ganglion of the preceding segment. The branches from the median nerve of the prothoracic ganglion go to the first pair of spiracles, which are primarily mesothoracic; those from the mesothoracic nerve go to the neighborhood of the rudimentary metathoracic spiracles; the metathoracic nerves go to the first abdominal spiracles, and so on. If the last two ganglia of the ventral nerve cord are united, as in *Malacosoma americana* (Fig. 246), the branches of the seventh median nerve, which go to the eighth spiracles, issue from the dorsal surface of the eighth ganglion. In *Malacosoma* the median nerves of the abdomen branch close to the succeeding ganglion. In some caterpillars the median nerve trunk continues to the following ganglion, and its lateral branches are given off through the first pair of lateral nerve trunks of this ganglion (Fig. 261, 1*Nv*).

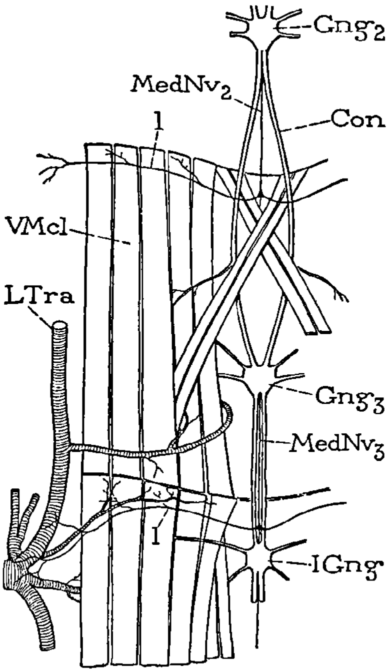

FIG. 262.—Mesothoracic, metathoracic, and first abdominal ganglion of a caterpillar, *Malacosoma americana*, showing median nerves (*MedNv*).

In the larva of *Aeschna,* it has been shown by Zawarzin (1924), each median nerve contains two motor fibers (Fig. 263 A, *MF*) and two sensory fibers (*SF*). The motor axons (*Axn*) originate from a pair of large unipolar cells (*MCl*) lying in the posterior part of the ganglion from which the nerve proceeds. In the thorax each motor axon (A, *Axn*), after giving off numerous branching collaterals within the ganglion, turns posteriorly to enter the median nerve trunk (*MedNv*) and, at the bifurcation of the latter, divides into right and left branches, which go outward in the lateral nerves. The sensory fibers (*SF*), which are very slender and varicose, enter through the lateral branches, and those from opposite sides unite in the median nerve to form two fibers that run forward into the ganglion, where they end in fine branching terminals.

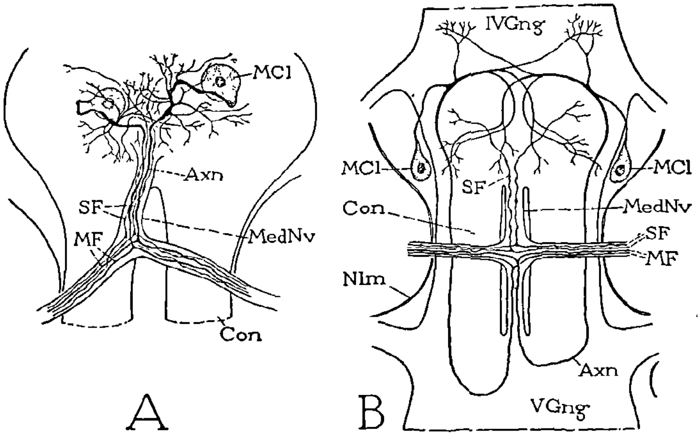

FIG. 263.—Histology of the median nerve roots of an *Aeschna* larva. (*From Zawarzin, 1924.*) A, a thoracic ganglion. B, an abdominal ganglion.

In the abdomen (Fig. 263 B) the course of the motor fibers of the median nerve is quite different from that in the thorax. The two motor neurocytes (*MCl*) are located superficially beneath the neurilemma (*Nlm*), and their axons (*Axn*) proceed posteriorly through the interganglionic connectives into the anterior part of the following ganglion. Here they turn mesally and forward into the posterior end of the median nerve, which connects the successive ganglia, and finally branch in the usual manner where the lateral nerves are given off from the median trunk. The sensory fibers (*SF*), on the other hand, take the same course as in the thorax, entering the preceding ganglion through the part of the median nerve trunk lying anterior to the lateral nerves. Whether this difference in the disposition of the motor fibers of the median nerve between the thorax and the abdomen is general in insects or applies only to the dragonfly larva has not been determined.

In its origin the median nerve appears to be derived from the median strand of nerve tissue formed in the embryo from the row of neuroblasts at the top of the ventral groove between the neural ridges (Fig. 17 B, *MC*). According to Escherich (1902), the median nerve system in the embryo of the blow fly *Lucilia* consists at first of ganglionic cell masses located over the intersegmental lines of the body, and of intraganglionic strands traversing the segmental areas. From the posterior end of each median ganglion there is given off a pair of lateral nerves, presumably associated with the tracheal invaginations. It would thus appear that the definitive ventral nervous system of insects is derived from two distinct sources, the primarily lateral nerve strands and a primitive median nerve strand. The embryonic ganglia of the median nerve described by Escherich must eventually be included in the posterior parts of the definitive composite segmental ganglia, and in many insects the median strand is either obliterated or entirely united with the lateral strands.

3. THE STOMODAEAL NERVOUS SYSTEM

The stomodaeal nervous system consists of sensory and motor neurones having their centers in small ganglia developed from the dorsal, or dorsal and lateral, walls of the stomodaeum. The nerve fibers are distributed to all the stomodaeal parts of the alimentary canal, and in certain insects they are continued over the entire length of the mesenteron. The labral muscles also, in some cases, appear to receive at least a part of their innervation from stomodaeal nerves, as do likewise the salivary ducts, the aorta, the corpora allata, and some of the mandibular muscles. This system centering in the stomodaeal ganglia is commonly called the "stomatogastric" or anterior "sympathetic" nervous system; but inasmuch as its ganglionic centers are derived from the stomodaeum, the term *stomodaeal nervous system* seems more fitting.

Since the stomodaeal nervous system has not been fully studied from a comparative standpoint, it is impossible to give a general description applicable to all its numerous variations in different insects. The one constant feature of the system is the presence of a median precerebral ganglion situated anteriorly on the dorsal wall of the pharynx. This is the *frontal ganglion* (Figs. 248, 249, 250 A, *FrGng*). The frontal ganglion is connected with the tritocerebral lobes of the brain by the *frontal ganglion connectives* (*FrCon*), and from it there is given off a median *recurrent nerve* (*RNv*), which goes posteriorly on the dorsal wall of the pharynx beneath the brain and the anterior end of the aorta (Fig. 249). Sometimes one or two nerves proceed forward from the frontal ganglion to the region of the clypeus.

In the back of the head there is usually a second nerve center of the stomodaeal system, which consists typically of a pair of ganglia lying just behind the brain (Fig. 250 B, *OcGng*). These ganglia may be termed the *occipital ganglia,* though they are variously called also "pharyngeal," "oesophageal," or "hypocerebral" ganglia. Each occipital ganglion is connected with the back of the brain by a short *occipital ganglion nerve* (*d*) and communicates with the frontal ganglion by a branch (*h*) from the recurrent nerve (*RNv*). In some insects the paired occipital ganglia are united in a single median occipital ganglion (Fig. 249, *OcGng*) situated beneath the aorta (*Ao*). In such cases the recurrent nerve ends in this ganglion, and the latter has two connectives (*d*) with the back of the brain. Several nerves are given off from the occipital ganglia, or ganglion, but the pattern of the postcerebral stomodaeal innervation varies much in different insects.

In a caterpillar, in which the occipital ganglia are widely separated (Fig. 250 B), the large recurrent nerve (*RNv*) proceeds posteriorly on the dorsal wall of the stomodaeum to the end of the crop, giving off along its course numerous lateral branches to the stomodaeal muscles. Each occipital ganglion (*OcGng*) has a connective (*d*) with the back of the brain, and another (*h*) with the recurrent nerve. From the second the aorta (*Ao*) is innervated. Laterally the ganglion gives off a short nerve (*e*) to the mandibular muscles, and a nerve (*c*) that goes forward and unites with the lateral nerve of the brain (*a*, *b*). From its posterior part a small nerve (*f*) goes to the duct of the silk gland (*SlD*), and a larger nerve (*g*) to the lateral wall of the crop.

A more simple pattern of innervation in the postcerebral region is shown in the acridid *Dissosteira* (Fig. 249), in which there is a single median occipital ganglion (*OcGng*) closely associated with the open, troughlike anterior end of the aorta, the latter being embraced by the short connectives (*d*) between the occipital ganglion and the brain. Three principal nerves are given off from each side of the ganglion. One (*i*) goes laterally to the corpus allatum (*CA*); the second (*j*) breaks up into branches distributed on the anterior part of the crop; the third and largest (*k*) goes posteriorly on the lateral wall of the crop, giving off branches along its course, and ends in a lateral *ingluvial ganglion* ("gastric" ganglion) on the rear third of the crop, from which the posterior parts of the stomodaeum are innervated.

According to the studies of Orlov (1924*a*) on the histology of the stomodaeal ganglia of the larva of *Oryctes nasicornis,* the frontal ganglion and the occipital ganglion contain sensory, motor, and association nerve cells. The distal processes of the sensory cells extend to the muscles and connective tissue of the stomodaeum. The frontal ganglion alone, however, contains associations between the motor and sensory fibers. The sensory neurones of the second ganglion have no collaterals in this ganglion, but their axons extend forward through the recurrent nerve into the frontal ganglion, where they form associations with the motor neurones. The frontal ganglion not only contains the sensory-motor associations of the stomodaeal system but has connections with the brain and the ventral nerve centers by way of the frontal connectives from the tritocerebrum. It is said to be the center of the peristaltic movements of the oesophagus.

4. THE PERIPHERAL NERVOUS SYSTEM

The peripheral nervous system includes the nerve trunks radiating from the ganglia, and the distal branches and terminal organs of the motor and sensory fibers contained in the nerve trunks. A full description of the peripheral nervous system, therefore, should contain an account of the distribution of all the nerves in the body; but since a subject of such magnitude could not be treated in a general text, we shall consider here only the terminals of the motor nerves and the distal endings of the sensory nerves.

The Sensory Neurones.—When the sensory fibers of a nerve trunk are traced outward from the central ganglia, they are found to end in cells lying either within the epidermis of the body wall, or immediately beneath it, or on the somatic muscles or the wall of the alimentary canal. These cells appear to be the true neurocytes of the sensory neurones, for in insects there are no other nerve cells in the course of the sensory fibers, such as those of the spinal ganglia of vertebrates.

The peripheral cells of the sensory nerves are either bipolar or multipolar. The distal processes of most of them go direct to specific ectodermal sense organs. Cells of this kind, which are always bipolar, are those designated *sensory cells of Type I* (Fig. 242 B). The others, which may be either bipolar or multipolar, but which are typically multipolar, are provided with one or more distal processes that branch elaborately and end with fine varicose fibrils, which terminate on the inner surface of the body wall, on the somatic muscles and connective tissue, and on the muscles and wall of the alimentary canal. Cells of this kind are those distinguished as *sensory cells of Type II* (Fig. 242 C). According to the nature of their neurocytes, therefore, the sensory neurones themselves may be classed as of Type I or Type II. The two groups of sensory neurones appear to be morphologically distinct. Those of the second type are undoubtedly the older, since they form the principal sensory innervation in the annelid worms, which consists of a diffuse branching of the terminal processes of the neurocytes on the inner surface of the epidermis. Sensory neurones of Type I are most numerous in arthropods having sclerotic plates in the body wall and are evidently developed as a means of circumventing the loss of sensitivity to external conditions, which would otherwise result from the hardening of the cuticula.

Sensory Neurones of Type I.—The neurocytes of the first type of sensory neurones are the so-called sense cells of the specific ectodermal sense organs (Fig. 267, *SCl*). They are always bipolar, and their distal processes (*d*) are immediately connected with the cuticular parts of the receptors. The proximal processes are the centripetal axons which end in terminal arborizations within the central ganglia. In most cases the sense cell (or cells) of a sense organ lies within the epidermis in close association with the constructive cells of the receptor (A); but in various larvae the sense cells of the tactile setae distributed over the body lie beneath the epidermis (B), and their long distal processes penetrate the basement membrane to enter the receptor.

The developmental history of the intraepidermal sense cells has been carefully studied, and all investigators agree that these sense cells take their origin from undifferentiated ectodermal cells. It seems certain, also, that the sense cells must in all cases be the neurocytes of the sensory nerves proceeding from them, and yet the growth of centripetal axons from the epidermal sense cells has not been demonstrated, and some investigators claim that the connection between the sense cells and the sensory nerves is established secondarily, which would imply, therefore, that the sense cells of insects are *secondary sense cells*, as are most of the sensory cells in the epidermis of vertebrates. The subject is fully discussed by Hanström (1928), who concludes that the arthropod sense cells are *primary sense cells*, but the exact origin of the nerves of the ectodermal sense organs of the Arthropoda appears yet to need further elucidation from the standpoint of development. Furthermore, the relation between the intraepidermal and subepidermal sense cells of Type I has not been determined.

Sensory Neurones of Type II.—Sensory neurones of this type are particularly abundant in the Annelida and in soft-skinned arthropods, such as the larvae of holometabolous insects, but they occur also in arthropods, including crustacea and insects, that have a sclerotized integument. Neurones of Type II are never connected with specific sense organs. Their neurocytes lie on the inner face of the body wall, on the muscles, or on the wall of the alimentary canal, and their finely branching distal processes end in free terminals which innervate the epidermis, the somatic muscles, connective tissue, and the muscles and epithelium of the alimentary canal. The centripetal axons go to the ganglia of the central nervous system. The ontogenetic origin of these neurones from the ectoderm has not been determined.

The integumentary innervation of the crayfish is well known. That of *Astacus fluviatilis* has recently been studied in detail by Tonner (1933), who finds that practically the entire inner surface of the body wall is covered by a network of branching and uniting fibers from numerous multipolar nerve cells lying in the connective tissue beneath the epidermis. In addition to this multipolar cell net, however, Tonner finds in *Astacus* also an inner integumental plexus of fibers branching from nerves given off from the ganglia of the ventral nerve cord. The two systems, moreover, are united by connecting fibers and together constitute an elaborate *integumentary nervous system.*

Among insects, sensory cells of Type II are particularly abundant in soft-skinned holometabolous larvae, where, in some forms, they give rise to an elaborate subepidermal nerve net. In the larva of *Aeschna,* Rogosina (1928) finds in each abdominal segment just 12 cells of this type, there being on each side of each segment one cell located on the sternal region, three on the lateral region, and two on the tergal region. The axons of these cells enter the ventral ganglion of the segment through the first and second lateral nerve trunks. The subepidermal innervation of the larva of *Melolontha vulgaris* is minutely described by Zawarzin (1912*a*). It consists of a network of large and small nerve branches distributed over the entire inner surface of the body wall (Fig. 264 B), including the appendages, but is particularly developed on the middle of

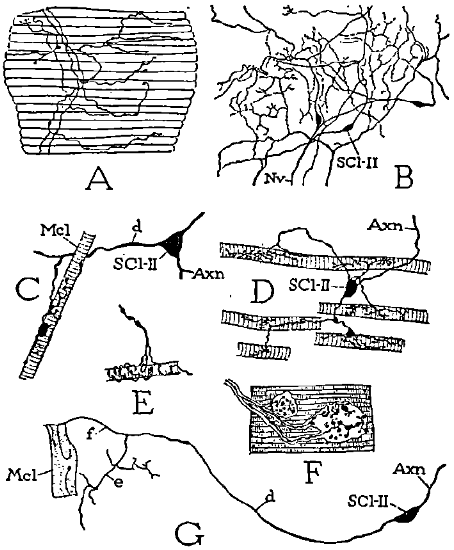

FIG. 264.—Examples of terminals of motor and sensory nerve fibers. A, motor innervation of diffuse type in ventral somatic muscle of *Aeschna* larva. B, sensory innervation of epidermis of *Melolontha* larva. C, D, sensory innervation of oesophageal muscles of *Oryctes* larva. E, sensory innervation of ventricular muscle of *Melolontha* larva. F, motor innervation of concentrated type in muscle fiber of rectum of *Oryctes* larva. G, sensory innervation of epidermis (*e*) and of a somatic muscle (*f*) of *Aeschna* larva. (A, G *from Rogosina,* 1928; B *from Zawarzin,* 1912*a;* C, D, E, F *from Orlov,* 1924.)

the back. The principal nerves of the net are the distal processes of irregular bipolar and multipolar sensory cells of Type II. The processes branch dichotomously into the fibers of the larger meshes, and these ramify to form the threads of the finer meshes. The fibers of the larger meshes in *Melolontha* are relatively smooth, but the finer branches are characteristically varicose, presenting numerous small swellings along their courses, a feature noted by most writers who have studied the subepidermal innervation of other insects. The actual endings of the fibrils have perhaps not been observed, but the terminal branches appear to end free on the inner surface of the basement membrane.

Little is known concerning the sensory innervations of the muscles of the body wall and appendages of insects. Orlov (1924) suggested that the skeletal muscles may be innervated from the subepidermal nerves, and Rogosina (1928) has found in the lateral region of the abdomen of an *Aeschna* larva the distal process from a sensory cell of Type II branching both to the epidermis and to a muscle fiber (Fig. 264 G). The terminals of the sensory muscle nerves (*f*) within the muscle fiber differ by their tufted structure both from the sensory terminals of the epidermis (*e*) and from the motor nerve endings in the somatic and visceral muscles (A). In addition to the muscle innervation, Rogosina describes also an innervation of connective tissue in the *Aeschna* larva proceeding from the two sensory cells of Type II found in the tergal region of each abdominal segment.

A sensory innervation of the alimentary canal has been described by Zawarzin (1916) in *Periplaneta americana* and by Orlov (1924) in larvae of scarabaeid beetles. Rogosina (1928) says there are no sensory nerves on the alimentary tract in the larva of *Aeschna*. Zawarzin finds numerous sensory cells of Type II, mostly multipolar, distributed over the walls of the crop of the cockroach. The distal processes break up into fine varicose fibers that innervate the epithelial cells of the crop and the neurilemma of the stomodaeal nerves and ganglia. The axons of these cells go to ganglia of the stomodaeal nervous system, where they terminate in neuropile arborizations. The alimentary canal of scarabaeid beetle larvae, as described by Orlov, is innervated both from the stomodaeal system and from the abdominal ganglia of the ventral nerve cord, there being in each group of nerves both motor and sensory fibers. The sensory neurocytes of the stomodaeal system are multipolar cells, the distal processes of which branch into varicose fibrils forming a network on the stomodaeum and ventriculus (Fig. 264, C, D, E), innervating the muscles and connective tissue. The sensory nerves of the proctodaeum, which have their roots in the abdominal ganglia, are distributed principally to the connective tissue of the anterior intestine and the posterior narrow part of the rectum.

The Motor Nerve Endings.—From the few studies that have been made on the terminations of the motor nerves in insects, it appears that there are two types of motor innervation of the somatic muscles. In one type, probably characteristic of the more generalized insects, the ends of the nerve fibers branch diffusely and the branches run lengthwise upon the muscle fibers or wind around them (Fig. 264 A). In the cockroach, according to Marcu (1929), the nerves do not enter the muscle fibers, the terminal branches ending free between them; but in a dragonfly larva, Rogosina (1928) says, the nerve terminals, as shown in cross sections, penetrate the sarcolemma and end among the fibrillae in the peripheral part of the muscle fiber.

In the second type of muscle innervation the motor fiber ends against the muscle in a small flattened or conical body (Fig. 264 F), sometimes called the "end plate," or "Doyères cone." These structures, however, as shown by Marcu in the somatic muscles of Coleoptera and Diptera, are merely the places on the muscle where the nerve suddenly breaks up into a brushlike group of fine branches that enter the muscle fiber directly and penetrate between the myofibrillae. A single nerve fiber in this type of muscle innervation goes to but one muscle fiber; in the simpler type a nerve fiber may branch to several neighboring muscle fibers. The motor nerve endings on the muscles of the alimentary canal appear to be the same as those on the body muscles. Thus, in the larva of *Aeschna*, according to Rogosina (1928), the nerves branch diffusely on the muscles of the alimentary canal, as they do on the somatic muscles. In the larvae of scarabaeid Coleoptera, on the other hand, the motor nerves of the alimentary canal, as described by Orlov (1924), end in swellings within which each breaks up into a group of small varicose fibrils (Fig. 264 F).

GLOSSARY OF TERMS APPLIED TO THE NERVOUS SYSTEM

Afferent Nerve.—A nerve that conducts from the periphery toward a nerve center; the axon of a sensory neurone.

Arborizations.—The fine branching terminal fibers of axons or collaterals.

Archicerebrum (*Arc*).—The ganglionic nerve mass of the prostomium in Annelida. (*Archencephalon.*)

Association, or Internuncial, Neurone.—A neurone lying within the central system that intermediates between sensory and motor neurones, or between other association neurones.

Axon, or Neurite (*Axn*).—The principal process, or nerve fiber, of a neurone.

Brain (*Br*).—The cephalic nerve mass situated above the stomodaeum, including the primitively postoral second antennal ganglia in insects.

Central Nervous System.—The part of the nervous system containing the motor neurocytes and the synaptic junctions between communicating neurones.

Chiasma (*Ch*).—The crossing of nerve tracts within a nerve center.

Circumoesophageal Connectives (*CoeCon*).—The connectives between the brain and the ventral nerve cord embracing the stomodaeum. Primitively the connectives from the archicerebrum to the first ventral ganglia; in insects the connectives between the tritocerebral ganglia and the mandibular ganglia.

Collateral (*Col*).—A lateral branch of an axon.

Commissure (*Com*).—A transverse tract of nerve fibers connecting the two ganglia of a segment or the lateral centers within a median ganglion.

Conductivity.—The property of nervous or other protoplasmic tissue by which changes in metabolic activity are propagated through it.

Connective (*Con*).—A longitudinal cord of nerve fibers connecting successive ganglia.

Cyton.—See *neurocyte.*

Dendrons, or Dendrites.—Finely ramifying branches given off from a nerve cell.

Deutocerebrum (*2Br*).—The part of the arthropod brain containing the first antennal nerve centers.

Distal Process.—The peripheral branch or one of several distal branches of a sensory nerve cell.

Effector.—One of the organs of the body activated by nerve stimuli, principally a muscle or a gland.

Efferent Nerve.—A nerve that conducts from a nerve center toward the periphery; the axon of a motor neurone.

Frontal Ganglion (*FrGng*).—The median precerebral ganglion of the stomodaeal system.

Frontal Ganglion Connectives (*FrCon*).—The connectives between the tritocerebral ganglia and the frontal ganglion.

Ganglion (*Gng*).—A central nerve mass; the term applied to a single primitive ganglion, or to a body formed of two or more united primitive ganglia.

Glia Tissue.—The cellular supporting tissue of the nervous system.

Globuli Cells.—Specialized association cells of the brain, usually distinguished by their small size, poverty of cytoplasm, and richly chromatic nuclei.

Glomerulus.—A small compact mass of intermingled terminal arborizations of nerve fibers within a nerve center.

Ingluvial Ganglion.—A paired ganglion of the stomodaeal nervous system in some insects, situated on the side of the crop. (*Gastric ganglion.*)

Median Nerves (*MedNv*).—Unpaired nerves arising from the ganglia of the ventral nerve cord between the roots of the connectives.

Medullary Substance.—The dense fibrous mass of nerve terminals forming the interior of a ganglion. (*Neuropile, punctate substance, Marksubstanz.*)

Motor Neurone.—A neurone of which the axon terminates in an effector.

Nerve (*Nv*).—Any one of the fibrous tracts of the peripheral nervous system, whether a single fiber or a group of fibers; a nerve trunk.

Nerve Fiber.—The axon or other branches of a neurocyte.

Nerve Tract.—A strand of nerve fibers; usually applied to tracts within a nerve center.

Nerve Trunk.—A bundle of nerve fibers in the peripheral system; the usual nerves.

Neurilemma (*Nlm*).—The nucleated sheath of nerve tissue, covering the ganglia, nerve trunks, and terminal branches.

Neurite.—See *axon.*

Neurocyte, or Cyton (*NCl*).—The cell body of a neurone, usually called the "nerve cell."

Neurone.—An entire nerve cell, including the neurocyte and axon and all their branches.

Neuropile.—The medullary substance, or mass of fibrous tissue within a ganglion.

Occipital Ganglion (*OcGng*).—A single or paired postcerebral ganglion of the stomodaeal nervous system. (*Pharyngeal, oesophageal,* or *hypocerebral, ganglion.*)

Peripheral Nervous System.—The outlying parts of the nervous system in distinction to the central ganglia and connectives, including the sensory neurocytes and their axons, and the axons of the motor neurones.

Protocerebrum (*1Br*).—The first part of the arthropod brain, containing the ocular and other association centers lying anterior or dorsal to the antennal (deutocerebral) centers.

Receptor (*SO*).—A so-called sense organ, or specialized structure of the integument responsive to external stimuli.

Recurrent Nerve (*RNv*).—The median stomodaeal nerve extending posteriorly from the frontal ganglion.

Sense Cell (*SCl*).—The neurocyte of a sensory neurone. A sense cell of Type I has an unbranched distal process going to a specific sense organ; a sense cell of Type II has one or more branched processes with a diffuse distribution.

Sense Organ (*SO*).—A receptor.

Sensitivity.—The labile property of protoplasm that makes it responsive to stimuli, highly developed in nerve tissue.

Stimulus.—Any change in the environment or in the internal conditions of the animal that produces activity in labile tissues.

Stomodaeal Nervous System.—The nervous system centering in the ganglia of the stomodaeum. (*Stomatogastric, visceral,* or *sympathetic, nervous system.*)

Suboesophageal Commissure (*ComI*).—The commissure of the tritocerebral ganglia, which goes below the stomodaeum.

Suboesophageal Ganglion (*SoeGng*).—The composite ventral nerve mass of the head in insects, formed of the united primitive ganglia of the gnathal somites.

Synapse.—The central mechanism of intercommunication between terminal fibers of two or more neurones.

Tritocerebrum (*3Br*).—The third part of the insect brain, formed of the ganglia of the postoral second antennal somite.

Ventral Nerve Cord (*VNC*).—The chain of connected ventral ganglia, morphologically beginning with the tritocerebral ganglia of the brain; in entomology the term usually applied to the thoracic and abdominal ganglia only.

CHAPTER XVII

THE SENSE ORGANS

The sense organs are often poetically said to be the "windows of the soul." Unfortunately, however, the simile has little basis in fact, for neither does the "soul" look out of the supposed windows nor does the external environment enter by way of them. Literally, the sense organs are places on the periphery of the animal where forms of energy existing in the environment may activate the form of energy latent in the nerve tissue of the animal. The activity thus aroused in a nerve terminal is propagated centripetally through the nerve to the nerve center. Here, in sentient animals, there may be generated a form of consciousness, which in ourselves we identify with the external energy that originated the impulse sent in over the receiving nerve; but with insects the only evidence we have of "perception" is a motor or glandular reaction of the individual to the external stimulus.

Sense organs are specifically receptive to certain forms of energy because of their physical structure, just as a telephone receiver is specifically receptive of sound vibrations because it is constructed for this purpose only. An organ of vision is stimulated by light waves because it permits the penetration of electromagnetic vibrations of certain lengths and does not respond to other kinds of stimuli, though many of the latter, such as sound vibrations and odor substances, may constantly impinge upon it. The eye membranes of a vertebrate may be irritated by volatile substances, to which the eye itself is impervious; but if these same substances fall upon the organs of smell, they find here a receptive apparatus specially prepared for them. The fact, however, that a volatile irritant may be perceived either as pain or as an odor shows that the effect of a stimulus depends also on the connections of the receptive end of the nerve with the central nervous system and not entirely on the nature of the stimulus.

Where there is no known conscious equivalent of a stimulus, it is perhaps inconsistent to speak of the receptor as a "sense organ" or to say that the animal has a "sense" of smell, sight, etc., but these terms are too conveniently useful to be thrown out on a technicality. Since insects give definite, visible muscular or glandular responses to most of the forms of energy in nature that produce sensory impressions in ourselves, and to some to which we are unconscious, insects possess at least corresponding mechanisms of reaction, and hence in entomology we use the terms "sense" and "sense organs" with the understanding that they are not literally significant.

The different manifestations of nature to which animals respond through sense organs include

1. The energy of moving masses or molecules of matter, and the energy of contact with stationary matter, giving us the sensation of touch (*tactile sense*).
2. Vibrations of matter that give us the sensation of sound (*auditory sense*).
3. Vibrations that give us the sensation of heat or of changes in temperature (*thermal sense*).
4. Substances in a chemically active state (ionization) that give us the sensation of taste (*gustatory sense*).
5. The impalpable state of matter that gives us the sensation of smell (*olfactory sense*).
6. Electromagnetic vibrations of certain magnitudes giving us the sensation of light (*visual sense*).
7. Gravity, for which there is no equivalent in consciousness, (*static*, or *geotropic*, *sense*).

To summarize more generally, we may say that animals are responsive to (1) *matter in most of its forms of activity*, (2) *electromagnetic energy*, and (3) *gravity*. The sense organs, however, are not attuned in all cases to the direct reception of the primary stimuli to which the animal reacts through them. The reaction to gravity, for example, is not by means of receptors stimulated directly by gravity; the known sense organs by which the animal orients itself in relation to gravity, or maintains itself in gravitational balance are functionally tactile organs, since the direct stimulus is the movement of a liquid or of solid bodies produced by gravity. The perception of sound might be said likewise to be a very delicate sense of touch, in which the stimulus is the alternating pressure of the sound waves.

The sense of taste and the sense of smell are often classed together as *chemical senses*, but they are not identical. Taste is produced by substances in solution, partly in a state of ionization; smell is a perception of emanations from odorous substances, often traveling long distances, the nature of which is but little understood. The quality of taste is not determined by chemical composition. The four taste varieties, sweet, sour, salty, and bitter, are distinguished by insects as by man, and insects are highly sensitive to many odors in a degree quite incomprehensible to us.

The eyes, being light-receptive organs, serve also as instruments for estimating form and for measuring distance; but all visual impressions are based on a perception of color and different degrees of color intensity. Much experimental proof has shown that insects, in their reactions, distinguish many of the colors that we see, and that they perceive as color some of the ultraviolet rays to which we are blind. However, since black is absence of light, and pure white does not occur in nature, all light perception is color perception in the physical sense.

In addition to the sense organs that respond specifically to the stimulus of environmental forces, there are also organs that are stimulated by changes in the tissues of the animal itself, such as pain receptors, and in general the proprioceptors that register the internal physiological conditions of the organism. Then there are also indefinite senses, such as that of muscle tension. Insects are not known to have any specific organs for the perception of temperature, though they are highly responsive to temperature changes, nor are they known to have pain receptors or proprioceptors other than the terminal endings of sensory nerve fibers on the skin, muscles, and other tissues.

1. GENERAL STRUCTURE AND CLASSIFICATION OF INSECT SENSE ORGANS

The anatomical elements of the sense organs of insects are derived from the cellular and cuticular parts of the integument, and all the numerous forms that the organs assume are produced by modifications and specializations of these primary elements. The known sense organs are located in the body wall or in the ectodermal parts of the alimentary canal.

The Structural Elements of a Sense Organ.—In its simplest form a sense organ consists of a *sense cell* connected with the distal end of a sensory nerve, and so situated as to be exposed to stimuli or to the secondary effects of primary stimuli. There are two known kinds of sense cells. Those of one kind are the peripherally situated cytons of sensory neurones, which receive the stimuli either directly (Fig. 265 A, 1*SCl*) or through a distal process (B, *d*). Those of the other kind are ectodermal cells secondarily innervated by distal branches of a sensory neurone (D, 2*SCl*). Sense cells of the first kind are sensory nerve cells and are termed *primary sense cells;* those of the second variety are sensory ectoderm cells and are distinguished as *secondary sense cells.* As shown in the preceding chapter, all sensory cells of insects, so far as known, appear to be primary sense cells, but they are divisible into two groups according to whether the distal processes go to a specific sense organ (Fig. 242 B) or are distributed in fine branches on an innervated surface (C). Those of the first group are primary sense cells of Type I, those of the second group are primary sense cells of Type II.

The sensory innervation of the epidermis in insects proceeds from primary sense cells of Type II. These cells have sometimes one, but generally several, branched terminal processes that end in fine fibrils on the inner surface of the body wall or between the epidermal cells (Fig. 265 C). Just how the terminals of these nerves are stimulated is not known; but if the stimuli are transmitted to them from the innervated cells of the epidermis, these cells (2*SCls*) are of the nature of secondary sense cells. Typical secondary sense cells (D, 2*Scl*) are characteristic of vertebrate animals, in which the cytons of the sensory neurones (1*SCl*) are located in the spinal ganglia near the spinal cord. A sensory structure of this kind is not known to occur in insects.

The sense cells of Type I in insects, which are the receptive elements of the specific sense organs, are generally regarded as primary sense cells (Fig. 265 A, B, 1*SCl*) because each is directly continuous with a sensory nerve that goes to a ganglionic center, and no other cell body has been found in the course of the nerve or in any way connected with it. Several writers, however, studying the development of insect sense organs, assert that the sense cells are specialized epidermal cells that make a secondary connection with the nerve by a centripetal process. Schön (1911) describes the outward growth of a sensory nerve through the leg of the honey bee, and its final connection with the tibial chordotonal organ, the latter being developed from the epidermis of the leg wall. Vogel (1923) reports that the sensory antennal nerve in Hymenoptera likewise penetrates distally through the entire length of the antenna before there is established any connection with the sense cells of the antennal sense organs. From such observations it would appear, as claimed by Berlese (1909), that the receptive cells of most insect sense organs are specialized epidermal cells that become sense cells secondarily by union with a sensory nerve. If this is true, the generative cytons of the sensory nerves are yet to be discovered. In the case of the eyes, however, there is no doubt that the retina cells are primary sense cells, since their centripetal processes form synaptic junctions with the terminals of association neurones in the optic lobes.

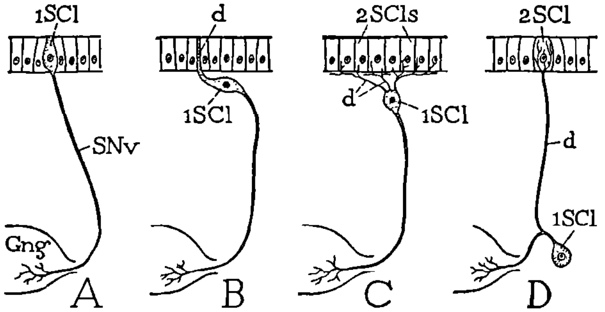

FIG. 265.—Various types of sensory innervation of the epidermis, diagrammatic. A, a primary sense cell (*1SCl*) located in the epidermis, connected with a nerve center (*Gng*) by a proximal nerve process (*SNv*). B, a subepidermal primary sense cell connected with the exterior by a single distal process (*d*). C, a subepidermal sense cell with branched distal processes (*d*) innervating epidermal cells, which become secondary sense cells (*2SCls*). D, a secondary sense cell (*2SCl*) innervated by a long distal process (*d*) from a far-distant primary sense cell (*1SCl*), the usual vertebrate type of sensory innervation.

Though the sense cell is the essential part of a sense organ, the sense organs of insects generally include associated structures formed of the cuticula and the epidermis. The cuticular part takes on various forms and appears to be largely responsible for specificity in the receptive quality of the sense organ, since the structure of the cuticular element determines the admission of the effective stimulus. The epidermal elements of a sense organ consist of one or more cells usually associated with the sense cell and are probably the chitinogenous matrix cells of the cuticular parts of the organ.

Classification of Insect Sense Organs.—Insects are provided with a great variety of external sense organs having characteristic structural differences in both the cuticular and the cellular parts. It is very difficult, however, to isolate the various types of organs for experimental purposes, and for this reason we can, in most cases, only form an opinion as to their probable function based on a study of their structure; and the structure is often so widely different from that of any organ of known function in other animals that many insect sense organs cannot yet be satisfactorily identified as receptors for any particular group of stimuli. The sense organs of insects, therefore, are generally classified on a purely anatomical basis. The receptor complex formed of the cuticula, the sense cell or group of sense cells, and the associated chitinogenous cells is called a *sensillum.*

The simplest type of insect sensillum is an innervated hair; that is, it is a seta having a direct connection with the distal process of a sensory cell. The external cuticular part, however, may take the form of a spine, a scale, or a minute peg, and it may be sunken into a pit or deep cavity of the integument. Organs bearing typical setae are termed *sensilla trichodea;* but if the external process is spine-like, they are distinguished as *senilla chaetica,* and when scale-like as *sensilla squamiformia.* If the external process is reduced to a small peg or cone, the organs are called *sensilla basiconica* when the process is freely exposed; but if the latter is sunken in a pit the organs become *sensilla coeloconica,* and if the cavity is a deep pouch they are *sensilla ampullacea.*

Two other groups of sense organs include sensilla which have no external processes corresponding to a seta, though possibly such organs have been derived from hair organs by the complete loss of the seta. Some of the organs here included are marked externally each by a minute pit in the cuticula and are hence often called *sense pores;* but, since most of them in section show a dome-like or bell-shaped thickening of the cuticula surrounding the distal process of the sense cell, they are more generally termed *sensilla campaniformia.* Others are covered externally by an oval or elliptical plate surrounded by a narrow ring of membrane, and these organs are distinguished as plate organs, or *sensilla placodea.*

A third group of sense organs also lacks a specific external structure, but each sense cell is associated in a special manner with two other cells, and its distal process ends in a characteristic rodlike structure, the scolops, or scolopale. These rod-bearing sense organs, therefore, are termed *sensilla scolopophora.*

Finally, the eyes, or *sensilla optica,* constitute a very distinct group of receptors having structurally little in common with the other sense organs. The external cuticula forms a transparent area that admits light to the receptive cells. The latter, composing the retina, are specialized ectodermal nerve cells, having centripetal axons that form the fibers of the optic nerve.

2. THE HAIR ORGANS

The sense organs in which the external part has the form of a seta, or is clearly derived from a hairlike process of the cuticula, retain essentially the structure of a seta with its associated cells in the body wall (Fig. 28 E), to which is added a sense cell (Fig. 266, *SCl*) having its distal process (*d*) connected with the base of the seta or extending into the hollow of the latter. The seta or other external process is generally set on a circular membrane, which covers the outer end of a cylindrical cavity of the cuticula, known as the *pore canal,* containing the outer ends of the cellular elements of the sensillum.

The trichogen cell of a hair sensillum is usually large (Fig. 266 A, *Trg*); in the formative stages it extends into the cavity of the external process, but in the mature organ it is generally retracted and more or less vacuolated (*Vac*). The sense cell, in most cases, is associated with the trichogen, and it is possible that it is a daughter cell of the latter, as are said to be the gland cells of certain stinging setae (Fig. 30). In some types of hair sensilla, instead of a single sense cell, there is a group of sense cells (Fig. 269, *SCls*), but these cells are evidently sister cells since they all branch from a common nerve (B), and their distal processes (*d*) unite in a single terminal strand (A, *TS*). The single sense cell in some insects, however, is entirely removed from the sensillum and lies beneath the basement membrane, though it retains its connections with the sense organ by means of its distal process (Fig. 267, B). Thus we must distinguish, among the hair sensilla, sense organs having intraepidermal sense cells, and sense organs having subepidermal sense cells. The sense cell, or group of sense cells, is covered by a nucleated neurilemma continuous with that of the connected nerve (Fig. 266 A, *Nlm*). A third cell (*Tmg*), which appears to be the tormogen, or the generative cell of the setal membrane, is often present as a part of the sensillum. It embraces the distal end of the trichogen. Surrounding the cellular elements of the sensillum are less specialized cells of the epidermis, which gradually merge into the ordinary epithelium of the integument (*Epd*). The basement membrane of the body wall (*BMb*) goes continuously over the inner surface of the sensillum, except where it is penetrated by the nerve (*Nv*).

The cellular elements of the sensillum do not always retain their more primitive relations to one another. Often the sensillum becomes elongate, and its three principal cells take a serial arrangement (Fig. 266 B). The tormogen, being the outermost cell, is then called the *cap cell* (*CpCl*), and the intermediate trichogen cell the *enveloping cell* (*ECl*). The innermost cell is the sense cell (*SCl*).

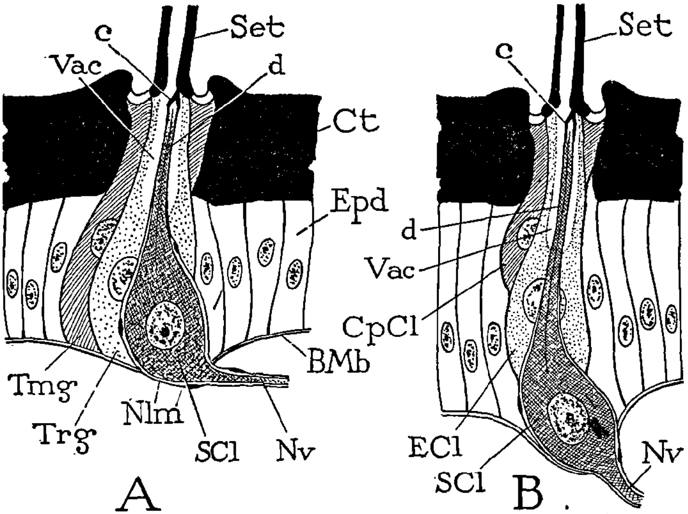

FIG. 266.—Diagrams of the relations of the cellular elements in a simple hair sensillum. A, the more generalized type. B, the cells in axial arrangement. *BMb*, basement membrane; *c*, connection of sense cell with cuticula; *CpCl*, cap cell (tormogen); *Ct*, cuticula; *d*, distal process of sense cell; *ECl*, enveloping cell (trichogen); *Epd*, epidermis; *Nlm*, neurilemma; *Nv*, sensory nerve; *SCl*, sense cell; *Set*, seta; *Tmg*, tormogen; *Trg*, trichogen; *Vac*, vacuole.

Though the various hair sense organs are generally classified anatomically according to the structure of the external process, on a more fundamental, and apparently physiological, basis they may be separated into two groups, according to whether the sensillum contains a single sense cell (Fig. 267) or a group of sense cells (Fig. 269). In organs of the first kind the external cuticular process, whatever its size or form, has thick walls and evidently could have only a mechanical function in stimulating the nerve. With organs of the second group the cuticular part is delicate and is usually very small; its thin, nonsclerotized wall suggests that these organs may be pervious to odor or taste substances. We may, therefore, on a structural basis, divide the setal sense organs into tactile organs, or *tangoreceptors*, having a single sense cell, and *chemoreceptors*, having a group of sense cells.

Sensilla trichodea.—In a sense organ of the typical setiform variety, the hairlike process is generally freely movable on the basal membrane. The hair socket may be flush with the general surface of the cuticula, elevated on a tubercle (Fig. 267 B), or set into an alveolar cavity (A). The sense cell usually has an intraepidermal position in adult insects (A, *SCl*), but in many larval insects (B) it is subepidermal, lying entirely outside the sensillum and connected with the latter by a long distal process (*d*). The innervation of sensory hairs from bipolar subepidermal sense cells has been described in larvae of Odonata, Coleoptera, Lepidoptera, and Diptera by Viallanes (1882), Monti (1893, 1894), N. Holmgren (1896), Hilton (1902), Zawarzin (1912*a*), H. Schneider (1923), and Orlov (1924). Since the origin and nature of the sense cell are not definitely known, the significance of its subepidermal position in larval insects is not understood. According to Bethe (1896), the sensory hairs on the mouth parts of the crayfish are likewise innervated from a subepidermal nerve plexus.

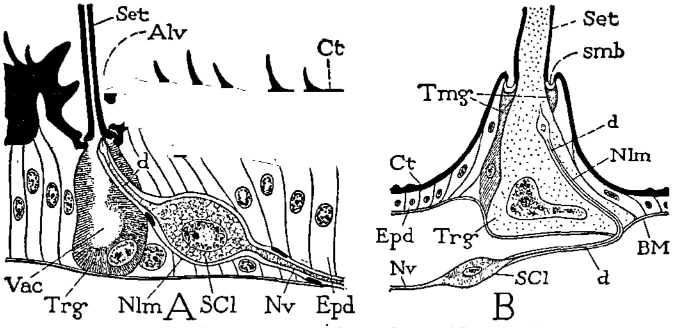

FIG. 267.—Two types of innervation of setal sensilla. A, sensillum with intraepidermal sense cell, organ on cercus of *Gryllus*. (*Adapted from Sihler*, 1924.) B, sensillum with subepidermal sense cell, body hair of cabbage caterpillar. (*Adapted from H. Schneider*, 1923.)

The distal process of the sense cell is usually attached to the base of the seta or to the setal membrane (Fig. 268 A, B, C), but in certain types of organs it extends into the hair (D). At the point of attachment there may be a small internal cuticular structure, and some writers have observed a differentiated body in the distal process.

It seems probable that most setae innervated through a single sense cell are organs of touch, the movement of the hair caused by contact with an object being the origin of the stimulus imparted to the sense cell through the distal process of the latter connected with the seta. Tactile hairs are of common occurrence in the Arthropoda; in insects they are distributed over most parts of the body and the appendages. The provision with innervated movable hairs offsets the loss of surface sensitivity in animals having a sclerotized integument and enables the animal, moreover, to become "aware" of the approach or nearness of an external object before coming into actual bodily contact with it.

Certain small, slender hairs with very delicate walls have been supposed to be receptive to odors and are distinguished as chemoreceptive hairs. Such hairs are said to be innervated each by a group of sense cells, and in this respect they resemble some of the still smaller peglike organs classed as sensilla basiconica (Fig. 269 A).

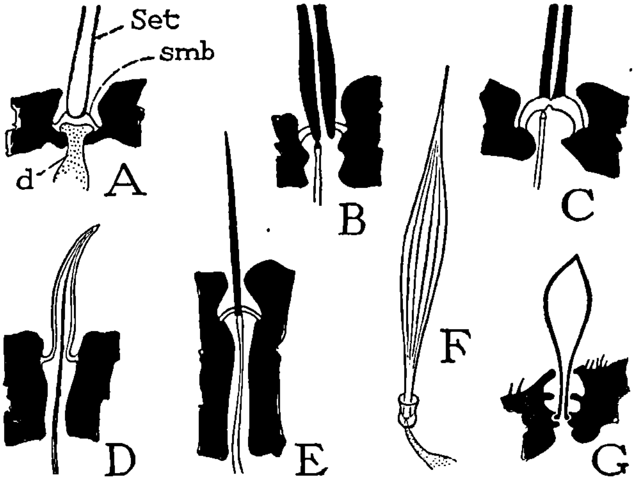

FIG. 268.—Various forms of the cuticular parts of setal sensilla. A–E, sensory hairs of *Dytiscus*. (*From Hochreuther*, 1912.) F, sensory scale on wing of *Notris verbascella*. (*From Freiling*, 1909.) G, club-shaped sensory hair on cercus of *Gryllotalpa*. (*From Sihler*, 1924.)

Sensilla chaetica.—The sense organs included here are merely trichoid sensilla in which the external process is bristle-like or spine-like rather than typically setiform. The thick walls of the process evidently preclude any possibility of penetration by odor or taste substances, and the sensilla chaetica are therefore probably tactile in function. The tactile mechanism, however, as already pointed out, may serve in a capacity that is not functionally one of touch. Static reactions in arthropods, for example, are brought about through organs that are essentially tactile in structure. In insects, static organs are not of general occurrence, but in certain aquatic Hemiptera it appears that special groups of innervated movable hairs serve to regulate the equilibrium of the insect. Organs of this kind have been described by Baunacke (1912) on the abdomen of *Nepa*, and on the antennae of *Notonecta* by Weber (1930, 1933). Organs on the terminal segment of certain mud-inhabiting tipulid larvae, described by Wolff (1922) as organs to enable the insect to orient itself according to the mud content of its medium, consist of pits of the integument containing innervated hairs.

Sensilla squamiformia.—Innervated scales have been described on the wings of Lepidoptera by Günther (1901), Freiling (1909), and Vogel (1911). According to Vogel, sensory scales occur in all groups of Lepidoptera, including *Hepialus*, and are found on both sides of the wings, but especially on the marginal veins, and also on the wing bases. A sensory scale is usually elongate fusiform in shape, with fewer ribs than the other scales, and the distal part is drawn out into a long tapering point (Fig. 268 F). Each scale is innervated by a single large sense cell, the distal process of which, Vogel says, is attached to the base of the scale. The innervated scales with their projecting points would appear to be tactile in function.

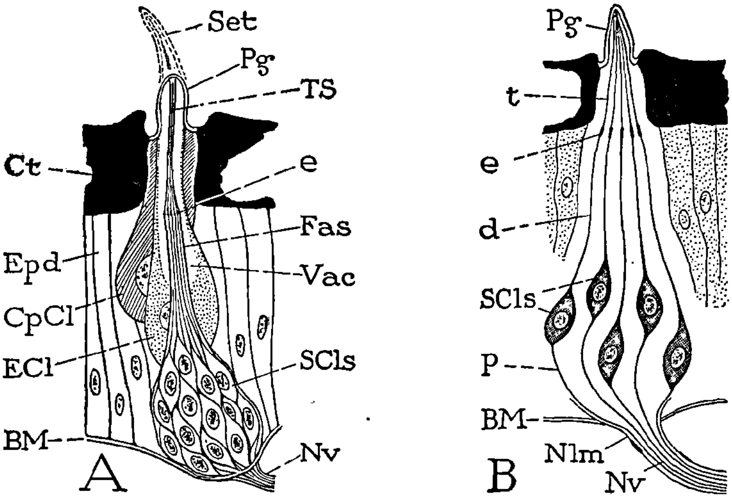

Fig. 269.—Structure of the chemoreceptive type of sensilla with thin-walled outer process (small seta or peg) and multiple sense cells. A, diagrammatic section of sensillum showing group of sense cells (*SCls*), fascicle (*Fas*) of distal processes of sense cells, terminal strand (*TS*) of fibers connected with cuticula, and minute bodies (*e*) at their inner ends. B, simplified diagram of separated sense cells with distal (*d*) and proximal (*p*) processes, and terminal connections (*t*) with the cuticula.

Sensilla basiconica.—Sensory pegs and cones are innervated hairs reduced in size, and there is no sharply dividing line between sensilla trichodea and sensilla basiconica, either in the character of the external parts or in the structure of the internal parts. In a typical sensillum basiconicum the external process is a small peglike or conical structure (Fig. 269 A, *Pg*). The walls of the process are thick or strongly sclerotic in some cases, while in others they are thin and transparent, or the process may terminate in a delicate membranous cap. Organs of the first type apparently can respond only to mechanical stimuli and must be regarded as tactile in function; those having thin membranous walls, however, may be supposed to be pervious to chemical stimuli, and such organs are usually regarded as receptors of taste or odor (chemoreceptors.)

The internal structure of the two groups of sensilla basiconica, as distinguished by the nature of the external process, is also characteristically different. The organs having thick-walled external processes are innervated by a single sense cell, as are the typical tactile hairs; those having thin-walled external processes, on the other hand, usually contain a group of sense cells (Fig. 269) and thus resemble the thin-walled chemoreceptive sensilla trichodea.

The cellular elements of a sensillum basiconicum with multiple sense cells (Fig. 269 A) include a distal cap cell (*CpCl*), a large vacuolated enveloping cell (*ECl*), and a compact group of sense cells (*SCls*). The cap cell appears to embrace the distal end of the enveloping cell, and the latter to be penetrated by the distal parts of the sense cells. The distal processes of the sense cells form a thick fascicle (*Fas*) ending in a terminal strand of fine fibers attached distally in the apex of the external process (*Pg* or *Set*). Near the middle of the bundle of terminal processes is a group of minute bodies (*e*), the number of which appears to correspond to the number of sense cells. These bodies have been particularly studied in the wasp by Vogel (1923), who calls them "olfactory rods" (*Riechstäbschen*), but they are so extremely minute that nothing satisfactory can be determined as to their nature or structure. While they appear to belong to the sense cell processes, it is perhaps possible that the terminal filaments beyond them (B, *t*) are cuticular processes to which the cell processes are attached, and that the bodies in question, therefore, might be themselves cuticular structures.

The possible chemoreceptive function of organs of this kind is suggested by the thinness and apparent permeability of the cuticular wall of the external process, and by the presence of a large vacuole surrounding the fascicle of sense cell processes. The latter are thus bathed in a liquid in which odor or taste substances might be dissolved if they can pass through the walls of the external cuticular process. Sense pegs and cones have been found on all parts of the body and appendages of various insects, but they occur principally on the antennae and mouth parts and in the preoral cavity.

Sensilla coeloconica and ampullacea.—Sense organs of these types are peg organs sunken into depressions of the body wall (Fig. 270). If the depression is shallow, the organ is termed a *sensillum coeloconicum* (A, B); if it is deep or flask shaped, the organ is distinguished as a *sensillum ampullaceum* (C, D). As with the hair organs and the exposed peg organs, some of the sunken pegs are thick walled or solid and are innervated each by a single sense cell; others have thin walls and contain each a group of sense cells. The second are regarded as chemoreceptors, but the function of the former is not clear since the external parts are removed from contact with mechanical stimuli. In some cases a number of pegs may occur in a single pit. Organs of this kind occur on the antennae of certain Diptera. Those of the house fly, as described by Röhler (1906), are in some cases simple cavities containing 10 to 20 sensory pegs, and others are compound, each cavity being divided into several shallow compartments, each with its group of pegs. The labial palpus of the cabbage butterfly (*Pieris*) has a deep apical cavity containing many sense pegs. Sensilla ampullacea occur particularly on the antennae of Hymenoptera. In some the cavity containing the sense peg is distinguished from that of a typical sensillum coeloconicum simply by being deeper and more flasklike in form (Fig. 270 C); in others (D) the "flask" is connected with the exterior by a long tubular neck.

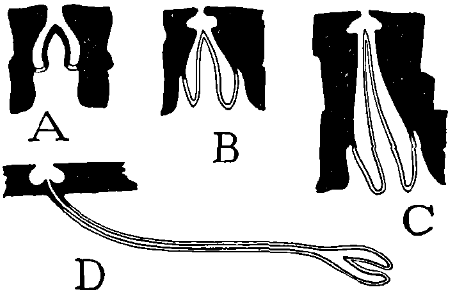

FIG. 270.—The cuticular parts of several varieties of sensilla coeloconica (A, B) and ampullacea (C, D).

3. THE CAMPANIFORM ORGANS

The sense organs included in this class have been called *vesicles, organs of Hicks, papillae, cupola organs, dome organs, umbrella organs, bell organs,* and *sense pores.* In vertical section the cuticular parts of the organs generally have the form of a small dome into which the sense cell process is inserted like the clapper of a bell. For this reason the organs are appropriately termed in general *sensilla campaniformia* (Berlese, 1909).

The external parts of the campaniform organs are, in some cases, small dome-like papillae, or but slightly convex swellings, usually less than 25 microns in diameter (Fig. 271); others (Fig. 272 B) are minute discs slightly sunken into the body wall, resembling in surface view vacant hair follicles, though they are usually distinguishable from the circular hair sockets by a more elliptical or oval form. The dome or disc in typical examples consists of a very thin outer lamella of the cuticula (Fig. 271 A, *a*), and of an endocuticular layer (*b*) generally having the form of an inverted cup or saucer. The inner layer is perforated by a central opening or by an axial slit through which the distal end of the sense cell process (*d*) is inserted on the under surface of the outer lamella. Beneath the cap is the usual canal of the cuticula.

Each campaniform organ is innervated through a single sense cell (Fig. 272 A, *SCl*); but since the organs often occur in groups, there may be a compact mass of sense cells in the neighborhood. The sense cells are long and narrow and generally project into the body cavity, though they are covered by the basement membrane of the epidermis. According to Newton (1931), the sense cells of the campaniform organs of the honey bee are doubly fusiform (B, *SCl*) and each swelling contains a nucleus. In the distal process of each cell is a "sense fiber" (*f*), the apex of which, Newton says, ends in a slightly swollen refractive body, which lies directly against the inner surface of the thin outer lamella of the external dome. It is possible that the presence of this body in the center of the cap has given rise to the idea that the nerve fiber penetrates to the exterior (McIndoo, 1914). In some insects the terminal body appears to be represented by a relatively large thickening of the cuticula (Fig. 271 C, *c*), while in others it takes the form of a small capsule receiving the end of the sense cell process (Figs. 271 A, B, D, 272 A, *c*). In any case it is probably only a cuticular modification at the point of attachment of the sense cell.

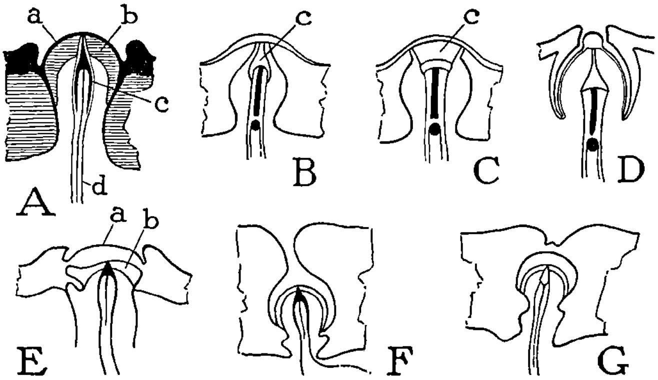

FIG. 271.—Structure of the cuticular parts of various types of sensilla campaniformia. A, diagrammatic section showing outer (*a*) and inner (*b*) lamella of the dome, and cuticular connection (*c*) of distal process (*d*) of sense cell. B, C, sections through short and long diameters of organ on halter of *Calliphora*. D, organ on halter of *Syrphus*. E, from cercus of *Periplaneta*. F, sunken organ from labium of *Dytiscus*. G, sunken organ on mandible of *Dytiscus* with no external opening. (B, C, D *from Pflügstadt*, 1912; E *from Sihler*, 1924; F, G *from Hochreuther*, 1912.)

Special epidermal cells associated with the sense cell have not generally been observed in the campaniform organs. Newton (1931) expresses the opinion that the sense cell is both chitinogenous and receptive in function. Various investigators, however, have found traces of other cells in the campaniform sensilla, and Sihler (1924) describes in *Periplaneta* a large cell (Fig. 272 A, *Cl*) ending in the canal of the cuticula, which is traversed by the distal process of the sense cell (*d*).

Campaniform organs occur on the head, thorax, abdomen, the antennae, mouth parts, legs, wing bases, cerci, and ovipositor of adult insects and have been observed in all the principal orders; they have also been found on the larvae of some species. The function of the organs is a subject on which there is some difference of opinion, but McIndoo (1914, 1915) has given much experimental reason for believing that the organs are receptors of odor stimuli, since there is scarcely any question that insects retain a "sense of smell" after removal of the antennae. Structurally, however, the campaniform organs would appear to offer but little surface for the penetration of odor substances, and, since each is innervated by a single sense cell, their receptive power must be of a low order, considering that most of the apparent chemoreceptors have multiple sense cells. The campaniform organs, however, usually occur in groups.

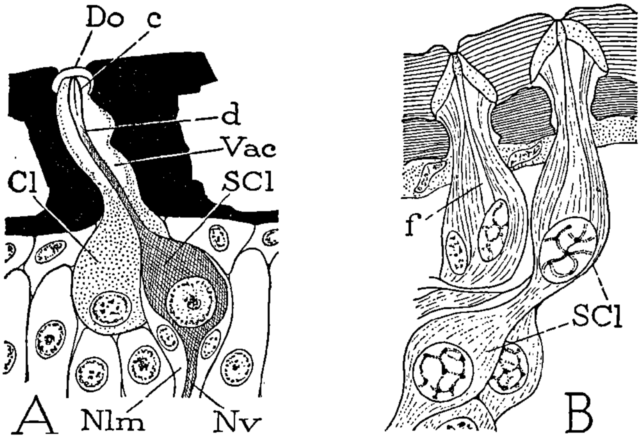

FIG. 272.—Sections of cuticular and cellular parts of sensilla campaniformia. A, organ on cercus of *Blatta orientalis* with single large cell (*Cl*) associated with the sense cell (*SCl*). (*Diagrammatic from Sihler*, 1924.) B, organs from base of hind wing of *Apis mellifica* with binucleate sense cells. (*From Newton*, 1931.)

4. THE PLATE ORGANS

The sensilla placodea present externally each a thin cuticular plate, elliptical, oval, or elongate in form, set over a large cavity in the cuticula (Fig. 273). The internal structure of these organs (Fig. 274) closely resembles that of sensilla basiconica having multiple sense cells. Plate-like organs occur on the antennae of certain Homoptera, Coleoptera, and Hymenoptera.

Among the Homoptera antennal plate organs are present in Aphididae, Aleurodidae, and Psyllidae, but the "plate" is here a thin membranous disc (Fig. 273 A). In Coleoptera (B, C, D) and Hymenoptera (E-K) the plate, though thin, is usually sclerotized and is generally separated from the surrounding antennal wall by a membranous ring or an inflection. According to Hochreuther (1912), there are from 4,500 to 5,000 plate organs on the antennae of *Dytiscus*, the plates being very small, measuring only 6 to 8 microns in diameter. In the Hymenoptera the plates are usually much larger and vary in form from an ellipse (J) to a narrow elongate oval (E, H). They are generally flush with the antennal surface (K) but are sometimes elevated (F) and may be surrounded by a deep groove (I). In the honey bee it is estimated that there are about 30,000 plate organs on both antennae of the drone, 5,000 to 6,000 in the worker, and 2,000 to 3,000 in the queen. Each plate is elliptical in shape, and from 12 to 14 microns in its longest diameter, which is lengthwise on the antenna. Surrounding the plate is a narrow membranous ring (J, K, *a*), within which is a concentric line formed by a submarginal groove (K, *b*) on the inner surface of the plate.

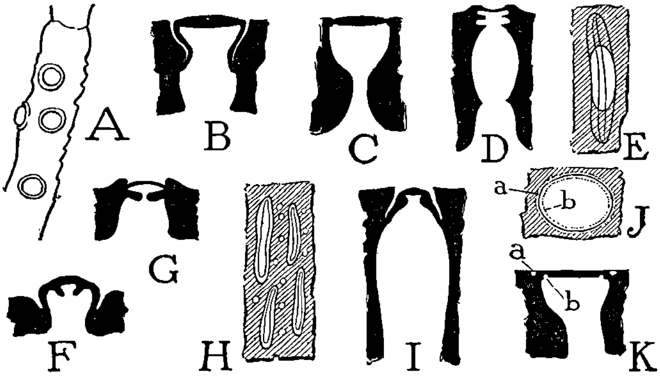

Fig. 273.—The cuticular parts of various forms of sensilla placodea. A, sensory plates on antenna of an aphis. B, section of antennal plate organ of *Dytiscus*. C, same of *Cetonia aurata*. D, same of *Necrophorus vespillo*. E, surface view of antennal plate of *Cynips gallae*. G, section of E. H, I, surface view and section of antennal plates of *Vespa crabro*. J, K, surface view and section of antennal plate of *Apis mellifica*: *a*, outer ring of clear cuticula; *b*, inner groove. (B *from Hochreuther*, 1912; C *from von Rath*, 1888; D–I *from Ruland*, 1888.)

The internal structure of a sensillum placodeum in Hymenoptera (Fig. 274 A) includes a large plate cell (*CpCl*), an elongate cell (*ECl*) enveloping the distal strand of the sense cells, and a compact mass of numerous sense cells (*SCls*). The enveloping cell (*ECl*) is attached by a slender neck to the external plate at a definite point in the submarginal groove of the latter. It contains a large vacuole (*Vac*) surrounding the distal processes of the sense cells (*Fas*) and the terminal strand (*TS*) connecting the latter with the plate. In a tangential section just below the plate, therefore, the large plate cell, or cap cell (B, *CpCl*), appears to surround the neck of the enveloping cell (*ECl*), which, in turn, contains the terminal strand (*TS*) of the sense cells. At a lower level (C) the fascicle of distal sense cell processes (*Fas*) is seen within the vacuole of the enveloping cell. The group of sense cells in each organ lies against the basement membrane of the epidermis (A, *SCls*), and the distal processes form a compact fascicle (*Fas*), which contracts into the terminal strand (*TS*) attached to the plate. At the distal end of the fascicle is a group of minute refringent bodies (*e*) as in the sensilla basiconica. In the antennal plate organs of Aphididae, as figured by Flögel (1905), the distal processes of the sense cells are short and their attachments are distributed over the entire inner surfaces of the membranous plates.

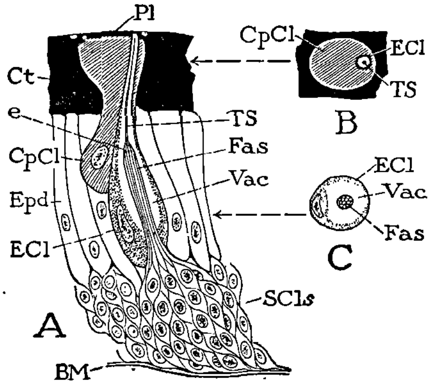

FIG. 274.—A sensillum placodeum of *Apis mellifica*, diagrammatic. A, vertical section showing large cap cell (*CpCl*) beneath outer plate, enclosing distal end of vacuolated enveloping cell (*ECl*), which contains the fascicle (*Fas*) of sense cell processes and the terminal strand (*TS*). B, horizontal section just below outer plate. C, horizontal section through base of enveloping cell.

The plate organs are commonly regarded as olfactory in function, and those of the aphids would appear to be well constructed for the reception of odor stimuli. In Coleoptera and Hymenoptera, however, the relatively thick sclerotic plates cannot be supposed to be pervious to odor substance, those of the honey bee being about 1.5 microns in thickness, and the narrowed distal stalk of the receptive cells attached in the groove of the plate presents a very restricted area at which stimuli could be effective. If the organs, nevertheless, are olfactory, the plate would appear at least to be an entirely superfluous adjunct.

5. THE SCOLOPOPHOROUS ORGANS

The scolopophorous organs are usually compound sense organs. each consisting of a bundle of simple sensilla having a common point of attachment on the body wall. There is no specific differentiation of the cuticula that forms structurally a part of the sensillum, as with the other sense organs, though the point of attachment on the cuticula may be marked by a pit, a thickened disc, or a sclerotic nodule. In some cases, however, a scolopophorous organ is immediately associated with a membranous area of the integument, known as a *tympanum,* and the latter then becomes functionally an essential part of the receptive apparatus. Frequently the inner end of the organ is united to the body wall by a ligament, and in such cases the entire organ may have the form of a thick cord stretched between two points on the body wall (Fig. 275 B). Since the scolopophorous organs first studied were of this type or were those found associated with tympanal membranes, they were given the name of *chordotonal organs* on the assumption that they were sound receptors. A wider knowledge of the organs, however, now shows that this term can apply literally only to certain types of scolopophorous organs.

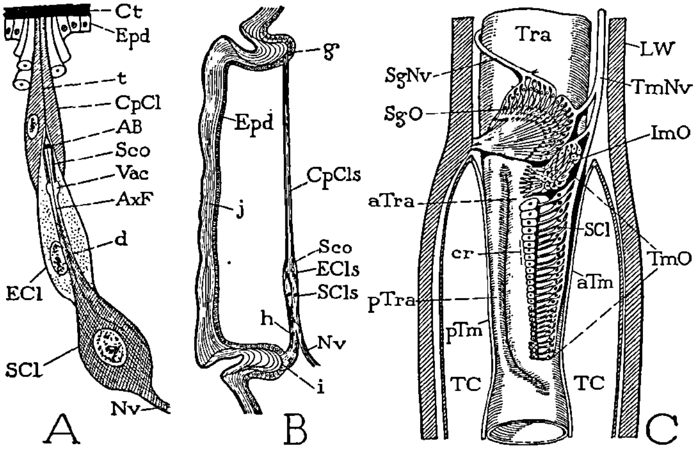

FIG. 275.—Sensilla scolopophora. A, diagrammatic structure of a single scolopophorous sensillum. B, chordotonal type of scolopophorous organ in abdominal segment of larva of *Monohammus confusor.* (*From Hess,* 1917.) C, scolopophorous organs in tibia of right foreleg of *Decticus.* (*Adapted from Schwabe,* 1906.) *AB,* apical body; *aTm,* anterior tympanum; *aTra,* anterior trachea; *AxF,* axial fiber; *cr,* crest; *g,* posterior attachment on cuticula; *h,* chordotonal ligament attached to cuticula at *i*; *ImO,* intermediate organ; *j,* pleural disc of body wall; *LW,* leg wall; *pTm,* posterior tympanum; *pTra,* posterior trachea; *SgNv,* subgenual nerve; *SgO,* subgenual organ; *TC,* tympanal cavity; *TmNv,* nerve of tympanal organ; *TmO,* tympanal organ.

Each scolopophorous sensillum (Fig. 275 A) consists of three distinct cells: a distal cap cell (*CpCl*) attached to the cuticula, an intermediate enveloping cell (*ECl*), and a basal sense cell (*SCl*). The inner end of the cap cell embraces the outer end of the enveloping cell, and the latter surrounds the elongate distal process of the sense cell (*d*), the apex of which is connected with the cuticula by a terminal fiber (*t*) traversing the cap cell.

The distinguishing feature of sensilla scolopophora is the presence of a well-differentiated, peg-shaped "sense rod," or *scolops,* at the apex of each sense cell (Fig. 275 A, *Sco*). The sense rod (*corpus scolopale, Stift* of German writers) is often called a *scolopale.* The term in this form, being an adjectival derivative, should be pluralized as *scolopalia*. The forms "scolopala" and "scolopalae" (Snodgrass, 1926, and others) have no grammatical standing.

The scolopes vary in length from a few microns to as much as 23 microns in different organs. In form some are slender and cylindrical, others are short and bulblike, but the typical rod (Fig. 275 A, *Sco*) is elongate, somewhat expanded toward the distal end, and then sharply tapering to an acute point. In the distal part is an "apical body" (*AB*), always conspicuous in stained specimens, to which is attached an axial fiber (*AxF*) of the sense cell. The walls of the rod are usually ribbed internally. Often there is no apparent connection between the rod and the body wall, but in most organs a fine terminal strand (*t*) extends from the apex of the rod to the cuticula. The connection with the cuticula suggests that the scolops itself may be a cuticular structure, but, according to the view of Eggers (1923), the scolops is a part of the wall of the sense cell, and its ribs are fibrous thickenings of the latter continued into the terminal strand, which may be likened to the tonofibrillae of a muscle.

Scolopophorous sense organs are widely distributed in insects, but until recently they have not been reported in other arthropods. In adult insects they have been found in the head, the thorax, the abdomen, the antennae, the legs, and the wing bases. Organs of the cordlike type of structure (Fig. 275 B) occur only in the abdomen of certain larvae, but organs of the usual form have been described in the labium, the legs, and even in the tarsi of larval insects.

Tympanal scolopophorous organs are well known in several groups of insects, as those on the base of the abdomen in Acrididae and Cicadidae, on the fore tibiae of Tettigoniidae and Gryllidae, on the thorax of Notonectidae, and on the thorax and abdomen of Lepidoptera. Most interesting and complex of these organs are those in the tibiae of the Tettigoniidae (Fig. 275 C). There are here in each leg three separate organs lying on the outer face of the leg trachea (*Tra*) between two tympana (*aTm, pTm*) concealed in small cavities (*TC*) of the tibial wall. Proximally, below the "knee," is a large fan-shaped subgenual organ (*SgO*), then a small intermediate organ (*ImO*), and finally a long tympanal organ (*TmO*). The cap cells of the last are arranged in a graduated series forming a crest (*cr*) on the outer wall of the trachea, with the sense cells (*SCl*) lying laterally along the nerve trunk (*TmNv*).

It seems probable that in general the scolopophorous organs are receptors of vibratory stimuli, and that those associated with tympanal membranes are organs of "hearing," that is, phonoreceptors.

The sense organ located in the second segment or, pedicel, of the antenna of nearly all insects, known as the *organ of Johnston*, is to be classed with the scolopophorous organs, though the sense rods of this organ are not typically scolopoid (Fig. 276). The numerous sensilla, innervated from the sensory antennal nerve (*Nv*), are arranged in the form of a cylinder within the pedicel, and their distal ends are attached in a circle to the articular membrane between the pedicel and the next antennal segment, which is the base of the flagellum (A), or to sclerotic processes radiating from the latter (B, *a*, *b*). In size and complexity the organ of Johnston varies much in different insects; it attains its highest development in Gyrinidae, Chironomidae, and Culicidae (B). There appears to be little doubt that the organ serves to register movements of the distal part of the antenna, which is freely implanted on the end of the pedicel (see Eggers 1923–1929).

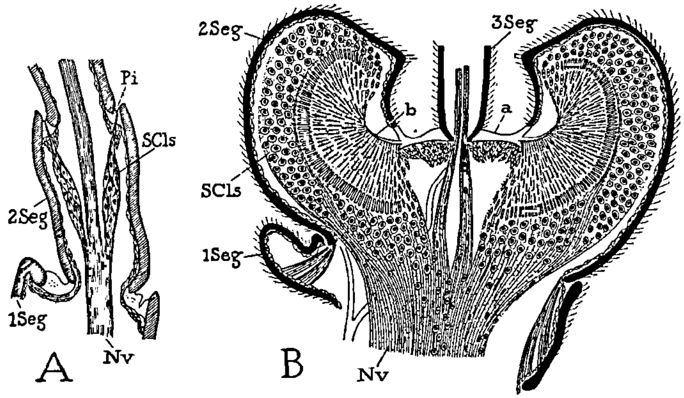

Fig. 276.—The organ of Johnston in simple and complex form. (*From Child*, 1894.) A, organ in second segment of antenna of *Melolontha vulgaris* showing distal ends of sense cell processes attached in pits (*Pi*) in articular membrane at base of third segment. B, organ in second segment of antenna of *Corethra* showing distal processes of sense cells attached to prongs (*b*) from circular plate (*a*) on base of third segment.

A very simple organ of the "chordotonal" type of structure, though it contains no sense rod, or scolops, has recently been found in the antennule of an amphipod crustacean *Caprella dentata* by Wetzel (1934). It consists of a series of three cells attached basally to the epidermis in the distal end of the second segment of the antennule, and distally by a long strand to the wall of the third segment. The proximal cell is the sense cell, with a fiber entering the antennular nerve; the other two cells appear to be an enveloping cell and a cap cell.

6. THE EYES

The word "eye" is used in general for any organ that is specifically sensitive to light rays impinging upon it, and capable of transmitting the effect on its sense cells to the central nervous system. A primitive eye, therefore, is merely a light-perceiving organ, or photoreceptor, and it is not to be assumed that all eyes are capable of registering impressions of form, color differences, or motion in external objects. The effect of the light stimulus must depend on the development of the eye and of the optic centers of the nervous system.

In some of the Annelida photoreceptive cells occur scattered through the epidermis and give the animal a general sensitiveness to degrees of light intensity. Among insects, the Collembola are said to exhibit a reaction to light thrown on the general body surface; but since the integument contains no photoreceptors, the sensitiveness probably arises from the effect of ultraviolet rays on the body tissues. The eyes of insects are always located on the head, and the optic centers lie in the protocerebral parts of the brain. The eyes belong, therefore, to the preantennal region of the procephalon and are probably prostomial organs in their origin.

The receptive elements of an eye sensillum, as of any other sensory organ, are specialized cells of the epidermis. An essential feature of a photoreceptor, therefore, is a transparency in the cuticula over the sense cells. It is conceivable that any sensory cells might be stimulated by light if light rays are able to reach them in sufficient strength, and it appears that certain organs on the head of the larvae of higher Diptera, having essentially the structure of the supposedly chemoreceptive organs, are photoreceptive in function by reason of the transparency and lenticular form of the external cuticular part. The sense cells of the usual optic organs of insects differ from the sensory cells of the other sense organs in that they lack terminal processes, and in that the receptive part of each cell is finely striated perpendicular to the receptive surface (Fig. 278 A, *a*). The striations appear to be terminal thickenings of neurofibrillae traversing the sense cell. Usually the striated parts of two or more adjacent cells are united to form an optic rod, or *rhabdom* (H, I, *Rhb*); the component elements of a rhabdom, representing the striated parts of the optic cells, are *rhabdomeres*.

The photoreceptors of insects, as of arthropods generally, include dorsal and lateral eyes. The dorsal eyes are always simple ocelli, but the lateral eyes may be either simple or compound in structure, and in many cases it is difficult to distinguish on an anatomical basis the two kinds of simple eyes. The usual optic organs, however, fall into three groups that are ontogenetically distinct in the individual and for descriptive purposes may be distinguished as *dorsal ocelli, lateral ocelli* (stemmata), and *compound eyes.* In actual position the morphologically dorsal ocelli are dorsal, anterior, or ventral according to the position of the facial area of the head. The apparent photoreceptors of muscoid maggots constitute a separate class of light-perceiving organs, since they have none of the characteristic features of true eyes.

The Photoreceptive Organs of Muscoid Larvae.—The maggots of the higher Diptera are negatively phototropic. Experiments show that the light-sensitive part of the animal is its extreme anterior end. There are here located on the apex of the larval "head" two pairs of small papillae, each bearing one or several minute cuticular processes, and containing the outer end of a large body of sense cells (see Lowne, 1890–1895). The structure of these organs in *Lucilia sericata* has recently been investigated by Ellsworth (1933). The external part of each organ (Fig. 277) is a transparent cuticular cone (*ln*) resembling a strongly biconvex lens of an ocellus. The internal part consists of a large ovate mass of elongate, bipolar sense cells (*SCls*), the distal processes of which form a thick cylindrical fasciculus (*Fas*) attached to a thin membrane beneath the cuticular lens. The proximal processes of the cells come together in a nerve (*Nv*). These organs appear to lack the characteristic features of photoreceptive organs, namely, the presence of striated bands on the receptive ends of the sense cells and the formation of rhabdoms among the distal processes. On the other hand, each organ clearly has the internal structure of a chemoreceptor with multiple sense cells. Hence, accepting the evidence that the organs are the photoreceptors of the maggot, we must conclude that they present a unique example of a sense organ having the usual chemoreceptive type of structure in its cellular parts that has become functionally a photoreceptor by an adaptation of the cuticular part for the transmission and condensation of light rays.

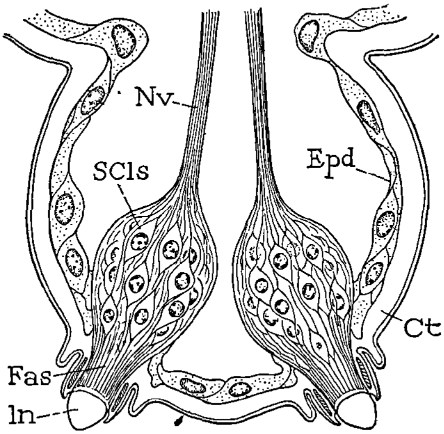

FIG. 277.—Sense organs, probably photoreceptors, in the cephalic lobe of the larva of *Lucilia sericata*. (*From Ellsworth*, 1933.)

General Structure of the Optic Organs.—Regardless of the diversity in structure of the several kinds of eyes, there are always to be distinguished in each organ two functionally distinct parts, namely, a *dioptric apparatus* and a *receptive apparatus*. The first transmits and usually also condenses the impinging light rays upon the receptive surface; the second consists of the sensory cells composing the *retina,* which present specialized receptive surfaces at the points where the light rays are focused, and are continued proximally into the optic nerve. Usually the photoreceptor includes also pigment cells, supporting connective tissue cells, and tracheae. Morphologically the two principal parts of the optic organ are not necessarily of different origin, since the dioptric apparatus, though it always includes the cuticula, may be in part or largely formed by specialized cells of the optic epidermis or of products of these cells. The receptive apparatus, on the other hand, is entirely epidermal. The optic centers of the brain, described in the last chapter, lie generally in extensions of the protocerebrum forming lobes or stalks capped by the eyes, in the outer ends of which are the terminals of the optic nerves. In some larval insects, however, the optic nerves are long trunks extending to the protocerebrum.

Simple eyes and compound eyes are not fundamentally different in their structure, and all types of eyes are developed from the ectoderm in practically the same way. A simple eye, or ocellus, is a photoreceptor having a single dioptric apparatus for all the sense cells. A compound eye has numerous individualized groups of sense cells, and a separate dioptric apparatus for each group. The anatomical elements of an insect's organ of vision include the following parts.

The Cornea.—The cornea is the cuticular covering of the eye, which is always transparent in order to admit light rays but is of a thickness presumably sufficient to exclude ultraviolet in harmful amount. The cornea may be but little differentiated from the surrounding cuticula, except for the lack of pigment (Fig. 279 A, *Cor*), but usually it is more or less dome shaped, or it is thickened to form a *corneal lens* (Figs. 279 F, 283 A, *Cor*), which may be either planoconvex or biconvex. Generally the lens shows a laminated structure in section, and it includes the entire thickness of the cuticula.

The Corneagenous Cells.—The epidermal matrix of the cornea consists of a layer of cells, which, in the formative stage of the eye, is a distinct outer stratum of the optic organ that secretes the cornea (Fig. 279 D, E, *CgCls*). In the mature eye the corneagenous cells are reduced in size and usually appear as a transparent (vitreous) epithelium underlying the cornea (F, *CgCls*), though they may be withdrawn from beneath the latter (Figs. 281 B, D, 283 B) and converted into pigment cells. In some cases the corneagenous cells form beneath the cornea a transparent crystalline body that becomes a part of the dioptric apparatus.

The Crystalline Body.—Many simple eyes and most compound eyes have a transparent *vitreous,* or *crystalline, body* beneath the cornea, which serves as an adjunct to the corneal lens or functionally replaces the latter when the cornea is not lenticular in form. The crystalline body generally has an oval shape in simple eyes (Fig. 281 A, B, D, *CB*), but in compound eyes it is typically conical with the apex directed toward the inner part of the eye (Fig. 283 A, *Cn*). It is a functional rather than a morphological part of the eye and is variously produced. In the ocelli of some insects a vitreous body is formed of elongate transparent corneagenous cells intervening between the cornea and the retina. A large oval crystalline body in the ocelli of Ephemerida consists of a compact mass of small vitreous cells lying beneath a subcorneal epithelium of corneagenous cells. The crystalline body here serves as the lens of the eye. In the lateral ocelli of certain larval insects an oval crystalline body lies beneath the cuticular lens (Fig. 281 A, B, D, *CB*), which may be a cellular structure, as in certain dipterous larvae (Fig. 280 C, F, *CB*), though more commonly it appears to be a secretion product of some of the surrounding cells. The crystalline cone of compound eyes (Fig. 283 B, *Cn*) is usually formed of four united transparent cells, but in some cases it is a vitreous transformation or secretion product of the cells.

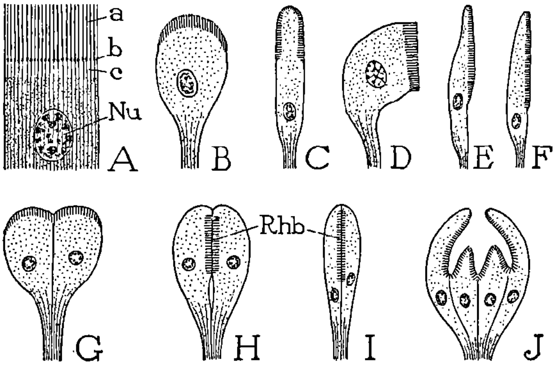

FIG. 278.—Structure of optic sense cells, diagrammatic. A, receptive pole of a sense cell: *a*, striated zone (rhabdomere) formed of ends of neurofibrillae; *b*, basal bodies; *c*, clear zone. (*From Hesse*, 1901.) B–J, different positions of the striated zones on ends of sense cells. H, I, union of the striated zones of adjacent cells to form a rhabdom (*Rhb*). (B–J *from Weber*, 1933.)

The Retina.—The retina is composed of the optic sense cells. It lies in the deeper part of the eye and usually consists of a single layer of elongate cells, the narrowed inner ends of which penetrate the basement membrane of the eye and become the fibers of the optic nerve. The receptive part of each optic sense cell (Fig. 278 A, *a*) is the striated band (*Stiftchensaum*), the striations of which appear to be rodlike thickenings of neurofibrillae traversing the cell. At the base of each rod is a small nodule (*b*). Proximal to the rods is a pale intermediate zone (*c*) separating the striated band from the plasmatic basal part of the cell, which contains the cell nucleus (*Nu*). The primary position of the striated band is probably on the distal surface of the sense cell (A, B), and the band may envelop the end of the cell (C), but more generally it is transferred to one side (D, E, F). In most cases the lateral striated bands of adjacent cells are united to form a rhabdom (H, I, *Rhb*). The rhabdom may be cylindrical, but often it shows a stellate or branched form in cross section due to the component elements, or rhabdomeres, contributed by the several encircling cells.

Pigment Cells.—A dark pigment usually occurs in some part of the eye and may be contained in various cells; it is commonly present in the retina cells, and generally there are special pigment cells surrounding the eye, or the separate elements of a compound eye, which optically isolate the sensillum and absorb the light that does not enter at such an angle as to reach the sense cells. The pigment cells in most cases are the epidermal cells surrounding the eye, or enclosing each group of rhabdom-forming retina cells, but in the compound eyes and in some simple eyes the corneagenous cells become pigment cells in the mature organ.

The Tapetum.—A reflecting surface, known as the tapetum, is variously developed in different eyes to give greater effectiveness to small amounts of light and is therefore more usually present in nocturnal species. It reflects the light from the depth of the eye back into the retina and gives a shining appearance to the eyes of many insects when seen in dim light. A tapetum is formed in some ocelli by a sheet of connective tissue through the base of the retina containing light-reflecting substances (Fig. 279 A, *Tap*). In the compound eyes the usual tapetum consists of dense masses of glistening air-filled tracheae that penetrate between the retinal elements and form a reflecting sheath enclosing each group of retinal cells.

The Basement Membrane.—The inner surface of the eye is always covered by a basement membrane continuous with that of the surrounding epidermis. The membrane is penetrated by the proximal processes of the retinal cells, which become the fibers of the optic nerve. The basement membrane of the compound eye is sometimes called the *membrana fenestrata.*

The Dorsal Ocelli.—The dorsal ocelli are the usual simple eyes of adult insects and of exopterygote larvae and nymphs. Typically there are three of them, one median, located on the upper part of the frons or the frontal area of the head, the other two more lateral on the postfrontal region. There is evidence that the median ocellus has been formed by the union of two primitive frontal ocelli. The median ocellus is often suppressed, seldom is it retained alone, but frequently all three ocelli are absent.

The dorsal ocelli have a relatively primitive structure in some of the Apterygota, as in *Orchesella* and *Machilis.* In *Machilis*, as described by Hesse (1901), the corneal cuticula is elevated over each ocellus (Fig. 279 A, *Cor*), but it is not thickened to form a lens. Beneath the cornea are the cellular elements of the eye, which consist of two sets of cells. The larger cells (*SCls*) are the sense cells forming the retina, and in this case some of the retinal cells extend from the cornea to the base of the eye. The smaller cells (*CgCls*), intercalated between the outer ends of the retinal cells, are the corneagenous cells. It is evident from the arrangement of the cellular elements in this eye that the two sets of cells have been differentiated side by side in the ocellular epidermis. The retinal cells are arranged in groups of four cells each, the rhabdomeres of which form rhabdoms (*Rhb*) irregularly X-shaped in cross section. The inner part of the retina is traversed by a sheet of reflecting connective tissue forming a tapetum (*Tap*), beneath which is a layer of dark pigment (*Pig*) at the proximal ends of the retinal cells. The eye is limited internally by a basement membrane (*BMb*) continuous with that of the surrounding epidermis (*Epd*).

In the usual dorsal ocelli of pterygote insects the corneagenous cells and the retinal cells form two distinct layers, the former intervening completely between the cornea and the retina (Fig. 279 F). The cornea may be a simple dome over the eye, but generally it is thickened to form a strongly biconvex lens (*Cor*). The corneagenous cells (*CgCls*) are transparent in order not to impede the transmission of light to the retinal cells, and when a corneal lens is developed the corneagenous cells are usually small and appear as a vitreous epithelium beneath the lens. In the absence of a corneal lens, however, the corneagenous cells may be enlarged to form a crystalline dioptric body. In some cases a vitreous mass of refractive fluid occurs between the epithelial corneagenous cells and the retina cells. The peripheral cells of the corneagenous layer, where the latter merge into the normal epidermis, usually contain a dark pigment forming an "iris" about the sensory elements. Rhabdoms (*Rhb*) produced by adjacent retinal cells are contained in the outer part of the retina, proximal to which the retinal cells are usually pigmented, and the retinal nuclei lie in the basal parts of the cells. Interspersed between the sensory cells of the retina are supporting cells that are purely mechanical elements in the structure of the eye.

The development of an eye of this type follows a very simple course and is well illustrated in the ant, as described by Caesar (1913). The first rudiment of the ocellus is a thickening of the epidermis in a fold at the back of the larval head (Fig. 279 B, *O*). According to Caesar, there are four ocellar rudiments in the ant larva, two of which subsequently unite to form the definitive median ocellus. The cells of each ocular area soon become differentiated into two sets (C), the cells of which, though at first interpolated among one another, soon draw apart toward opposite ends of the eye (D). The outer cells become the corneagenous cells (*CgCls*), the inner ones the retina cells (*SCls*). The corneagenous cells next become greatly enlarged, while the retina cells condense to a compact group (E). Then the corneagenous cells begin an active secretion of chitin, which increases the thickness of the superlying cuticula until the latter takes the form of a large biconvex lens (F, *Cor*); but the secretion activity at last reduces the corneagenous cells to a thin transparent epithelium separating the lens from the retina, and the cells remain thus in the fully mature eye (F, *CgCls*).

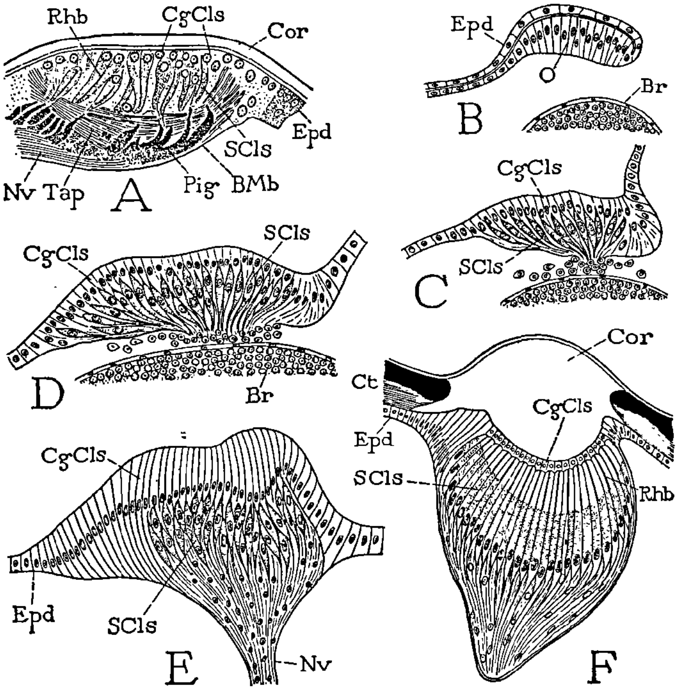

FIG. 279.—Examples of the structure and development of dorsal ocelli. A, dorsal ocellus of *Machilis*. (*From Hesse*, 1901.) B–F, stages in the development of a dorsal ocellus of male of *Formica pratensis*, and mature median ocellus of same. (*From Caesar*, 1913.) *BMb*, basement membrane; *Br*, brain; *CgCls*, corneagenous cells; *Cor*, cornea; *Ct*, cuticula; *Epd*, epidermis; *Nv*, nerve; *O*, ocellar rudiment in epidermis; *Pig*, pigment; *Rhb*, rhabdom; *SCls*, sense cells; *Tap*, tapetum.

The ocelli of Ephemerida, as described in *Cloëon* by Hesse (1901), present an exceptional structure in that each eye contains a large lenslike cellular body enclosed between a thin outer epithelium of corneagenous cells lying immediately beneath the dome-shaped cornea, and a thick inner layer of elongate vitreous cells distal to the retina. The lenticular body is composed of many distinct, transparent, nucleated cells, and at one point on its outer surface it is continuous with the subcorneal epithelium, suggesting that it is a product of the latter. The retina has the usual structure, with short rhabdomes in the outer ends of its cells, but it contains no pigment. The entire eye is invested in a densely pigmented epithelium.

The Lateral Ocelli of Holometabolous Larvae.—The eyes of holometabolous larvae are of the ocellar type of structure and are precursors of the compound eyes of the adult. The larval ocelli, however, do not become the ommatidial elements of the compound eye; the latter are developed independently from the epidermis, while the larval ocelli usually degenerate, though in a few insects they are said to be retained in the imago along with the compound eyes. In some cases rudiments of the degenerating larval ocelli are to be found withdrawn into the head and attached to nerve strands of the compound eyes (Fig. 281 F, *O*).

The larval ocelli generally occur on the sides of the head in the neighborhood where the compound eyes will be developed. In number they vary from one to six and sometimes seven on each side. They are often termed "stemmata" to distinguish them from the dorsal ocelli, probably in allusion to the fact that those of each lateral group are frequently arranged in a circle or "wreath" about a central pigmented area, though in this sense the term "stemma" would more properly apply to the entire circle of ocelli than to a single organ. There is much variation in the structure of the larval ocelli in different groups of insects, but it is probable that these eyes are homologous structures in all cases, and that they have variously diverged in their evolutionary development. Since the larval ocelli and the compound eyes of the adult are both innervated from the optic lobes of the brain, it would appear that the two sets of eyes are genetically related, though ontogenetically they are distinct developments from the lateral ocular rudiments in the epidermis.

In their simpler forms, and in their growth, the lateral ocelli do not differ essentially from the dorsal ocelli. Each is developed by differentiation of the cells in the ocular region of the epidermis into a corneagenous layer and a retinal layer. The cornea is sometimes flat or dome shaped, but usually it has the form of a biconvex lens. The corneagenous cells may form a thick vitreous layer between the lens and the retina, or they may be reduced to a thin epithelium; in certain types of larval ocelli they are withdrawn completely from beneath the cornea in the mature eye. Usually there is a dioptric body below the cornea, either composed of vitreous corneagenous cells or produced as a vitreous secretion of the cells. Rhabdoms are generally present in the outer part of the retina, formed in the usual manner between the distal ends of the retinal cells. Pigment is variously distributed in the eye, or sometimes absent.

A simple type of lateral ocellus is found in the larvae of Tipulidae, in which there is a group of five very small ocelli on each side of the head. Each ocellus, as described by Constantineanu (1930), consists of a thick corneal lens (Fig. 280 A, *Cor*), a subcuticular epithelium of transparent corneagenous cells (*CgCls*), and an inner mass of sense cells (*SCls*) containing rhabdoms (*Rhb*) in their outer ends. In certain other nematocerous larvae, in which the cornea is not lenticular, some of the corneagenous cells take on a vitreous character and form a dioptric apparatus beneath the cornea, which, as in the mosquito larva (B, *VCls*), may be but little differentiated from the rest of the corneagenous layer, or which, as in *Simulium* (C, *CB*), may be a well-defined crystalline body of large transparent cells. A crystalline body is shown by Constantineanu to be particularly well developed in the pigmented ocelli of various genera of Chironomidae, in which it is a compact lenslike structure composed of four or five large vitreous cells (F, *CB*). Accompanying each pigmented ocellus (*O*) there may be an imperfect, nonpigmented accessory ocellus (*O′*) lacking a crystalline body. The chironomid larval eyes, which were formerly supposed to be very primitive photoreceptive organs, are thus shown by Constantineanu to be well developed and specialized in their structure.

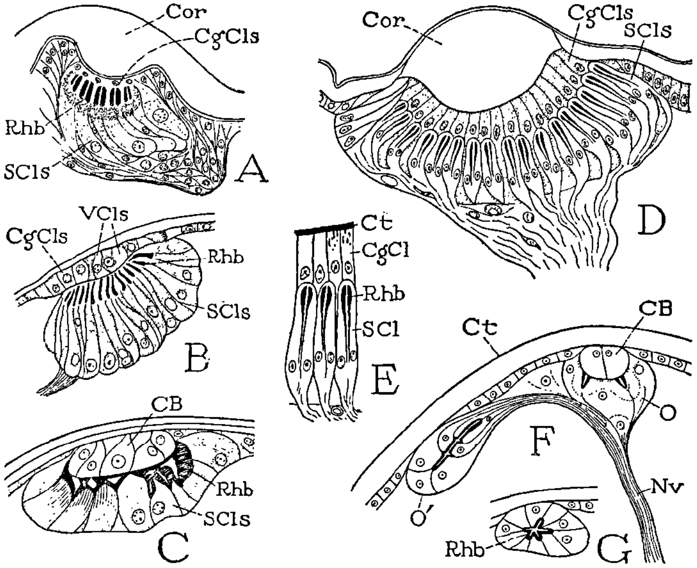

FIG. 280.—Lateral ocelli of dipterous and tenthredinid larvae. A, *Tipula*. B, *Culex pipiens*. C, *Melusina* (*Simulium*). D, *Allantus togatus* (Tenthredinidae), pigment removed. E, detail of corneagenous and retinal layers of same. F, *Tendipes* (*Chironomus*), outer pigmented ocellus (*O*), inner pigment-free ocellus (*O′*). G, horizontal section of pigmented ocellus of same. (A–C, F, G *from Constantineanu*, 1930; D, E *from Corneli*, 1924.)

The larvae of Tenthredinidae and related families have a characteristic and distinctive appearance by reason of the single large ocellus on each side of the head. This eye in its structure (Fig. 280 D) much resembles a typical dorsal ocellus (Fig. 279 F). The corneagenous cells form a thick layer (*CgCls*) between the large biconvex corneal lens (*Cor*) and the retina, and the sense cells (*SCls*) are united in retinular groups forming rhabdoms in their distal ends (E, *Rhb*). The single tenthredinid larval eye, however, is in no respect structurally different from the simple lateral ocelli of a tipulid larva (A), and in its development, as described by Corneli (1924), it follows the usual course of differentiation of the primitive ocellar epidermis into two superposed layers of cells.

The larva of the antlion *Myrmeleon* has several minute ocelli on each side of the head. The structure of these eyes (Fig. 281 A), as shown by Hesse (1901), is relatively simple in that each organ has a well-developed outer layer of corneagenous cells (*CgCls*) beneath the corneal lens, while the rhabdom-bearing sense cells (*SCls*) form a compact inner layer. In a space between the corneagenous cells and the cup-shaped outer surface of the retina lies a large oval crystalline body (*CB*). The periphery of the crystalline body is surrounded by long corneagenous cells that extend from the cornea to the sides of the retina. The rhabdoms have the usual form of rods converging toward the dioptric apparatus.

Ocelli in which the corneagenous cells are withdrawn from the inner surface of the cornea in the mature eye have, in section, the appearance of a cellular invagination beneath the cornea, and each may contain a deep lumen. Ocelli of this type occur in the larva of *Dytiscus* and in the larvae of Trichoptera and Lepidoptera.

The larva of *Dytiscus* has on each side of the head six functional ocelli and one rudimentary ocellus, or "eye spot." Each fully developed ocellus has the form of a deep cellular sac beneath the lenticular cornea (Fig. 281 B), the lumen of which is a narrow cleft through the longer axis of the eye. Just beneath the corneal lens (*Cor*) is a large crystalline body (*CB*). The cells of the distal part of the ocellar sac turn inward from the epidermis surrounding the crystalline body and form a pigmented "iris" (*ICls*). Continuing from the latter are the sensory retinal cells of the deeper part of the eye. The retinal cells include vertical median cells (*cSCls*) arranged in two axial rows at the bottom of the ocellar sac, and long peripheral cells (*pSCls*) converging distally beyond the outer ends of the median cells. Both sets of retinal cells contain rhabdoms in their exposed ends (*Rhb*), those of the vertical cells forming two parallel rows at the bottom of the sac, those of the convergent peripheral cells being directed toward one another in the lateral walls of the eye beyond the vertical rhabdoms. The tapering proximal ends of all the retinal cells come together to form the ocellar nerve (*Nv*).

The rudimentary ocellus in each lateral group of ocelli in the *Dytiscus* larva, as shown by Günther (1912; Korschelt, 1924), is more primitive in structure than the other ocelli. The organ lies immediately beneath the cuticula (Fig. 281 C) and has no cuticular lens. The corneagenous cells (*CgCls*), however, form a continuous layer between the cuticula and the sense cells (*SCls*) and enclose a small mass of vitreous cells (*CB*) evidently representing the crystalline body. The structure of this ocellus may be supposed to represent an arrested early stage in the development of the other ocelli.

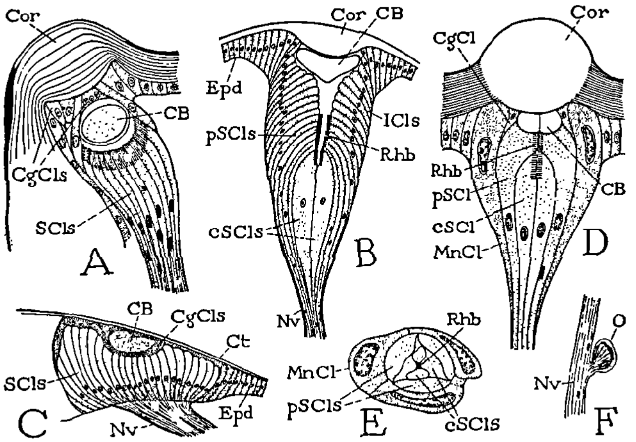

Fig. 281.—Lateral ocelli of holometabolous larvae. A, *Mermeleon.* B, *Dytiscus,* section through short axis of ocellus. C, rudimentary ocellus of *Dytiscus* larva. D, diagram of ocellus of a caterpillar. E, horizontal section of ocellus of *Arctia caja.* F, degenerating larval ocellus of *Dytiscus* attached to nerve strand of compound eye. (A, E *from Hesse,* 1901; B, C, F *from Günther,* 1912; D, *based on Pankrath,* 1890, *and Hesse,* 1901.) *CB,* crystalline body; *cSCls,* central sense cells; *ICls,* iris cells; *MnCl,* mantle cell; *pSCls,* peripheral sense cells.

The lateral ocelli of trichopterous and lepidopterous larvae have the same type of structure as those of the *Dytiscus* larva, but the cellular elements of each eye are fewer in number, and the lumen is obliterated by a contiguity of the inner ends of the retinal cells (Fig. 281 D). Lying immediately beneath the thick cuticular lens (*Cor*) is a small oval crystalline body (*CB*). The corneagenous cells (*CgCl*) lie at the sides of the crystalline body, and those at the periphery form long mantle cells (*MnCl*) surrounding the retina. The retina consists of a central group of vertical cells (*cSCl*), and of peripheral cells (*pSCl*) convergent distally over the central cells. The rhabdomeres of all the retinal cells form an axial rhabdom (*Rhb*) beneath the crystalline body. In a horizontal section through the distal part of the retina (E), the retinal cells appear as two concentric cell groups surrounding the rhabdom, there being four cells in the central group (*cSCls*), and three in the peripheral group (*pSCls*). Surrounding the sensory cells are three large corneagenous mantle cells (*MnCl*) ensheathing the retina. The eyes of the caterpillar closely resemble in structure the lateral eyes of certain Apterygota.

Simple Lateral Eyes of Adult Insects.—Certain adult insects, both apterygote and pterygote, are provided with simple lateral eyes in place of compound eyes. These eyes usually occur in groups, but their structure, though variable, never closely resembles that of an ommatidium of a typical compound eye.

Among the Apterygota simple lateral eyes are found in Collembola and in Lepismatidae. Those of Collembola form a group on each side of the head, the number of ocelli in each group being variable but never more than eight. The cuticula is elevated in a simple dome-shaped cornea over each eye (Fig. 282 A, *Cor*). Beneath the cornea are two flat corneagenous cells (*CgCl*), which cover the outer surface of a large spherical crystalline body (*CB*). The crystalline body of *Orchesella*, Hesse (1901) says, shows no evidence of cellular structure except for indistinct traces of nuclei, but in *Podura*, according to Willem (1900), the body consists of four crystalline cells. The retina has the form of a cellular pocket beneath the crystalline body, composed of four distal, or peripheral, cells (*pSCl*) and of three proximal central cells (*cSCl*). The retinal cells have striated borders directed toward the lumen of the eye, but they do not form a true rhabdom. Dense masses of pigment (*Pig*) surround the crystalline body and the receptive parts of the retinal cells.

In *Lepisma*, as described by Hesse (1901), each lateral eye consists of a complex of 12 simple eyes separated by a few intermediate pigmented epidermal cells. The cornea forms a biconvex lens over each eye (Fig. 282 B, *Cor*). Immediately beneath the center of the lens is a crystalline body (*CB*) composed of four distinct vitreous cells. Two corneagenous cells (*CgCl*) surround the crystalline body but are only slightly inserted between the latter and the lens. The retina is made up of four peripheral cells (*pSCl*) and three central cells (*cSCl*), the former being convergent distally beyond the central cells. Each retinal cell has a rhabdomere (*a*) on its inner surface, and the seven rhabdomeres compose a hollow axial rhabdom.

The adult eyes of Collembola and *Lepisma* are thus seen to be very similar to the larval eyes of Lepidoptera (Fig. 281 D), with the exception that the latter have three cells in the peripheral group of retinal cells and four in the central group (E), the number being the reverse in the apterygote forms. The eyes of both Collembola and *Lepisma*, however, have two features characteristic of compound eyes, namely, the presence of only two corneagenous cells in each eye, and of four component cells in the crystalline body. For this reason some writers claim that these composite simple eyes are dissociated and more or less degenerate ommatidia of compound eyes. In the Arachnida and Myriapoda also, groups of simple lateral eyes replace the compound eyes of the more primitive xiphosurans, eurypterids, and certain extinct myriapods. The relation of the various forms of lateral arthropod eyes to one another is not known, but it seems probable that they are simply different modes of development proceeding from a common lateral eye fundament with its nerve roots in the lateral optic lobe of the brain.

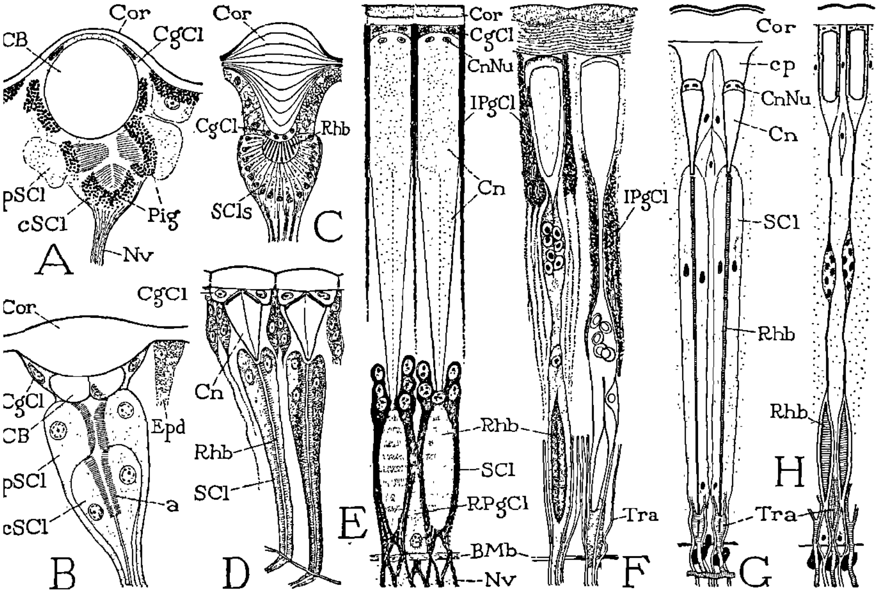

FIG. 282.—Lateral eyes of adult arthropods. A, single eye of lateral group of eyes *Orchesella rufescens.* B, single eye of composite lateral eye of *Lepisma saccharina.* C, single eye of composite lateral eye of *Xenos rossii.* D, two ommatidia of compound eye of *Machilis.* E, two ommatidia of compound eye of *Astacus fluviatilis.* F, two ommatidia of compound eye of *Osmylus chrysopa.* G, diagram of ommatidia of appositional compound eye of diurnal Lepidoptera. H, diagram of ommatidia of superpositional eye of nocturnal Lepidoptera. (A, B, D *from Hesse,* 1901; C *from Strohm,* 1910; E *from Bernhards,* 1916; F *from Ast,* 1920; G, H *from Nowikoff,* 1931.)

The Siphonaptera have two small simple eyes in the adult stage, one on each side of the head, near the usual position of the compound eyes, the latter being absent in the fleas. The structure of these lateral eyes of the flea, as shown by Hesse (1901), resembles that of the usual dorsal ocelli of other insects. Each eye has a single biconvex lens, beneath which are long cells reaching, as in the ocellus of *Machilis,* from the base of the eye to the lens. These cells are evidently the sense cells, though they do not form rhabdoms. Between their outer ends are a few small corneagenous cells. The entire inner part of the eye is invested in a pigmented sheath. It has been supposed that these lateral ocelli of the adult flea are the lateral dorsal ocelli transposed to the sides of the head, but their true nature cannot be decided until the source of their innervation is known.

Lateral eyes unquestionably of an ocellar structure occur in some adult Strepsiptera. The males of *Xenos rossi*, as described by Strohm (1910), have a large projecting composite eye on each side of the head composed of about 50 closely appressed simple eyes. The individual lenses are large and each has a long peglike projection on the inner surface (Fig. 282 C) surrounded by a pigmented fold of the epidermis. Beneath the lens is a nucleated corneagenous epithelium (*CgCl*) in which cell boundaries are lost. The retina consists of about 50 to 55 slender cells with hexagonal rhabdoms among their distal ends converging toward the inner surface of the lens. The eye elements of *Xenos*, Strohm contends, are not ommatidia but are "ocellar compound eyes," since the structure of each is that of a typical ocellus.

Simple eyes of the structure above described should not be confused with reduced compound eyes, which may consist of only a few ommatidia, or even a single ommatidium, as in certain worker ants.

The Compound Eyes.—Compound eyes are an ancient heritage of the Arthropoda. They were possessed by the trilobites and the eurypterids; among modern forms they have descended to the xiphosurans, on the one hand, and to the crustaceans and the insects, on the other. In modern arachnids and myriapods the compound eyes have been replaced by groups of lateral simple eyes, but certain Permian diplopods are said to have had well-developed compound eyes. It is not to be supposed, however, that the compound eyes of primitive arthropods closely resembled the highly organized compound eyes of modern crustaceans and insects. The compound eyes of *Xiphosura* are comparatively very simple structures, each consisting of a large cornea with numerous peglike processes on its inner surface, beneath which are corresponding groups of rhabdom-forming epidermal sense cells. The origin of the compound eye is lost in antiquity, since the trilobites are the oldest of known arthropods. In its ontogeny the compound eye is formed directly by the differentiation of its cellular elements from the lateral ocular region of the epidermis; in its growth it enlarges by the addition of new elements to its margin.

A typical, fully developed compound eye is present only in Crustacea and Insecta. Among the insects such eyes occur in Machilidae and in nearly all the Pterygota. In Collembola, Lepismatidae, Strepsiptera, Siphonaptera, and holometabolous larvae, the site of the compound eyes is occupied by simple lateral eyes. In a few apterygote and pterygote insects lateral eyes are entirely suppressed.

A compound eye is made up of individual eye elements known as *ommatidia* (Fig. 283 A, B). Each ommatidium includes a cylindrical group of elongate sense cells, the *retinula* (A, *Ret*), enclosing a long axial rhabdom (*Rhb*), and has an individual dioptric apparatus formed of a corneal lens (*Cor*) and a vitreous body, the latter being typically a *crystalline cone* (*Cn*). The cone is surrounded by two pigmented corneagenous cells (*CgCl*), and the entire ommatidium is more or less isolated by a sheath of epidermal pigment cells (*PgCls*). The tapering proximal ends of the retinula cells penetrate the basement membrane (membrana fenestrata) and become the optic nerve fibers (*Nv*), which end in the lamina ganglionaris (*I*) of the optic lobe of the brain. Generally the inner surface of the eye has an even contour limited by the basement membrane, but in the dorsal eyes of the male of *Simulium*, as described by Dietrich (1909), each retinula protrudes as a long free process at the base of the eye.

The margin of the corneal surface of the eye is usually surrounded by an apodemal inflection of the head wall, which forms a collarlike ocular ridge surrounding the retina (Fig. 283 A, *OR*). The external groove of the ridge is the ocular suture (*os*), and the narrow rim of the head wall next to the eye (*OSc*) is the so-called ocular sclerite (Fig. 57 A). The lenses of the cornea are sixsided in insects, though they may be quadrate in Crustacea, and give the cornea its faceted appearance. If the ommatidial lenses are convex externally, they form elevations on the general corneal surface corresponding to the positions of the ommatidia, but in some insects the outer surface of the cornea is smooth, and the lenticular swellings are internal. The number of facets in the cornea varies greatly in different insects according to the number of ommatidia in the eye. Usually there are from a few hundred to several thousand; the maximum, in Odonata, has been estimated as being close to thirty thousand. The surface of the compound eye is generally bare, but in some insects setiform hairs are borne on the interspaces between the lenses.

The several elements of an ommatidium vary considerably in their structure, but their principal modifications may be briefly stated.

The Lens.—Each ommatidial lens is typically biconvex, but it may be planoconvex and is sometimes but little rounded on either surface. It is often very thick and probably has a protective as well as a dioptric function. In many Lepidoptera the inner surface of each lens is produced in a long transparent corneal process (Fig. 282 G, *cp*). The lens is a cuticular product of the corneagenous cells and generally shows a laminated structure in cross section.

The Corneagenous Cells.—The corneagenous cells of the compound eyes are invariably found to be only two in number. Usually in the mature eye they lie at the sides of the crystalline cone and are densely pigmented, for which reason they are known as the primary pigment cells (*Hauptpigmentzellen*). In *Machilis* (Fig. 282 D) and in Crustacea (E), however, the corneagenous cells (*CgCl*) are inserted between the lens and the base of the cone. This is undoubtedly their primitive position, and it has been observed that in developmental stages of exopterygote insects the corneagenous cells temporarily assume this position at the beginning of each instar in order to regenerate the cornea. The Crustacea moult throughout life and their corneagenous cells, therefore, retain the normal position beneath the lens.

The Crystalline Cone.—The crystalline body of the compound eye, both in insects and in Crustacea, is formed of four cells. Though the structure is typically a crystalline cone, with its base against the lens and its apex in proximity to the distal end of the rhabdom (Fig. 283 B), it is not produced in the same way in all insects, and in some it is imperfectly developed. The cone cells, sometimes called the cells of Semper after their discoverer, are probably specialized corneagenous cells. The cone varies somewhat in relative size among insects, in some Crustacea it is very long as compared with the length of the retina (Fig. 282 E), and it is not always strictly conical in shape.

According to whether the cone cells form a true conical structure or not, and according to the manner in which the cone, when typically present, is produced by the cone cells, the compound eyes of insects are classed as *acone eyes*, *eucone eyes*, and *pseudocone eyes*. The characteristic and variable features of these three kinds of eyes are summarized by Weber (1933) as follows: (1) In acone eyes the cone cells are present but they do not form a true cone. Either the plasma of the cells is entirely uniform (many Heteroptera, Nematocera, Brachycera, and some Coleoptera) or a part of it is transformed into a vitreous mass (Reduviidae, Silphidae, Bibionidae). (2) In the eucone type of eye the cone cells are almost completely transformed into a four-part crystalline cone (Fig. 283 B, C, *Cn*), leaving only a small plasmatic zone at the base of the latter containing the nuclei, and a thin plasmatic sheath investing the cone. This is the usual structure of the cone in the majority of insects. (3) In eyes of the pseudocone type the cone is an extracellular body formed by a vitreous secretion of the cone cells, the nucleated remnants of which in this case lie at the apex of the cone. The substance of the pseudocone either remains soft and clearly distinguishable from the cornea (many Cyclorrhapha) or becomes hard and optically continuous with the cornea, giving the impression that the eye is of the acone type (many Diptera and some Coleoptera).

It is evident that the degree of development of the cone and its manner of formation are not dependent on phylogenetic relationships. The eucone eye and the pseudocone eye, as Weber points out, are fundamentally different, since each forms the cone in a different way, but there is no sharp distinction between either of these types and the acone type.

The Retinula.—The retinal part of each ommatidium consists primarily of 8 elongate sense cells arranged in a cylindrical fascicle between the apex of the cone and the basement membrane of the eye (Fig. 283 A, *Ret,* B, *SCl*), though in rare cases as many as 10 and even 12 nuclei have been observed in the retinular fascicle. The rhabdomeres are on the apposed surfaces of the cells and together form an axial rhabdom (*Rhb*). In cross section a retinula appears as a rosette of cells surrounding the rhabdom (D). Generally the rhabdom is narrow and cylindrical in form (Fig. 282 D, G), but it is sometimes club shaped, or ellipsoid (E, F, H), and it may have a laminated appearance in sections.

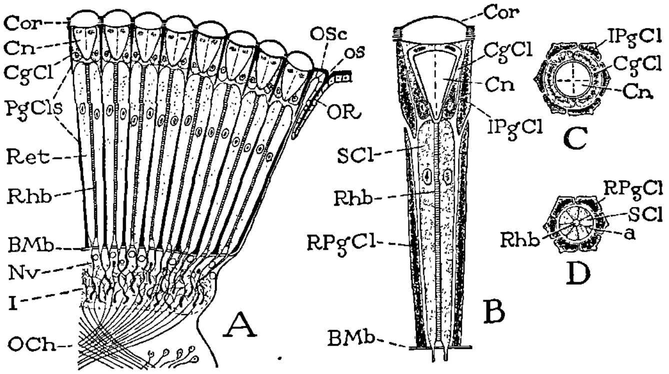

FIG. 283.—Structure of a compound eye, diagrammatic. A, vertical section of part of eye. B, typical structure of an ommatidium. C, horizontal section of ommatidium through cone. D, same through retinula. *a,* eccentric retinula cell; *BMb,* basement membrane (membrana fenestrata); *CgCl,* corneagenous cell; *Cn,* crystalline cone; *Cor,* corneal lens; *I,* lamina ganglionaris; *IPgCl,* iris pigment cell; *Nv,* nerve; *OCh,* outer chiasma; *OR,* ocular ridge; *os,* ocular suture; *OSc,* ocular sclerite; *PgCls,* pigment cells; *Ret,* retinula; *Rhb,* rhabdom; *RPgCl,* retinal pigment cell; *SCl,* sense cell (retinula cell).

The eight cells of the retinula are usually not equally developed along the entire length of the rhabdom. Generally one or two of them are reduced in the distal part of the retinula and are thus more or less restricted to the basal part, where at least the nuclei remain visible in sections. In many insects, however, one or both of the reduced cells disappear completely, and the retinula then contains only seven or six cells. In some of the Coleoptera one cell becomes reduced and finally eliminated from the retinula, while another takes a proximal position in the axis of the retinula, surrounded by the six other cells, and the base of the rhabdom is imbedded in the distal end of the axial cell. Or again, in certain insects, the retinula cells are more equally separated into a distal group and a proximal group.

In the Neuroptera and Lepidoptera the retinula of the compound eye becomes differentiated into two types of structure, one characteristic in general of day-flying species, the other of crepuscular and nocturnal species (see Johnas, 1911; Ast, 1920; Nowikoff, 1931). Eyes of the first type have cylindrical retinulae of the usual form, and long slender rhabdoms reaching from the apex of the cone to the base of the eye (Fig. 282 G). In eyes of the second type the retinula becomes more or less constricted between a distal part containing most of the retinular nuclei, and a proximal part containing one nucleus and the short, thick rhabdom (F). The distal part of the retinula, in such eyes, may be reduced to a mere filament (H), with a fusiform swelling in its course containing the distal nuclei. This modification is found in the eyes of nocturnal species and is an adaptation to the "superposition" principle of vision by compound eyes, since it allows the oblique rays of light from each cone to be thrown upon the rhabdoms of several surrounding ommatidia.

The Pigment Cells.—Each ommatidium is enclosed in a sheath of cells containing an abundance of dark pigment (Fig. 283 A, *PgCls*), by which it is optically more or less isolated from its neighbors. These cells are probably undifferentiated epidermal cells of the parts of the eye between the ommatidia. Usually there are two sets of them, an outer set having their bases on the cornea and reaching to the distal end of the retinula (B, *IPgCl*), and an inner set (*RPgCl*) resting on the basement membrane and extending a varying distance toward the distal end of the retinula. In cross sections, therefore, the outer pigment cells, or *iris pigment cells,* form a circle around the corneagenous cells (C, *IPgCl*), and the inner cells, or *retinal pigment cells,* encircle the retinula (D, *RPgCl*). The number of pigment cells surrounding an ommatidium varies from a few to many. In addition to these interommatidial pigment cells, as we have already observed, the corneagenous cells of the mature eye in pterygote insects become pigment cells ensheathing the crystalline cone (B, C, *CgCl*). The *corneagenous pigment cells* are often termed the primary pigment cells (*Hauptpigmentzellen*) of the iris, and the outer iris cells distinguished as the secondary or accessory pigment cells (*Nebenpigmentzellen*). Pigment also occurs abundantly in the retinula cells themselves.

Tracheae from the optic lobe penetrate the basement membrane of the eye and ramify between the retinal pigment cells. Here, in crepuscular and nocturnal species, they may form a dense network of fine branches (Fig. 282 H, *Tra*), constituting a tracheal tapetum that reflects light from the walls of the ommatidia back into the retina. In some of the Crustacea, as in *Astacus* (E), the retinal pigment cells (*RPgCl*) contain dense masses of a golden-brown pigment, which, however, reflects the light and thus forms a pigment tapetum.

In the eyes of diurnal insects the retinulae are generally entirely surrounded by pigment, so that each ommatidium is an optically isolated element of the eye. In such eyes only perpendicular light rays passing the dioptric apparatus affect the retina through the rhabdom, oblique rays being absorbed in the pigmented walls of the ommatidium. Thus the light from any part of an external object stimulates a retinula directly opposite to it in the eye. The result is that the stimulated area in the retina represents a mosaic pattern of the points of the object reflected into the eye. An eye that works on this principle is termed an *apposition eye.* On the other hand, in eyes that function in dim light, pigment is restricted to the iris region and to the basal parts of the retina. In such eyes there is no light wasted by absorption, since oblique rays entering any one ommatidium may pass into neighboring ommatidia and there become effective stimuli. Eyes of this type are distinguished as *superposition eyes.*

The eyes of insects have no focusing mechanism and no mechanical means of adaptation to different degrees of light. In many insects, however, an adaptation to light intensities is effected by changes in the extent of the pigmented areas. When the insect is brought from the dark into the light, the pigment moves outward in the retinal pigment cells or extends inward in the iris cells (Fig. 282 F, *right*) but retreats again when the insect is placed in the dark (F, *left*). The eye thus becomes accommodated to the amount of light by changing from the appositional to the superpositional condition. A permanent structural adaptation to dim light may be brought about, as shown in nocturnal Lepidoptera (Fig. 282 H), by the differentiation of the retina into a distal nonsensitive part in an unpigmented region of the eye and into a proximal sensitive part containing the rhabdoms. In the clear distal part of the eye there is a free crossing over of oblique light rays from one ommatidium to another.

The ommatidia are often different in two areas of the same eye. They may differ in diameter and in optical construction, and the two sets may be quite apparent on the exterior of the eye, or even so distinctly separated that the eye becomes double. In some cases one part of a divided eye is dorsal and the other ventral.

The optical mechanism of the compound eye is a subject that has been much discussed and is perhaps fairly well known, but we are far from understanding the physiological and "psychological" effects of light on the insect. Experiments show that insects distinguish in their reactions variations of light intensity, color, form, and distance, but there is no doubt that the compound eyes function most effectively for the perception of motion in external objects.

GLOSSARY OF TERMS APPLIED TO THE SENSE ORGANS

Cap Cell (*CpCl*).—The distal or peripheral cell of a sense organ, or of one of the component units of the organ, probably corresponding to the tormogen, or socket-forming cell of a seta. (*Deckzelle.*)

Chemoreceptor.—A sense organ supposedly sensitive to chemical properties of matter (a "taste" receptor or an "odor" receptor).

Chordotonal Organ.—A sense organ of the scolopophorous type, the cellular elements forming an elongate structure attached at both ends to the body wall, but not necessarily containing sense rods, or scolopes.

Compound Eye (*E*).—A composite optic organ having a dioptric apparatus for each receptive unit.

Cone (*Cn*).—The usually conical crystalline body of a compound eye.

Cornea (*Cor*).—The cuticular part of an eye.

Corneagenous Cells (*CgCls*).—The epidermal cells that generate the cornea.

Crystalline Body.—A transparent subcorneal part of the dioptric apparatus of an eye, formed of cells or of cell products, having an oval or conical shape. (*Vitreous body, crystalline cone.*)

Dioptric Apparatus.—The outer transparent part of an optic organ, consisting of the cornea and usually of a subcorneal crystalline body.

Distal Process.—The peripheral process of a sense cell.

Enveloping Cell (*ECl*).—The intermediate cell of a sense organ, or of one of the component sensory units of the organ, probably corresponding to the trichogen of a seta. (*Hüllzelle.*)

Eye.—In general a photoreceptor, but usually meaning one of the more complex types of light-perceptive organs.

Iris.—Dark pigment surrounding the dioptric apparatus of an eye.

Iris Pigment Cells.—Cells containing the iris pigment.

Johnstonian Organ.—An organ of the scolopophorous type located in the second segment, or pedicel, of the antennae of nearly all insects.

Lens (*Ln*).—A lenticular outer part of the eye, generally formed of the cornea.

Ocellus (*O*).—A simple eye, or photoreceptor having a single dioptric apparatus, including the dorsal ocelli, and lateral ocelli (stemmata).

Ommatidium.—One of the component units of a compound eye.

Phonoreceptor.—A sense organ responsive to sound.

Photoreceptor.—A sense organ responsive to light.

Pore Canal.—The channel of the cuticula beneath the seta or other external part of many sense organs.

Receptive Apparatus.—The part of a sense organ primarily responsive to the stimulus transmitted by or through the peripheral parts, formed of the sense cell or cells.

Retina (*Ret*).—The receptive apparatus of an eye.

Retina Cells.—The cells composing the retina.

Retinal Pigment Cells (*RPgCls*).—Pigment cells in the retinal region of the eye.

Retinula.—The group of retinal cells in a single ommatidium of a compound eye.

Rhabdom (*Rhb*).—A rodlike structure formed of the united sensory borders of adjacent retina cells.

Rhabdomere.—The receptive area of a retina cell that is one of the component parts of a rhabdom.

Scolops, Scolopale (*SR*).—A "sense rod," or minute rodlike capsule enveloping the distal end of the sense cell in certain sense organs. (*Stift.*)

Sense Cell (*SCl*).—The receptive cell of a sense organ, with a proximal nerve process going to a nerve center.

Sensillum.—A simple sense organ, or one of the structural units of a compound sense organ.

Sensillum basiconicum.—A sense organ of which the external part has the form of a minute projecting cone or peg.

Sensillum campaniformium.—A sense organ without an external process, in which the cuticular part has typically the form of a bell or hollow cone receiving the distal process of the sense cell.

Sensillum chaeticum.—A sense organ of which the external part is spine-like.

Sensillum coeloconicum.—A sense organ in which the external process is sunken in a cavity of the body wall.

Sensillum opticum.—A photoreceptor of the eye type of structure, or one of the ommatidia of a compound eye.

Sensillum placodeum.—A sense organ having a flat, plate-like external part.

Sensillum scolopophorum.—A sense organ in which the sense cells contain "sense rods" of the scolops type.

Sensillum squamiformium.—A sense organ of which the external part is scale-like in shape.

Sensillum trichodeum.—A sense organ of which the external part is a seta.

Stemmata.—A name sometimes given to the lateral ocelli of holometabolous larvae, which are often arranged in a circle.

Tangoreceptor.—A sense organ responsive to touch.

Tapetum (*Tap*).—A reflecting surface within an eye, formed either of pigment or of densely massed tracheae.

Vitreous Body (*CB*).—See *crystalline body.*

CHAPTER XVIII

THE INTERNAL ORGANS OF REPRODUCTION

The reproductive organs differ from all the other organs of the body in that their functions do not contribute primarily to the welfare of the individual of which they are a part; their chief concern lies with the succeeding generation. On the other hand, many of the activities of the organism must be correlated with the reproductive functions. This correlation is largely brought about in vertebrate animals by the secretion of hormones in the gonads, but with insects there is no evidence that the reproductive organs have a regulatory effect on the activities of the body organs or on the development of secondary sexual characters.

The reproductive system of insects is a complex of organs derived from three anatomical sources. Its parts, therefore, may be classed in three morphological groups as follows: (1) primary internal mesodermal organs, (2) secondary ectodermal parts, produced from invaginations of the body wall, forming the usual exit apparatus; and (3) external appendicular structures. In a study of the reproductive system, however, it will be found more convenient to divide the subject into *internal genitalia* and *external genitalia*, each division including some of the parts classed above in the second group. The internal genitalia serve to lodge the germ cells, to provide for their nutrition, and to furnish them a protected space within the body where they may undergo a part or all of the development that brings them to a stage ready for conjugation; they include devices for insuring fertilization, and glands for the production of mucous or an adhesive or protective medium; and, finally, they discharge the germ cells from the body at the proper time. The external genitalia accomplish the union between the sexes and enable the female to deposit the eggs according to the manner fixed in the instinct of each particular species.

Insects, with rare exceptions, are bisexual, in so far as the male and female germ cells are matured in separate individuals; but in some species males are not known to exist, and parthenogenesis is of frequent occurrence, the unfertilized eggs in some cases producing males, in other females. A condition approaching hermaphroditism is said to occur in a species of Plecoptera, *Perla marginata*. In the male organs of this insect, illustrated by Schoenemund (1912), the genital ducts are united in a transverse arch, as they are also in the female, and in young males the median part of the arch bears, between two lateral groups of sperm tubules, a number of smaller tubules containing egglike cells. These "male eggs," however, in the diploid stage, according to Junker (1923), have the same chromosome formula as the sperm cells, each being provided with two unlike heterochromosomes, and, though they undergo a partial development like that of a normal egg cell, they never reach maturity, and the tubules containing them degenerate when the insect approaches the time for transformation to the adult.

The occurrence of functional hermaphoditism has been demonstrated by Hughes-Schrader to occur in the cottony-cushion scale *Icerya purchasi*, in which, she says (1930), the so-called females "are in reality hermaphrodites capable of self-fertilization of their own eggs by their own sperm." The gonad of these hermaphroditic females, which are diploid in chromosome constitution, is primarily a pair of ovaries united anteriorly above the alimentary canal. The organ at an early stage contains no lumen, and in the first instar some of its central cells become reduced to the haploid condition and proliferate a solid central core of haploid cells. The outer cells of the gonad remain diploid and form the ovarioles with their contained oöcytes and nurse cells. The central haploid cells develop into spermatozoa. The oöcytes undergo normal maturation, resulting in haploid ova, and when the latter are fertilized they give rise to diploid hermaphrodites; unfertilized eggs develop parthenogenetically into haploid males. Males of this species are rare; they have been observed to copulate with the females, but it is not known that they accomplish fertilization.

The majority of insects are amphigonous and oviparous. The spermatozoa are stored in a receptacle of the female at the time of mating. The eggs in most cases are fertilized as they are extruded from the oviduct and thus undergo their entire development outside the body of the female. Viviparity, however, is of frequent occurrence among insects of various orders, the eggs, or even the larvae, being retained within the body of the female where they complete a part or all of their development. Usually, in such cases, the egg is deposited just before the time of hatching and almost immediately gives issue to an active young insect. Hatching may take place, however, within the egg passage of the female, where the larva then spends a varying length of time before its extrusion, as in the viviparous Diptera that give birth to living maggots. In the tsetse fly and Hippoboscidae the larva completes its development within the body of the parent female and pupates on emergence.

In the viviparous Diptera the developing egg or larva is retained in a dilatation (uterus) of the vaginal section of the median egg passage (Fig. 290 E, *Utrs*), where in pupiparous forms the larva is nourished from special glands (Fig. 291). In other cases, however, as in viviparous Aphididae and Coccidae, and in the viviparous beetle *Chrysomela varians*, the embryos are developed within the egg tubes of the ovaries. Probably in most cases development within the ovaries is parthenogenetic, but the eggs of *Chrysomela varians*, according to Rethfeldt (1924), are fertilized in the egg follicles by spermatozoa that travel upward into the ovarial tubes. The female of this beetle has no sperm receptacle, and copulation takes place during immature stages.

1. THE FEMALE ORGANS

The essential parts of the reproductive system in female insects (Fig. 284 A) consist of a pair of *ovaries* (*Ov*), two *lateral oviducts* (*Odl*) converging posteriorly from the ovaries, and generally a *median oviduct*, or *oviductus communis* (*Odc*), receiving the lateral ducts anteriorly, and opening posteriorly to the exterior at the *gonopore* (*Gpr*). In addition to these primary parts, there are usually a saclike *receptaculum seminis*, or *spermatheca* (*Spt*), for the reception and storage of the spermatozoa, a pair of *accessory glands* (*AcGl*) having various functions, and a copulatory pouch of the body wall, which is either an open *genital chamber* (*GC*), or a tubular exit passage from the median oviduct, known as the *vagina*.

The Ovaries.—Each ovary, in most insects, consists of a group of cylindrical or tapering units, the *ovarioles* (Fig. 284 A, *Ovl*), which ordinarily converge upon the anterior end of the corresponding lateral oviduct (*Odl*), though in many of the more generalized insects the ovarioles of each ovary arise serially from one side of the oviduct (Figs. 287, 290 A). The anterior parts of the ovarioles consist of threadlike filaments, and usually all the ovariole filaments in each ovary are united distally with one another in a *suspensory ligament* (Fig. 284 A, *Lg*). The ligament may end in the neighboring fat tissue, but generally it is attached either to the body wall or to the dorsal diaphragm. In some cases the ligaments from the two ovaries are combined in a single *median ligament*, which is inserted in the ventral wall of the dorsal blood vessel. In young stages the entire ovary is usually incased in a *peritoneal sheath* of adventitious connective tissue; in the adult this sheath is generally absent, though it may be retained, as in some Diptera (Fig. 290 F), in the form of a membrane enveloping the ovarioles.

The number of ovarioles in an ovary varies greatly in different insects. Usually it is not large, four, six, or eight ovarioles being perhaps typical, but in some Hymenoptera and Diptera the number may be increased to 100 or even 200, and in the Isoptera it is said to reach 2,400 or more. On the other hand, the number of ovarioles may be reduced to two or to one (Fig. 290 B, E).

Structure of an Ovariole.—A typical ovariole (Fig. 284 B) consists of three parts: a *terminal filament* (*TF*), an *egg tube* (*ET*), and a supporting stalk, or *pedicel* (*Pdcl*). The principal part is the egg tube, which contains the germ cells and their derivatives; the terminal filament continued from the anterior end of the egg tube is a part of the suspensorial apparatus of the ovary; the pedicel is the ovariole duct uniting the egg tube with the lateral oviduct.

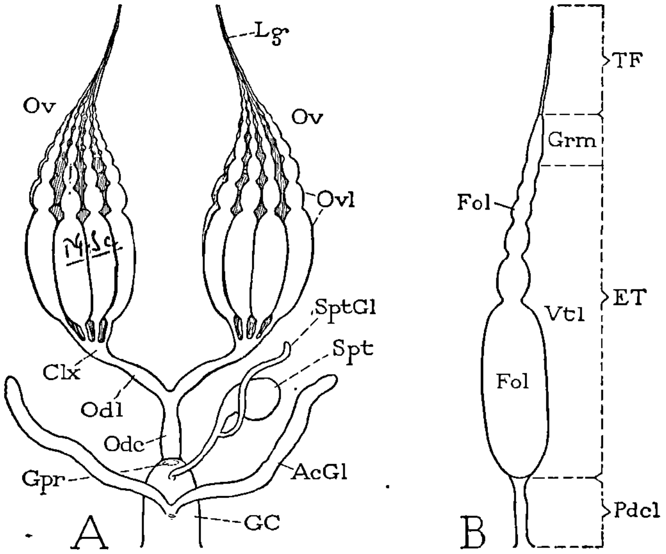

Fig. 284.—Structure of the female reproductive organs. A, diagram of the ovaries, exit ducts, and associated structures. B, diagram of an ovariole. *AcGl*, accessory gland; *Clx*, calyx; *ET*, egg tube; *Fol*, follicle, or egg chamber; *GC*, genital chamber (vagina); *Gpr*, gonopore; *Grm*, germarium; *Lg*, ovarial ligament; *Odc*, oviductus communis; *Odl*, oviductus lateralis; *Ov*, ovary; *Ovl*, ovariole; *Pdcl*, ovariole pedicel; *Spt*, spermatheca; *SptGl*, spermathecal gland; *TF*, terminal filament; *Vtl*, vitellarium.

The usual covering of an ovariole is a thin structureless membrane, known as the *tunica propria* (Fig. 285 C, *Tp*), which stretches over the terminal filament, the egg tube, and the pedicel. In some insects, however, there is to be seen outside the tunica an *epithelial sheath* of flat cells. This outer cellular sheath is generally better developed in younger stages of the ovary (B, *ESh*). It is sometimes regarded as a connective tissue layer, but according to K. Schneider (1917) its cells in the moth *Deilephila* originate within the body of the embryonic gonad. The epithelial sheath, therefore, is probably of mesodermal origin and represents the original mesodermal wall of the gonad. In early developmental stages it is continuous over the entire ovarial rudiment; but when the latter becomes divided into compartments that are to form the definitive ovarioles, the epithelial sheath is inflected between the lobes and eventually forms a covering about each ovariole.

The Terminal Filament.—The slender, threadlike filament that forms the anterior part of an ovariole (Fig. 248 B, *TF*) is a solid strand of cells (Fig. 285 C) ensheathed in the tunica propria (*Tp*). The group of terminal filaments in each ovary is derived from the embryonic sheet of mesoderm by which the primitive ovarial rudiment was suspended from the splanchnic wall of the coelom (Fig. 294 E, *a*), and, as we have seen, the terminal filaments form in the adult the suspensory apparatus of the mature ovary. In some insects the terminal filaments are not united with one another, and in a few cases they are absent.

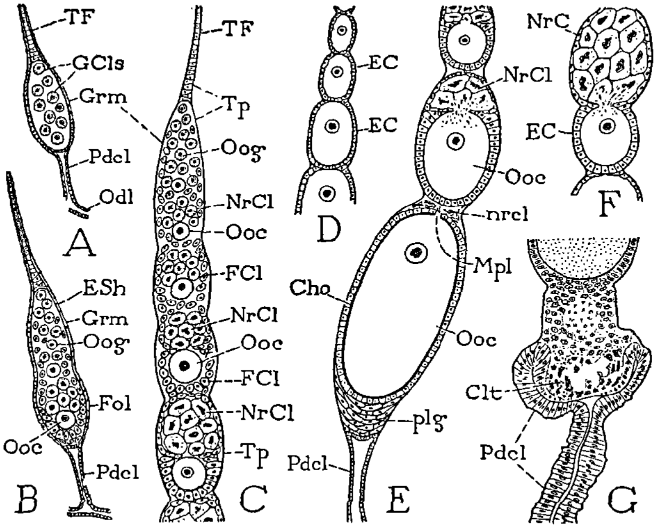

FIG. 285.—Histology of an ovariole, mostly diagrammatic. A, B, C, stages in the development of an ovariole. D, ovariole egg chambers containing oocytes only. E, each egg chamber containing an oocyte and nurse cells. F, alternation of egg chambers and nutritive chambers. G, lower end of an egg tube from which an egg has been discharged, *Dytiscus marginalis*. (*From Demandt*, 1912.) *Cho*, chorion; *Clt*, corpus luteum; *EC*, egg chamber; *ESh*, epithelial sheath; *FCl*, follicle cell; *GCls*, primary germ cells; *Mpl*, micropyle; *NrC*, nutritive chamber; *NrCl*, nurse cell; *nrcl*, remnants of nurse cells; *Ooc*, oocyte; *Oog*, oögonium; *plg*, epithelial plug; *Tp*, tunica propria. (Other lettering as on Fig. 284.)

The Egg Tube.—The middle section of an ovariole, the egg tube (Fig. 284 B, *ET*), represents the intermediate part of the embryonic gonad, which contains the germ cells (Fig. 294 E, *Grm*). In the adult organ it is an elongate sac filled with a mass of cells (Fig. 285 C) derived from the germinal elements, some of which become the ova. The wall of the egg tube is formed of the tunica propria (*Tp*), outside which there may be a cellular epithelial sheath, but the latter, as we have observed, is often not evident in adult insects. Most of the length of the egg tube is lined inside the tunica propria by a layer of *follicular epithelium* (*FCl*).

In each mature egg tube there are to be distinguished two principal parts. At the anterior end is a region containing the germ cells in an active state of division and incipient differentiation. This region is the *end chamber*, or *germarium* (Fig. 284 B, *Grm*). Beyond the germarium is the region in which the egg cells grow and attain their mature size. This part of the egg tube is the *zone of growth*, or *vitellarium* (*Vtl*).

The germarium represents the primary egg tube of the young ovary in which the germ cells are lodged (Fig. 285 A, *Grm*). The germ cells, however, soon develop into *oögonia* (C, *Oog*), and from the latter are formed the *oöcytes*, or young egg cells (*Ooc*), which are generally accompanied by nutritive *nurse cells* (*NrCl*). In the germarium there are usually also smaller cells, which become the *follicle cells* (*FCl*) in the lower part of the egg tube. In more general terms we may designate the follicle cells *cystocytes*, and the nutritive cells *trophocytes*, since both types of cells accompanying the true reproductive cells are found in various forms in both the ovary and the testis.

The vitellarium is formed during the development of the insect as an extension of the egg tube beyond the germarium (Fig. 285 B). It enlarges rapidly as the oöcytes multiply and mature and varies in length according to the number and size of the eggs it contains. At the upper end of the vitellarium the follicle cells take a peripheral position in the tube and show the beginning of a definite epithelial arrangement (C, *FCl*), while the oöcytes (*Ooc*) and nurse cells (*NrCl*) assume an axial position.

The growth of the oöcytes distends the vitellarium into a series of *egg chambers*, or *follicles* (Fig. 284 B, *Fol*), which become successively larger toward the posterior end of the tube. The follicular walls are formed by the follicle cells, which enclose each egg, or each egg and its accompanying nurse cells, in a cystlike sac. Beyond the last egg chamber a mass of follicle cells forms a "plug" that closes the rear end of the egg tube (Fig. 285 E, *plg*). Different types of ovarioles result from the presence or absence of nutritive cells or from differences in their position in the egg tube, but these modifications will be noted later.

Since the oöcytes are produced continuously from the oögonia, the first encysted oöcyte (Fig. 285 B, *Ooc*) becomes the lowermost and the first mature oöcyte in the vitellarium. With each successive addition of an oöcyte to the series the egg tube becomes lengthened between the last formed egg chamber and the germarium by a rapid multiplication of the follicle cells in this region. The ovarioles thus undergo a great increase in size during the growth period of the eggs, which is usually the early part of the imaginal stage of the insect.

The last egg in each egg tube, when fully formed, is usually abruptly larger than any of those preceding it and is enclosed in the chorion, but it is still in the oöcyte stage, since maturation does not ordinarily take place until the egg is laid. Hence it is not strictly proper to speak of the full-grown ovarial oöcytes as "mature" or "ripe" eggs. If an oöcyte is fully formed in all the ovarioles at the same time, the insect may deposit at one laying as many eggs as there are ovarioles in the ovaries. Some insects, however, such as the queen bee and the queen termite, eject the eggs singly in a continuous succession. With a few insects the full-grown oöcytes are produced alternately first in one ovary and then in the other. Finally, a large number of eggs may accumulate in the exit passages before they are discharged. Thus in Ephemerida and Acrididae the elongate calyx and wide lateral ducts (Fig. 287), prior to oviposition, become distended with eggs ready to be laid, and in some of the Lepidoptera the greatly lengthened pedicels of the ovarioles form storage tubes filled with long series of eggs, in which the latter are held until the moth is inseminated (Fig. 288).

The Ovariole Pedicel.—The pedicels, or stalks, of the ovarioles (Fig. 284 B, *Pdcl*) are short ducts connecting the egg tubes with the lateral oviduct. They are formed from the strand of mesodermal cells along the lower margin of the embryonic gonad (Fig. 294 E, *b*), which is continuous posteriorly with the primitive oviduct. Each pedicel develops a lumen communicating with that of the duct but closed at the upper end beneath the epithelial plug of the egg tube (Fig. 285 E). At the time the first egg is ready to be laid the cells of both the plug and the retaining wall of the pedicel are dissolved to open a passage through the pedicel from the egg tube into the oviduct. The walls of the mature pedicels consist of a simple elastic epithelium, and in some insects the muscle sheath of the oviduct is continued upon them.

The Trophic Function of the Egg Tubes.—The growth of the eggs in the ovary, which is mostly the accumulation of yolk, involves the utilization of much nutrient material. This material is supplied either from the daily food of the insect absorbed into the blood or from the food reserves stored in the body, principally in the fat tissue. With insects that do not feed in the imaginal stage, all the added egg material must be drawn from the latter source.

Since the eggs in the egg tubes do not have direct access to the nutrient elements of the blood, an important function of the ovary is that of an intermediate trophic organ between the blood and the eggs. It discharges this function in various ways. It is possible that the eggs in some cases utilize material that passes by diffusion directly through the walls of the ovarioles; but observations on the histology of the epithelial layer of follicle cells indicate that more generally the walls of the egg chambers play an active physiological role in the nutrition of the eggs. On the one hand, the follicular cells apparently absorb food material from the blood and elaborate it in their cytoplasm, while, on the other hand, either they discharge the products into the egg tubes, where the material is directly or indirectly taken up by the egg cells, or the highly nutritious plasma itself of the follicle cells is absorbed by the egg cells. The first process is the more usual one.

The structure of the egg tubes differs somewhat according to the manner in which the oöcytes are nourished. In general two principal types of structure are distinguished by the presence or absence of special nutritive cells within the follicular tubes. When there are no nutritive cells, an egg tube is classed as *panoistic* (that is, "all eggs"); when nutritive cells are present the tube is *meroistic* ("part eggs"). The meroistic type is again subdivided into two groups known as *polytrophic* and *acrotrophic* according to the position of the trophocytes in the egg tube.

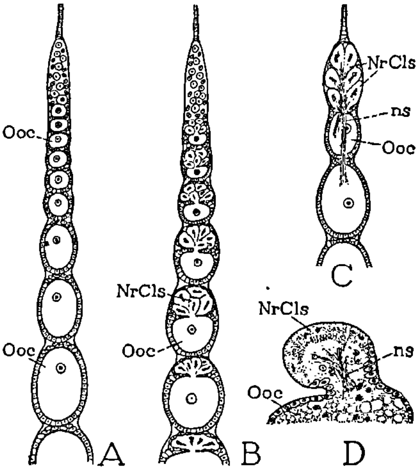

FIG. 286.—Three principal types of egg tubes, diagrammatic. A, panoistic type. B, polytrophic type. C, acrotrophic type. D, upper end of an acrotrophic ovariole of *Pseudococcus*. (*From Shinji*, 1919.)

The Panoistic Type of Egg Tube.—In an egg tube of this type there are no special nutritive cells differentiated from the egg cells; the food products elaborated by the follicular epithelium are absorbed directly by the oöcytes. There is within the vitellarium, therefore, only a series of egg cells (Fig. 286 A, *Ooc*), each of which is generally contained in a distinct follicular egg chamber. Insects having panoistic ovarioles occur in the Apterygota, Ephemerida, Odonata, Orthoptera, and Siphonaptera.

The Polytrophic Type of Egg Tube.—An egg tube of the polytrophic type contains an alternating succession of oöcytes and trophocytes (Fig. 286 B). In most cases the trophocytes, or nurse cells, are descendants along with the oöcytes from the oögonia, but in some insects they are said to be derived from the follicle cells.

Where the trophocytes are of germ-cell origin, the cells produced by the division of a single oögonium adhere in compact groups and maintain connections with one another in the form of protoplasmic strands. Only the most posterior cell in each group becomes a functional oöcyte (Fig. 286 B, *Ooc*); the others specialize in the trophic function and become differentiated as the nutritive cells (*NrCls*).

Usually there is a definite number of nurse cells to each oöcyte. In muscoid Diptera, according to Verhein (1921), the proportion is 16 to 1, while in the honey bee, according to Paulcke (1901), the ratio is 48 to 1. In the first case it would seem that the egg cell and the nurse cells are differentiated from the cells of the third generation produced from a single oögonium; in the second, the egg is one of the daughter cells of the first division, and the nurse cells the descendants of the other by four succeeding divisions. In *Deilephila euphorbiae,* it is said by K. Schneider (1917) that, of the five nurse cells accompanying each oöcyte, four are daughter cells of the oögonium and one a sister cell of the oöcyte. On the other hand, the number of nurse cells accompanying each egg may be highly variable, as in Carabidae, described by Kern (1912). In *Carabus violaceus* Kern found a maximum of 127 nurse cells with a single egg cell, and the total of 128 cells he presumes to have been produced by seven successive divisions from one oögonium.

The polytrophic type of egg tube is characteristic of Anoplura, Neuroptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera.

In some insects with polytrophic ovarioles, such as Coleoptera and Lepidoptera, each oöcyte and its accompanying nurse cells occupy the same ovariole chamber (Figs. 285 E, 286 B); in others there is an alternation of egg chambers and nutritive chambers (Fig. 285 F), the nutritive chambers in such cases being the larger in the upper parts of the tubes, while in the lower parts the size relation is the reverse owing to the growth of the egg at the expense of its nurse cells. The nurse cells at first increase in size presumably by absorbing material elaborated by the cells of the egg-tube walls. From histological studies it is generally evident that the oöcytes are nourished by an active streaming of the plasmatic contents of the nurse cells into the cytoplasm of the eggs along the strands originally connecting the cells in the group produced from a primary oögonium. When the oöcyte is mature, its nurse cells are exhausted and reduced to mere remnants in a state of degeneration (Fig. 285 E, *nrcl*).

The production of special groups of nutritive cells from the follicular epithelium has been described in Apterygota by Willem (1900), in the May beetle *Melolontha vulgaris* by Mollison (1904), in a moth, *Deilephila euphorbiae,* by K. Schneider (1917), and in Tenthredinidae by Peacock and Gresson (1928). In some of the Apterygota, according to Willem, the epithelial nurse cells form large protoplasmic masses of nutritive material in the egg tubes alternating with groups of oöcytes. Earlier students of these insects, Willem claims, mistook the egg cells for the nurse cells and regarded the masses of epithelial nutritive cells as the oöcytes. In *Melolontha,* as described by Mollison, the follicle cells of the egg tubes form a mass of nutritive cells in the upper part of each egg chamber, many of which become connected with the oöcyte by protoplasmic strands through which their contents are passed into the cytoplasm of the oöcyte. A similar condition is reported by Peacock and Gresson in Tenthredinidae, where certain cells of the egg follicles appear to become nutritive cells since the chromatin of their nuclei is discharged into the oöcytes.

The Acrotrophic Type of Egg Tube.—In a few insects, particularly in the Hemiptera and some Coleoptera, the cells produced with the oöcytes from the oögonia, but which are destined to become nurse cells, remain in the upper part of the egg tube (Fig. 286 C, D, *NrCls*), while the oöcytes become removed from them as the series of egg cells increases in the vitellarium. The original protoplasmic connections between the two sets of cells are maintained, however, as long plasmatic strands (*ns*) through which the oöcytes in the egg tube continue to receive the yolk-forming material from the nurse cells. The germarium in the acrotrophic type of egg tube, therefore, is also an apical feeding chamber for the oöcytes. A good illustration of the acrotrophic type of egg tube in Hemiptera is given by Malouf (1933).

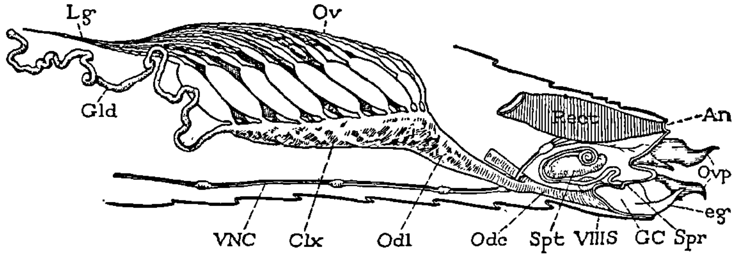

FIG. 287.—Female reproductive system of a grasshopper, *Dissosteira carolina*, lateral view. *eg*, egg guide; *GC*, genital chamber; *Spr*, spermathecal aperture; *Spt*, spermatheca.

Origin and Relation of the Cellular Elements of the Egg Tubes.—There has been much difference of opinion as to the derivation of the various cell groups composing an ovariole and found within the egg tube. The terminal filament, the outer epithelial sheath of the egg tube (which may be absent in the adult organ), and the pedicel are without doubt mesodermal parts of the ovariole derived from the primitive mesodermal covering of the germ cells. The tunica propria is probably a product or a remnant of the outer epithelial wall of the egg tube. The oögonia are direct descendants of the primary germ cells. The oöcytes and the usual trophocytes, or nurse cells that accompany the oöcytes, are produced from the oögonia by mitotic division and nuclear changes. The principal question of origin, then, pertains to the derivation of the follicular cells.

It is claimed by K. Schneider (1917) that in the moth *Deilephila* the ovarial follicle cells are proliferated anteriorly during the growth of the egg tube from the mass of cells that closes the posterior end of the tube. The origin of the posterior cells Schneider did not discover, but he asserts that only the oöcytes and the nurse cells are produced from the oögonia. There seems to be no question, however, that the generative cells of the follicle cells referred to by Schneider are of mesodermal origin. Seidel (1924) states definitely that the follicle cells of *Pyrrhocoris apterus* are formed from the epithelial cells of the upper ends of the pedicels, and more recently Lautenschlager (1932), in a study of the developing female organs of *Solenobia triquetrella* (Psychidae), finds that both the follicle cells and the posterior masses of cells that give rise to the ovariole pedicels are derived from the mesodermal sheath of the primitive gonad. It seems most probable, therefore, that the follicular egg tube, which, during the multiplication of the oöcytes, is interpolated between the germarium and the pedicel of the ovariole, is formed by cells proliferated from the upper end of the pedicel and is hence of mesodermal origin. Earlier investigators believed that the follicle cells are descendants of the oögonia along with the oöcytes and the usual trophocytes, though some claimed that they are derived from the mesodermal sheath of the gonad.

Formation of the Chorion and the Discharge of the Eggs.—The mouth of each egg tube, as we have seen, is closed behind the last oöcyte by a plug of the follicular epithelial cells, and the plug abuts against a transverse septum formed of the terminal wall of the ovariole pedicel (Fig. 285 E). The last oöcyte is thus completely enclosed in the follicular egg chamber and is prevented from escaping prematurely into the oviduct. When the egg is fully formed, the epithelium of the chamber begins a secretive activity producing a substance which is discharged upon the egg and there hardens to form the egg shell. This shell is the *chorion* (*Cho*). The substance of the chorion resembles in appearance the harder parts of the body wall cuticula, but it is invariably found to be nonchitinous. On its outer surface the chorion retains the marks of the cells that produced it in the form of a honeycomb pattern of fine ridges reproducing the outlines of the cells of the follicular wall. Only at the upper end of the egg is the chorion incomplete, there being left here a point not covered by the chorion deposit, which becomes the *micropyle* of the egg (E, *Mpl*), an opening in the shell through which the spermatozoa gain entrance to the interior of the egg. In some insects there are several apertures in the micropyle area.

When the egg is finally ready to be discharged from the ovary, the epithelial plug behind it and the adjoining wall of the pedicel degenerate and open a passage through which the egg slips into the lumen of the pedicel and then goes through the calyx, through the lateral oviduct, into the median oviduct, and finally reaches the exterior. As the egg passes the mouth of the spermathecal duct a small mass of spermatozoa is discharged upon its micropylar surface, and some of the spermatozoa here enter the egg. Thus the egg is inseminated just as it leaves the oviduct. It is usually deposited at once, but with some insects it is held a varying length of time in an external genital chamber of the female. The egg now undergoes its maturation divisions, and shortly thereafter a sperm nucleus unites with the nucleus of the ovum, and the fertilized egg is ready for development when external conditions are favorable.

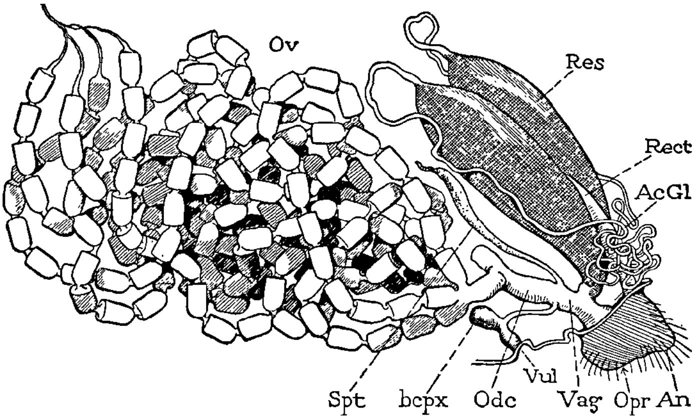

FIG. 288.—Female reproductive system of a moth, *Malacosoma americana*, lateral view. *An*, anus; *AcGl*, accessory glands; *bcpx*, bursa copulatrix; *Odc*, oviductus communis; *Opr*, oviporus (egg exit); *Ov*, ovary; *Res*, reservoir of accessory glands; *Spt*, spermatheca; *Vag*, vagina; *Vul*, vulva (copulatory opening).

After an egg has left the follicle, the walls of its chamber collapse. The epithelial cells, including the remnants of those that formed the closing plug, degenerate (Fig. 285 G) and are at last mostly dissolved and absorbed. The mass of degenerating cells in the lower end of an egg tube (*Clt*) is sometimes called a *corpus luteum* in reference to its likeness to the degenerating Graafian follicle of a vertebrate ovary. With the disappearance of the posterior chamber in the egg tube, the next oöcyte and its investing follicle assume a terminal position as the egg tube is lengthened by a growth in its cellular walls. The successive eggs thus probably do not literally pass down the egg tubes, as they are often said to do; more exactly, the tube shortens posteriorly by the degeneration of each emptied chamber and increases its length anteriorly by renewed growth to accommodate the newly forming oöcytes.

The Lateral Oviducts.—The ducts that lead posteriorly from the ovaries are probably for the most part the primary mesodermal exit tubes of the gonads, though in some of the higher insects the mesodermal ducts are largely or entirely replaced by ectodermal tubes formed as branches of the median oviduct. In the early developmental stages of many insects the lateral oviducts are attached posteriorly to the body wall at the posterior margin of the seventh abdominal venter; but it is only in the Ephemerida that the lateral ducts have their permanent openings in this position. With all other insects the lateral oviducts discharge into a median invagination of the body wall, which becomes the oviductus communis (Fig. 284 A, *Odc*). The anterior end of each lateral duct is generally somewhat expanded, forming a receptacle known as the calyx (*Clx*), into which open the pedicels of the ovarioles. When the ovarioles open serially into the oviduct the calyx is lengthened and may be greatly enlarged for the reception of the eggs (Fig. 287, *Clx*). Other than this the oviducts are generally simple tubes without accessory structures of any kind, though in the Acrididae the anterior end of each is prolonged into a tubular gland (Fig. 287, *Gld*). The cellular walls of the ducts are usually covered by a muscular sheath consisting of circular or longitudinal fibers or both.

The Oviductus communis.—The median oviduct is not a part of the primitive genital system; it belongs to the secondary exit apparatus formed as a series of invaginations of the body wall. The first rudiment of the oviductus communis is an ectodermal pouch behind the seventh abdominal sternum receiving the two approximated mesodermal lateral ducts (Fig. 289 A, *Odc'*). The median duct retains this primitive condition in Dermaptera, but in other insects it has been extended into the eighth segment (B, *Odc*) by the closure of a groove continued from it on the venter of the eighth segment. Generally the definitive median oviduct opens into an invagination of the body wall on the eighth segment, which is the genital chamber (Figs. 284 A, 287, 289 C, *GC*) or a derivative of the latter known as the vagina (Fig. 289 D, *Vag*).

The posterior opening of the median oviduct is the *female gonopore.* Primarily it is located on the rear part of the seventh abdominal segment (Fig. 289 A, *Gpr'*); but, by the posterior extension of the oviduct, it occurs generally at the posterior end of the eighth segment (B, *Gpr*), where usually it is concealed in the genital chamber (C, *GC*) or the vagina (D, *Vag*). The gonopore serves for the discharge of the eggs from the oviduct and is not a copulatory opening. It should be distinguished, therefore, from the *vulva,* which is the external opening of the genital chamber (C, *Vul*) or of the vagina (D, F).

The oviductus communis has a cuticular lining continuous with the cuticula of the body wall, and the entire epithelial tube is surrounded by a strong muscular sheath consisting of circular and longitudinal fibers. The length of the tube varies much in different insects, and its anterior end is sometimes bifurcate. In some insects branches of the median duct partially or entirely replace the mesodermal lateral ducts.

The Genital Chamber and Its Derivatives.—The median oviduct extended into the eighth segment does not ordinarily open directly to the exterior. Its aperture, the gonopore, is generally concealed in an inflection of the body wall behind the eighth sternum. The cavity thus formed is the *genital chamber* (Figs. 287, 289 C, *GC*). The genital chamber receives the median oviduct (*Odc*) and the duct of the spermatheca (*Spt*) into its anterior end. It serves as a copulatory pouch during mating and is therefore properly termed the *bursa copulatrix.* Its external opening is the *vulva* (Fig. 289 C, *Vul*). The genital chamber in its more primitive form is an open pocket of the body wall (Fig. 287, *GC*); but in many insects it becomes an internal pouch or takes the form of a tubular passage continuous with the median oviduct, in which case it is distinguished from the latter as the *vagina* (Fig. 289 D, *Vag*).

Since the vagina is a derivative of the genital chamber, it opens primarily on the posterior part of the eighth abdominal segment. In many insects, however, as in some Cicadidae, Panorpidae, most Trichoptera, Lepidoptera, and Coleoptera, the vagina is continued through the ninth segment and has acquired an opening on this segment (Fig. 289 E, F). In most such cases the primary anterior opening on the eighth segment is closed, and the posterior opening on the ninth segment becomes the functional vulva (F, *Vul*), serving both for copulation and for the discharge of the eggs. In the majority of Lepidoptera, however, the anterior aperture is retained as a copulatory opening (Figs. 288, 289 E, *Vul*). The posterior vaginal opening, serving only for the discharge of the eggs, may be distinguished in this case as the *oviporus* (*Opr*). The vulva of Lepidoptera having two genital openings leads into a passage connected with the vagina, which usually has a diverticulum (*bcpx*) serving as a copulatory pouch. The vagina, the seminal passage, and the copulatory pouch of the latter collectively represent the genital chamber of more generalized insects. The vagina is continuous with the median oviduct (*Odc*), and the spermatheca (*Spt*) opens dorsally into its anterior end. A similar condition exists in certain species of Cicadidae. It should be observed that, in the continuous egg passage, the point of union between the true oviduct and the vagina is marked approximately by the opening of the spermatheca into the anterior end of the latter.

Some confusion has arisen in the terminology of the female exit apparatus owing to a failure to distinguish between the true oviductus communis and the vagina, and because it has not been perceived that the vagina is a direct derivative of the genital chamber and not a continuation of the oviduct. When the genital chamber is an open external pocket of the body wall (Fig. 289 C, *GC*), the facts are clear, and it should be recognized that an internal pouch or tube receiving both the oviduct and the spermatheca, though called the "vagina" (D, E, F, *Vag*), is still the genital chamber or a part of it. Thus, in the Diptera, the saclike posterior part of the median egg passage (Fig. 290 F, *Vag*), receiving the spermathecal ducts (*Spt*) into its dorsal wall, and continuous anteriorly with the median oviduct (*Odc*), is the homologue of the open genital chamber of the Orthoptera (Fig. 287, *GC*). In the honey bee (Fig. 290 D) there is a shallow genital cavity concealed above the seventh abdominal sternum at the base of the sting, but from this external depression there open a large internal median pouch (*Vag*) and two lateral pouches (*P*). The median pouch is functionally the vagina, but the fact that both the spermatheca (*Spt*) and the oviduct (*Odc*) discharge into it shows that it is a part of the genital chamber (*GC*), as are also the lateral pouches.

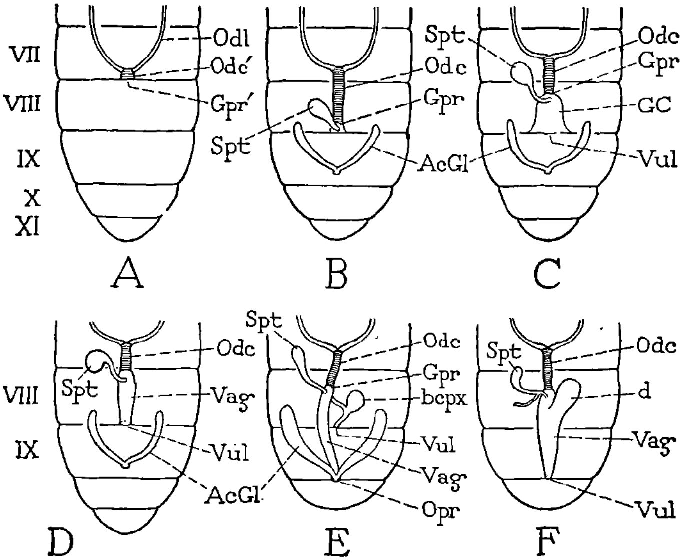

FIG. 289.—Diagrams illustrating the evolution of the median exit apparatus of the female reproductive system. A, primitive median gonopore (*Gpr′*) behind seventh abdominal segment. B, oviduct extended through eighth segment, definitive gonopore (*Gpr*) at end of this segment. C, genital chamber (*GC*) invaginated behind eighth segment. D, genital chamber converted into a vagina (*Vag*). E, vagina extended through ninth segment, but copulatory opening (*Vul*) retained on eighth. F, vagina extended through ninth segment, anterior opening lost, posterior opening becomes the vulva (*Vul*). *AcGl*, accessory gland; *bcpx*, bursa copulatrix; *d*, vaginal pouch; *GC*, genital chamber; *Gpr*, definitive gonopore; *Gpr′*, primitive median gonopore; *Odc*, oviductus communis; *Odc′*, primitive median oviduct; *Odl*, oviductus lateralis; *Opr*, oviporus; *Spt*, spermatheca; *Vag*, vagina (genital chamber); *Vul*, copulatory opening, or vulva.

In the viviparous Diptera the anterior part of the genital chamber forms a pouch known as the *uterus* (Fig. 290 E, *Utrs*), into the anterior end of which open the oviduct (*Odc*), the ducts of the spermathecae (*Spt*), and the accessory glands (*AcGl*). The egg is fertilized and in some species hatched, and the larva retained a varying length of time, even to maturity, within the uterus, where it may be fed from the secretion of the accessory glands (Fig. 291). Keilin (1916) distinguishes two groups of viviparous flies according to whether the larva receives no nourishment from the mother or is fed from uterine glands. With some species of the first group the egg is extruded from the uterus, but the larva hatches as oviposition occurs; in others hatching takes place within the uterus and the larva passes the first stage or several stages of its life in the uterine chamber. In the second group, including the tsetse fly *Glossina* and the Hippoboscidae, in which the larva is nourished within the uterus (Fig. 291), the young insect is deposited as a full-grown larva or as a pupa.

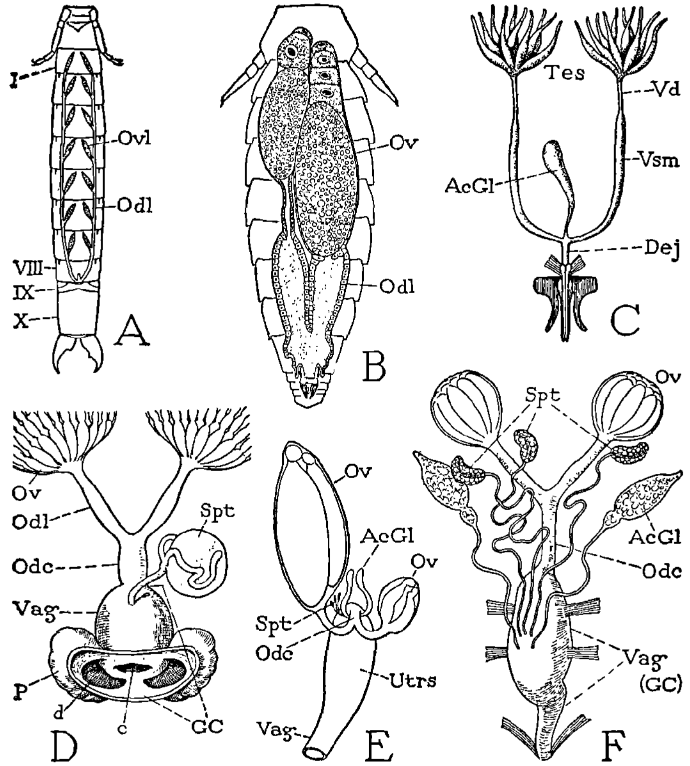

FIG. 290.—Examples of unusual types of reproductive organs. A, *Heterojapyx gallardi*, female. (*From Tillyard*, 1930.) B, *Acerentulus confinis*, female. (*From Berlese*, 1910.) C, stonefly, *Leuctra prima*, male. (*From Mertens*, 1923.) D, honey bee, queen, diagrammatic. E, *Mesembrina meridiana*, female. (*From Keilin*, 1916, *after Cholodkowsky*.) F, *Rhagoletis pomonella*, female.

The Spermatheca, or Receptaculum seminis.—Since with insects insemination of the eggs is not generally accomplished during the act of mating but takes place a varying length of time afterward, most female insects are provided with a sperm receptacle in which the spermatozoa are stored, and from which they can be ejected upon the eggs as the latter are extruded from the oviduct. This organ is the *receptaculum seminis,* or *spermatheca* (Fig. 284 A, *Spt*).

The spermatheca is primarily an invagination of the integument at the posterior end of the venter of the eighth abdominal segment (Fig. 289 B, *Spt*). Its opening, therefore, comes to be enclosed in the genital chamber when a copulatory pouch is formed behind the eighth sternum (Figs. 287, 289 C, *Spt*), or it lies in the dorsal wall of the vagina when the genital chamber has the form of a vaginal tube (Fig. 289 D, E, F). Usually the spermatheca is a single organ; but since it is sometimes double or consists of two branches of unequal size, it is possible that it is primitively bifurcate or paired, though in some Diptera it is triple (Fig. 290 E, F).

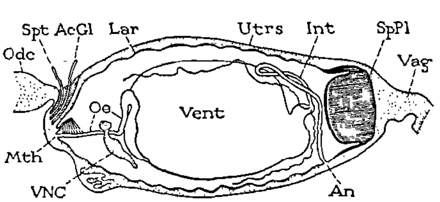

FIG. 291.—Larva of *Glossina palpalis* in uterus of the fly. (From Keilin, 1916, after Roubaud, figure reversed and relettered.) *AcGl,* accessory gland; *An,* anus; *Int,* intestine; *Lar,* larva; *Mth,* mouth; *Odc,* oviductus communis; *Oe,* oesophagus; *SpPl,* spiracular plate of larva; *Spt,* spermatheca; *Utrs,* uterus; *Vag,* vagina; *Vent,* ventriculus; *VNC,* ventral nerve cord.

The size, shape, and structure of the usual single spermatheca are highly variable in different insects, but generally the organ is saclike in form with a slender duct (Figs. 287, 288, 290 D, *Spt*). Very commonly a diverticulum of the duct forms a tubular spermathecal gland (Fig. 284 A, *SptGl*), which secretes a fluid in which the sperm are discharged. On the outer surface of the duct there is a muscular sheath, and the muscle fibers are sometimes so arranged as to form a special pumping apparatus for ejecting the sperm, or a certain quantity of sperm-containing fluid, upon each egg as it issues from the oviduct into the genital chamber or vagina.

The Female Accessory Glands.—The pair of glands associated with the exit apparatus of the female genital organs (Fig. 284 A, *AcGl*) usually has some function connected with the laying of the eggs. These glands, therefore, are known as the accessory glands of the reproductive system. In the more generalized insects the opening of the accessory glands lies on the venter of the ninth abdominal segment (Fig. 289 B, C, *AcGl*) between the bases of the second valvifers of the ovipositor. When the genital chamber is converted into a vaginal pouch or tube, however, the accessory glands open either at the end of the latter or in its dorsal wall (Figs. 288, 289 E, *AcGl*). Their proximal parts are sometimes enlarged to form reservoirs (Fig. 288, *Res*). The accessory glands and their duct are the only ectodermal parts of the female reproductive system that may possibly be homologous with parts of the male system; in position at least they correspond to the ejaculatory duct and accessory glands of the male.

In the majority of female insects the accessory glands produce an adhesive substance for attaching the eggs to a support or for gluing them together in a mass as they are laid, and for this reason they are commonly termed *colleterial glands.* But in some insects an abundance of secretion from the accessory glands is used to form a covering over the egg mass, or an egg case. The egg-covering material, however, may be secreted in special glandular parts of the oviducts, as in the Acrididae (Fig. 287, *Gld*). At least one of the accessory glands in the stinging Hymenoptera produces an irritating or toxic liquid and has become an essential adjunct to the stinging apparatus evolved from the ovipositor. In some viviparous Diptera, as we have seen, there are accessory glands having a nutritive function, but since they open into the anterior end of the uterus (Figs. 290 E, 291, *AcGl*) it is possible that they are special food glands not homologous with the usual accessory glands of the ninth segment.

2. THE MALE ORGANS

The internal organs of reproduction in male insects having a single genital opening are in many respects similar to those of the female. In an adult insect the essential parts of the male reproductive system include a pair of *testes* (Fig. 292 A, *Tes*), a pair of lateral ducts, the *vasa deferentia* (*Vd*), corresponding to the lateral oviducts of the female, and a median ectodermal exit tube, or *ductus ejaculatorius* (*Dej*), functionally comparable with the median oviduct of the female. Besides these constant parts there are generally present also accessory structures of a more variable nature. Frequently a section of each vas deferens, for example, is enlarged to serve as a sperm reservoir, or *vesicula seminalis* (*Vsm*), or, again, a considerable length of the duct is thrown into a compact coil of irregular convolutions, forming an *epididymis.* Ectodermal *accessory glands* (*AcGls*) are commonly present in the form of pouches or blind tubes branching from the upper end of the ejaculatory duct. The external opening of the exit duct, or *male gonopore* (*Gpr*), is generally situated on or within a median intromittent organ, the *penis* (*Pen*), or *phallus.*

The Testes.—Each testis consists typically of a group of short *sperm tubes* (Fig. 292 B, *SpT*). The tubes contain the male germ cells in successive stages of development, and other cells associated with the germ cells in various capacities. The sperm tubes in their origin and development correspond to the egg tubes of the ovaries, but they are usually called the testicular "follicles."

General Structure of a Testis.—The testis in some of the more generalized insects closely resembles an ovary in that the sperm tubes arise serially from the distal part of the exit duct (Fig. 292 B). Each tubule is attached to the vas deferens by a small stalklike *vas efferens* (*Ve*), but the testicular tubes have no terminal filaments. In some insects, as in Apterygota and Plecoptera, the sperm tubes are free from one another in the adult stage (Fig. 290 C), as are the ovarioles of the ovary, but generally they are all contained in an investing *peritoneal sheath* (Fig. 292 B, *PSh*). Frequently the two testes of opposite sides are united in a single median organ. In the higher insects the testes usually have a more compact structure because of the incomplete separation of the sperm tubes within the peritoneal sheath (C). The number of sperm tubes in a testis varies in different insects; it is generally less than the number of egg tubes in the ovary, but in most Lepidoptera there are four tubules in each sex. In certain insects, as in some Apterygota, Coleoptera, and Diptera, each testis is a simple saclike organ, which in most cases is probably a single sperm tube, though in some Diptera it is said to be partially subdivided.

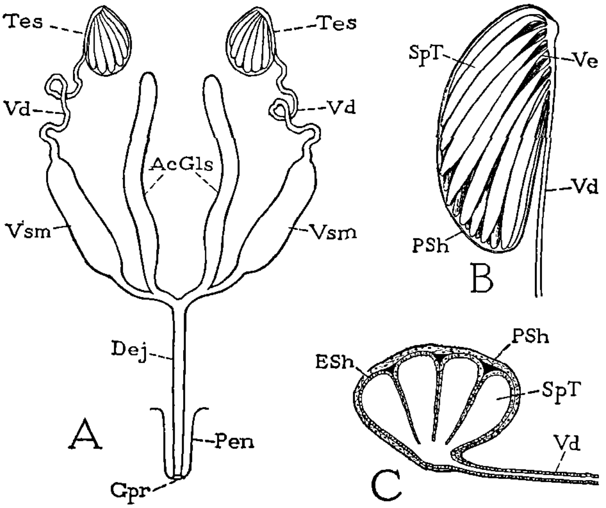

FIG. 292.—General structure of the male reproductive organs, diagrammatic. A, the male reproductive system. B, structure of a testis. C, section of a testis and duct. *AcGls*, accessory glands; *Dej*, ductus ejaculatorius; *ESh*, epithelial sheath; *Gpr*, gonopore; *Pen*, penis; *PSh*, peritoneal sheath; *SpT*, spermatic tube; *Tes*, testis; *Vd*, vas deferens; *Ve* vas efferens; *Vsm*, vesicula seminalis.

Structure of a Sperm Tube.—The wall of a testicular tubule consists of a cellular *epithelial sheath* (Fig. 293 A, *ESh*), which is sometimes divided into two layers, forming an outer epithelium and an inner epithelium. The sperm tubes, however, do not have a true follicular epithelium such as that which forms the walls of the egg chambers in the ovary. If the testis is but incompletely divided into sperm tubes, as in Lepidoptera, the septa between the compartments appear as folds of the epithelial sheath extending posteriorly toward the mouth of the duct (Fig. 292 C, *ESh*), while the entire organ is invested in the peritoneal sheath (*PSh*).

The walls of the testicular tubules probably serve as trophic intermediaries between the blood surrounding the gonads and the germ cells within them, as do the walls of the ovarioles. The single long, coiled tube forming the testis of *Dytiscus*, according to Demandt (1912; Korschelt, 1924), is covered by two epithelial sheaths inside the peritoneal sheath. The thick outer epithelium consists of a spongy, granular plasma in which cell boundaries are not visible, but the cytoplasm is vacuolated by numerous small cavities, indicating that the outer epithelium has a secretory function and probably elaborates nutritive products discharged into the lumen of the tube. The outer epithelium is bounded externally by a basement membrane. The inner epithelium is a thin elastic layer having a fibrillated appearance and containing a large number of small nuclei. The single saclike testis of Diptera also is said to be surrounded by two envelopes, distinguished as the *tunica externa* and *tunica interna* by Keuchenius (1913). The outer tunic, as described by Lomen (1914) in the mosquito, is a thick connective tissue layer abundantly vacuolated by small spaces filled apparently with stored nutritive material. The inner tunic forms the lining of the testis. In Lepidoptera, according to Ruckes (1919), the walls of the incompletely separated testicular compartments have the appearance of connective tissue and apparently serve for storage of reserve materials, including fat in some cases. In species with colored testes this coat is the repository of the pigment granules.

Within each sperm tube there are to be distinguished successive regions according to the state of development of the germ cells. The upper part containing the primary spermatogonia is the *germarium* (Fig. 293 A, *Grm*), as in the ovary; beyond the germarium is a *zone of growth* (*I*) in which the spermatogonia enter a stage of multiplication and are usually encysted; next is the *maturation zone* (*II*) in which the maturation divisions take place; and lastly comes the *zone of transformation* (*III*) where the spermatocytes develop into spermatids and finally into mature spermatozoa. The entire process of spermatogenesis thus takes place regularly within the tubes of the testis.

The Cellular Elements within a Testicular Tube.—A characteristic feature of the testicular tubes is the presence of a large cell or nucleated mass of protoplasm in the apex of the germarium. This cell is known as the *Versonian cell*, or *apical cell* (Fig. 293 A, B, *ApCl*). Earlier investigators believed the apical cell to be the primary spermatogonium of the tube, from which by division all the other spermatogonia are produced. The majority of recent workers, however, regard the apical cell as a spermatogonium specialized as a trophocyte.

The apical cell is particularly well developed in the Lepidoptera, where it consists of a large mass of cytoplasm containing a nucleus (Fig. 293 B, *ApCl*). Surrounding the apical cell are several concentric rows of spermatogonia (*Spg*), of which those nearest the apical cell are seen to be connected with the latter by protoplasmic strands containing dark granules that appear to originate in the apical cell. The spermatogonia of Lepidoptera, therefore, as pointed out by Grünberg (1903), must be nourished directly from the apical cell. The nutritive material utilized by the apical cell, it is claimed both by Grünberg and by Zick (1911), is derived from certain spermatogonia in the immediate neighborhood of the apical cell which are dissolved and absorbed by the latter. According to this view, then, the apical cell of a testicular tube in the Lepidoptera is a spermatogonial nurse cell, which, on the one hand, dissolves and absorbs some of the adjacent spermatogonia and, on the other hand, feeds a second set of spermatogonia with the material from the first set elaborated in its cytoplasm and delivered to the recipient

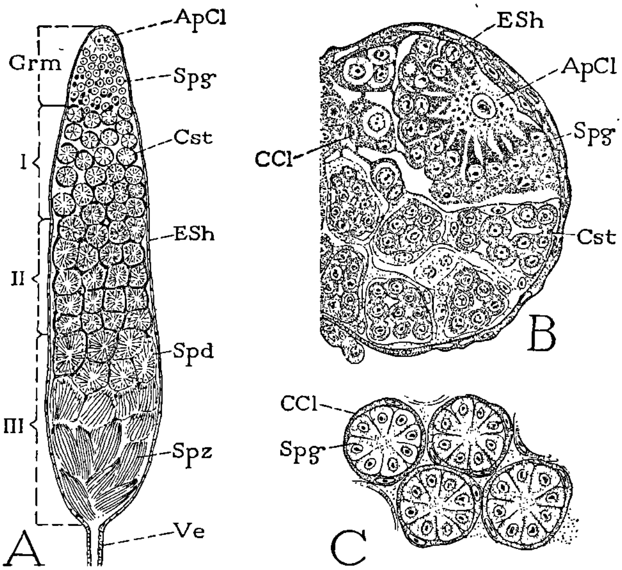

FIG. 293.—Histology of the testis. A, lengthwise section of a sperm tube, diagrammatic. B, section of a larval sperm tube of *Pieris*. (*From Knaben*, 1931, *after Zick*, 1911.) C, diagram of the typical structure of spermatogonial cysts. *ApCl*, apical cell; *CCl*, cyst cell; *Cst*, sperm cyst; *ESh*, epithelial sheath; *Grm*, germarium; *I*, zone of growth; *II*, maturation zone; *III*, transformation zone; *Spd*, spermatids; *Spg*, spermatogonia; *Spz*, mature spermatozoa; *Ve*, vas efferens.

cells through the connecting cytoplasmic strands. These specially nourished spermatogonia become spermatocytes and develop into the spermatozoa. In the first place, however, the nutrient material of the male germ cells, as in the case of the female germ cells, comes from the blood and is primarily elaborated in the trophic sheath of the gonadial tube.

An apical cell is also well developed in Diptera. According to Friele (1930), it is a conspicuous structure in the upper end of the testicular lumen in *Psychoda alternata* during the larval stages, but it degenerates and disappears in the pupa and is not to be found in the adult testis. Friele claims that the apical cell of *Psychoda* is a secretion cell only, the products of which dissolve the spermatogonia adjacent to it and convert them into a fluid plasma, which is dispersed through the testicular lumen where the developing sperm cells can make use of it.

The spermatogonia that are destined to become spermatozoa undergo a series of divisions, but the cells produced from each primary sperm cell usually remain attached to one another centrally by protoplasmic strands and assume a radial position, giving a rosette pattern to the spherical mass in cross section (Fig. 293 C). Each spermatogonial group in most insects soon becomes enclosed in a cellular envelope, known as a *sperm cyst* (A, B, *Cst*, C).

The origin of the male cyst cells has not been definitely observed in many insects, but, while some investigators have believed that these cells are derived from the sheath of the sperm tube, most writers regard them as products of the germ cells. According to Zick (1911), the differentiation between the secondary spermatogonia and the cyst cells in Lepidoptera is a matter of nutrition. The primary spermatogonia (Fig. 293 B, *Spg*) immediately surrounding the apical cell (*ApCl*), and which are directly nourished by the latter, he says, become the functional spermatogonia; those of the next rank, receiving little nourishment from the apical cell, become the cyst cells (*CCl*). Adjacent cells of these two groups attach to each other in pairs; the poorly nourished cell by division forms the cyst, the other produces the enclosed group of spermatogonia.

On comparing the internal cellular organization of a testicular tube with that of an ovarial tube, it becomes evident that the cyst cells of the former correspond functionally at least to the follicle cells of the latter, though investigations seem to show that the ovarial follicle cells and the testicular cyst cells have different origins. In the ovary the cystocytes produce a continuous epithelium lining the egg tube; in the testis they invest groups of spermatogonia separately. In some insects it has been observed that the testicular cysts are connected by strands of cells forming a network throughout the lumen of the sperm tube.

The spermatogonia within each cyst continue to multiply, forming successively spermatocytes, spermatids, and finally spermatozoa in advancing stages of development (Fig. 293 A). The cysts finally degenerate and are dissolved, but the spermatozoa (*Spz*) generally remain grouped in bundles as they were in the cysts. The details of the maturation of the male germ cells, the differentiation of the two sex-determining types of sperm cells, and the development of the spermatozoa have been described in many special papers on spermatogenesis in insects and need not be given here. As the sperm cells mature, others are produced in the apical part of the sperm tube, and the sperm tube increases in length between its two ends. The ripe spermatozoa are thus always located at the posterior ends of the testicular tubes in proximity to the exit ducts.

The Vasa deferentia.—The ducts leading from the testes (Fig. 292 A, *Vd*) are usually simple tubes, each having a thick cellular epithelium limited by a basement membrane, outside which is a strong muscular coat of circular fibers. Frequently a part of each duct is much convoluted, and the coils may form a definite epididymis. In some insects an enlargement of the duct in the shape of a dilatation or diverticulum constitutes a vesicula seminalis (*Vsm*) for the storage of the mature sperm as the latter leave the testis. The spermatozoa are generally found closely massed in the vesicula, with their heads imbedded in the epithelial wall and their vibratile tails projecting like cilia into the lumen.

The vasa deferentia are primarily of mesodermal origin, but they may be extended posteriorly by ingrowths from the ectoderm or more or less replaced by the latter. Thus, in Ephemerida, as shown by Wheeler (1893), the terminal parts of the male ducts may be lined with an ectodermal cuticula, and in the Diptera, according to Brüel (1897) and Friele (1930), the definitive ducts of the testes are formed entirely as lateral diverticula from the ectodermal ductus ejaculatorius. The lateral genital ducts of the male open separately to the exterior in Protura, Ephemerida, and some Dermaptera; in other insects they unite with the anterior end of a median ejaculatory duct.

The Ductus ejaculatorius.—The usual common exit tube of the male genital system is formed as a median ventral invagination of the ectoderm at the posterior end of the ninth abdominal segment, with which the vasa deferentia become connected. The ejaculatory duct, therefore, and all parts derived from it have a cuticular lining continuous with that of the body wall. The epithelial wall of the duct is surrounded by a strong muscular sheath, usually consisting of circular fibers, and sometimes containing longitudinal fibers, but the relation of the two sets of fibers to each other appears not to be the same in all cases. Though the ejaculatory duct is always described as unpaired in its embryonic origin, its anterior end is frequently forked, especially when accessory glands arise from it. The external aperture of the exit duct, or male gonopore, is usually situated on an intromittent organ, the phallus, but the latter often contains an invagination cavity, or endophallus, within which the true gonopore is concealed. The endophallus, which is either a permanently enclosed cavity of the phallus or an eversible vesicle or tube, is sometimes mistaken for the terminal part of the ductus ejaculatorius.

The Male Accessory Glands.—Glandular structures associated with the male organs usually have the function of secreting a mucous or viscid substance, which either is discharged as a liquid with the spermatozoa or hardens about them to form a covering or capsule known as a *spermatophore.* The male accessory glands generally arise from the anterior end of the ejaculatory duct or from short divergent anterior branches of the duct. Typically they have the form of elongate sacs or tubes, and the tubular variety is often greatly looped and coiled. Usually there is but one pair of accessory glands (Fig. 292 A, *AcGl*), but in some insects a series of glands arises from each side of the ejaculatory duct, while in others there may be a compact mass of tubules about the terminus of each vas deferens. The walls of the accessory glands may have a muscular sheath continuous with that of the ejaculatory duct.

Glands associated with the external opening of the ductus ejaculatorius are termed *preputial glands.* Groups of one-celled preputial glands are described by Demandt (1912; Korschelt, 1924) in *Dytiscus marginalis.*

3. GENERAL MORPHOLOGY OF THE REPRODUCTIVE ORGANS

The gonads of the simpler metazoic animals are merely epithelial swellings or simple capsules of somatic cells surrounding the germ cells and retaining them until the latter are ready to perform their destiny independent of the soma. The mature germ cells either are discharged directly into the surrounding medium or are liberated into the body cavity. In the second case the germ cells must find an exit through the body wall to the exterior.

In the Annelida, the gonads are developed from the coelomic epithelium, and frequently they occur on the posterior surfaces of the intersegmental septa that divide the body cavity. Typically, the ripe germ cells fall into the coelomic cavities, where they mature and from which the ova and spermatozoa finally escape to the exterior, in some species through ruptures of the body wall, but generally by way of the nephridial tubes or through special genital ducts. In some forms the genital ducts are continuous with the walls of the gonads, and they may be united distally in a common outlet tube.

The reproductive system of the Arthropoda is entirely closed, the exit ducts being continuous with the walls of the ovaries or testes. The ducts either open separately to the exterior, generally on the bases of segmental appendages, or unite in a median terminal duct. Considering the evident relationship between the arthropods and annelids, as expressed in various fundamental features of their structure, it will be interesting to learn if in the development of the arthropod reproductive organs there is any suggestion of an early condition resembling that found in adult annelids.

Though the germ cells of insects are known in some cases to be differentiated from the somatic cells at the time of cleavage, this early origin of the reproductive elements cannot be demonstrated in all species. Visible differences between the germ cells and the somatic cells appear in most insects only after the formation of the germ layers of the embryo, when the germ cells are found imbedded in the splanchnic layer of the abdominal mesoderm. The rudiments of the gonads now appear as thickenings of the mesoderm, known as the *genital ridges,* in the anterior parts of which the germ cells are lodged. With the dorsal extension of the germ layers, the genital ridges are carried to the dorsal part of the abdominal cavity, where they protrude from the splanchnic wall.

According to the detailed study by Heymons (1892) on the development of the female reproductive organs in the roach *Blatella germanica,* the germ cells are at first mostly aggregated in groups opposite the intersegmental grooves, so that, when the coelomic sacs appear, the cells lie dorsally in the intercoelomic walls. This early position of the germ cells in the roach is thus, as Heymons points out, suggestive of the condition in many Annelida, in which the germ cells are grouped in the intersegmental septa. Wherever the germ cells assemble in the Annelida, the gonad is formed as a mesodermal covering over them, from which the germ cells are eventually liberated into the coelomic cavities. In the female roach, Heymons finds, the germ cells at an early stage are likewise extruded from the mesoderm into the coelomic cavities, but, though an occasional cell may be entirely liberated, most of them remain attached to the dorsal coelomic walls, where they migrate posteriorly and are soon again overgrown by the mesodermal epithelium. After the disappearance of the intercoelomic septa, the germ cells lie in a continuous series along each side of the body, imbedded in the splanchnic mesoderm, which grows out as the genital ridges, or first rudiments of the reproductive organs (Fig. 294 A).

As development proceeds, the germ cells become limited to the anterior part of each genital ridge, which increases in thickness until it forms a fold hanging from the dorsal area of the splanchnopleure and eventually becomes the ovary or testis, while the posterior narrow part of the ridge becomes the lateral genital duct. In the gonadial rudiment

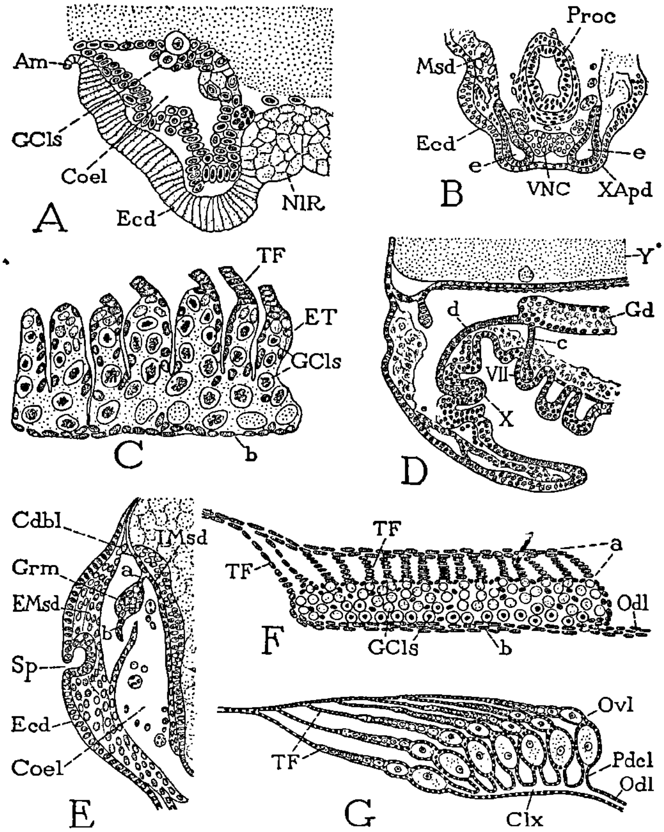

Fig. 294.—Development of the gonads, the ovary, and the genital ducts. A, section of coelomic sac of *Blattella germanica* with group of germ cells in splanchnic wall. (*From Heymons*, 1892.) B, section of posterior end of embryo of *Conocephalus*, with terminal ampullae of male ducts in appendages of tenth abdominal segment. (*From Wheeler*, 1893.) C, differentiation of female gonad of *Blattella* into egg tubes of ovary. (*From Heymons*, 1892.) D, showing branching of gonadial ducts in embryo of *Forficula* to seventh and tenth abdominal segments. (*From Heymons*, 1895.) E, coelomic sac of embryo of *Leptinotarsa* with rudiment of gonad attached to splanchnic wall. (*From Wheeler*, 1889.) F, G, two late stages in development of ovary of *Blattella*. (*From Heymons*, 1892.) *a*, suspensorium of gonad; *Am*, amnion; *b*, ventral strand of gonad; *c*, anterior branch of gonadial duct; *Cdbl*, cardioblasts; *Clx*, calyx; *Coel*, coelomic cavity; *d*, posterior branch of gonadial duct; *e*, terminal ampulla of gonadial duct; *Ecd*, ectoderm; *EMsd*, somatopleure; *ET*, egg tube; *GCls*, germ cells; *Gd*, gonad; *IMsd*, splanchnopleure; *Msd*, mesoderm; *NlR*, neural ridge; *Odl*, oviductus lateralis; *Ovl*, ovariole; *Pdcl*, ovariole pedicel; *Proc*, proctodaeum; *Sp*, spiracle; *TF*, terminal filament; *VNC*, ventral nerve cord; *XApd*, appendage rudiment of tenth abdominal segment.

there is soon to be distinguished a *suspensorium* (Fig. 294 E, *a*), or dorsal strand of cells by which the gonad is attached to the coelomic wall, a median part, or *germarium* (*Grm*), containing the germ cells, and a cellular *ventral strand* (*b*), which is continuous posteriorly with the duct. During the embryonic period the germ cells increase in number without other change from their earlier condition.

The next stage in the development of the gonad is that in which the single organ becomes subdivided into a series of compartments—the ovarioles of the ovary or the sperm tubes of the testis. In the female roach, according to Heymons, the cells of the gonadial suspensorium become flattened and arranged in vertical series (Fig. 294 F, *a*), there being finally thus formed about 20 columns of regularly stratified cells, which become the terminal filaments (*TF*) of the mature ovary. Now, the intermediate part of the gonad, containing the germ cells, loses its even contour and is produced dorsally into a series of swellings corresponding to the bases of the filament columns (C), while the intervening depressions are extended ventrally. When the clefts reach the ventral strand of the gonad, the ovary is divided into its definitive egg tubes (*ET*), each surmounted by a terminal filament, and is connected basally with the ventral strand (*b*), which is continuous with the duct (*Odl*). The final inclined or horizontal position of the ovarioles (G) is attained by a shortening of the ventral strand and a compensating differentiation in the length of the terminal filaments.

In other insects the formation of the ovarial or testicular tubes may be a more simplified process, consisting merely of the outgrowth of the tubes from the primitive organ or of a division of the latter by an inflection of its epithelial walls. In any case, it is evident that the egg or sperm tubes are but secondary outgrowths or subdivisions of a primitively simple gonad, and that there is no basis in ontogeny for regarding the gonadial tubes as a series of primitive segmental reproductive organs secondarily united by a common lateral duct. On the other hand, the segmental arrangement of the gonadial tubes in certain Apterygota (Fig. 290 A) might be taken as suggestive that the tubes originated as segmental pouches of a primitively continuous gonad. However, in many of the Apterygota the arrangement of the genital tubes has no close relation to the metamerism of the body, and the gonad may consist of a single large saclike ovary or testis on each side.

In the Protura both the ovary and the testis, as described by Berlese (1910), consist of a simple elongate sac, the walls of which consist of a layer of epithelial cells covered externally by a sheath of connective tissue. Each ovary (Fig. 290 B, *Ov*) has the structure of a typical panoistic ovariole, except that it lacks a terminal filament. The anterior end, which is deflected, contains the germarium, and there are from 13 to 15 oöcytes in the rest of the tube in successive stages of growth. The eggs attain their mature size first in one ovary, then in the other. The oviducts unite in the eighth abdominal segment to form a median duct.

The testis is almost a replica of the ovary; the male ducts, however, are long and coiled, and they open separately through the terminal spines of the external genital organ exserted from between the eleventh and twelfth abdominal segments.

Among apterygote insects the gonads have likewise a simple saclike form in Collembola, in *Campodea*, and in the male of *Japyx*. In *Campodea*, each testis and ovary, as described by Grassi (1887), consists of a single long tube extending forward into the posterior part of the thorax. In *Japyx* the testes are similar to the testes and ovaries of *Campodea*, but the vasa deferentia are long and convoluted. Posteriorly the lateral ducts unite in a very short median ejaculatory duct, which opens between the ninth and tenth segments of the abdomen.

In other Diplura and Thysanura, including the female of *Japyx*, each gonad consists of several or numerous tubules, which in some cases are segmentally arranged on the lateral ducts. Thus, in *Japyx*, there are seven ovarioles in each side of the body, one in each of the first seven abdominal segments, opening into a long lateral oviduct (Fig. 290 A). The same type of structure occurs in the ovaries of *Machilis*, though there are here only six pairs of ovarioles. In young specimens of Lepismatidae, according to Grassi, the ovarioles are also segmentally disposed, but in adults the metameric arrangement is lost. In the males of these forms the number of testicular tubes is variable, and they do not have a segmental arrangement.

Since the ovaries and the testes in Protura, Collembola, and *Campodea* consist each of an undivided sac, it might be supposed that the adult organs in these forms represent the simple undivided embryonic gonads of the higher insects. However, if the fact is considered that the ovarial or testicular sac in these lower forms has the structure of a single ovariole or sperm tube and not that of an embryonic gonad, and it is recalled that the ovary of some of the more specialized insects may likewise consist of but one ovariole, it seems more probable that the simple gonads of the groups above mentioned are cases of reduction rather than examples of primitive structure. On the other hand, there can be little doubt that the primary compound ovary or testis consisted of only a few egg tubes or sperm tubes, and it may be conceded that the tubes were perhaps at first segmentally arranged on the duct. The further evolution of the gonad has been generally in the direction of an increase in the number of tubes, which have kept their serial arrangement in the ovary of some of the more generalized insects but in most forms have assumed a clustered arrangement owing to the shortening of the duct.

The primary exit apparatus of the reproductive system consists in the female of the pedicels of the ovarioles, the calyces, and the lateral oviducts; in the male it includes the vasa efferentia and the vasa deferentia. The ovariole pedicels, the vasa efferentia, and the oviducal calyx are developed from the cellular ventral strands of the gonads; the lateral ducts are direct derivatives of the posterior unspecialized parts of the genital ridges, which are continuous with the ventral strands of the gonads.

There is no evidence that the lateral reproductive ducts of arthropods ever served any other than their present purpose. It is probable that their mesodermal parts represent closed grooves of the splanchnic mesoderm that primarily conducted the reproductive elements to openings in the body wall. Their lumina are to be regarded, therefore, as parts of the coelomic cavity. In immature stages of many insects the female ducts are attached posteriorly to the ectoderm of the seventh abdominal segment, and those of the male to the ectoderm of the tenth segment. As described in Orthoptera by Wheeler (1893), and in Dermaptera and Orthoptera by Heymons (1892, 1895), the embryonic ducts terminate in hollow swellings, or ampullae, within the rudiments of the appendages of these segments (Fig. 194 B, *e*). It seems probable, therefore, that the primitive reproductive ducts of insects opened on the bases of segmental appendages.

The median exit apparatus of the genital system of modern insects is a secondary development from the ectoderm. In some of the higher insects branches from the median duct have partly or entirely supplanted the primary mesodermal lateral ducts.

GLOSSARY OF TERMS APPLIED TO THE INTERNAL REPRODUCTIVE ORGANS

Accessory Glands (*AcGl*).—In the female, a pair of glands opening primarily on the venter of the ninth abdominal segment, secreting an adhesive substance or material forming a covering or a case (oötheca) for the eggs; in the male, mucous glands opening into the ejaculatory duct.

Acrotrophic Egg Tube.—A type of egg tube in which the trophic cells remain in the apical chamber. (*Telotrophic type.*)

Apical Cell (*ApCl*).—A special, usually large, trophic cell in the upper end of the testicular tube in some insects. (*Versonian cell.*)

Bursa copulatrix (*Bcpx*).—A copulatory pouch of the female, usually the genital chamber or a part of the latter.

Calyx (*Clx*).—The widened anterior end of the lateral oviduct receiving the ovariole pedicels. (*Eierkelch.*)

Chorion (*Cho*).—The egg shell secreted by the follicle cells of the ovarial egg chamber.

Colleterial Glands.—Accessory glands of the female secreting an adhesive substance used to fasten the eggs to a support.

Corpus luteum (*Clt*).—The mass of degenerating follicle cells left in an egg chamber after the discharge of the egg.

Cystocytes.—The cells enclosing the germ cells in a gonadial tube; the follicle cells of the ovary, the cyst cells of the testis.

Ductus ejaculatorius (*Dej*).—The median ectodermal outlet tube of the male genital system.

Egg Chamber (*EC*).—One of the compartments, or follicles, of an ovarial egg tube, formed of the follicle cells, containing an oöcyte. (*Eikammer.*)

Egg Tube (*ET*).—The tubular part of an ovariole containing the germ cells, the oöcytes, the nurse cells, and the follicle cells.

Ejaculatory Duct (*Dej*).—See *ductus ejaculatorius.*

End Chamber (*Grm*).—The germarium of a gonadial tube.

Epididymis.—A convoluted part of the vas deferens. (*Nebenhode.*)

Follicle (*EC*).—See *egg chamber.*

Follicle Cells (*FCls*).—The inner epithelial cells of an ovarian egg tube.

Genital Chamber (*GC*).—In the female, primarily an invagination cavity behind the eighth abdominal sternum containing the gonopore and the spermathecal aperture, often converted into a *vagina* or *uterus*, and in some insects opening secondarily on or behind the ninth sternum; in the male, an invagination cavity behind (above) the ninth sternum containing the intromittent organ.

Genital Ridge.—One of the embryonic gonadial rudiments, a ridge-like swelling of the splanchnopleure wall of the mesoderm containing the germ cells.

Germ Cells (*GCls*).—The reproductive cells as distinguished from the somatic cells, or, more specifically, the early undifferentiated reproductive cells. (*Keimzellen.*)

Germarium (*Grm*).—The end chamber of an ovarial or testicular tube, containing the primary oögonia or spermatogonia. (*Endkammer.*)

Gonad (*Gd*).—The ovary or testis, or the embryonic rudiment of either, formed of splanchnic mesoderm cells enveloping the germ cells.

Gonopore (*Gpr*).—The external opening of a genital duct.

Lateral Oviduct (*Odl*).—See *oviductus lateralis.*

Median Oviduct (*Odc*).—See *oviductus communis.*

Meroistic Egg Tube.—A type of egg tube containing both oöcytes and trophocytes, including the acrotrophic and polytrophic types.

Nurse Cells (*NrCls*).—The trophocytes of the ovary or testis.

Oöcytes (*Ooc*).—The egg cell differentiated from the oögonium, before maturation.

Oögonium (*Oog*).—The first stage in the differentiation of an egg cell from a primary female germ cell.

Ovarial Ligament (*Lg*).—A ligamentous strand attaching the terminal filaments of an ovary to the dorsal diaphragm or to the body wall, sometimes united with that from the opposite side in a median ligament attached to the ventral wall of the dorsal blood vessel.

Ovariole (*Ovl*).—One of the secondary divisions of the ovary, composed of a *terminal filament*, an *egg tube*, and a *pedicel.*

Ovary (*Ov*).—The female reproductive organ containing the egg cells. (*Eierstock.*)

Oviductus communis (*Odc*).—The median ectodermal outlet duct of the female genital system, usually opening into a genital chamber, or vagina. (*Eiergang.*)

Oviductus lateralis (*Odl*).—One of the paired lateral ducts of the female system connected with the ovary, mesodermal in origin, but sometimes partly or entirely replaced by an ectodermal branch of the median duct. (*Eileiter.*)

Ovum.—The mature (unfertilized) egg cell.

Panoistic Egg Tube.—A type of egg tube in which the vitellarium contains eggs only.

Pedicel (*Pdcl*).—One of the ovariole stalks (*Eiröhrenstielen*), or short ducts from the egg tubes to the oviduct.

Polytrophic Egg Tube.—A type of egg tube in which groups of trophocytes accompany the oöcytes.

Sperm Cyst (*Cst*).—One of the cellular capsules in the testis containing the spermatocytes.

Sperm Tube (*ST*).—One of the secondary divisions of the testis.

Spermatheca, or Receptaculum seminis (*Spt*).—The sperm receptacle of the female.

Spermatid.—An immature spermatozoon.

Spermatocyte (*Spc*).—The sperm cell differentiated from a spermatogonium, before maturation.

Spermatogonium (*Spg*).—The first stage in the differentiation of a sperm cell from a primitive male germ cell.

Spermatozoon *Spz*).—The mature sperm cell.

Terminal Filament (*TF*).—The cellular end thread of an ovariole. (*Endfaden.*)

Testis (*Tes*).—The male reproductive organ containing the primary germ cells, and in which the sperm cells undergo maturation. (*Hode.*)

Trophocytes (*NrCls*).—The nutritive cells, or nurse cells, of the ovary or testis. (*Nährzellen.*)

Uterus (*Utrs*).—A compartment of the genital chamber, or vagina, in which the embryonic and a part of the postembryonic development of the young insect may take place.

Vagina (*Vag*).—A part of the definitive egg passage in many insects posterior to the true oviductus communis, derived from the genital chamber. (*Scheide.*)

Vas deferens (*Vd*).—One of the lateral ducts of the male reproductive system. (Plural, *vasa deferentia.*)

Vas efferens.—One of the short ducts connecting the sperm tubes of the testis with the vas deferens, corresponding to the pedicel of an ovariole.

Versonian Cell.—See *apical cell.*

Vesicula seminalis (*Vsm*).—A dilatation of the vas deferens in which the spermatozoa may be retained.

Vitellarium (*Vtl*).—The part of an ovariole egg tube in which the oöcytes grow by the accumulation of yolk and attain their mature size. (*Zone of growth.*)

CHAPTER XIX

THE ORGANS OF COPULATION AND OVIPOSITION

The organs specifically concerned with sexual mating and the deposition of the eggs are known collectively as the *external genitalia.* The copulatory organs pertain to both sexes, though they are particularly developed in the male; the female organs of oviposition are external genitalia in the sense that they are accessory to the reproductive function.

The copulatory apparatus of the male includes primarily an organ for conveying the spermatozoa into a sperm receptacle of the female, and usually a group of associated structures adapted for grasping and holding the female. The recipient organ of the female is a copulatory pouch (genital chamber or vagina) or a spermathecal diverticulum of the latter.

The principal clasping organs of the male are generally movable appendicular structures of the ninth segment, which serve as a pair of grappling hooks (harpagones), though accessory copulatory processes of various forms may occur on the same segment or on any of the neighboring segments, and in some cases the cerci are transformed into grasping organs. Coition, in most insects, is effected by a median intromittent organ located on the conjunctival membrane behind the ninth abdominal sternum, with which there may be associated various accessory structures forming a group of phallic organs; but in some of the Apterygota an intromittent organ is absent, and in Odonata it is functionally replaced by a secondary copulatory structure on the anterior part of the abdomen. In certain lower pterygote insects there is a pair of intromittent organs.

The external genitalia of the female, in addition to the copulatory pouch, consist of structural adaptations for the disposal of the eggs. In the Thysanura (Machilidae and Lepismatidae) and in many of the pterygote orders, the female is provided with a special egg-laying organ, known as the *ovipositor*, which appears to be formed of the appendages of the eighth and ninth abdominal segments. By means of the ovipositor the female is enabled to deposit her eggs in the ground, in the leaves, stems, and wood of plants, or into the bodies of other insects. With many insects, however, especially in those having the genital aperture from which the eggs are discharged located on the ninth abdominal segment, the ovipositor is reduced or absent, and in such cases the terminal segments of the abdomen are usually slender and tapering and capable of being protracted as a tube, from which the eggs are extruded and may be attached to smooth surfaces or concealed in crevices.

1. THE MALE GENITALIA

The morphology of the male organs of copulation is not definitely known, notwithstanding the efforts that various investigators have given to the subject. In the following discussions, therefore, a minimum of attention will be given to theoretical views that do not appear to be in harmony with anatomical facts. Moreover, in order to avoid the nomenclatural confusion that has resulted from the lack of an understanding of the fundamental nature of the male organs, and in order to present simply the facts of structure, a terminology has been adopted that can be applied consistently to the major structural elements regardless of what may be the morphological relations of the latter. In each order, however, many special structures must be named individually, since it is clear that there are numerous modifications of the genital organs that have only a local significance.

The primary mesodermal outlet tubes of the male genital system, as we learned in the last chapter, are attached during embryonic development in some orthopteroid insects to the ectoderm of the ventral wall of the tenth abdominal somite, or in some cases they terminate in ampullae located within the appendage rudiments of this segment. In certain hexapods (Protura, Ephemerida, Dermaptera) the vasa deferentia retain their separate openings in the adult, though each may terminate in an exit duct of ectodermal origin, and in such cases the gonopores are borne on a pair of penes or on paired processes of a single organ. Since, however, the position of the intromittent organ in these several hexapod groups varies from the ninth to the eleventh segment, it seems doubtful that the paired adult structures represent rudimentary limbs, though we might conclude from the embryological evidence given above that the primitive male ducts opened on the bases of the appendages of the tenth abdominal segment.

With the majority of adult insects the vasa deferentia open into the proximal parts of the ectodermal accessory glands (Fig. 292 A), and the latter then unite in a common outlet tube, the ductus ejaculatorius. The ejaculatory duct opens usually on a median intromittent organ arising from the ventral conjunctival membrane between the ninth and tenth abdominal segments; this membrane is probably the posterior part of the venter of the ninth primary somite. It would appear, therefore, that the original orifices of the vasa deferentia in such cases have migrated forward to open in common with the accessory glands on the ninth abdominal venter, and that a median invagination of the body wall at this point has formed the common ejaculatory duct. This theoretical origin of the male exit apparatus, however, is not necessarily recapitulated in ontogenetic development, since in many insects the embryonic vasa deferentia have not been traced beyond the eighth or ninth abdominal somite, where they are said to unite directly with the ectodermal ductus ejaculatorius. The median gonopore, or external opening of the ejaculatory duct, may remain flush with the surface of the membrane in which it is situated; but, with the majority of insects, it is situated on a tubular intromittent organ, the *median penis*, or *phallus*.

Male Genitalia of Hexapoda Having Paired Gonopores.—Here are included the Protura, the Ephemerida, and the Dermaptera, though some of the last have secondarily a single gonopore.

Protura.—The males of Protura, as described by Berlese (1910) and by Prell (1913), have an elaborate bipartite intromittent organ (Fig. 295) eversible from between the sternal plates of the eleventh and twelfth abdominal segments, but they have no accessory lateral copulatory structures. The bifid distal part of the genital organ ends in a pair of long hollow processes on which the two genital ducts open separately through subterminal apertures (*Gprs*). The position of the male organ in Protura would appear to preclude the possibility of any homology with the usual intromittent organ of insects, located on the ninth abdominal segment.

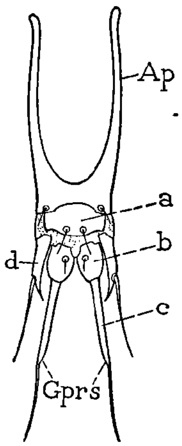

Fig. 295.—Male genital organ of Protura (*Eosentomon germanicum*), ventral view. (*From Prell*, 1913.)

Ephemerida.—The vasa deferentia of Ephemerida terminate in exit ducts of ectodermal origin that open separately on a pair of penes. The ephemerid penes are small, flattened, conical processes arising ventrally at the base of the tenth abdominal segment (Fig. 296, B, C, *Pen*). It is not clear whether the membrane supporting the organs (C) belongs to the ninth segment or represents the venter of the tenth segment. Associated with the intromittent organs is a pair of lateral segmented claspers (B, *Sty*), arising either separately from basal lobes or from a common basal plate (B, *Cxpd*) borne by the ninth sternum. These claspers, which are individually movable by basal muscles (*smcl*), are evidently the styli of the ninth segment and therefore belong to the appendages of this segment. The presence of paired penes in male Ephemerida is correlated with the presence of two separate oviducal openings in the female.

Dermaptera.—The terminal ectodermal parts of the genital ducts of male Dermaptera in some forms open separately on a pair of penes, while in others they unite in a common exit duct that opens on a single median penis (Fig. 297 A, C). The ovarial ducts of the female come together in a short median pouch with a single opening. The male organ in this order, however, is basally an unpaired structure, since the terminal parts, whether double or single, arise from a common median plate. The basal plate is situated anterior to the tenth abdominal sternum in the membranous floor of a genital chamber above the ninth sternum. Proximally it is produced into a long apodemal process (*Ap*). Styli are absent in Dermaptera, and there are usually no other accessory structures associated with the intromittent organ.

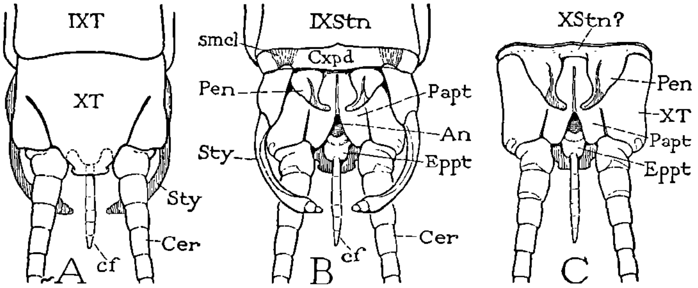

FIG. 296.—Male genitalia of Ephemerida (*Hexagenia*). A, end of abdomen, dorsal view. B, same, ventral view. C, segments beyond the ninth, ventral view. *An*, anus; *Cer*, cercus; *cf*, caudal filament; *Cxpd*, basal plate of styli; *Eppt*, epiproct; *Papt*, paraproct; *Pen*, penis; *smcl*, stylus muscles; *Sty*, stylus.

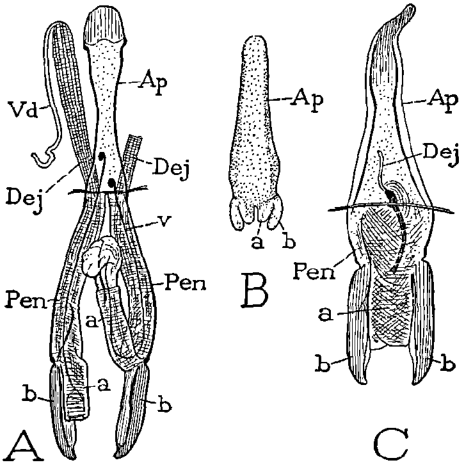

FIG. 297.—Male genitalia of Dermaptera. A, *Anisolabis maritima*, ventral view. B, same, last instar nymph. C, *Forficula auricularia*.

The bipartite type of intromittent organ is well shown in *Anisolabis maritima* (Fig. 297 A), in which there are two elongate penes (*Pen, Pen*) arising from a common basal apodemal plate (*Ap*). Each penis ends in a distal lobe (*a*) and bears a strong lateral process, or "paramere" (*b*), arising at the base of the lobe. The left lobe is turned proximally in the usual condition. A strongly musculated ejaculatory duct (*Dej*) penetrates each penis and opens into an eversible sac at the end of the terminal lobe. The immature intromittent organ of *Anisolabis*, even in a full-grown nymph (B), has the form of four small simple lobes arising from a long thin apodemal plate. The double or deeply bipartite penis with two ejaculatory ducts opening separately to the exterior is characteristic, according to Walker (1922), of the superfamilies Protodermaptera and Paradermaptera.

The unpaired type of organ occurs in Eudermaptera, where, as shown in *Forficula* (Fig. 297 C), there is a single median penis (*Pen*) with one terminal lobe (*a*) but provided with two lateral processes (*b*, *b*). The vasa deferentia of *Forficula*, Walker says, unite in a single ejaculatory duct (*Dej*) that opens on the median lobe, but there is present also a vestigial second duct with no external orifice, suggesting that one lobe of a primitively double penis has been suppressed.

It is difficult to estimate the significance of the presence of paired penes in two such unrelated orders of the Pterygota as the Ephemerida and Dermaptera, when there is no suggestion of a double origin of the penis in any of the more primitive apterygote insects, nor any evidence that the single organ of other Pterygota is formed by the union of a pair of primitive penes. The essential differences in structure between the paired organs of Ephemerida and those of Dermaptera should not be overlooked.

The Male Genitalia of Thysanura.—The genital equipment of male Thysanura is deserving of special attention because it presents in a simple form a structural complex of the type found in many pterygote insects, consisting of an unpaired median intromittent organ and of paired lateral accessories.

In Machilidae and Lepismatidae the intromittent organ is a simple tubular median penis, or phallus (Fig. 298 B, C), arising from the membrane behind the narrow membranous venter of the ninth abdominal segment. The organ is somewhat differentiated into a proximal part, or *phallobase* (*Phb*), and a distal part, or *aedeagus* (*Aed*). In Diplura the penis is rudimentary.

Closely associated with the penis are the appendages of the ninth segment, which are well developed in the Thysanura. Each genital appendage, or gonopod, consists of a large, flat coxopodite (Fig. 298 B, C, *Cxpd*) and of a slender distal stylus (*Sty*) movable by muscles arising in the coxopodite. In some species there arise from the mesal angles of the bases of the coxopodites of the ninth segment a pair of short gonapophyses (B, 2*Gon*), which closely embrace the penis. Certain species of *Machilis* have also a pair of smaller anterior gonapophyses arising at the corresponding angles of the coxopodites of the eighth segment (A, 1*Gon*). With such species, therefore, the appendages of the eighth and ninth abdominal segments of the male are identical in structure with those of the same segments in the female (Fig. 313 B, C), except for the greater length of the gonapophyses in the latter. Both pairs of gonapophyses, however, may be absent in the male (Fig. 298 C).

The ontogenetic origin of the median penis of Thysanura has not been carefully studied, but the simple structure of the adult organ suggests that the latter is merely a tubular outgrowth of the body wall around the mouth of the ejaculatory duct.

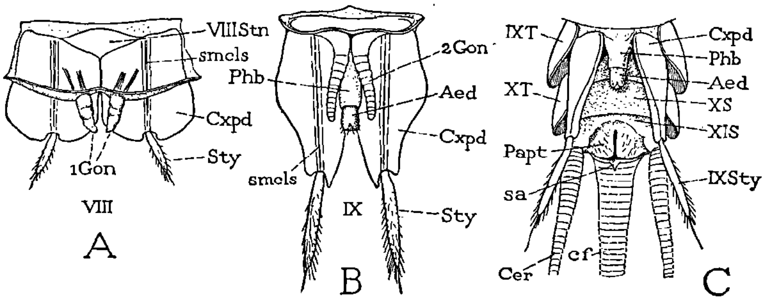

FIG. 298.—Male genitalia of Thysanura. A, *Machilis variabilis*, dorsal view of first gonopods, showing gonapophyses of eighth segment. B, same, dorsal view of second gonopods and median copulatory organ. C, *Nesomachilis maoricus*, ninth and terminal segments, ventral view.

General Structure of the Male Genitalia of Pterygote Insects.—The primary external genital organs of male pterygote insects are located medially on the venter of the ninth abdominal segment. This segment, therefore, is the *male genital segment*, or *gonosomite*. Accessory genital structures, however, may be present on the periphery of the genital segment or on the pregenital or postgenital segments. The genital parts, therefore, can be classed in two distinct groups of structures. Those of one group constitute the median intromittent apparatus of the ninth segment and may be designated the *phallic organs*. Those of the other group are the peripheral accessory structures of the ninth or other segments and may be termed collectively the *periphallic organs*. The phallic organs are immediately concerned with the function of coition; they include the phallus and various accessory or supporting structures associated with the latter. The periphallic organs are movable or immovable lobes or processes that have for the most part a grasping or clasping role in the function of copulation.

The Male Genital Segment.—The genital segment of the male (ninth abdominal somite) may be a simple segmental annulus resembling those that precede it; but usually it is more or less modified, and it is sometimes greatly distorted, asymmetrical, turned upon its axis, or even inverted. Generally the tergum and the sternum of the genital segment are distinct plates. They are sometimes separated by lateral pleural plates bearing a pair of appendicular lobes, but more usually the pleural and sternal areas of the genital segment are united in a definitive pleurosternal plate, and frequently the entire segment is a continuously sclerotized annulus.

The phallic organs (Fig. 299 A, *Phl*) arise from the conjunctival membrane behind the ninth sternum, but this membrane is usually invaginated within the ninth segment to form the *male genital chamber* (*GC*), in which the phallic organs are ordinarily mostly concealed. The ninth sternum (*IXS*) is thus, in most cases, the *male subgenital plate* ("hypandrium"), but often the external plate beneath the male genital apparatus is the eighth or the seventh sternum.

The periphallic organs of the genital segment may include a pair of lateral movable claspers (Fig. 299 B, *Hrp*) and various immovable lobes or processes arising from the tergum or the sternum. In some of the more generalized pterygote insects a pair of styli is borne on the sternum or on coxosternal lobes of the ninth segment of the male (A, *Sty*), but it should be observed that typical styli never occur in conjunction with movable claspers (harpagones).

The Phallic Organs.—The phallic organs of most insects other than Ephemerida and Dermaptera are the median genital outgrowths of the ninth segment, surrounding or containing the gonopore, that, as already defined, are immediately concerned with the function of coition. They take the form either of lobes, *phallomeres,* or of a median tubular penis, the *phallus,* and various accessory processes or supporting plates associated with the latter.

In the Blattidae and Mantidae the phallic organs consist of three phallomeres arising close to the gonopore from the anterior wall of the genital chamber. These structures in the young nymph of *Blatta* are simple membranous lobes (Fig. 302 C), two of which are lateral and the other ventral with respect to the gonopore. In the adults of both families, however, the phallomeres become greatly enlarged, somewhat altered in position, and take on highly irregular forms (F, G, H).

Studies on the development of the male genitalia in Trichoptera, Lepidoptera, and Hymenoptera have shown that the tubular phallic organ of these insects is formed during larval development by the union of a pair of genital lobes that grow out at the sides of the gonopore (Zander, 1900, 1901, 1903; Singh Pruthi, 1924, 1925; Mehta, 1933). It is possible, therefore, that these larval phallic lobes of the higher insects are homologues of the lateral phallomeres of Mantidae and Blattidae. According to Zander, the primitive phallic lobes divide each into a median lobe and a lateral lobe, the two median lobes uniting to form the intromittent organ, while, in Trichoptera and Lepidoptera, the lateral lobes move to the sides and become articulated to the margins of the annulus of the ninth segment, where they develop into the movable claspers of this segment. We might, therefore, regard the median lobes as gonapophyses of the gonopods, and the lateral lobes (valvae, or harpagones) as the styli. However, since it is claimed by Mehta that the lateral lobes in Lepidoptera arise separately from the median lobes, we cannot accept it as established that the gonopods of the male insect take any part in the formation of the intromittent organ, though there appears to be little doubt that they give rise to the styli or to the movable claspers of the genital segment.

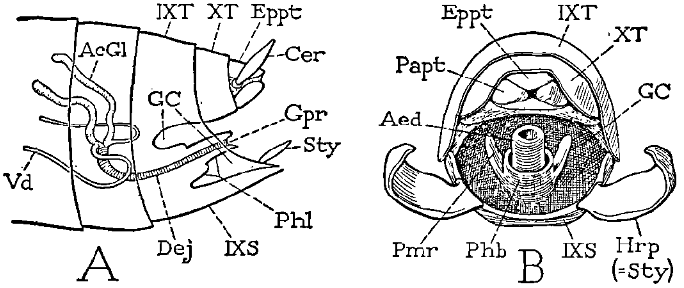

Fig. 299.—Diagrams of the basic structure of the male genitalia of pterygote insects A, end of abdomen, with phallic organ in genital chamber, lateral view. B, same, end view, with clasperlike modifications of styli. *AcGl*, accessory gland; *Aed*, aedeagus; *Dej*, ductus ejaculatorius; *GC*, genital chamber; *Gpr*, gonopore; *Hrp*, harpago (stylus); *Phb*, phallobase; *Phl*, phallus (median penis); *Pmr*, paramere; *Sty*, stylus; *Vd*, vas deferens.

Some male Thysanura, as we have seen (Fig. 298 A, B), have gonapophyses that are without doubt homologous with the processes of the female ovipositor, but there is here present also a well-developed median phallic organ between the gonapophyses of the ninth segment, and the gonapophyses may be entirely absent (C). The lateral phallic lobes of nymphal blattids (Fig. 302 C) are far removed from the styli (*Sty*) carried on the margin of the ninth sternum, and in the adult stage (F, G) they are widely different in both form and musculature from the gonapophyses of the female.

The typical phallus is a conical or tubular structure containing the terminus of the ejaculatory duct. The organ, however, is highly variable in form and in the extent of its secondary modifications. Its musculature is simple or complex and so variable that in most cases it is impossible to trace any consistent scheme of homology in the various muscle patterns of the organ. The current view that male gonapophyses are involved in the formation of the phallus is disregarded in the present discussion because of the absence of positive ontogenetic evidence, and because of the entire lack of conformity in the phallic musculature. It is assumed tentatively that the phallus is an independent median outgrowth of the body wall, independently musculated, and bound by no phylogenetic influences to conform with the structure of any ancestral appendage. On the other hand, the gonopods of the ninth segment appear undoubtedly to contribute the movable claspers to the male genital complex.

A simple tubular phallus, similar to that of the Thysanura, is present in Plecoptera, though in the latter order the organ may have sclerotic plates in its walls, and it is ordinarily retracted into a pouch of the conjunctival membrane above the ninth sternum, from which it is exserted during copulation.

With the majority of insects the phallus is differentiated into several more or less distinct parts, and it may be provided with various accessory structures. Externally there is very commonly to be distinguished a proximal part, or *phallobase* (Figs. 299 B, 300 A, *Phb*), and a more slender terminal part, the *aedeagus* (*Aed*). When the basal differentiation is not evident the entire organ is generally called the aedeagus. The walls of the phallobase and the aedeagus constitute together the *ectophallus* in distinction to an inner chamber, or *endophallus*, which is usually invaginated at the end of the organ (Fig. 300 A, *Enph*) and contains the true gonopore (*Gpr*), or aperture of the ductus ejaculatorius (*Dej*). The endophallus is sometimes eversible (B) and is sometimes a permanently internal structure. Its opening at the end of the aedeagus is the *phallotreme* (A, *Phtr*).

The phallobase is an important part of the phallic organ in many insects, but in some it is reduced or represented only by basal sclerites supporting the aedeagus, and again it may be entirely absent. Usually the phallobase gives attachment to phallic muscles from the body wall, as well as to muscles of the aedeagus, and may be provided with a *basal apodeme*. Sclerites in its wall are termed the *basal plates* of the phallus. Very commonly the distal part of the phallobase forms a fold about the base of the aedeagus (Fig. 300 D), and this fold is sometimes produced into a tubular sheath, the *phallotheca*, which partly or wholly encloses the aedeagus (E, *Thc*). In such cases the aedeagus may be reduced (G, *Aed*) or entirely suppressed (H); the phallic tube is then the theca (*Thc*), and its lining is the *endotheca* (*Enth*). In some insects in which there is no evident phallobase, the aedeagus is more or less sunken into a *phallocrypt* (C, *Crpt*), or pocket in the genital chamber wall, which possibly represents the endotheca. The walls of the crypt may be membranous or variously sclerotized; the sclerotic part sometimes forms a ring or tube from which the aedeagus projects.

Lobes or processes arising from the phallobase are of frequent occurrence. Lateral basal lobes are particularly characteristic genital structures in the Coleoptera, where they are commonly called *parameres* (Fig. 303 C, *Pmr*). The term, however, is applied also to other processes of the genital armature and has been used by Walker (1922) and other writers as synonymous with "male gonapophyses," which are supposed to be components of the phallus. Since, however, as already shown, it appears doubtful that the gonapophyses are retained in the males of pterygote insects, the term "paramere" is here defined according to the current usage by coleopterists as lateral process of the phallobase. Dorsal and ventral processes of the phallobase may then be named, respectively, *epimeres* or *hypomeres.*

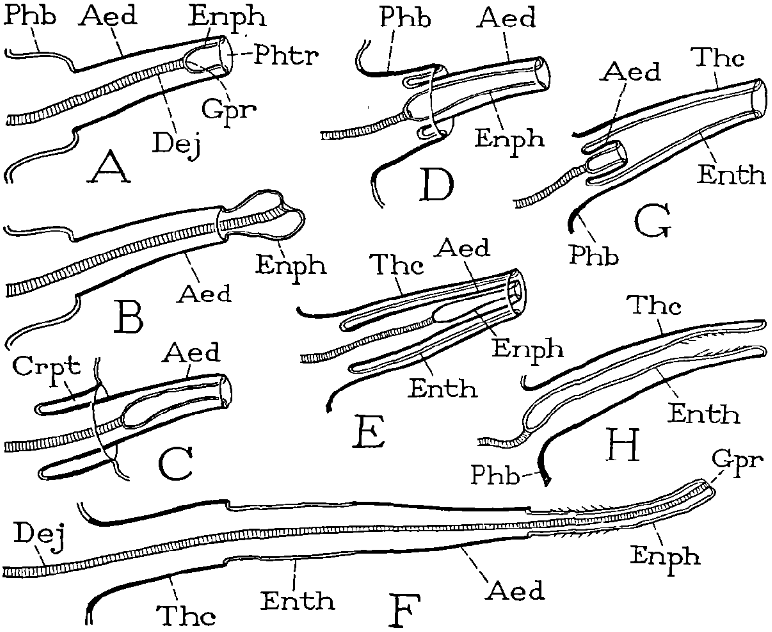

FIG. 300.—Modifications of the phallus, diagrammatic. A, simple structure. B, endophallus everted. C, aedeagus partly retracted into a phallocrypt. D, aedeagus partly retracted into phallobase. E, aedeagus enclosed in a phallotheca. F, phallus extended by eversion of endophallus and endotheca. G, aedeagus reduced, theca enlarged. H, aedeagus suppressed and replaced by the theca. *Aed*, aedeagus; *Crpt*, phallocrypt; *Dej*, ductus ejaculatorius; *Enph*, endophallus; *Enth*, endotheca; *Gpr*, gonopore; *Phb*, phallobase; *Phtr*, phallotreme; *Thc*, phallotheca.

The aedeagus is usually tubular in form (Fig. 303 D, *Aed*), though it assumes a great variety of shapes, and its walls are characteristically strongly sclerotized, except often for a terminal membranous part known as the *preputial sac*, or *vesica* (*Vsc*). The organ is usually provided with its own muscles, and its base may be produced into one or more apodemal processes (*Apa*). The distal extremity is frequently armed with spines, small plates, or slender processes often called *titillators.* Though the aedeagus is generally the conspicuous part of the phallic organ, it may be much reduced or even practically obliterated, and in such cases, as already mentioned, a tubular thecal extension from the phallobase may replace the aedeagus (Fig. 300 G, H, *Thc*).

The endophallus varies from a small invagination in the end of the aedeagus, containing the gonopore (Fig. 300 A, *Enph*), to a long inner tube (D) or an elaborate internal chamber of the phallus. In its tubular form the endophallus is often mistaken for the ejaculatory duct. When its walls are membranous, the endophallus is usually eversible (B, F), and, when everted during copulation, it becomes the functional intromittent organ (sometimes called "the penis"), since it is the part of the phallus projected into the copulatory receptacle of the female. The length of the endophallus in such cases is probably correlated with the length of the genital tract of the female between the copulatory entrance and the mouth of the spermatheca. The inner walls of the endophallus are often armed with spicules, spines, and plates, which become external with eversion (F). When the phallobase, the aedeagus, and the endophallus are each retracted one within the other, the fully everted organ may become an extraordinarily long slender tube (F). On the other hand, when the endophallus is a permanently internal part of the phallus, it sometimes attains a high degree of development. An endophallus of this type is characteristic of the Acrididae, where it forms a complex, strongly musculated apparatus for discharging the spermatophores through the relatively small aedeagus.

The Periphallic Organs.—The periphallic organs, in contrast to the median phallic organs, arise peripherally, generally from the annulus of the ninth abdominal segment but also from the other segments often closely associated with the latter in the genital complex. In the Thysanura the periphallic organs are the gonopods of the ninth abdominal segment; in the Pterygota they include movable lobes (harpagones) and various accessory immovable genital processes.

The gonopods of the Thysanura (Fig. 298), as we have already observed, consist each of a large basal coxopodite (*Cxpd*) and of a slender distal stylus (*Sty*) movable by muscles arising in the coxopodite. Gonapophyses may be present on the appendages of the ninth segment (B, *2Gon*) or absent (C); rarely they occur on the appendages of the eighth segment (A). When present on the ninth segment they closely embrace the penis but do not form a part of the phallic organ.

The movable periphallic genital lobes of pterygote insects are typically lateral appendages and, when present, always pertain to the annulus of the ninth abdominal segment (Fig. 299 B, *Hrp*). They are to be identified by the fact that they are individually provided with muscles inserted on their bases. In form they vary from slender processes to broad lobes or from small hooks to long falciform arms, and frequently they are armed with secondary outgrowths. In general these *movable* periphallic organs serve as copulatory claspers, and for this reason they are here designated the *harpagones* (from ἁρπάγη, a "grappling hook"). They occur principally in Ephemerida, Hemiptera, Neuroptera, Mecoptera, Lepidoptera, and Diptera but are frequently absent in members of groups in which they are typically present.

The harpagones always arise from some part of the lateral or ventral walls of the genital segment, never from the tergal region. In some insects they are borne on independent basal plates, which either are interpolated laterally between the tergum and sternum of the genital segment or are attached to the sternum. When such plates are present the muscles of the claspers take their origins upon them; otherwise the claspers are borne on the sternal (coxosternal) plate of the segment and their muscles arise on this plate. The position and musculature of the harpagones at once suggest that these movable genital claspers represent the styli of the more generalized insects, and that the basal plates on which they are sometimes supported are the coxopodites of the gonopods. When the basal plates of the claspers are not individually evident, it is to be supposed that they have united with the sternum, producing the same condition as in some Thysanura and Orthoptera where the styli arise directly from a coxosternal plate of the genital segment. Movable genital lobes and typical styli, as we have observed, do not occur together in any insect, though both may be absent.

The numerous fixed or merely flexible processes arising from the walls of the genital segment, or also from the other segments associated in the genital complex, are so variable in their occurrence that there can be little homology between those occurring in the different major groups of insects, though their presence and form are often highly characteristic of smaller groups and of species. Such structures are never specifically provided with muscles, though in rare cases they may be movable by segmental muscles attached at their bases. The immovable genital processes are of such diverse forms that they can have no constant function; in general they appear to be adapted for grasping or holding various parts of the female apparatus, but only a close study of insects in copulation will reveal their exact uses in the genital mechanism.

Characteristics of the Male Genitalia in the Principal Pterygote Orders.—It is impossible to give an adequate treatment of the many modifications in the copulatory apparatus of male insects within the space that may be allotted to the subject in a general text. The following descriptions, therefore, present only a sketch of the salient or distinctive features of the male genitalia in the principal orders, with suggestions as to how the various parts may be related to one another.

Odonata.—The Odonata are of particular interest in a study of the male genitalia because of the development of a secondary copulatory organ on the anterior part of the abdomen. The true gonopore of the male (Fig. 301 C, *Gpr*) is situated on a rudimentary penis of the ninth abdominal segment concealed beneath two small plates (*e*), which possibly represent the gonopods. A large postgenital plate (*f*) appears to be a secondary sclerotization of the intersegmental area behind the genital organ.

The functional intromittent organ of the Odonata is a secondary structure situated in a median depression, or genital fossa, on the ventral wall of the second abdominal segment (Fig. 301 A, *Pen*). This organ is a strongly sclerotized tubular structure composed of several segment-like parts movable upon each other (B). Various accessory lobes (A, *a*, *b*), differing much in different species, may arise from the surrounding walls of the first and second abdominal segments. The copulatory organ contains a chamber open to the exterior which serves as a sperm receptacle. Before copulation the male dragonfly transfers spermatozoa from the genital opening on the ninth segment to the receptacle of the intromittent organ by flexing the abdomen ventrally and forward until the two apertures are in contact. In copulation the male grasps the female with the cerci by the neck or the back of the thorax, or sometimes by the head, and the female brings the end of her abdomen forward beneath that of the male to effect a union with the anterior genitalia of the latter. Details of the structure of the male organs in Anisoptera and Zygoptera have been described by Ingenitzsky (1894), Backhoff (1910), E. Schmidt (1916), and Kennedy (1917, 1922).

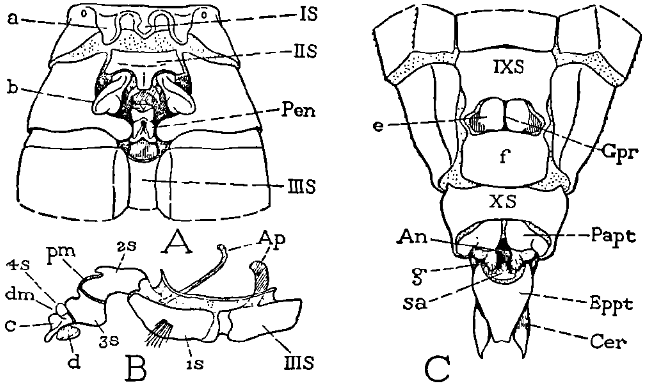

FIG. 301.—Male genitalia of Odonata (*Plathemis lydia*). A, base of abdomen, under surface, showing secondary copulatory organs. B, secondary penis of second abdominal segment, lateral view. C, posterior end of abdomen, under surface, showing true gonopore (*Gpr*) on ninth segment between two valve-like plates.

Orthoptera.—The external genitalia of male Orthoptera are mostly phallic structures. Styli of the ninth segment are present in several families, but they take no part in the genital apparatus and depart but little from the typical stylus form (Fig. 302 A-E, *Sty*). The coxopodites of the styli are plates distinct from the ninth sternum in Grylloblattidae (A, *Cxpd*), but otherwise the genital coxopodites are united with the sternum in the definitive sternal plate of the ninth abdominal segment.

In Mantidae and Blattidae the male organs consist typically of three phallic lobes surrounding the gonopore, contained in a genital chamber between the ninth sternum and the paraprocts (Fig. 302 E). Of the three phallomeres, two are situated above the gonopore, one to the left (E, *F*), the other to the right (*G*), while the third (*H*) lies ventral to the genital opening. The right lobe usually assumes a position dorsal to the others and its base may extend almost completely across the wall of the genital chamber. In the adults of most members of these families the lateral phallic lobes become extraordinarily complex in structure by the development of secondary lobes and processes of various forms (F, G). The ventral lobe (H) is usually more simple, and, since the ejaculatory duct (*Dej*) opens in a membranous fold at its base (*Gpr*), it is often called the "penis." An intricate system of muscles arising in the ninth segment is inserted on the bases of the phallomeres, and in addition there are numerous muscles within the lateral lobes inserted on their various secondary parts. In some of the roaches the phallic organs are simpler, and in certain forms, as in *Ectobia*, the lateral lobes are retracted into deep pouches of the genital chamber.

In the nymph of *Blatta* the highly complex genital organs of the adult are represented by three simple lobes projecting from the anterior wall of the genital chamber (Fig. 302 C), two of which (*F*, *G*) lie immediately laterad of the gonopore, and the third (*H*) below it. These three simple phallic structures appear to be merely outgrowths of the genital chamber wall in the immediate neighborhood of the gonopore. The lateral lobes have been regarded as gonapophyses of the ninth segment, but in the nymph there is nothing to suggest that they have any relation to the gonopod bases incorporated in the ninth sternum.

Among other Orthoptera the male genital structures are very different in the several families. The Phasmidae have a short compact intromittent organ, which possibly is formed by the union of primitive phallic lobes about the gonopore. In Tettigoniidae and Gryllidae the lateral lobes are reduced and retracted, while the ventral lobe becomes enlarged and may be the only phallic structure ordinarily visible. In Acrididae the phallus is a large conical structure distinctly divided into a phallobase and aedeagus and contains a highly developed endophallus forming a sperm ejection pump into which opens the ejaculatory duct.

A large, often complex sclerite, known as the *epiphallus*, or "pseudosternite," lies dorsally at the base of the phallic organs in Tettigoniidae,

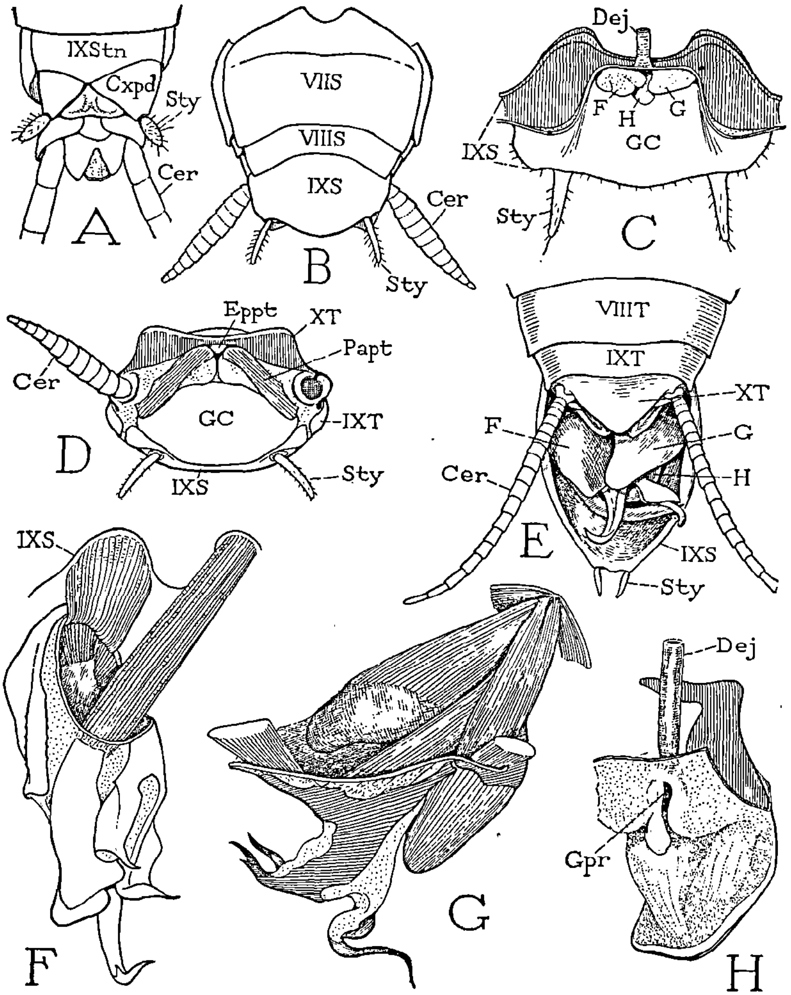

Fig. 302.—Male genitalia of Orthoptera. A, *Grylloblatta campodeaformis*, end of abdomen, ventral view. (*From Walker*, 1922.) B, *Blatta orientalis*, end of abdomen, ventral view. C, same, young nymph, genital chamber above ninth sternum, showing phallic lobes (*F*, *H*, *G*) surrounding gonopore. D, same, adult, end of abdomen, terminal view. E, *Paratenodera cinensis* (*Mantidae*), end of abdomen, dorsal view, with phallic lobes in place. F, *Blatta orientalis*, adult, left phallic lobe, dorsal surface. G, same, right phallic lobe, dorsal surface. H, same, ventral phallic lobe and gonopore, dorsal view.

Gryllidae, and Acrididae and forms an important element of the copulatory mechanism.

Coleoptera.—The male genitalia in Coleoptera, as in Orthoptera, are phallic structures only, there being in general no accessory or periphallic armature on the genital segments. There are, therefore, no elements of the genital complex that can be referred directly to the gonopods; movable claspers (harpagones) of the ninth segment are always absent, and, in the male at least, styli are never present in any form. The ninth and tenth segments of the abdomen are usually much reduced and retracted into the eighth segment, and in some forms the eighth is concealed within the seventh. The phallic organs consist essentially of a tubular aedeagus and a variously developed phallobase usually provided with parameres. The innumerable variations in the genital apparatus of male Coleoptera have been described by Sharp and Muir (1912), but the fundamental structure of the parts involved may be understood from a few typical examples.

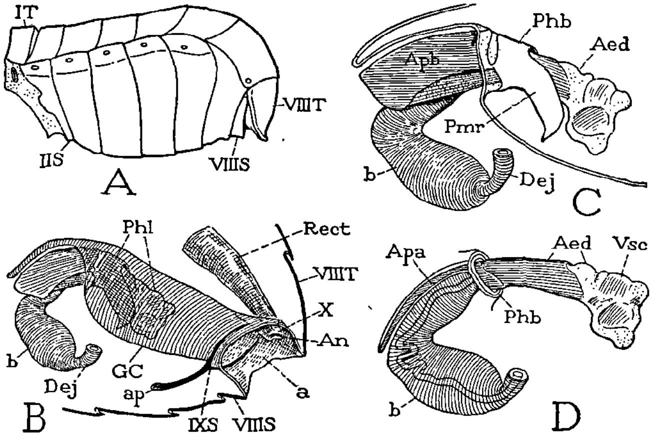

FIG. 303.—Abdomen and male genitalia of Coleoptera (*Phyllophaga chiriquiana*). A, male, abdomen. B, genital chamber and phallus of rudimentary ninth segment, and anogenital vestibule (*a*) inflected from eighth segment. C, the phallus and end of ejaculatory duct, showing apodeme (*Apb*) and paramere (*Pmr*) of phallobase (*Phb*), and distal aedeagus (*Aed*). D, the aedeagus, with aedeagal apodeme (*Apa*) and terminal vesica (*Vsc*).

The external part of the abdomen consists usually, as illustrated in *Phyllophaga* (Fig. 303 A), of the first eight segments. Within the eighth segment is an invagination cavity (B, *a*) into which are retracted the reduced ninth and tenth segments, but which is continued forward through the narrow annulus of the ninth segment as a large genital chamber (*GC*) containing the phallic organs (*Phl*). The tenth segment (*X*) appears as a small projection from the dorsal wall of the entrance chamber, bearing the anus (*An*). The region of the ninth segment that encircles the mouth of the genital chamber may contain a complete, though narrow, sclerotic annulus, as in Carabidae, but generally only a sternal sclerite is present, and this, as in *Phyllophaga* and various other beetles, is reduced to a U-shaped or V-shaped bar (B, *IXS*), often provided with a ventral apodeme (*ap*), which gives it a Y-shaped form.

The phallic organs arise from the anterior wall of the genital chamber (Fig. 303 B, *Phl*). The phallobase (*tegmen* of Sharp and Muir) is usually well differentiated from the aedeagus (C, *Phb*) but varies much in form and character; it may be a membranous fold about the base of the aedeagus containing several basal plates, but often it is a sclerotic ring and sometimes forms a cylindrical theca completely investing the aedeagus. Generally the phallobase bears a pair of parameres (*Pmr*) and in some cases a median dorsal lobe, or epimere; from its base an apodeme (*Apb*) projects into the body cavity for muscle attachments. The aedeagus (C, D, *Aed*) is typically a sclerotic tube with a membranous distal part (*Vsc*); from its base an apodeme (D, *Apa*) projects into the body cavity beneath the apodeme of the phallobase. An endophallic chamber or tube is usually present and is generally eversible; when everted in coition it becomes the functional intromittent organ.

In some beetles the eighth segment also is partly or entirely retracted, and, as in Oedemeridae, it may take the form of a sheath enclosing the ninth and tenth segments, the genital chamber, and the phallic organs, the last, finally, consisting of a phallobase, an aedeagus, and an endophallus. In such cases the genital apparatus assumes the complicated form of numerous folds successively ensheathing each other, all of which probably are protracted during the act of copulation.

Hemiptera.—In the Hemiptera there are present, in addition to well-developed phallic organs, various periphallic structures having the form of lobes or processes arising from the eighth, ninth, and tenth abdominal segments. Among these structures there is usually one pair movably articulated to some part of the ninth segment and individually provided with muscles. These movable claspers are thus to be identified as the harpagones, that is, as derivatives presumably of the styli of the gonopods of the ninth segment. The harpagones vary from small hooks to long slender processes or broad spatulate lobes, often of irregular shapes. In some cases they are absent. In Homoptera they arise from the floor of the genital chamber, where their bases are usually associated with one of the sclerites of the phallobase or supporting plates of the aedeagus (Fig. 305 E, *Hrp*). In Heteroptera the harpagones are small but strongly musculated processes (Figs. 304 B, C, 305 G, *Hrp*) articulated to the sclerotic wall of the ninth segment inflected into the genital chamber.

The principal segment involved in the genital modification of the hemipterous abdomen is the ninth (Figs. 304, 305 A, H, *IX*), but in Heteroptera the eighth is often reduced and closely associated with the ninth (Fig. 304 A, B, *VIII*). In most Homoptera the tenth and eleventh segments are distinct annuli (Figs. 304 D, 305 H, *X*, *XI*), the tenth being sometimes provided with accessory genital processes in the form of lateral lobes (Fig. 304 D, *c*). In Heteroptera the two postgenital segments apparently are united in a tubular proctiger (A, B, C, *Ptgr*). The ninth segment in Homoptera often bears, in addition to the harpagones, accessory periphallic structures having the form of short processes (Fig. 304 D, *a*, *b*) or of long arms or broad lobes (Fig. 305 H, *a*, *b*). Such structures may be flexible at their bases and they have been mistaken for the harpagones (styli), but they are to be distinguished from the latter by the fact that they are never provided with muscles.

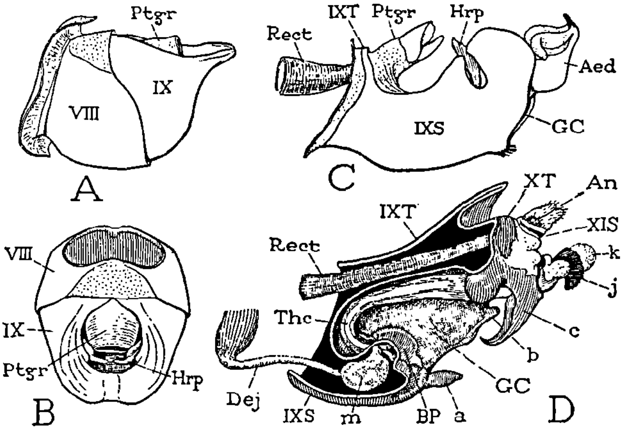

FIG. 304.—Male genitalia of Hemiptera. A, *Anasa tristis*, genital segments and proctiger, lateral view. B, same, dorsal view, showing tips of harpagones. C, *Notonecta variabilis*, ninth segment and proctiger. D, *Magicicada septendecim*, section of ninth segment and genital chamber, with tenth and eleventh segments attached, showing thecal tube, which replaces the true aedeagus, supported on basal plate (*BP*).

The phallus of the Hemiptera comprises in most cases a phallobase and an aedeagus, though either one or the other may be suppressed. The aedeagus in its simplest development is a tubular structure (Fig. 305 E, *Aed*), but more usually it takes on an irregular shape (Figs. 304 C, 305 F, *Aed*), which by exaggeration may produce bizarre forms, often with curious terminal outgrowth (Fig. 305 D, *g*). It is usually provided with apodemal processes for muscle attachment (Fig. 305 D, *h*, *i*). The phallobase is variously developed. It may consist merely of one or two basal plates in the wall of the genital chamber (Fig. 305 E, F, *1BP*, *2BP*) supporting the aedeagus (*Aed*) and giving attachment to phallic muscles. In the cicada the single large basal plate of the phallus (I, J, *BP*) is articulated upon fulcral arms (*l*) of the sternal margin of the ninth segment. In some cases the phallobase bears parameral processes (F, *Pmr*), or again it may be produced into a thecal sheath more or less investing the aedeagus (C, *Thc*) and subject to many variations in form. When the theca is well developed the aedeagus is sometimes greatly reduced, as in Fulgoridae and Cicadellidae (D, *Aed*), except for terminal processes (*g*) that may protrude through the theca (C, *g*). In the Cicadidae it is evident that the aedeagus has been almost entirely suppressed, and that the long tubular intromittent organ is the theca (Figs. 304 D, 305 J, *Thc*). The inner tube of the organ is therefore the endotheca (Fig. 305 J, *Enth*). The only remnant of the aedeagus in the cicada is an apodemal process (*i*) attached to the inner extremity of the endotheca where the ejaculatory duct (*Dej*) opens into the latter. The homologies of the various genital structures of male Hemiptera can be determined only by a very close study of the relations of the parts to one another.

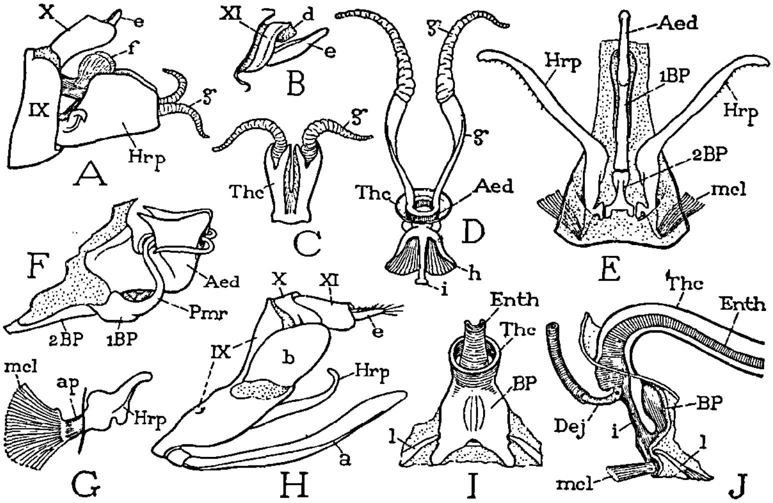

FIG. 305.—Male genitalia of Hemiptera. A, *Poblicia fuliginosa* (Fulgoridae), ninth and tenth abdominal segments. B, same, eleventh segment removed from tenth. C, same, the phallic theca with ends of aedeagal cornua projecting. D, same, the reduced aedeagus exposed by removal of theca, showing aedeagal cornua (*g*) and apodemes (*h*, *i*). E, *Idiocerus atkinsoni* (Cicadellidae), phallus and harpagones, ventral view. F, *Amblydisca gigas* (Cicadellidae), phallus with parameres arising from basal plates. G, *Euschistus variolarius* (Pentatomidae), left harpago and muscle. H, *Idiocerus atkinsoni*, ninth, tenth, and eleventh segments, showing accessory lobes (*a*, *b*) of ninth segment. I, J, *Magicicada septendecim*, base of phallus, ventral and lateral views, showing thecal and endothecal tubes; aedeagus obliterated except for apodeme (*i*) supporting endotheca at union with ductus ejaculatorius.

Mecoptera.—In the Mecoptera the periphallic genital claspers of the ninth abdominal segment are distinctly two segmented. The basal segments appear to be the coxopodites, the distal segments the true harpagones (styli). Each segment is individually movable by muscles. In *Panorpa* the organs are strongly developed, but the harpagones extend but little beyond the ninth segment; in *Merope tuber* they are long slender, weakly sclerotized appendages, each of which is bifid terminally and bears a suckerlike disk on its inner surface.

The abdomen of the typical scorpionflies ends with a recurved bulbous structure formed of the ninth segment and its appendages (Fig. 306 A, *IX*), which contains the phallic organs and mostly conceals the tubular proctiger (B, *Ptgr*). In *Panorpa* the genital segment is a continuously sclerotized annulus, the tergal region of which is greatly prolonged posteriorly (B, C, *IXT*), and the short sternal region produced into two long lobes (B, *a*). The large lateral coxopodites are broad oval lobes (B, C, *Cxpd*) articulated basally to the annulus of the ninth segment. Distally each bears a strong, hooked harpago (*Hrp*), which is individually movable by antagonistic muscles arising in the coxopodite (E). The aedeagus, a flat irregular structure (D, *Aed*) with a pair of distal arms (*g*), arises from the wall of the genital pouch between the bases of the claspers. At its sides are two slender parameres (*Pmr*) supported on a U-shaped bar (*BP*) in the ventral wall of the genital chamber proximal to the base of the aedeagus. The morphology of the phallic structures is difficult to understand in *Panorpa.* A more comparative study of the mecopteran genitalia, as given by Issiki (1933), shows much variation in the structure of the organs and suggests that the phallus is composed primarily of two united lateral phallic lobes, provided with protractor and retractor muscles, between which opens the large saclike ductus ejaculatorius.

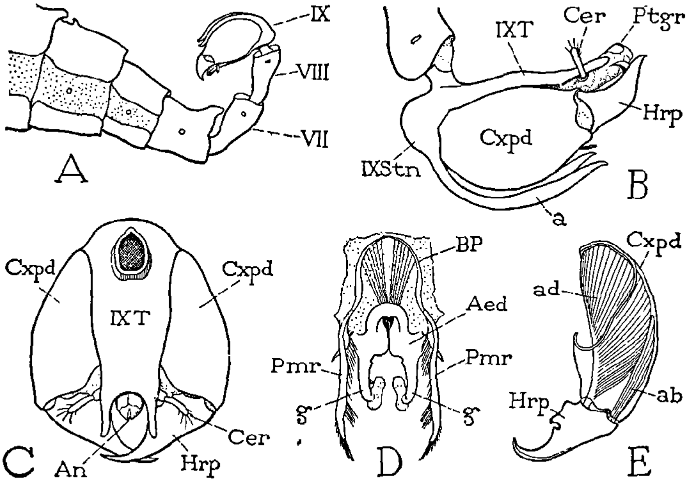

FIG. 306.—Male genitalia of Mecoptera (*Panorpa consuetudinis*). A, end of abdomen. B, genital segment and proctiger, lateral view, showing 2-segmented gonopod (*Cxpd, Hrp*) and accessory lobes (*a*) of ninth sternum. C, same, dorsal view. D, phallus, dorsal view. E, gonopod, showing muscles of harpago arising in coxopodite.

Trichoptera.—In most of the Trichoptera, as in the Mecoptera, the genital claspers are two segmented, each consisting of a proximal coxopodite and a distal stylus, or harpago (Fig. 307 A, B, *Cxpd, Hrp*). The coxopodite is movable on the annulus of the ninth segment by muscles inserted on its base (B), and the harpago is movable on the coxopodite by muscles arising within the latter. In some forms each clasper consists of a single segment, which appears to be the coxopodite rather than the harpago, since the harpago is often reduced and is sometimes not separated from the coxopodite, though it retains its basal muscles. The coxopodites are generally united with each other medially by a transverse bridge, or *pons coxalis* (C, *Pncx*), lying in the floor of the genital chamber, and from the bridge a median process (*BP*) extends upward in the genital chamber wall to give support to the sheath of the aedeagus (E). The aedeagus is tubular (*Aed*); its base may be sunken in a crypt of the genital chamber (*Crpt*), or the entire organ may be ensheathed in a thecal fold.

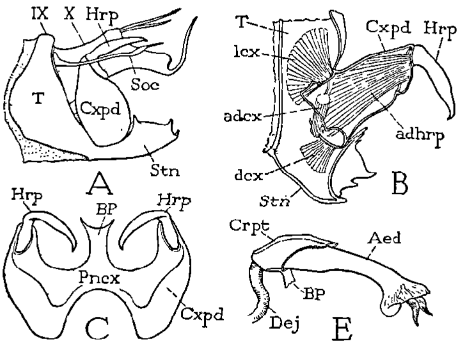

FIG. 307.—Male genitalia of Trichoptera (*Neuronia semifasciata*). A, ninth and tenth abdominal segments and appendages. B, right gonopod, inner view, showing muscles. C, ventral view of gonopods united by pons coxalis (*Pncx*) supporting basal plate of phallus. E, aedeagus (*Aed*) and basal crypt (*Crpt*).

The single postgenital segment present in Trichoptera appears to be the tenth (Fig. 307 A, *X*). It varies greatly in shape and is often provided with terminal processes of various forms. Paired lateral processes (*Soc*) sometimes arising from the base of the segment appear to be homologues of the so-called socii of male Lepidoptera and are possibly the pygopods of the tenth segment.

Lepidoptera.—The genital complex of male Lepidoptera includes the eighth, ninth, and tenth abdominal segments. The eighth segment forms at least a protractile base for the copulatory apparatus (Fig. 308 H), and in some cases it bears accessory genital lobes. The ninth segment may be a simple sclerotic ring (H, *IX*), but usually it is irregular in form, with distinct tergal and coxosternal areas of sclerotization (D).

The tergum (*IXT*) is the *tegumen* of lepidopterists, and the coxosternal arc the *vinculum*. The sternal region of the vinculum is often extended forward in a deep inflection known as the *saccus* (A, D, E, *c*), the membranous ventral wall of which (E, *d*) is usually adnate with the sternal surface (*Stn*). The tenth segment may be a simple membranous tube (H, *X*), but usually it presents a variously modified tergal structure called the *uncus* (B, C, D, *e*) and a mandible-like ventral lobe, the *gnathos* (*f*). A pair of lateral processes, termed the *socii*, often arise from the base of the tenth segment; they are usually membranous hairy appendages, and there is some evidence that they are derived from the pygopods (postpedes) of the tenth segment of the larva.

Movable genital claspers (the *harpes* of lepidopterists) are characteristic of the male genitalia of Lepidoptera and assume a great variety of forms (Fig. 308 D, H, I, *Hrp*). Typically they are borne on the coxopodite areas of the vinculum, in which their muscles take their origin (D, E). In such cases there can be little doubt that the organs are the harpagones (stylus derivatives) of other insects. In some of the Microlepidoptera, however, the claspers are articulated ventrally to a median triangular plate (I, *BP*) that supports the sheath of the aedeagus, and their muscles (*6*) take their origins medially on a sclerotization of the aedeagal sheath. Here the intimate relation between the claspers and the phallobase suggests that the clasping organs in such cases are parameres, and that they are not homologous with the typical dorsolateral harpagones of other Lepidoptera (D, *Hrp*), the muscles of which arise in the coxopodite areas of the vinculum (E).

The phallic organs of the Lepidoptera include an aedeagus (Fig. 308 A, D, F, I, *Aed*), usually an eversible endophallic tube often of much greater length than the aedeagus (F, *Enph*), and various supporting structures that may be referred to the phallobase. In its simplest development the phallobase is a mere inflection of the genital chamber wall forming a pocket (phallocrypt) containing the base of the aedeagus; but the lips of the pocket may be produced as a tubular theca (D, F, *Thc*) more or less enclosing the aedeagus. The inner walls of the sheath, however, are usually variously sclerotized, forming in some cases a sclerotic ring or tube, the *anellus*, from which the aedeagus protrudes (I, *Anl*). The ventral lip of the anellus may be continuous with a median arm from a supporting basal plate (*BP*) in the ventral wall of the genital chamber.

Hymenoptera.—The male genitalia of Hymenoptera appear to be phallic structures only, periphallic appendicular organs being absent in most cases. The phallus is usually a large, highly complex structure (Fig. 309 C, D) arising from the wall of the genital chamber above the ninth sternum (A). It consists of a central aedeagus (C, D, *Aed*), often provided with lateral or terminal processes, and of a large two-segmented phallobase (*Phb*) bearing various lobes and processes surrounding the aedeagus. The proximal segment, or basal ring ("cardo"),

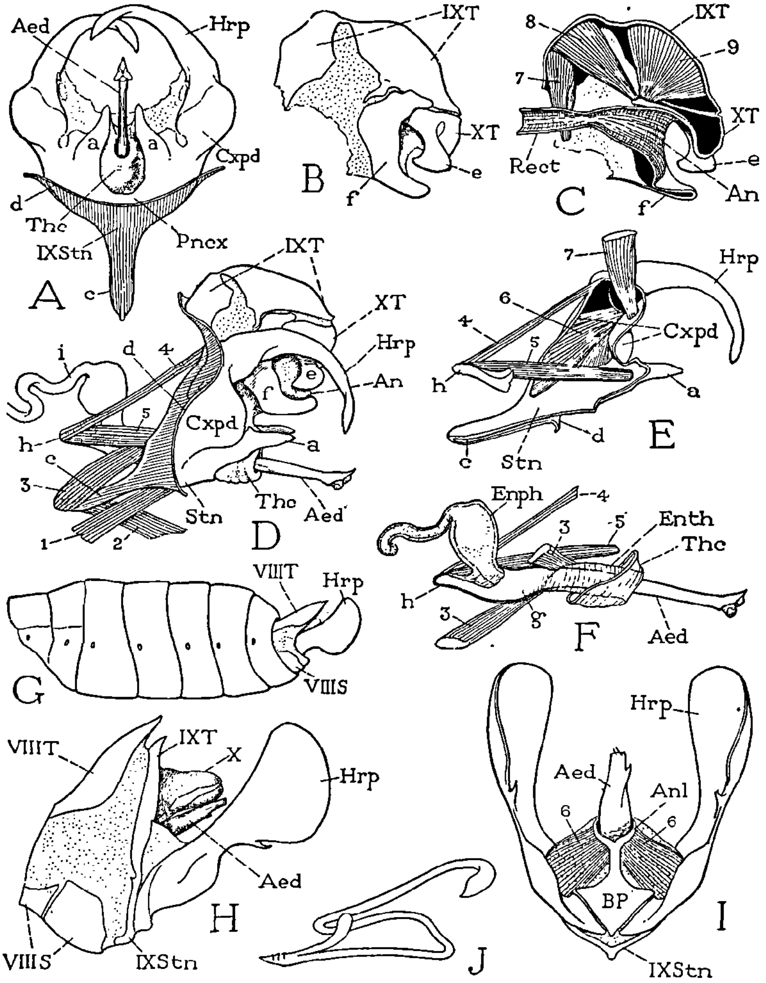

FIG. 308.—Male genitalia of Lepidoptera. A, *Bombyx mori*, ventral view of genital segment. B, same, ninth tergum and tenth segment. C, same, inner view of right half. D, same, genital and tenth segments with phallus, appendages, and muscles. E, same, right harpago and half of ninth sternum, inner view. F, same, phallus and phallic muscles. G, *Carpocapsa pomonella*, abdomen. H, same, eighth, ninth, and tenth segments. I, same, genital segment and aedeagus, ventral view. J, a lepidopterous spermatophore from bursa copulatrix of female.

of the phallobase (*BR*) opens from the body cavity by a large foramen (D) that gives passage to the ejaculatory duct. The distal segment bears usually one or two pairs of movable lobes provided individually with muscles. Of these the more lateral ventral pair (C, D, G, *Pmr*) may be termed *parameres*, since they are at least analogous with the parameres of Coleoptera (Fig. 303 C, *Pmr*), though the dorsal lobes (Fig. 309 C, G, *b*) are accessory structures of the same nature. Hymenopterists generally call the ventral lobe on each side the *volsella*, and the dorsal lobe the *squama*. Some, however, regard the basal parts of the genital organ as being formed of the united coxopodites of the ninth segment, and therefore regard the appendicular lobes as stylus derivatives.

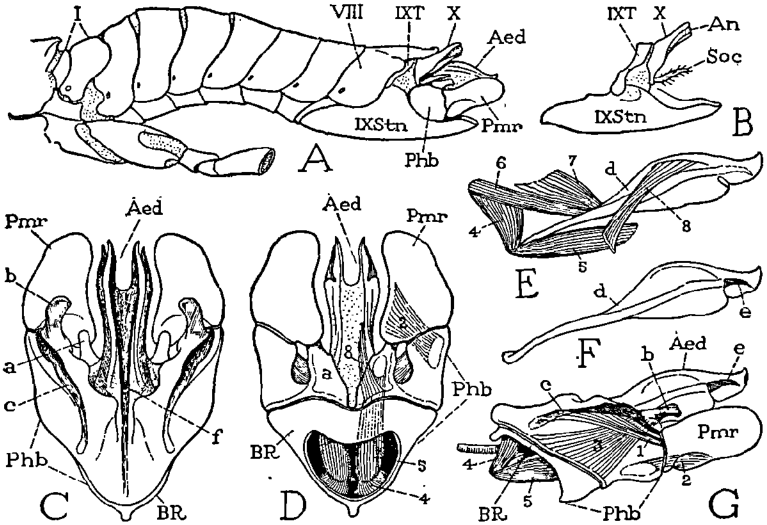

Fig. 309.—Male genitalia of Hymenoptera (*Pteronidea ribesii*). A, abdomen and base of thorax. B, ninth and tenth abdominal segments. C, phallus, dorsal surface. D, same, ventral surface. E, right lateral plate of aedeagus and muscles. F, left lateral plate of aedeagus. G, phallus and muscles, lateral view.

The aedeagus is a relatively simple structure. As represented in *Pteronida* (Fig. 309 C, D, *Aed*) it is mostly membranous but contains two lateral plates (E, F, *d*) produced proximally as apodemes on which the aedeagal muscles are attached (E, G). A median dorsal groove leads into a proximal aperture (C, *f*) from which a membranous endophallus is eversible. In the Apidae the aedeagus commonly bears a pair of proximal lateral processes (*sagittae*), and often a dorsal lobe (*spatha*). In the honey bee the entire phallic organ is much simplified; the basal structures so characteristic of other Hymenoptera are absent, and the organ appears to consist of the aedeagus with a highly developed eversible endophallus.

In the ontogenetic development of the Hymenoptera, as shown by Zander (1900), the entire group of phallic structures proceeds from two primary genital lobes at the sides of the gonopore. First, each lobe divides into two, then those of the resulting median pair unite to form the aedeagus, while those of the outer pair become the lateral lobes of the phallobase. The basal ring is said to be differentiated as a circular fold of the wall of the genital chamber.

Only one postgenital segment is present in Hymenoptera, which, judging from the larva, is the tenth abdominal segment (Fig. 309 A, B, *X*). In some of the lower families it bears a pair of cercuslike appendages (B, *Soc*), which, since they occur on the tenth segment, are perhaps to be identified with the socii of Trichoptera and Lepidoptera (Fig. 307 A, *Soc*).

Diptera.—The male genitalia of Diptera show a great proclivity toward the development of secondary lobes and processes, both phallic and periphallic. In the more generalized families the genital segments have a tendency to form a terminal enlargement (hypopygium) of the abdomen (Fig. 310 A); in higher families the distinction between the genital and visceral regions of the abdomen becomes accentuated by a reduction of the sixth and seventh segments and a close association between the eighth, ninth, and tenth segments to form a genital complex (F), which becomes mostly concealed within the fifth segment (E). Asymmetry is of frequent occurrence in the genital region, and the ninth segment is sometimes partly revolved upon its axis or completely inverted.

The harpagones are well developed in lower Diptera (Fig. 310 A, *Hrp*); they are often bilobed (B) and sometimes are bipartite. In some of the Tipulidae the genital coxopodites are distinct pleural plates on the sides of the ninth segment (A, D, *Cxpd*), and they may be partly exserted from between the tergum and sternum as in Mecoptera and Trichoptera; but more commonly the coxopodites unite with the sternum or entirely lose their identity in the continuously sclerotized annulus of the ninth segment. The venter of the genital segment may be entirely membranous (C, *V*), but usually it contains a sternal plate.

The greatly specialized type of abdomen characteristic of higher Diptera is well exemplified in *Pollenia rudis* (Fig. 310 E-J). The visceral part of the abdomen consists of segments *I-V* (E), but the first segment is usually obscured by reduction and union with the second. In *Pollenia*, segment *VI* appears to be obliterated, and segment *VII* contains only a small tergal plate (F, *VIIT*). Segment *VIII* has a well-developed tergum (*VIIIT*), but its sternum is reduced to a narrow sclerotic band (*VIIIS*), which is incomplete on the right side. Segment *IX* presents externally a small tergal plate (*IXT*) behind and below the eighth tergum; the sternum of the ninth segment (*IXS*), however, ordinarily projects forward and upward from the lower angles of the tergum in the dorsal wall of a large pouch with membranous walls (*g*) invaginated within the eighth sternum. This pouch contains the phallic organs. Seen from below, the ninth sternum is a broad plate (G, *IXS*) having its posterior angles produced as two arms (*h*) in the membranous wall beneath the ninth tergum, from which a pair of lateral bars (*i*) extends to the tenth segment. Two median plates (*a*, *a*) arise from the posterior margin of the ninth sternum and support a pair of free lobes (*b*) that embrace the base of the aedeagus.

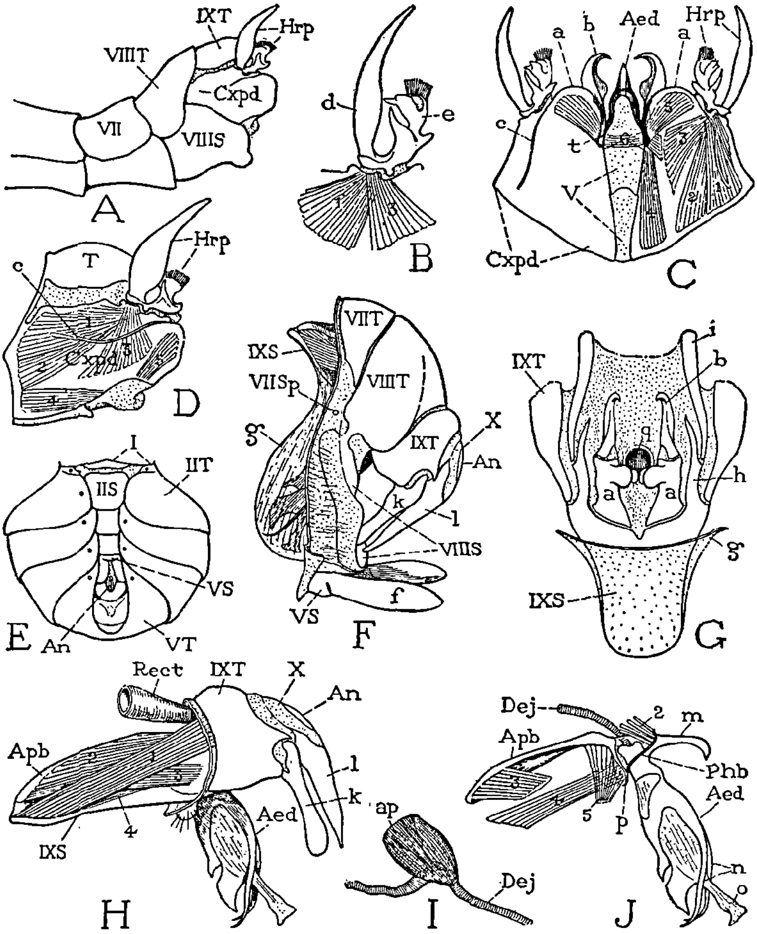

FIG. 310.—Male genitalia of Diptera. A, *Nephrotoma ferruginea* (Tipulidae), end of abdomen. B, same, harpago and muscles. C, same, genital segment, ventral view. D, same, lateral view. E, *Pollenia rudis* (Calliphoridae), ventral view of abdomen. F, same, segments of genital complex, lateral view. G, same, ninth segment (aedeagus removed), ventral view. H, same, ninth and tenth segments with aedeagus. I, *Phormia regina*, ejaculatory bulb. J, *Pollenia rudis*, phallus, with basal apodeme and muscles.

Movable claspers that can be identified with the harpagones, or styli of the gonopods, are absent in muscoid Diptera, but the ninth tergum commonly bears on its lower posterior angles a pair of long lobes

(Fig. 310 F, H, *k*), which may be flexible at their bases but are not provided with muscles. The small flat membranous tenth segment (*X*), in which the anus appears as a median slit (*An*), also is usually provided with a pair of lateral lobes (*l*) associated with those of the ninth tergum. On the bases of these lobes of the tenth segment is inserted a pair of muscles from the ninth tergum.

The phallic organs of Diptera consist principally of a variously developed aedeagus, though supporting basal structures also may be present. The aedeagus in its simpler forms varies from a short tapering process (Fig. 310 C, *Aed*) to a long slender tube usually curved or coiled. The typical muscoid aedeagus is a large irregular structure (J, *Aed*) with basal, lateral, and ventral lobes or processes. The phallobase (*Phb*) is represented by a low thecal fold surrounding the base of the aedeagus, in the walls of which are two small plates (*p*) supporting a large basal apodeme (*Apb*) for muscle attachments. Ordinarily the aedeagus is turned forward in the phallic pouch above the eighth sternum (F). The ductus ejaculatorius is provided with an ejaculatory bulb (I), a syringe-like structure with a thick muscular sheath supported on a flat central apodeme (*ap*) arising from one side of the cuticular lining of the duct. Distal to the bulb the duct enters the base of the phallus (J, *Dej*).

2. THE FEMALE GENITALIA

The primitive individual openings of the lateral ducts of the female genital system, situated on the seventh abdominal segment, are retained in modern adult insects only in the Ephemerida, the females of this order having a pair of gonopores located in the conjunctival membrane behind the seventh sternum, from which the eggs issue in two distinct masses (Fig. 311 B). In Dermaptera the lateral oviducts unite in a very short median oviductus communis (A, *Odc'*) opening immediately behind the seventh abdominal sternum (*Gpr*). In all other insects the median egg passage is extended posteriorly, and the exit aperture is located either on the eighth abdominal segment or on the ninth. When the genital opening is established on the eighth segment, there is generally associated with it an organ formed of appendicular parts of the eighth and ninth segments serving for the deposition of the eggs. This organ is the *ovipositor* (Fig. 311 C, *Ovp*).

An ovipositor having a uniform basic plan of structure is of wide occurrence among pterygote insects, and an organ of the same type though of more primitive structure occurs in the Thysanura. Hence there is little reason to doubt that the common ancestors of the Pterygota and Thysanura were equipped with an egg-laying organ from which the modern ovipositor has been evolved. The ovipositor of present-day insects is nearly always rudimentary or suppressed in insects having the egg exit on the ninth segment, and it is often reduced or absent in forms having the genital opening on the eighth segment. Insects in which the ovipositor is absent or never fully developed include Collembola, Diplura, most Odonata, Ephemerida, Plecoptera, Mallophaga, Anoplura, the tubuliferous Thysanoptera, Coleoptera, most Neuroptera, Mecoptera, Trichoptera, Lepidoptera, and Diptera.

Insects lacking an ovipositor, or in which the organ is not functionally developed, may have no special provision for placing the eggs; but with many of them the posterior segments of the abdomen are so modified that they can be protracted in the form of a slender telescopic tube having the opening of the egg passage near its distal end. A substitutional "ovipositor" of this kind is characteristic of the tubuliferous Thysanoptera, the Mecoptera (Fig. 312 D), the Lepidoptera (A), the Coleoptera, and the Diptera (B, C). Most insects of these groups insert their eggs into crevices or attach them to smooth surfaces by a cementing substance discharged from the colleterial glands. In some cases, however, the end of the abdomen forms a piercing or cutting organ, or it may have a simple modification for manipulating or placing the eggs. The abdomen of the fruit flies (Trypetidae, Lonchaeidae), the distal part of which is narrowed and tapering (B) or sometimes greatly elongate (C), terminates in a sharp point that enables the insects to pierce the skin or rind of fruit in which they deposit their eggs. In most Lepidoptera the female abdomen is provided with two terminal lobes at the side of the egg exit, which serve to grasp the issuing eggs, or which, when spread out flat, form a disc for pressing the eggs against the surface on which they are attached by the secretion of the cement glands.

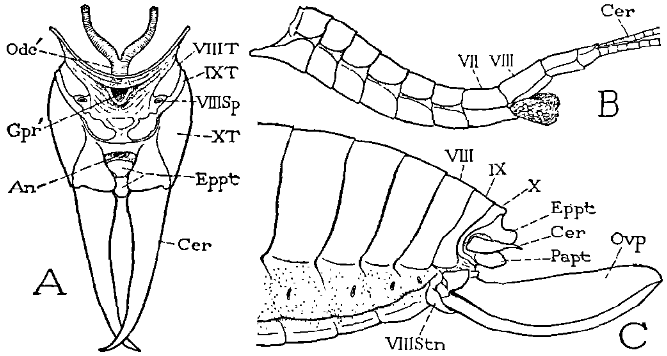

FIG. 311.—Three types of external genital structure of the female abdomen. A, genital and terminal segments of a dermapteron, *Anisolabis maritima*, with median gonopore immediately behind seventh abdominal sternum. B, abdomen of a mayfly, *Hexagenia*, with paired gonopores behind seventh sternum, eggs issuing in two masses. C, nymph of *Scudderia*, illustrative of insects with an appendicular ovipositor and gonopore behind eighth abdominal sternum.

The Ovipositor of Thysanura.—The ovipositor of the Thysanura presents in a simple form structural elements from which, there can be little question, the more highly perfected ovipositor of pterygote insects has been evolved. More than this, its basal parts show an exact serial identity with ventral plates of the pregenital segments that are almost certainly rudiments of abdominal limbs.

The under surfaces of the pregenital segments of Machilidae, as was shown in Chap. XI, have each three plates (Fig. 138 A), namely, a small triangular median plate, which is the true sternum (*Stn*), and two large lateral plates (*Cxpd*), which appear to be the coxopodites of the otherwise rudimentary limbs. The coxopodites of each pair are united medially behind the sternal plate, and each bears a slender appendage known as a stylus (*Sty*), which is movable by muscles arising in the supporting basal plate.

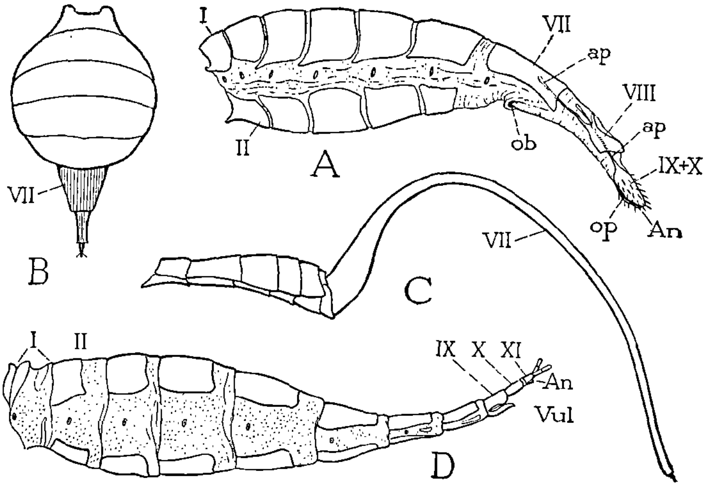

FIG. 312.—Examples of an "ovipositor" formed of the terminal segments of the abdomen. A, a moth, *Lymantria monacha*. (*From Eidmann*, 1929.) B, a fruit fly, *Paracantha culta*. C, a fruit fly, *Toxotrypania curvicauda*. D, *Panorpa consuetudinis*.

In the genital segments of female Thysanura the coxopodites are free plates or flat lobes (Fig. 313 A, *Cxpd*), and sternal plates are absent. Each coxopodite bears distally a stylus (*Sty*), but in addition it has a long slender genital process, or *gonapophysis*, arising from the mesal angle of its base (B, C, *1Gon*, *2Gon*), the four of which are closely associated to form the shaft of the ovipositor (A, *Ovp*). Since the gonapophyses are never represented on the pregenital segments they would appear to be special developments of the gonopods. If so, judging from their position, they are of the nature of coxal endites. Each is provided with a short muscle arising in the supporting coxopodite (B, C, F, *gmcl*).

The principal movements of the gonapophyses, however, are probably brought about by muscles of the coxopodites, which arise on the corresponding terga of the genital segments (F). In some cases the second gonapophyses are fused at their bases (C), and in others they may be united throughout their length, but the first gonapophyses are always entirely free from each other and are apparently capable of independent movement.

The two pairs of gonopods are practically alike in Machilidae (Fig. 313 D, E); but in *Thermobia* (G), and probably in other Lepismatidae, the coxopodites of the second pair are each divided into an anterior plate (*a*) bearing the gonapophysis, and a posterior plate (*b*) supporting the stylus. The tergal muscles of the coxopodite are inserted on the anterior sclerite. This division of the second coxopodite occurring in the Lepismatidae is most interesting since it suggests the similar condition that is characteristic of most pterygote insects.

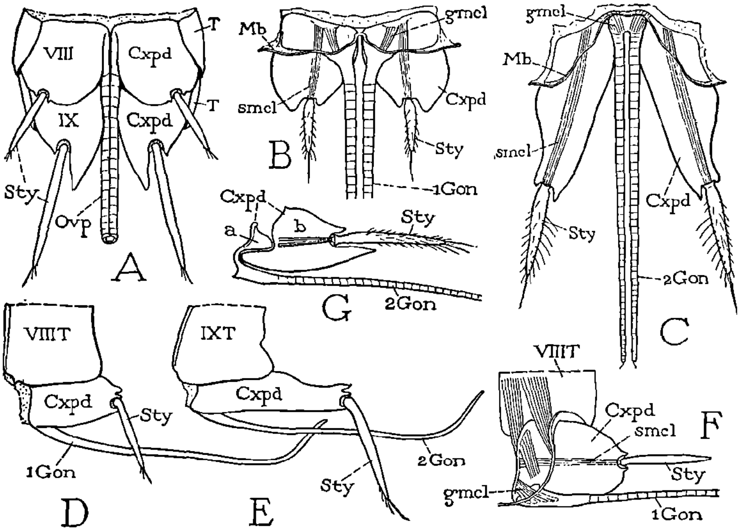

FIG. 313.—The ovipositor of Thysanura. A, *Thermobia*, eighth and ninth abdominal segments, ventral view. B, *Nesomachilis maoricus*, dorsal view of first gonopods. C, same, second gonopods. D, E, *Machilis*, lateral view of right gonopods and supporting tergal plates. F, *Thermobia*, muscles of first gonopod, diagrammatic. G, same, second gonopod, showing subdivision of coxopodite.

General Structure of the Ovipositor of Pterygote Insects.—The ovipositor of pterygote insects, in its typical form, consists of a *shaft* and a *basal apparatus* and usually includes a pair of accessory lobes (Fig. 314 A). The shaft, in most insects, is composed of two pairs of closely appressed elongate processes, the *first* and the *second valvulae* (*1Vl*, *2Vl*), the first valvulae being usually ventral, the second dorsal.

The second valvulae are often united in a single median dorsal piece. The basal apparatus consists essentially of two pairs of lobes or plates, the *first* and the *second valvifers* (*1Vlf*, *2Vlf*), which support the ovipositor shaft by the bases of the valvulae. The proximal parts of the valvulae, by which the latter are attached to their respective valvifers, are distinguished as the *rami of the valvulae.* The accessory lobes, or *third valvulae* (*3Vl*), are borne on the posterior ends of the second valvifers. They usually ensheath the distal part of the shaft, but in Orthoptera they form a third pair of blades in the shaft. The ventral body wall between the bases of the second valvifers sometimes contains sclerites, which are termed *intervalvulae* (B, *aiv*, *piv*).

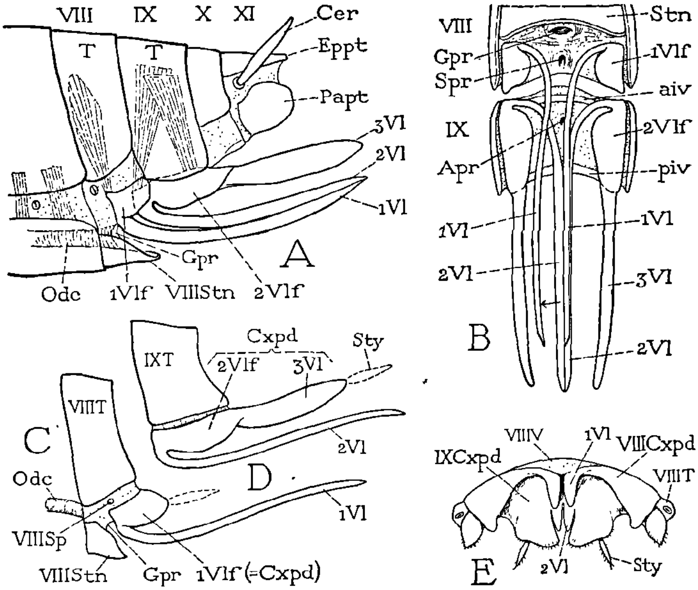

FIG. 314.—Structure of the ovipositor of pterygote insects (A–D, diagrammatic). A, showing segmental relations of the parts of the ovipositor. B, ventral view of genital segments and ovipositor. C, D, lateral view of genital segments and parts of ovipositor dissociated. E, nymph of *Blatta orientalis*, ventral view of genital segments with lobes of ovipositor. *aiv*, anterior intervalvula; *Apr*, aperture of accessory glands; *Gpr*, gonopore; *Odc*, oviductus communis; *piv*, posterior intervalvula; *Spr*, spermathecal aperture; *Sty*, stylus; 1*Vl*, 2*Vl*, 3*Vl*, first, second, and third valvulae; 1*Vlf*, 2*Vlf*, first and second valvifers.

The principal muscles of the ovipositor are inserted on the valvifers. The dorsal muscles of the first valvifers take their origin on the tergum of the eighth abdominal segment, those of the second valvifers on the tergum of the ninth segment (Fig. 314 A). It is thus evident that the first valvifers pertain to the eighth segment and the second valvifers to the ninth segment. The second valvifers usually retain a close connection with the tergum of the ninth segment, but the first valvifers are often more or less dissociated from the eighth segment. An exception to the general structure and musculature of the ovipositor occurs only in the Acrididae and Tridactylidae.

When the separated elements of the pterygote ovipositor (Fig. 314 B, C, D) are compared with those of the thysanuran ovipositor (Fig. 313 D, E), it is to be seen at once that there is almost an exact correspondence between the parts of the organ in the two cases. It becomes evident, therefore, that the first and second valvifers (1*Vlf*, 2*Vlf*) of the pterygote ovipositor are derived from the coxopodites of the gonopods respectively of the eighth and ninth abdominal segments, and that the first and second valvulae (1*Vl*, 2*Vl*) are respectively the first and second gonapophyses. The third valvulae of the Pterygota (Fig. 314 D, 3*Vl*), which are carried by the second valvifers, are also derivations of the second coxopodites (*Cxpd*), but they are not the styli (*Sty*). True styli are present on the second coxopodites of a few pterygote insects, as in nymphs of Blattidae (E, *Sty*) and in the adults of some Odonata. We may now recall that in *Thermobia* (Fig. 313 G) each coxopodite of the ninth segment is divided into a proximal plate (*a*) carrying the gonapophysis and a distal stylus-bearing plate (*b*). Styli of the coxopodites of the eighth segment are never present in Pterygota.

The development of the pterygote ovipositor is entirely in accord with the homology of its parts suggested by the structure of the adult organ. The first valvulae (Fig. 314 E, 1*Vl*) are median outgrowths of the coxal areas of the eighth abdominal segment (*VIIICxpd*), the latter developing into the first valvifers. The primary genital processes of the ninth segment are the third valvulae, which are distal outgrowths of the coxopodites of the second gonopods (*IXCxpd*), which become differentiated proximally into the second valvifers, while mesal (endite) processes become the second valvulae. Styli never appear on the coxopodites of the eighth segment, and those of the ninth segment (*Sty*), if present in immature stages, are lost with the transformation to the adult, except in some Odonata. While the theory of the origin of the parts of the ovipositor from the primitive limbs of the genital segments may thus seem to be well substantiated by ontogenetic development, due consideration should be given to the evident fact that all outgrowths of the body wall must necessarily look much alike in their early stages of growth, whether they represent primary or secondary organs. Similarity in such structures, therefore, is no proof of identity.

The principal groups of pterygote insects in which the ovipositor is well developed are the Orthoptera, Hemiptera, Thysanoptera, and Hymenoptera.

The Ovipositor of Orthoptera.—The ovipositor of Orthoptera is in some respects more generalized than that of other insects, while, on the other hand, it has one unique feature and certain structural specializations that adapt it to the particular mechanism developed in this order.

The orthopteroid ovipositor is generalized in that the coxopodites of the ninth segment are not anatomically separated into second valvifers and third valvulae, though each is distinctly differentiated into a basal valvifer region (Fig. 315 A, C, E, *2Vlf*) and a distal valvular process (*3Vl*). Also there are present in some families anterior and posterior

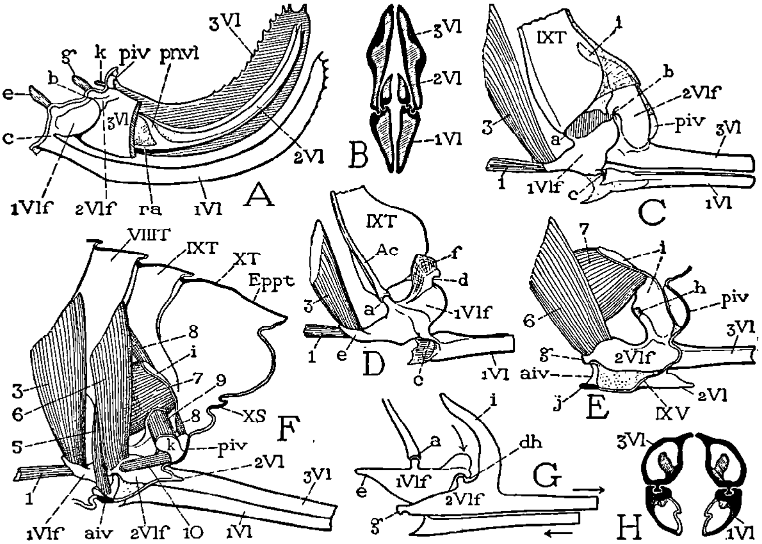

Fig. 315.—The ovipositor of Orthoptera. A, *Scudderia* (third valvula cut off near base). B, *Locusta viridissima*, cross section of shaft of ovipositor. (*From Weber*, 1933.) C, *Gryllus assimilis*, base of ovipositor. D, E, same, first and second valvifers with muscles, inner view of right side. F, same, base of ovipositor with muscles, inner view of right side. G, same, diagram of mechanism of ovipositor. H, same, cross section of shaft of ovipositor.

intervalvular sclerites in the venter of the ninth segment between the second valvifers (F, *aiv*, *piv*), and muscles from the ninth tergum (*5*, *8*) and from the valvifers (*9*, *10*) that do not generally occur in higher insects are inserted on these sclerites.

The unique feature of the orthopteroid ovipositor is the inclusion of the third valvulae as a pair of blades in the shaft of the organ (Fig. 315 A, C, *3Vl*). When the three pairs of valvulae, therefore, are all well developed, the shaft consists of three pairs of valvular lobes or blades (A, B). In such cases, the first valvulae (*1Vl*) are ventral, the third valvulae (*3Vl*) dorsal, and the second valvulae (*2Vl*) median and usually concealed between the others. The first valvulae may be movable on both the second and the third valvulae by interlocking grooves and ridges (B). The second valvulae, however, are in some cases reduced or rudimentary, as in Acrididae and Gryllidae (E, F, *2Vl*), and the shaft then consists of only two pairs of blades (H), which, it should be noted, are the first and third valvulae, and not the first and second as in the usual four-valve ovipositor of other insects.

The particular mechanical features characteristic of the orthopteroid ovipositor are in the relations of the valvifers to the terga of the genital segments, and in the interrelation of the valvifers to each other. The first valvifer is never closely attached to the eighth tergum, and it may be displaced so far posteriorly that it appears to belong to the ninth segment. By its posterior angle it articulates with the second valvifer (Fig. 315 A, C, *b*), and it may also have a strong articulation with the ninth tergum (C, D, *a*). Internally the two valvifers of *Gryllus* osculate by special articular processes (D, *d*, E, *h*, G, *dh*)—a feature of much importance in the mechanism of the gryllid ovipositor. The second valvifer has no direct articulation with the ninth tergum, its fulcrum of movement being the articulation (E, *h*) with the first valvifer (G, *dh*). It is interesting to note that this same anatomical relation of the valvifers to each other and to the ninth tergum is characteristic of Hymenoptera also, though the structure and mechanism are not exactly the same in the two orders. The definitive first valvifer of Gryllidae is a composite structure formed of the true first valvifer and a small plate derived from the coxopodite of the ninth segment.

The musculature of the ovipositor, as illustrated in *Gryllus* (Fig. 315 F), is somewhat more complex than in insects of other orders owing to the presence of the muscles inserted on the intervalvular sclerites. Each first valvifer has a muscle from the seventh sternum (*1*) and a large muscle (*3*) from the eighth tergum, both inserted on an anterior apodemal arm of the sclerite (C, D, *e*). In its musculature, therefore, the first valvifer asserts its relation with the eighth abdominal segment regardless of its mechanical connections. Each second valvifer has a pair of large antagonistic muscles (E, F, *6*, *7*) arising on the ninth tergum. This pair of muscles recurs in nearly all insects provided with an ovipositor. The muscles of the intervalvular sclerites (F, *aiv*, *piv*) include a pair of tergosternal muscles (*5*, *8*) of the ninth segment, and two pairs of muscles (*9*, *10*) between the posterior intervalvula and the first and second valvifers, respectively.

The motion of the valvifers produced by the tergal muscles inserted on them results in an alternate back-and-forth movement of the valvulae on each other (Fig. 315 G). The articulations of the first valvifers with the ninth tergum (*a*), and the articulation of the two valvifers on each side with each other (*dh*) constitute a mechanism of such a nature that any motion of either pair of valvifers is communicated reversely to the other pair, with the result that the corresponding valvulae have opposite movements.

The Phasmidae, Mantidae, Blattidae, Grylloblattidae, and Tettigoniidae retain the three pairs of valvulae in the ovipositor, but otherwise the ovipositor has essentially the same structure in these families as in Gryllidae, though it is reduced and more or less modified in the first four and attains its highest mechanical perfection in Gryllidae. In the Acrididoidea and Tridactylidae, however, the organ departs widely in structure, musculature, and mechanism, not only from the ovipositor of other Orthoptera, but from that of all other insects, since the four terminal processes work by a divergent motion instead of sliding upon each other.

The Ovipositor of Hemiptera.—The morphology of the pterygote ovipositor is perhaps best shown in the Hemiptera, because here the valvifers more nearly than in the other orders retain their proper segmental connections. In most of the Heteroptera the ovipositor is reduced or rudimentary, but in Homoptera, except parasitic forms, it is generally well developed. The eighth abdominal sternum is reduced or practically obliterated in all Hemiptera, and the subgenital plate is the seventh sternum.

The shaft of the ovipositor in Homoptera, as illustrated in the cicada (Fig. 316 A), issues at the base of the ninth segment between the eighth tergum and the seventh sternum. When dissected (B, C) the parts belonging to the two genital segments are easily distinguished. The first valvifers (1*Vlf*), implanted in the membranous ventrolateral parts of the eighth segment (A), are small triangular plates carrying the first valvulae. Each articulates posteriorly with the ninth tergum, and a small plate on the inner surface (F, *m*), continuous with the dorsal margin of the first valvula, is directly fused with a lobe (*n*) of the ninth tergum. This feature is characteristic of all Hemiptera, and generally the base of the first valvula is produced into two rami, the outer of which is attached to the valvifer, while the inner one is fused with the ninth tergum. In the cicada a short muscle extends between the outer and inner plates of the first valvifer (F, *4*). Other muscles of the first valvifer comprise a muscle from the seventh sternum (H, *1*) and two muscles from the eighth tergum (*2*, *3*), all inserted on an apodeme (*e*) of the dorsal margin of the valvifer.

The second valvifers of the cicada are elongate plates (Fig. 316 A, C, G, 2*Vlf*) mostly concealed within the projecting lower parts of the ninth tergum (A). At their anterior ends the second valvifers are directly continuous with the bases of the second valvulae (C, G, 2*Vl*), and the third valvulae (3*Vl*) arise at their posterior ends. Each second valvifer is articulated at a point near the middle of its dorsal margin with a condyle on the ventral margin of the ninth tergum (F, G, *p*). Two large muscles (G, *6*, *7*) arising on the ninth tergum are inserted on each second valvifer respectively anterior and posterior to the articular fulcrum. The second valvifers of the Hemiptera, therefore, rock directly on the ninth tergum, and not on the first valvifers as in Orthoptera and Hymenoptera. There are no other muscles in the ninth segment connected with the ovipositor, since intervalvular sclerites and their muscles, such as those of the cricket (Fig. 315 F), are absent in Hemiptera.

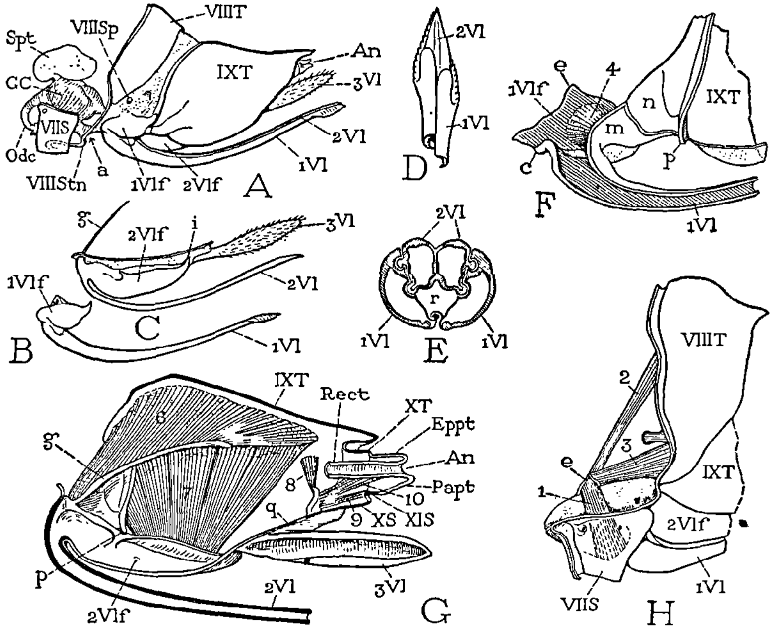

FIG. 316.—The ovipositor of a cicada, *Magicicada septendecim*. A, end of abdomen, with ovipositor, genital chamber (*GC*) and spermatheca (*Spt*) exposed. B, C, parts of ovipositor dissociated. D, tip of ovipositor, ventral view. E, cross section of shaft of ovipositor. F, first valvifer and associated parts, inner view of right side. G, muscles of second valvifer and terminal segments, inner view of right side. H, base of ovipositor, showing muscles of concealed first valvifer.

The shaft of the cicadid ovipositor consists of only three distinct parts, since the second valvulae are united with each other (Fig. 316 E, 2*Vl*) to form a strong median rod, to the sides of which the first valvulae (1*Vl*) are attached by the usual ridge-and-groove device. The lateral position of the first valvulae with respect to the second valvulae is characteristic of Homoptera, but more commonly the valvulae have the form of flattened blades. When the ovipositor is not in use it is ensheathed between the concave inner surfaces of the third valvulae.

The Ovipositor of Hymenoptera.—The ovipositor of Hymenoptera, in its general form and in the composition of its shaft, resembles the ovipositor of Hemiptera more closely than that of Orthoptera, but it has one special character, namely, the articulation of the second valvifers with the first valvifers and not with the ninth tergum, that is a highly developed feature in the mechanism of the ovipositor of Gryllidae.

The basic structure of the hymenopterous ovipositor is well shown in the Tenthredinidae, though the organ here does not have the form typical of the ovipositor of clistogastrous Hymenoptera, in which it is usually long and slender. The shaft of the tenthredinid ovipositor, as illustrated in *Pteronidea ribesii* (Fig. 317 A, B), is short and broad with an acute apex and strong lateral ridges. It is composed of the first and second valvulae (B, 1*Vl*, 2*Vl*), and is ordinarily ensheathed between the broad third valvulae (3*Vl*). The basal part of the ovipositor consists of the first and second valvifers (B, 1*Vlf*, 2*Vlf*) lying beneath the long lower margin of the ninth abdominal tergum (*IXT*). The first valvifer (B, C, 1*Vlf*) is a small triangular plate articulated by its dorsal angle (*a*) with the ninth tergum (B) and by its posterior ventral angle (*b*) with the second valvifer. Anteriorly the first valvifer is continuous with the narrow ramus of the first valvula (C). The second valvifer is a relatively large, elongate plate (B, E, 2*Vlf*) with the ramus of the second valvula (E, *r*2*vl*) attached to its anterior extremity, and the third valvula (3*Vl*) forming a broad lobe at its posterior end. The second valvifer

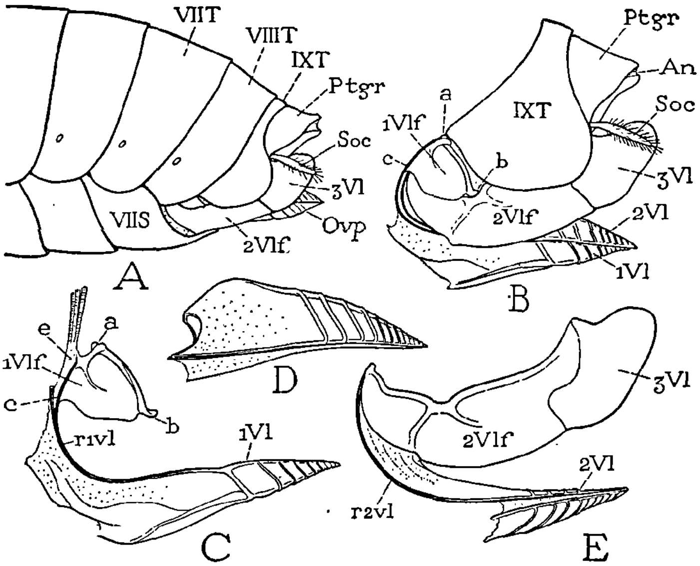

FIG. 317.—The ovipositor of a tenthredinid, *Pteronidea ribesii*. A, end of abdomen. B, showing relation of basal parts of ovipositor to each other and to ninth tergum. C, first valvifer and valvula. D, second valvula. E, second valvifer with second and third valvulae.

has no articular connection with the ninth segment, its point of movement being the articulation (B, *b*) with the first valvifer. The two second valvulae are united to each other by a median membrane (E).

It should be observed that in the Tenthredinidae the terga of the eighth and ninth abdominal segments are normally developed and fully exposed plates (Fig. 317 A). There are, however, as in all Hymenoptera, no sternal plates in these segments, the subgenital plate being the seventh sternum. In the higher hymenopterous families the eighth and ninth segments are retracted into the seventh, and the terga of these segments are progressively reduced, until, in the bees, they consist only of two pairs of lateral sclerites associated with the base of the sting.

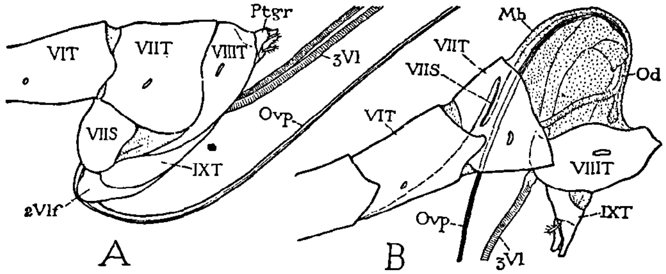

FIG. 318.—The ovipositor of *Megarhyssa*. A, *M. atrata*, end of abdomen and base of ovipositor with parts in usual position. B, *M. lunator*, showing position of abdominal segments and base of ovipositor during oviposition.

In the more typical form of the hymenopterous ovipositor the shaft is long and slender, and the ensheathing third valvulae are correspondingly lengthened, but the general structure of the organ is in no way essentially different from that of the Tenthredinidae. An extreme development of the slender type of shaft occurs in some of the Ichneumonidae, as in *Megarhyssa* (Fig. 318) and related genera. During oviposition by such species the terminal part of the abdomen is turned downward (B), exposing the wide conjunctival membrane (*Mb*) between the seventh and eighth terga. The base of the ovipositor is now dorsal and is contained in a large pouch formed by inflection of the membranous ventral part of the body wall including the seventh sternum (*VIIS*). The ovipositor shaft (*Ovp*) protrudes from the pouch at right angles to the length of the abdomen and is ensheathed distally in the slender third valvulae (3*Vl*); but, as the shaft penetrates the wood in which the female lays her eggs, the sheath valves separate from the shaft and may curve upward at the sides of the body, as shown in various familiar illustrations.

In the stinging Hymenoptera the ovipositor loses its egg-laying function and is converted into a poison-injecting instrument, but even here there is little change in the structure of the organ except in the development of valvular lobes on the first valvulae for driving the poison liquid through the shaft. The stinging apparatus of the bees (Fig. 319 A) includes not only the usual parts of the ovipositor but also the lateral sclerites (quadrate plates) of the ninth tergum (*IXT*) and the lateral spiracular plates of the eighth tergum (D, *VIIIT*). The united second valvulae form an inverted trough, the enlarged proximal part of which is the bulblike swelling of the shaft (A, *blb*), and the tapering distal part the median *stylet* (*stl*). The slender first valvulae, or *lancets* (*Lct*), slide on the lower margins of the bulb and stylet. Proximal to the bulb the rami of the valvulae (*r1vl, r2vl*) diverge on each side to their attachments with the valvifers. The reservoir of the poison gland (*PsnSc*) discharges directly into the base of the bulb; the tubular left accessory gland opens ventrally between the rami of the valvulae. When the sting is in repose it is concealed in a sting chamber within the seventh abdominal segment, where it is ensheathed between the third valvulae. To be used effectively, the sting must be protracted from the sting chamber and deflected at right angles to the basal plates (D).

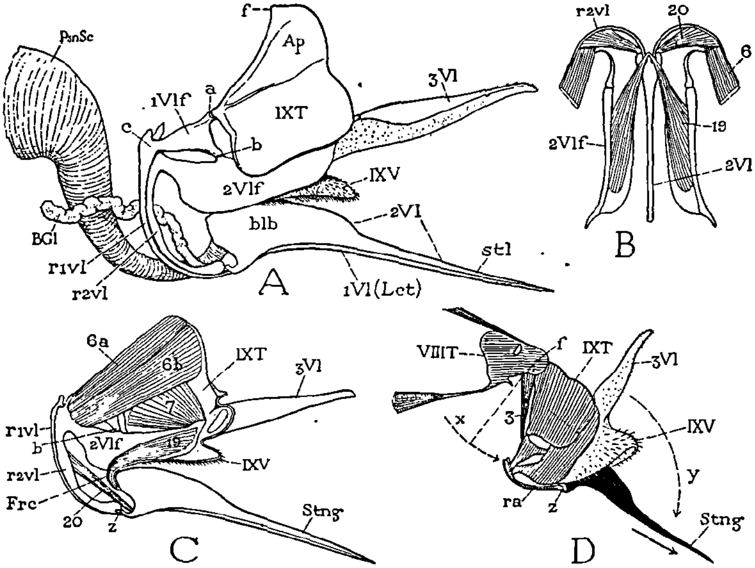

FIG. 319.—The ovipositor (sting) of Hymenoptera. A, *Apis mellifica*, shaft and basal apparatus of sting, showing relation of valvifers to ninth tergal plate. B, *Atanycolus rugosiventris* (Braconidae), basal part of ovipositor and muscles, dorsal view. C, *Apis mellifica*, muscles of sting, inner view of right side. D, same, position of parts of sting when shaft is extruded, diagrammatic.

The protraction of the bee's sting is brought about by pressure engendered in the anterior part of the abdomen, which causes the entire organ to swing backward on the connections between the eighth and ninth tergal sclerites (Fig. 319 D) as shown by the arrow at *x*. At the same time the shaft is depressed in the direction of the arrow at *y*, and the membranous venter of the ninth segment (*IXV*) is protruded as a hood over the base of the bulb. The depression and elevation of the shaft are effected by two pairs of muscles common to all Hymenoptera, but which appear to have no homologues in other insects. The depressor muscles (B, C, 19) arise on the second valvifers and are inserted on the base of the bulb of the shaft; the levators (20) stretch between the extremities of the rami of the second valvulae.

The principal mobile elements of the shaft of the sting are the first valvulae, or lancets, which are moved by motions of the first valvifers produced by the muscles of the second valvifers. The first valvifers have each only a single small muscle arising on the tergal plate of the eighth segment (Fig. 319 D, 3). The second valvifers are provided with the usual antagonistic muscles arising on the ninth tergal plates (C, 6, 7); but since these plates themselves are movable on account of the membranization of the median part of the dorsum, the pull of the muscles on the second valvifers vibrates the tergal plates, and the motion of the latter is communicated to the first valvifers, which in turn move the lancets back and forth in the shaft of the sting. The valves on the bases of the lancets drive the poison liquid through the channel of the united second valvulae, from which it escapes ventrally between the tips of the lancets.

With most Hymenoptera the eggs traverse the channel of the ovipositor shaft, regardless of the diameter of the latter. In the very slender bristle-like ovipositors of some parasitic forms, as shown by Fulton (1933), the eggs are compressed and stretched to an extreme degree in their transit through the narrow passage. In the stinging Hymenoptera the eggs are ejected from the opening of the genital chamber at the base of the ovipositor.

GLOSSARY OF TERMS APPLIED TO THE EXTERNAL GENITALIA

The Male Organs

Aedeagal Apodeme (*Apa*).—An apodeme of the aedeagus.

Aedeagus (*Aed*).—The distal part of the phallus, usually the principal part of the intromittent organ, typically a sclerotic tube.

Anellus (*Anl*).—A sclerotization of the inner wall of the phallocrypt or phallotheca, often forming a ring or tube about the base of the aedeagus.

Basal Apodeme (*Apb*).—An apodeme of the phallobase.

Basal Plates (*BP*).—Sclerites of the phallobase.

Ectophallus.—The outer phallic wall in distinction to the endophallus.

Ejaculatory Duct (*Dej*).—The ectodermal outlet duct of the male genital system.

Endophallus (*Enph*).—The inner chamber of the phallus invaginated at the end of the aedeagus, into which the ejaculatory duct opens; typically an eversible sac or tube, but sometimes a permanently internal phallic structure.

Endotheca (*Enth*).—The inner wall of the phallotheca.

Epimere.—A dorsal process of the phallobase.

Epiphallus.—A sclerite in some Orthoptera in the floor of the genital chamber proximal to the base of the phallus. (*Pseudosternite.*)

Genital Chamber (*GC*).—A ventral invagination of the conjunctival membrane between the ninth and tenth abdominal segments containing the phallic organs.

Genital Segment.—Specifically the ninth segment of the abdomen in the male, though other segments are frequently associated with the ninth in the genital complex. (*Gonosomite.*)

Genitalia.—The genital organs collectively, but usually applied only to the external genitalia.

Gonapophyses (*Gon*).—Median proximal processes of the coxopodites of the gonopods, present in the male in some Thysanura.

Gonopore (*Gpr*).—In the male the external opening of the median ejaculatory duct, usually concealed in the endophallus, or one of the apertures of paired exit ducts.

Gonosomite.—See *genital segment.*

Gonostyli.—The styli of the ninth segment, when present, generally modified to form clasping organs (harpagones).

Harpagones (*Hrp*).—Movable periphallic processes of the ninth segment individually provided with muscles, probably derivatives of the gonostyli, usually having a clasping function. (Termed *harpes* in Lepidoptera.)

Hypandrium.—See *subgenital plate.*

Hypomere.—A ventral process of the phallobase.

Parameres (*Pmr*).—Lateral processes or lobes of the phallobase. (The term is here defined as used in Coleoptera, but it is also applied to the gonapophyses.)

Penis (*Pen*).—One of the paired intromittent organs of certain insects, or the usual median phallic organ. (See *phallus.*)

Periphallic Organs.—Peripheral genital processes of the ninth segment, or also of other segments in the genital complex, including the movable claspers, or harpagones.

Phallobase (*Phb*).—The proximal part of the phallus, highly variable in its development, sometimes a large structure supporting the aedeagus, often produced into a thecal fold or sheath about the aedeagus, sometimes represented only by basal phallic sclerites in the wall of the genital chamber.

Phallocrypt (*Crpt*).—A pocket of the phallobase or of the genital chamber wall containing the base of the aedeagus.

Phallomeres.—Genital lobes formed at the sides of the gonopore in the ontogeny of some insects; in most cases they unite to form the phallus, but in Blattidae and Mantidae they develop separately into complex genital organs of the adult.

Phallotheca (*Thc*).—A fold or tubular extension of the phallobase about the aedeagus.

Phallotreme (*Phtr*).—The distal opening of the endophallus, usually at the end of the aedeagus.

Phallus (*Phl*).—The unpaired penis, or median intromittent organ, including the phallobase, the aedeagus, the endophallus, and various processes of the phallobase and the aedeagus if present.

Sagittae.—Proximal lateral processes of the aedeagus in Hymenoptera.

Socii (*Soc*).—Lateral appendicular processes of the tenth segment in Trichoptera and Lepidoptera, possibly homologous with the cercuslike appendages of the tenth segment in lower Hymenoptera.

Spatha.—A dorsal lobe of the aedeagus in Hymenoptera.

Squama.—A dorsal lateral lobe of the phallobase in Hymenoptera.

Subgenital Plate.—Usually the ninth abdominal sternum of the male extended beneath the genital chamber, but sometimes the eighth or the seventh sternum. (*Hypandrium.*)

Titillators.—Terminal processes of the aedeagus.

Uncus.—A process of the tenth abdominal tergum overhanging the anus in Lepidoptera.

Vesica (*Vsc*).—A terminal membranous part of the aedeagus. (*Preputial membrane.*)

Vinculum.—The entire coxosternal plate of the ninth abdominal segment in Lepidoptera.

Virga.—A terminal phallic spine, usually arising from the endophallus.

Volsellae.—Ventral lateral processes (parameres) of the phallobase in Hymenoptera.

THE FEMALE ORGANS

Basivalvulae.—Small sclerites sometimes occurring at the bases of the first valvulae, often confused with the first valvifers.

Egg Guide.—A median process of the subgenital plate behind the genital opening, particularly developed in Acrididae.

Genital Chamber (*GC*).—In the female a copulatory invagination cavity behind or above the eighth abdominal sternum containing the gonopore and the orifice of the spermatheca, often narrowed to form a pouchlike or tubular vagina. (*Bursa copulatrix.*)

Gonapophyses (*Gon*).—Mesal processes of the bases of the gonopods, perhaps endites, forming the first and second valvulae of the ovipositor.

Gonopore (*Gpr*).—In the female either one of the paired primitive openings of the lateral oviducts, or the median opening of the oviductus communis.

Intervalvulae (*iv*).—Sternal sclerites in the venter of the ninth abdominal segment between the second valvifers.

Lancets (*Lct*, 1*Vl*).—The first valvulae.

Ostium bursae (*ob*).—The opening of the bursa copulatrix in Lepidoptera, equivalent to the vulva of female insects having the genital opening on the eighth segment.

Oviporus (*op*).—The posterior opening of the vagina in most Lepidoptera, serving only for the discharge of the eggs when there are two genital apertures.

Ovipositor (*Ovp*).—The egg-laying organ formed of the gonopods of the eighth and ninth abdominal segments; or also, in a functional sense, the egg-laying tube of some insects formed of the protractile terminal segments of the abdomen.

Rami valvularum.—The proximal, often slender, parts of the first and second valvulae by which the latter are attached to the valvifers.

Stylet (*stl*).—A median dorsal element in the shaft of the ovipositor formed of the united second valvulae.

Subgenital Plate.—In the female the eighth abdominal sternum, or the seventh when the eighth is reduced or obliterated.

Valvifers (*Vlf*).—The basal plates of the ovipositor, probably derived from the coxopodites of the gonopods, carrying the valvulae, including *first valvifers* (1*Vlf*) of the eighth abdominal segment, and *second valvifers* (2*Vlf*) of the ninth segment.

Valvulae (*Vl*).—The three pairs of processes forming the blades and ensheathing lobes of the ovipositor. The *first* and *second valvulae* (1*Vl*, 2*Vl*) are gonapophyses of the gonopods; the *third valvulae* (3*Vl*) are distal outgrowths of the coxopodites of the ninth abdominal segment.

Vestibulum (*Vst*).—An external genital cavity formed above the seventh abdominal sternum when the latter extends beyond the eighth.

Vulva (*Vul*).—The external opening of the genital chamber or vagina serving in most cases for both copulation and the discharge of the eggs; sometimes on the eighth abdominal segment, sometimes on the ninth.

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