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THE MORPHOLOGY OF INSECT SENSE ORGANS AND THE SENSORY NERVOUS SYSTEM

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INTRODUCTION

There are no facts of structure presented in this paper that are not recorded elsewhere; but a mere lack of new information should not be held to lessen the value of a piece of work, or to make it unworthy of scientific consideration. Facts are the food of science, and, like all food, they do not contribute to growth of the body until digested, distributed, and assimilated.

It is time for entomology to be taking stock of what it has acquired, to assemble its facts, and to get them into form that will facilitate progress, dropping a few old ideas, if necessary, and taking on a few new ones. A science, in its growth, is likely to be something like a caterpillar—it increases rapidly during a period when its skin is soft and elastic, but after a while it begins to become hidebound in its own cuticula; then the old skin must be cast off, and a new one formed that will again allow of growth and development.

A mere review of the known facts on any particular subject, scattered as the records are likely to be through many scientific journals and presented often in highly technical language, may render at least the double service of making the facts more easily available and of showing more plainly the bare spots of ignorance; but it may, also, give an insight into general truths heretofore unrecognized.

Concerning the anatomy of insect sense organs, and the intimate structure of the insect nervous system, much is known, *i. e.,* to those who have studied the sense organs and the nervous system of insects. To the general entomologist, little is known of these subjects. A knowledge of mere structure, however, is of no use in itself, it is only a prerequisite to a study of function. A knowledge of insect physiology, furthermore, is still of no particular importance until it helps us to understand the nature of the insect as a living organism. An understanding of the nature of an insect, again, has real significance only as it enables us to understand the nature of life in general. So, everything we take up in science is of value, in the minds of those to whom a knowledge of the universe is the ultimate aim, only through the superstructure it supports.

To the practical entomologist, however, the value of knowledge may be judged within more finite limits. The acquisition of any information that will help in the control of injurious insect species, or that will further the propagation of useful or beneficial species is to him in itself an end worth attaining. There can be no doubt that the accomplishment of practical results in entomology will be greatly facilitated when we have acquired a better understanding of the physiology, the senses, and the tropisms of insects, and an insight into how these properties enable insects to maintain so successfully their place in nature in spite of our efforts to dislodge them.

The following résumé, therefore, of the known facts concerning the structure of insect sense organs and the sensory nervous system is offered in the hope that it will be found useful to the experimental worker who is attempting to obtain knowledge of the life processes of insects, with the purpose of rendering practical benefits to mankind from his discoveries, while the generalizations that are suggested from a study of the assembled facts are given as an attempt to further the science of pure morphology.

I. THE NERVOUS SYSTEM OF INSECTS

In complex animals the ectoderm is the body layer that comes into direct contact with the environment. It may be supposed, therefore, that its cells retained from the first a higher degree of the properties of irritability and conductivity than did the cells of those layers that are infolded to form the strictly internal organs. It is not surprising, then, to find that, later, from the ectoderm are developed the sensitive, conductive, and receptor elements of the fully evolved animal.

Insects possess two nervous systems, which, though united with each other in the mature condition, appear to be independent in their origin. One constitutes the *ventral nerve cord* of ganglia and connectives, including the brain; the other consists of the ganglia of the stomodeum and their nerves, forming the *stomatogastric system,* or the so-called " sympathetic " system.

THE ORIGIN OF NERVOUS TISSUE

All true nervous tissue, comprising the nerve cells and their prolongations known as nerve fibers, are formed from the ectoderm. The investing tissue, or neurilemma, may be of mesodermal origin, but some investigators claim that even this in insects comes from the ectoderm.

The ganglia and commissures of the ventral nerve cord arise in the embryo from the ventral part of the germ band. At an early stage of development there appear two longitudinal *neural ridges* (fig. 1 A, *NlR*) on the under side of the embryo, with a median *neural groove* (*NlG*) between them. The ectoderm (*Ect*) both of the ridges and the groove proliferates from its inner surface a layer of large cells, the *neuroblasts* (*Nbl*), which are to generate the tissues of the future ventral nervous system. By multiplication, these cells form a *lateral cord* of cells in each ridge, and a *median cord* above the groove. According to Wheeler (1891), there are in insects typically, as exemplified by the Orthoptera, four rows of primitive neuroblasts in each ridge, and a median row above the neural groove. The neuroblasts divide repeatedly, those of the ridges giving rise to the vertical columns of ganglion cells (fig. 1 B, *GngCls*) that form the lateral cords, those above the groove producing a strand of cells which is the median cord (*MC*). From these cells are later formed the cellular and fibrous tissues of the ventral nerve cord.

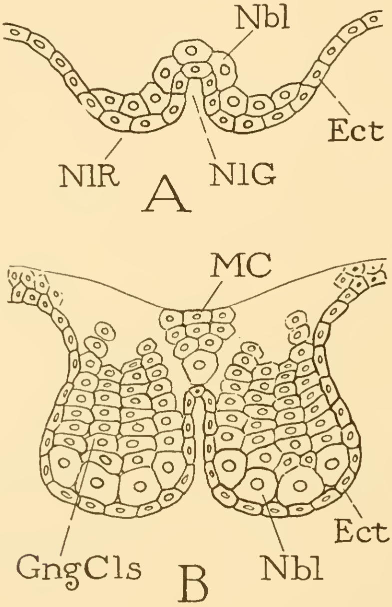

FIG. 1.—Diagrammatic cross-sections of median ventral part of insect embryo, showing origin of ventral nervous system.

A, formation of neuroblasts (*Nbl*) from ectoderm (*Ect*) of neural ridges (*NlR*) and neural groove (*NlG*). B, later stage (diagram based on drawing by Wheeler, 1891) showing formation of median cord (*MC*) and lateral cords of ganglion cells (*GngCls*) formed from the original neuroblasts (*Nbl*).

The ganglia of the stomatogastric nervous system are developed from the dorsal wall of the stomodeum, which is of ectodermal origin, but the details of their formation and separation from the epithelium have not been as fully described as in the ventral ganglia.

An animal with its nervous centers once buried within its body must establish connections between these centers and its own exterior, if it is to be aware of what concerns its welfare in the outside world; and it must also have paths of communication from the nerve centers to its muscles and other organs, if it is to control its activities in accord with the information it receives from without. These bonds extending between the nerve centers and the rest of the organism are the *nerve trunks,* which, all together, constitute the *peripheral nervous system.*

THE STRUCTURE OF NERVOUS TISSUE

All nerve fibers are connected with nerve cells; according to the modern conception of the morphology of nervous tissue, nerve fibers are in all cases prolongations of nerve cells. A nerve cell, in the broadest sense, then, consists of the cell body, or *cyton* (fig. 2, *Cy*), together with all of its nerve processes. The entire system is called a *neuron.* A nerve cyton is said to be unipolar, bipolar, or multipolar, according to the number of processes that arise from it. Of the cell processes, several may be short and branching, but one is usually a long, smooth, continuous axis with few branches. The first are known as *dendrons,* or *dendrites* (*a*), the second is the *axon,* or *neurite* (*Axn*), and constitutes the true nerve fiber from the cell. Branches given off from an axon are distinguished as collaterals (*Col*). The axons, collaterals, and dendrons terminate in fine branches (*b*), often spoken of as *arborizations.*

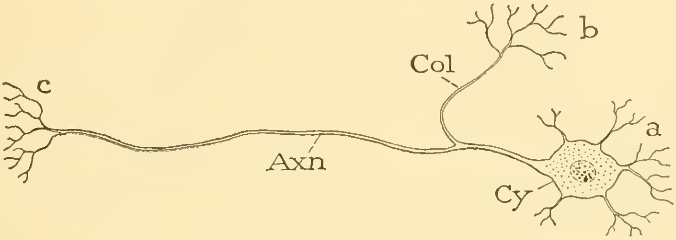

FIG. 2.—Diagram of a nerve cell, or neuron.

a, dendrons; *Axn,* axon; *b, c,* terminal arborization; *Col,* collateral; *Cy,* nerve cell body, or cyton.

The principal function of nervous tissue is the transmission of *stimuli.* Stimuli originate either from influences outside the body (sensory stimuli) or from influences within the body. According as the stimuli travel along the nerve fibers toward or away from the nervous centers, the fibers are said to be *afferent fibers* or *efferent fibers.* The fibers which receive stimuli directly, either from without or from within, and transmit them to the nerve centers, constitute the *sensory nervous system.* The efferent nerves and their root branches, receiving their stimuli secondarily from the central roots of the afferent fibers, constitute what is in general known as the *motor nervous system*, though the out-going stimuli induce not only muscular contraction, but glandular and all other cell activities.

Besides the long nerves that enter or depart from the central ganglia, there are shorter nerves, arising from cytons within the ganglia, that are confined to the limits of one ganglion, and longer nerves which go from one ganglion to another through the commissures. These nerves and their cytons constitute the *association system*, consisting of connective fibers and commissural fibers, which place different parts of the same ganglion, or parts of different ganglia, in communication with one another.

Finally, within the brain, there are two special regions with neurons of their own, which receive association terminals from all parts of the brain and the ventral nerve cord. These regions, known on account of their shape as the *mushroom bodies*, constitute the centers of the entire central nervous system.

The motor nerves are in all cases outgrowths of cells located in the nerve centers. The motor nerve cytons of insects lie either within the ganglia of the brain and the ventral nerve cord, or in the ganglia of the stomatogastric system. The peripheral sensory nerves of most animals, on the other hand, arise from cells lying outside the principal ganglionic centers, which cells either retain a peripheral position or are withdrawn more or less deeply into the body.

In vertebrate animals, most of the sensory cytons are derived from the neural crests of the embryo, ridges of ectodermal cells that are separated from the ectoderm along the line of closure of the neural tube, and which finally come to lie in the spinal ganglia. These cells (fig. 7 B, *SCy*) send out axons which branch in one direction (*SNv*) to the outlying parts of the body, and in the other to the spinal cord, thus establishing sensory connections between the peripheral sense receptors of the body wall (*BW*) and the main nerve centers. Only the nerves of the olfactory organs in vertebrates have their origin in cells that remain permanently in the peripheral ectoderm.

With insects, no neuroblastic cells are known that are analogous to those of the spinal ganglia of vertebrates. The origin and growth of the sensory nerves have not been traced in any insect, but all investigators agree that the sensory nerves end in the central ganglia in finely-branching terminal fibrils (fig. 7 A, *SNv*), which constitute the sensory neuropiles. This is attested by the works of vom Rath (1896), Kenyon (1896), Jonescu (1909), Haller (1910), Zawarzin (1924), and Orlov (1924).

THE VENTRAL NERVOUS SYSTEM

The lateral cords of the neural ridges of the insect embryo extend from the first segment of the head to the eleventh segment of the abdomen. Each forms a lateral mass of ganglionic cells in each segment, and intersegmental connecting commissures of fibrous tissue between them. Then the ganglionic masses of each segment become united by transverse commissural fibers, forming, in most cases, a compact double ganglion in the segment. The first three primitive pairs of ganglia in the head consolidate to form the *brain,* the next three unite to form the *subœsophageal ganglion;* the last four body ganglia consolidate to form the eighth abdominal ganglion of the adult, the others may remain separate, or they may unite in various combinations. After the formation of the alimentary canal, the brain comes to occupy a dorsal position in the head above the œsophagus, but in its origin it is a part of the ventral nerve cord.

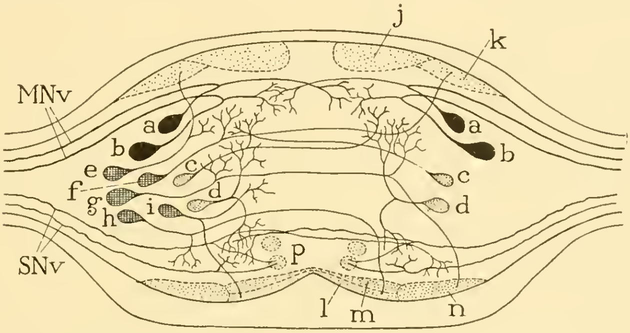

Fig. 3.—Diagrammatic cross-section of an abdominal ventral ganglion (based on diagram by Zawarzin, 1924 *a*).

a, b, motor cytons; *c,* cytons of transverse connectives; *d.* cytons of dorso-ventral connectives; *e, f, g, h, i,* cytons of longitudinal commissural connectives; *j, k, l, m, n, p,* dorsal and ventral fibrous tracts of the longitudinal commissures.

The body ganglia.—In a fully-formed ganglion of the thorax or abdomen the principal cellular elements are arranged peripherally (fig. 3, *a-i*), mostly in the lateral and dorso-lateral parts, while the central and ventral regions are occupied by fibrous tissue, consisting of connective and commissural fibers and the branching roots of sensory nerves and collaterals from motor axons. This fibrous core of the ganglion is known as the *medullary tissue,* or the *punctate sub-*

stance. Within it there are often more or less definite areas formed by the finely-branching terminals of associated fibers. Such areas are known as the *neuropiles* of the ganglion. When the fibers of a neuropile are scattered and the limits of the region are not well defined, the neuropile is said to be diffuse; when the fibers constitute a definite mass, the neuropile is called a *glomerulus.* In each body ganglion there is a dorsal motor neuropile region, and a ventral sensory neuropile region.

The principal ganglionic nerves issue as paired lateral trunks from the sides of each ganglion, but there is often also a posterior, unpaired, median nerve, which may be continued from one ganglion to that following. The fibers of the lateral nerve trunks separate within the ganglion into dorsal and ventral bundles, or *roots,* in which the fibers of the dorsal roots (fig. 3, *MNv*) are motor axons, and those of the ventral roots (*SNv*) are sensory axons. This arrangement is just the reverse of that which exists in the spinal cord of vertebrates (fig 7 B); but the main nerve centers of the Arthropoda and the Vertebrata are developed from opposite surfaces of the body—they are alike, therefore, in that the sensory roots in each are those nearest the exterior.

In each body ganglion there are five principal elements: (1) the cytons and roots of the motor fibers of the lateral nerves; (2) the roots of the sensory fibers of the lateral nerves; (3) the cytons and fibers of the intraganglionic connectives; (4) the cytons and fibers of the longitudinal commissural nerves; (5) the cytons and roots of the median nerve.

The nerve cytons, or nerve cell bodies, of the motor fibers of the lateral nerves, according to the diagram of Zawarzin (fig. 3, *a, b*), lie in the dorso-lateral parts of the ganglion. Each cell gives off a nerve process which soon divides into two branches. One branch, the collateral, goes inward and ends with a fine aborization in the motor neuropile of the ganglion; the other, the axon, turns outward in the dorsal root of a lateral nerve to become a peripheral motor fiber (*MNv*). The sensory fibers (*SNv*), coming in from the periphery, separate from the motor root fibers of the nerve trunk, and enter the ganglion through the ventral nerve root. Some of the sensory fibers end in the ventral sensory neuropile of the ganglion; others merely give off branching collaterals into the sensory neuropile, while the main axon proceeds forward through a longitudinal commissure to the sensory neuropile of some anterior ganglion. According to Zawarzin (1924), all the sensory fibers of the abdominal ganglia of a dragonfly larva (*Aeschna*) end in ganglia anterior to the one they enter. In the thoracic ganglia, however, Zawarzin says, while the sensory nerves from the body of the segment end in the same manner, *i. e.*, in an anterior ganglion, those from the legs terminate mostly in the ganglia of their respective segments. This evidently has the effect of making each thoracic ganglion a more independent center than are the individual abdominal ganglia.

The intraganglionic connectives in the ganglia of the dragonfly larva, as described by Zawarzin, comprise two sets of fibers and their respective cytons. One set consists of transverse fibers (fig. 3, *c*) which intermediate, by means of basal collaterals and terminal arborizations, between the two sides of the ganglion; the other set consists of T-shaped neurons (*d*), the two branches of which intermediate between the dorsal motor neuropile and the ventral sensory neuropile.

The fibers of the longitudinal commissures have their cytons (*e, f, g, h, i*) in the lateral parts of the ganglion; the axons, after giving off collaterals in the ganglion, proceed through the commissures to other ganglia of the chain. Some of these are motor connectives (*e, f*), sending their collaterals into the motor neuropile of the ganglion; others (*g, h, i*) are sensory connectives, sending their collaterals into the sensory neuropile. Zawarzin distinguishes three types of commissural fibers in the abdominal ganglia of the dragonfly larva: *tautomeric fibers* (*e, i*) that leave the ganglion through the commissure of the same side, after giving off one collateral into this side; *heteromere* fibers (*f, h*) that give off one collateral and then cross to the opposite side of the ganglion to enter the commissure of this side; and *hekateromere* fibers (*g*) that cross the ganglion but give off a collateral in each side.

The commissural tracts pass superficially through the dorsal and ventral parts of each ganglion. Zawarzin distinguishes on each side of the dorsal part of each ganglion in the dragonfly larva a median tract (fig. 3, *j*) which contains fibers that go long distances through the nerve chain, and a lateral tract (*k*) that contains the shorter dorsal fibers; and, on each side of the ventral part, an external median tract (*l*) of long fibers, an internal median tract (*m*) of short fibers, and a lateral tract (*n*) of short fibers. Besides these, finally, he says there are two internal ventral tracts (*p*) on each side that contain the sensory fibers which traverse the commissures.

The cytons and roots of the median nerves of the ventral ganglia, according to Zawarzin, lie in the posterior parts of the ganglia; but we are not here concerned with these nerves.

The brain and its nerves.—The brain of an insect consists of the ventral ganglia of the first three head segments united into one mass. The first pair of ganglia constitutes the *protocerebrum* (fig. 4, *1Br*), the second the *deutocerebrum* (*2Br*), and the third the *tritocerebrum* (*3Br*). The transverse commissures of the first and second pair form fibrous tracts (*1Com, 2Com*) within the brain, but the connectives of the tritocerebral ganglia (*3Com*) form an independent commissure beneath the œsophagus (*Œ*). The tritocerebral ganglia, therefore, really belong to the post-oral series of ganglia.

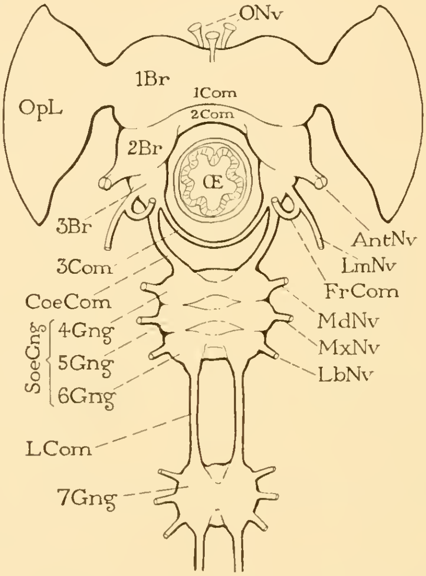

FIG. 4.—Diagrammatic structure of brain and subœsophageal ganglion.

The brain consists of the protocerebral (*1Br*), deutocerebral (*2Br*), and tritocerebral ganglia (*3Br*), the first two connected by transverse commissures (*1Com* and *2Com*) above the œsophagus, the third by a commissure (*3Com*) beneath the œsophagus. The subœsophageal ganglion (*SoeGng*) consists at least of the united fourth, fifth and sixth head ganglia, with nerves to the mandibles, maxillæ, and labium, and with other nerves from its posterior part (not shown).

In the brain, the same essential elements are to be found that are present in the ganglia of the ventral cord, except that in it cells of longitudinal commissural fibers have not been distinguished as such. The internal structure of the brain, however, in the higher insects, is far more complicated than that of a ventral ganglion, first, because of the composit nature of the brain, second, because of the presence of the great sensory tracts of the eyes and the antennæ, and third, on account of the development of the *corpora pedunculata,* or so-called *mushroom bodies,* in which there come together association fibers from all parts of the brain and the ventral cord.

The mushroom bodies, apparently, have no counterparts in any of the ganglia of the ventral cord. Each consists of a double fibrous *stalk* (fig. 5, *b*), buried in the lateral lobe of the protocerebrum, and of two cup-like fibrous masses, the *calyces* (*a*, *a*), supported on the ends of the stalks in the dorsal part of the brain. The calyces are filled with nerve cells (*c*), the axons of which (*f*) penetrate the stalks of the bodies and give off finely-branching collaterals (*e*) into the tissue of the calyces. At the lower end of the stalk of each body the fibers separate into a ventral and an anterior root. The mushroom bodies receive association fibers (*d*) from nearly all other parts of the brain, from the subœsophageal ganglion, and from the other ganglia of the ventral nerve cord, most of which end in fine branches within the calyces. If the insect, therefore, has intelligence, or consciousness of external things that affect it, or of its own actions, the seat of this faculty must surely be in the mushroom bodies. Or, if insects are but living mechanisms, the chief regulatory centers must again be these bodies, which are to the ganglia what the ganglia are to the peripheral nerves—they are the centers of the central nervous system. The mushroom bodies appear to be present in nearly all insects, but they are much more highly developed in the Diptera and Hymenoptera than in the lower orders.

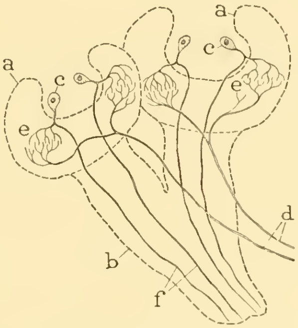

FIG. 5.—Diagram of a "mushroom body," or corpus pedunculatum, of the brain.

a, *a*, calyces; *b*, stalk; *c*, calyx cells giving axons (*f*) into the stalks, and collaterals (*e*) into the neuropiles of the calices; *d*, association fibers from other parts ending in arborizations within the calices.

The first division of the brain, the protocerebrum (fig. 4, *1 Br*), supports the simple and the compound eyes, but a discussion of the optic tracts and the ocellar nerves is omitted here because the structure of the organs of vision will be but briefly treated in this paper. The protocerebral segment of the head has no true appendages, and there are probably no muscles innervated from the protocerebrum. Therefore, this part of the brain contains few motor cytons. Kenyon (1896) says there are motor fibers in the ocellar nerves of the honeybee, but he believes that they regulate the activities of the pigment in the ocelli.

The deutocerebrum, or second division of the brain (fig. 4, *2Br*), consists mostly of the large antennal lobes and the fibrous tracts of the deutocerebral commissure (*2Com*). The appendages of the deutocerebral head segment are the antennæ. These organs in insects are highly sensitive structures, being provided with sense receptors of many different kinds. They are also delicately mobile, and are responsive to subtile influences from all parts of the body. Each contains muscles that move its flexible parts, while the appendage is moved as a whole by muscles within the head inserted upon its base. Each antenna is transversed by a nerve trunk, commonly double, which contains, at least in its proximal part, both sensory and motor fibers, and each trunk gives off from its base a motor branch to the antennal muscles of the head. The roots of the antennal nerves lie within the antennal lobes of the deutocerebrum.

The motor cytons of the antennal nerve, according to Jonescu (1909), in the honeybee, are arranged in two groups corresponding with the two divisions of the nerve trunk, one group being in the upper part of the antennal lobe, the other in the ventral part. Kenyon (1896) says that collaterals from some of the motor axons branch upon the bases of the mushroom bodies, but that the majority of them go backward to the tritocerebral region of the brain and to the subœsophageal ganglion, where they come in contact with nerve ends from this ganglion and from the ventral cord. The motor cytons thus mark the roots of the antenno-motor fibers as belonging to the deutocerebrum; but the stimuli received by the fibers may come from all possible sources.

The sensory antennal fibers end in fine branches within neuropile bodies, or glomeruli, of the antennal lobes. These bodies contain also the end branches of connective fiber collaterals, the principal axons of which go to the mushroom bodies, in the calices of which they break up into terminal aborizations. Here these fibers come into close relation with the branches of the mushroom body nerves themselves, and with the terminations of all the other nerves that center in these bodies. The sensory stimuli received by the antennæ may thus be transmitted to motor nerves going out to all parts of the body. The similarity of the glomeruli of the antennal lobes of insects to those of the olfactory lobes of a vertebrate brain has strengthened the idea that the sense receptors of the antennæ are chiefly organs of smell.

The third division of the brain consists of the tritocerebral ganglia (fig. 4, *3Br*), but since the connecting commissure (*3Com*) lies beneath the œsophagus, these ganglia do not form an intimate part of the brain. The tritocerebral segment of the head has a pair of vestigial appendages in the embryonic stage of some insects, but the appendages disappear in all adult insects, except possibly in *Campodea,* one of the Thysanura. Each tritocerebral lobe gives off two nerves, a labral nerve (*LmNv*) and a frontal ganglion nerve, or frontal commissure (*FrCom*), but the two are usually united at their bases into one labro-frontal, or tritocerebral, nerve trunk. The labral nerve innervates the labrum and some of the dorsal muscles of the pharynx. It is said to be composed of sensory fibers, the roots of which, according to Jonescu (1909), in the honeybee, are distributed in the protocerebrum, within and beneath the deutocerebral commissure, and in the antennal lobes. Kenyon (1896) says that some of its roots go also into the subœsophageal ganglion. The frontal commissure is said to consist of motor fibers, the cytons of which lie in the tritocerebral lobes.

The subœsophageal ganglion.—The composit ganglionic mass lying in the lower part of the head, known as the subœsophageal ganglion, (fig. 4, *SœGng*) on account of its position below the œsophagus, consists at least of the united ganglia of the fourth, fifth, and sixth head segments (*4Gng, 5Gng, 6Gng*). Its principal nerves innervate the mandibles, the maxillæ and the labium, but besides the three pairs of mouth part nerves there is commonly a fourth pair, and sometimes several pairs, issuing from the posterior part of the ganglion. One of these posterior nerve pairs has been traced in some insects to the salivary glands; the others when present go to the neck region and into the prothorax. The origin of nerves other than those of the mouth parts from the subœsophageal ganglion might suggest that this ganglion is a composit of more than three primitive ganglia, and Verhoeff (1903) has argued that here is positive evidence of the presence formerly of a neck segment, or "microthorax," in insects, homologous with the segment of the poison fangs in the Chilopoda, the ganglionic center of which is united with the ganglia of the true mouth part segments. Ontogeny, however, has not recorded the presence of a neck segment rudiment in any insect embryo, and entomologists mostly still regard the sclerites of the neck in insects as secondary developments. Likewise, embryology has not demonstrated a fourth component in the insect subœsophageal ganglion. Verhoeff's idea of the quadruple structure of this ganglion should not be confused with the claim, now pretty well discarded, that the ganglion comprises a pair of ganglionic centers between those of the mandibles and the maxillæ, innervating the lateral lobes (superlinguæ) of the hypopharynx. A more detailed investigation of the internal structure of the subœsophageal ganglion, which has been less studied than that of the brain or the body ganglia, should be made before any definite statement can be given of the exact composition of the ganglion or the homologies of its posterior nerves.

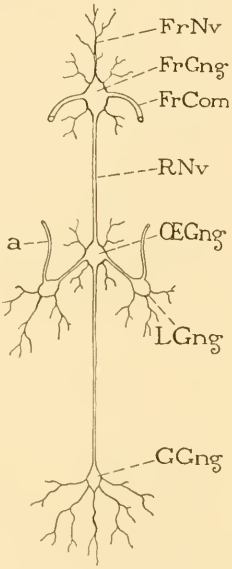

Fig. 6.—Diagram of a typical arrangement of ganglia in the stomatogastric nervous system.

FrGng, frontal ganglion, connected with tritocerebrum by frontal commissures (*FrCom*) and giving off posteriorly the recurrent nerve (*RNv*) to œsophageal ganglion (*ŒGng*); the latter connected by lateral nerves with lateral ganglia (*LGng*), each of which is united with back of brain by small nerve (*a*), and by median nerve with gastric ganglion (*GGng*).

THE STOMATOGASTRIC NERVOUS SYSTEM

The ganglionic centers of the stomatogastric nervous system are located on the dorsal surface of the stomodeal parts of the alimentary canal, from the epithelium of which they are formed in the embryo. The number and arrangement of the ganglia differ much in different insects, but a typical scheme of the ganglia and the principal nerves of this system is shown diagrammatically in figure 6. The most anterior ganglion is the median *frontal ganglion* (*FrGng*), situated on the dorsal wall of the pharynx before the base of the brain. It is united laterally by the *frontal commissures* (*FrCom*) with the tritocerebral regions of the brain, as already described (fig. 4). Anteriorly it gives off a small median *frontal nerve* (*FrNv*) with branches to the pharynx and the clypeal region of the wall of the head. Posteriorly a median *recurrent nerve* (*RNv*) goes back from the ganglion beneath the brain to a second median ganglion on the pharynx below or behind the brain. This ganglion is known as the *œsophageal ganglion* or *hypocephalic ganglion* (*ŒGng*). From it is given off on each side a short nerve to a *lateral ganglion* (*LGng*) located on the dorso-lateral part of the pharynx or œsophagus (the "œsophageal ganglion" of Berlese). Each of these lateral ganglia is connected with the posterior part of the brain by a small nerve (*a*). The median œsophageal ganglion may also give off posteriorly a long median nerve which ends in a gastric ganglion (*GGng*) on the wall of the stomach. Besides the main nerve trunks, many smaller nerves arise from all the ganglia of the stomatogastric system, which are mostly distributed on the stomodeal and ventricular parts of the alimentary canal, but some go to the walls of the head, the surface of the brain, to the aorta, and to other neighboring organs.

Janet (1899) has proposed the interesting theory that the three median ganglia of the stomatogastric chain are the primitive ventral ganglia of three pre-cerebral segments that have been invaginated to form the stomodeum. This theory, however, must assume first that, prior to the stomodeal invagination, the first six pairs of ventral ganglia migrated upward in the sides of the body and then came together dorsally, the two ganglia of each segmental pair uniting above the alimentary canal. Then, with the retraction of the supposed stomodeal segments, the three pre-cerebral ganglia were drawn inward with their segments, the first one becoming the gastric ganglion, the third becoming the frontal ganglion. Next, the theory must assume that the posterior roots of the frontal-protocerebral connectives became shifted from the protocerebrum to the tritocerebrum; while, finally it assumes that the transverse commissures of the stomatogastric ganglia have been lost, and that those of the brain ganglia are all united in the subœsophageal commissure. None of these assumptions is supported by the known facts either of the development or of the structure of the parts concerned. The median ganglia of the stomatogastric system, moreover, are so variable in number that the scheme given above can scarcely be regarded as representing a primitive arrangement. The frontal ganglion is the only one of constant occurrence; one or both of the other median ganglia may be lacking. The lateral ganglia must in any case be regarded as of secondary origin. They are apparently always connected with the median system, but each has also one or two connectives with the back of the brain. In caterpillars the lateral ganglia are entirely separated from the walls of the alimentary canal, and their principal nerves go to muscles of the anterior dorsal and lateral parts of the head.

According to the accounts of Zawarzin (1916) and Orlov (1924), the nerves of the stomatogastric system contain both motor fibers and sensory fibers, the former having their cytons in the ganglia, the latter arising from cells distributed over the innervated parts of the alimentary canal and ending in fine terminal arborizations within the ganglia.

THE ORIGIN OF THE SENSORY NERVES

Since no sensory cytons have been found in the central ganglia of insects, or anywhere associated with them, students of the central nervous system follow vom Rath (1896) in insisting that the generative cells of the sensory nerves must be found in the periphery, presumably in the ectodermal tissue of the body wall and the alimentary canal.

When the sensory fibers are traced outward from the central ganglia, each is found to end in a cell. Some of the cells are bipolar, others are multipolar. The distal process of some of the bipolar cells goes direct to a sense organ of the ectoderm, either one in the hypodermis, or one in the epithelium of the alimentary canal. Bipolar cells of this kind, connected with specific sense organs, constitute the sensory cells of Type I of Zawarzin (1912 *a*). The other cells, which may be either bipolar or multipolar, but which are characteristically multipolar, give off terminal processes that end in fine branches on the inner surface of the hypodermis, perhaps also on the tendons of the skeletal muscles, and on the walls and muscles of the alimentary canal. Cells of this kind constitute the sensory cells of Type II of Zawarzin. The cells of both types lie either within or just beneath the ectodermal tissues they innervate, and they are the only cells yet found in the courses of the sensory nerves. This has given rise to the idea that they are the true cytons of the sensory fibers, according to which, all the sensory nerves of insects are analogous to the olfactory nerves of vertebrates, being the centripetal axons of nerve cells developed in the peripheral ectoderm.

The developmental origin of the sensory cells of Type I that lie within the hypodermis has been studied by many investigators, and all agree that they are specialized hypodermal cells. No one has demonstrated the growth of a nerve axon from these cells, while, on the other hand, several investigators have claimed that a nerve fiber grows outward and unites with the sense cell. Berlese (1909), for example, after studying the postembryonic developmental stages of several kinds of sense organs, says that, in all cases, it is found that a sensory nerve proceeds outward from the central nerve chain and elongates until it attains the basement membrane of the body wall at the point where the sense organ is to be formed. Here it remains until the sense organ is ready to receive it, when it penetrates the basement membrane and unites with the sensory complex that has formed in the hypodermis. Vogel (1923) says that in a mature larva of a wasp the antennal nerve has already reached the tip of the antenna without penetrating the basement membrane of its walls. During an early stage of the pupa, however, branches of the nerve enter the hypodermis, where a single fiber unites with the base of each sense cell. The base of the sense cell, Vogel says, may elongate slightly toward the nerve, but the connection with

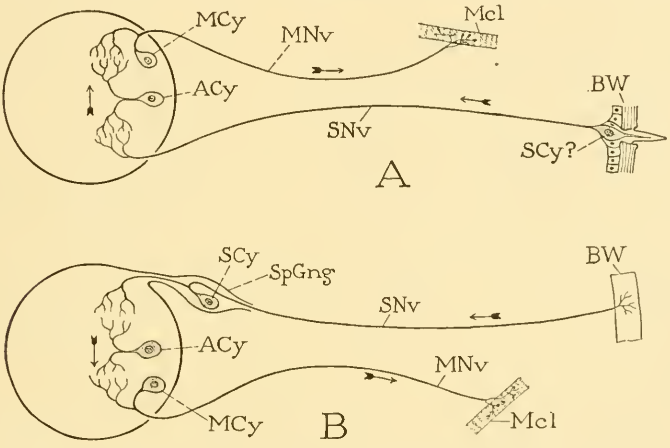

Fig. 7.—Comparative diagrams of central and peripheral nervous systems of an insect (A) and a vertebrate (B). In the vertebrate most of the sensory cytons (*SCy*) are in the spinal ganglia (*SpGng*); in the insect the apparent sensory cytons (*SCy?*) are in the hypodermis.

the latter is made in the immediate neighborhood of the cell. From his observations, made on specimens stained by the Golgi method, Vogel claims that the antennal nerve of insects is not to be likened to the olfactory nerve of vertebrates, and that the innervated cell of an insect sense organ becomes secondarily a sense cell by union with a sensory nerve fiber.

It still, therefore, appears to be true, as Berlese (1909) has said, that those writers "who had hoped for a demonstration of the hypodermal cells themselves becoming ganglion cells, have awaited in vain that this should be proved." Yet, Vogel's conclusion that there must be found in the deutocerebrum a ganglionic center from which the sensory antennal nerves take their origin, has also not been substantiated, for the elaborate studies of vom Rath, Kenyon, Haller, and Jonescu have failed to reveal anywhere within the central ganglia of insects the cytons of the sensory fibers. Perhaps they lie somewhere between the extreme periphery and the nerve centers. The subject of the origin of the sensory nerves in insects or other invertebrates is one on which the embryologists are strangely silent, and until further investigations shall give us more light upon it, we cannot reconcile the two apparently contradictory sets of observations. Either the claims from one side or the other are incorrect, or there is some undiscovered source of the sensory axons, possibly corresponding with the neural crests of the vertebrate embryo.

II. THE PERIPHERAL ENDINGS OF THE SENSORY NERVES

Some nerve trunks consist entirely either of motor or of sensory fibers; but, for the most part, the two kinds of fibers, after leaving the central ganglia, are bound together in the same nerve trunks. Toward the periphery, however, the two sets of fibers again separate, and individual axons proceed to their own destinations.

The peripheral ends of the sensory fibers, as we have already seen, end in bipolar or multipolar cells, the distal processes of which either go direct to specific ectodermal sense organs, or they break up into fine branches beneath the hypodermis and on the wall and muscles of the alimentary canal. The bipolar cells with unbranched distal processes going to the external sense organs are distinguished, according to the classification of Zawarzin (1912 *a*), as sensory cells of Type I; the bipolar and multipolar cells, with branching terminals or dendrons, as sensory cells of Type II. Since the former belong to the cellular complexes of the sense organs they will be described in following sections of this paper treating of the general and specific structure of the sense organs; this section will deal with the cells of Type II.

For convenience of description, the sensory nerve endings of the body wall, and those of the alimentary canal will be described under separate headings. Nearly all the axons of the nerve endings of the body wall proceed to the ganglia of the ventral nervous system; those of the alimentary canal go both to the ventral ganglia, and to the ganglia of the stomatogastric system.

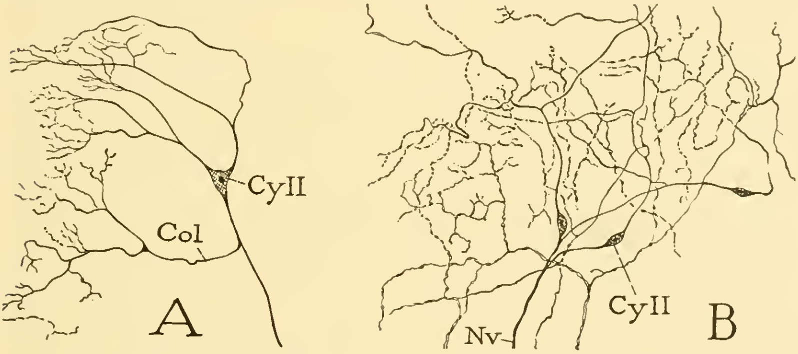

FIG. 8.—Peripheral endings of sensory nerves on inner surface of hypodermis.

A, a subhypodermal multipolar sensory nerve cell of Type II (*CyII*) of a dragonfly larva with branches on articular membrane between trochanter and femur (Zawarzin, 1912). B, part of subhypodermal network of nerves from cells of Type II in larva of *Melolontha* (Zawarzin 1912 *a*).

THE SENSORY INNERVATION OF THE HYPODERMIS

In many soft-bodied larvæ of insects there is an extensive network of nerves on the inner surface of the hypodermis, which is formed by the finely-branching terminals of the bipolar and multipolar peripheral sensory cells of Type II. This network (fig. 8 A, B) constitutes the so-called *subhypodermal plexus,* though the fibers composing it probably do not unite with one another.

The extent to which this hypodermal innervation occurs in different insects, especially in adults, has not been determined; it is known to exist chiefly in soft-skinned larvæ. A subhypodermal nerve net was first noted by Viallanes (1882) in the larvæ of Diptera (*Stratiomys, Eristalis, Musca*). It was described later in more detail by Monti (1893, '94) in the larvæ of Cerambycid beetles, by Holmgren (1896) in the caterpillar of *Sphinx ligustri,* by Hilton (1902) in the silkworm, and finally by Zawarzin (1912 *a*) in the larva of *Melolontha* *vulgaris* (fig. 8 B). Zawarzin (1912) says also that there are branching nerve fibrils in some places beneath the membranous parts of the cuticula in dragonfly larvæ (fig. 8 A), and Monti reports the presence of a rich arborization of nerve fibers arising from multipolar cells on the inner surface of the hypodermis in adult Orthoptera. Several writers have described a nerve net beneath the body wall of other arthropods; Bethe (1896), for example, found it in the freshwater crayfish, Němec (1896) in land isopods, where, he says, the nerve endings lie between the hypodermal cells, and Holmgren (1896) reports a plexus similar to that of insects in various groups of Crustacea.

The writers mentioned above all assert that the cells of the subhypodermal net are nervous elements, but Duboscq (1897) claims that similar cells present in Forficulidæ are connective tissue cells, and he discredits the idea that the cells are in any case nerve cells. All studies of the subhypodermal network and its cells have been made by the methylenblue method of staining nerve tissues.

The most concise account of the subhypodermal innervation of an insect is that by Zawarzin (1912 *a*) made on the larva of *Melolontha vulgaris*. Beneath the skin of the larva, Zawarzin says, there is a finely-branching system of nerve fibrils forming a network of large and small meshes over all parts of the body (fig. 8 B), including the appendages, but particularly developed on the middle of the back. The nerves (*Nv*) that break up to form the net proceed from small, irregular cells of Type II (*CyII*), some bipolar, other multipolar. The distal processes of the cells branch dichotomously into the fibrils of the larger meshes, and these ramify to form the threads of the finer meshes. None of the fibrils, Zawarzin says, unite with one another, though they often appear to do so when they lie close together. Monti noted the same in studying the subhypodermal nerve net of Cerambycid larvæ. The fibrils of the larger meshes in *Melolontha* are relatively smooth, but the finer branches are characteristically varicose, presenting numerous small swellings along their courses. All investigators have noted this varicosity of the end branches of the subhypodermal nerves of insects, and the same feature is described for the branches and fibrils of the sensory nerves in the human epidermis. The actual endings of the fibrils in insects have not been definitely observed, but the terminal branches appear to end free on the basement membrane.

The character of the fibrils in the subhypodermal nerve net apparently leaves no doubt that they are the terminals of sensory nerves, since the fibrils of the sensory roots in the central ganglia have the same varicose structure. It is reasonable to suppose that they are sensitive to external stimuli, to mechanical stimuli, at least, and possibly to changes of temperature. Sparsely-haired caterpillars react to gentle pressure on the skin between the tactile hairs, and naked, soft-bodied larvæ are well known to be highly sensitive to touch anywhere on the body surface, showing that a sense of touch is not dependent on the presence of special tactile organs. Viallanes noted that naked fly larvæ possess peripheral cells of Type II, though lacking those of Type I which innervate the body hairs of other species. Since the nerve endings of cells of Type II, however, are apparently all alike, and are not associated with specialized cells of the hypodermis, it may be questioned whether they receive differentiated sensations. Possibly, perceptions received through them, whether of mechanical, thermal, or chemical stimuli, are merely general sensations akin to degrees of pain.

It is suggested by Orlov (1924) that the skeletal muscles of insects receive a sensory innervation through their tendons from the subhypodermal nerves. Orlov, however, remarks that there is no literature on the sensory nerves of the skeletal muscles of invertebrates, except for the negative statement of Döflein that no such nerves are present in the Arthropoda.

The peripheral sensory cells of Type I, the single distal processes of which are non-varicose, non-branched, and go direct to the tactile hairs or other cuticular sense organs, are associated with the cells of Type II in hairy larvæ, since they commonly lie beneath the hypodermis, more or less removed from the bases of the sense organs. These cells are usually larger than the others, and have more regular, oval, or fusiform shapes (fig. 11, *SCl*). The sense cells of adult insects generally lie within the hypodermis (fig. 12) and, in their origin, are clearly modified hypodermal cells. The subhypodermal sense cells of larval insects, and the intrahypodermal sense cells of adults are possibly not of the same origin, but on this subject we have no light at present.

THE SENSORY INNERVATION OF THE ALIMENTARY CANAL

There are only two papers, known to the writer, treating of the sensory nerves of the alimentary canal in insects, and the endings of the nerves in the various tissues of the tract. One of these is by Zawarzin (1916), describing the stomatogastric system of *Periplaneta americana;* the other is by Orlov (1924) on the innervation of the alimentary tract of Lamellicorn beetle larvæ.

In the cockroach, as described by Zawarzin, there are numerous sensory nerve cells of Type II, mostly multipolar, distributed over the walls of the crop. Some of these cells lie free on the outer surface of the epithelium, some are more or less inclosed within the nerve trunks, and others lie beneath the covering membranes of the ganglia. The distal processes of the free cells break up into fine varicose fibrils that terminate between the epithelial cells; the distal processes of the other cells apparently innervate the neurilemma of the nerves and ganglia. The main axons, in all cases, go to the principal stomatogastric ganglia where they terminate in neuropile arborizations. Zawarzin does not describe sensory nerves ending in the muscles of the crop.

The alimentary canal of larvæ of Lamellicorn beetles, as described by Orlov, is innervated both from the stomatogastric system and from the abdominal ganglia of the ventral nerve cord. In the larvæ of *Oryctes* and *Melolontha,* there is a nerve ring around the posterior end of the œsophagus, connected by lateral nerves with the œsophageal ganglion, from which six equally spaced, parallel nerve trunks go posteriorly on the walls of the ventriculus. From the ganglia and from the nerve trunks there are given off numerous ramifying nerve branches, containing both motor and sensory fibers, that spread over all parts of the œsophagus and stomach.

The sensory fibers, Orlov says, end peripherally in multipolar nerve cells, the terminal processes of which branch into a network of fine varicose fibrils similar to the sensory network beneath the hypodermis. The fibrils terminate on the œsophagus and the ventriculus, some in the connective tissue, and some in the sarcolemma of the muscle fibers. Several types of nerve endings on the muscles are distinguished by Orlov. In typical cases, a nervous network surrounds the muscle fiber, and the nerve fibrils contain flat swellings from which are given off fine varicose terminal threads with free ends (fig. 9 A); in other cases, the nerve fibers end directly in varicose branches on the muscles (B); while, again, the nerve may make a complicated spiral tangle about the muscle fiber (C). In most cases, the branches of one sensory nerve cell are localized on one fiber, but in some they spread over adjoining parts of several fibers (B). The character of the sensory endings always distinguishes them from the endings of the motor fibers.

The proctodeum of Lamellicorn larvæ, according to Orlov, is innervated by abdominal ganglia of the ventral nerve cord, from which it receives both motor and sensory fibers. On the small intestine the sensory fibers are distributed principally on the connective tissue layers surrounding the epithelium and uniting the muscles. The rectal sac has no sensory innervation, but the posterior straight part of the rectum is provided with sensory networks of varicose fibers, arising from multipolar cells, lying between the epithelium and the muscular coat, and on the outer surface of the latter. On the terminal part of the rectum, Orlov notes, besides these cells of Type II, also bipolar cells of Type I, the distal processes of which go to sense organs in the rectal wall (fig. 22).

The brief descriptions of the sensory nerves given in this section summarize practically all that is known of the sensory innervation of insects. It is evident that much must yet be done in this field before we can pretend to have anything approximating a comprehensive knowledge of the subject, and we should feel grateful to the few workers who have contributed what information we now possess.

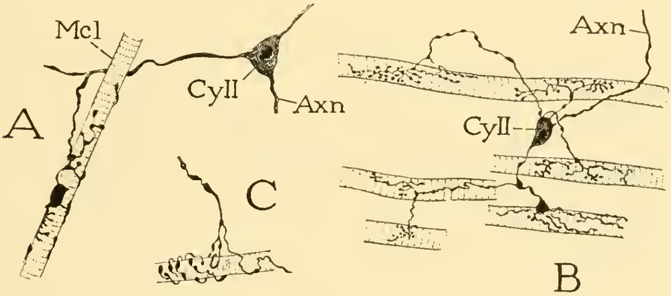

FIG. 9.—Various types of sensory innervation of muscles of alimentary canal of Lamellicorn beetle larvæ by nerves of stomatogastric system (Orlov, 1924).

A, B, from œsophagus of larva of *Oryctes*. C, from ventriculus of larva of *Melolontha*.

III. THE GENERAL STRUCTURE AND CLASSIFICATION OF INSECT SENSE ORGANS

The true sense organs of insects are more or less complex structures formed, in all cases, from a part of the body wall. Usually there is a specialized cuticular element having the shape of a hair, peg, dome, plate, or lens, and there are always cellular elements consisting of specialized hypodermal cells, of which one at least is connected with the end of a sensory nerve. Any study of the structure of insect sense organs must, therefore, be based on an understanding of the general structure of the body wall and the particular structure of its cuticular appendages.

THE STRUCTURE OF THE BODY WALL AND ITS APPENDAGES

The foundation of the body wall is the ectodermal layer of cells commonly known in insect anatomy as the *hypodermis* (fig. 10 A, *Hy*). The cells are lined on their inner surfaces by the *basement membrane* (*BM*), which is either a homogeneous product of the cells themselves, or is perhaps itself, in its origin, a cellular tissue derived from the mesoderm. The outer surface of the hypodermal layer is covered by the *cuticula* (*Ct*), a secretion from the cells containing chitin as its characteristic component. In sections, the cuticula usually shows a horizontally lamellate structure, and a differentiation into an outer denser part, the *epidermis,* or *exocuticula* (*Epd*), and a clearer, softer internal part, the *dermis,* or *endocuticula* (*Dm*).

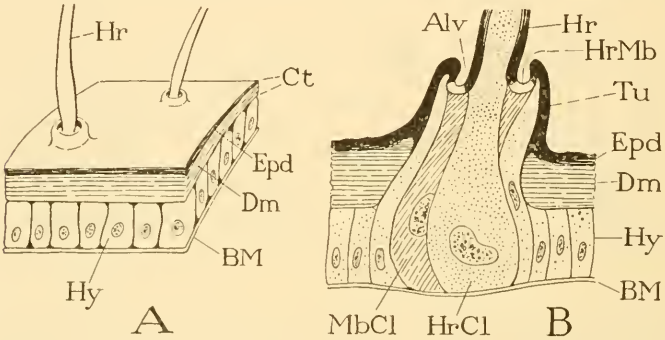

FIG. 10.—Diagrammatic structure of the body wall, and of a tuberculate hair, or seta.

A, piece of body wall bearing two setæ. B, section of base of a seta showing two cells associated with it, the seta-forming cell, or trichogenous cell (*HrCl*), and the cell of the hair membrane (*MbCl*).

The commonest types of external appendages of the body wall have the form of hollow hairs or *setæ*. A seta (fig. 10 B, *Hr*) is an outgrowth of the cuticula formed by a large hypodermal cell, known, on account of its special function, as a *trichogenous cell*, or *trichogene* (*HrCl*). The base of the seta is commonly attached by a membranous ring, the *hair membrane* (*HrMb*), to the surrounding cuticula. Sometimes the hair stands on the surface of the body wall, but more usually it is sunken into a cup or *alveolus* (*Alv*). The rim of the alveolus may be flush with the general cuticular surface, or it may be elevated to form a *tubercle* (*Tu*) supporting the hair base.

Beneath the hair and its membrane there is a large cavity in the cuticula, open proximally, but distally prolonged into the hollow of the hair. This cavity is known as the *hair canal,* or *pore canal.* The hair canal is usually occupied by the outer ends of several cells that have formed the distal cuticular parts. One of these is the trichogene, another is the formative cell of the hair membrane, the *membrane cell* (*MbCl*), while others are unspecialized hypodermal cells of the canal wall, being more prominent where the hair is situated on a tubercle (fig. 11, *b*). The distal end of the membrane cell normally surrounds the neck of the trichogene at the base of the hair, though after the hair is formed at any molt the trichogenous cell may withdraw from the seta and retract from its base, leaving a vacuole beneath the seta (fig. 12, *Vac*). Especially is this true in the adult stage.

The various cells associated with the hair are not always easily distinguishable in sections, and they have not always been included in descriptions and figures of the cuticular organs; yet, theoretically, we must assume that they are present, in most cases, though perhaps variously modified. It is especially important to take them into account, particularly the hair cell and the membrane cell, in any study of the morphology of insect sense organs.

SENSORY HAIRS

A seta sensitized by a nerve connection is the commonest form of insect sense organ. The innervation is always through a special bipolar sense cell, the proximal process of which is continuous with a sensory nerve, while the distal process is associated with the seta. In adult insects the sense cell is situated within the hypodermis (fig. 12, *SCl*), being limited internally by the basement membrane, though its size or position may cause it to project into the body cavity beyond the general level of the hypodermis (fig. 13 B). In some larval insects, on the other hand, the sense cell may lie beneath the hypodermis (fig. 11, *SCl*) some distance removed from the base of the cuticular organ, with which it is connected by a long distal process (*d*) that penetrates the basement membrane (*BM*). The sense cells of adult insects are unquestionably modified hypodermal cells; the origin of the larval sense cells that lie beneath the hypodermis has not been determined. The two sets of cells will, most likely, prove to be homologous, for Zawarzin (1912 *a*) notes that the sense cells of the sense organs of Lamellicorn beetle larvæ lie in some cases within the subsetal canal, in others in the hypodermis, and in others beneath the hypodermis; but, for the present, we apparently must distinguish between *intrahypodermal* sense cells, and *subhypodermal* sense cells. The latter constitute the subhypodermal sensory cells of Type I, already noted.

Sensory hairs with subhypodermal sense cells.—A good description of the structure of a setal sense organ innervated through a subhypodermal sense cell may be found in the recent paper by Schneider (1923) on the sense organs of the cabbage worm (*Pieris brassicæ*). The body of the caterpillar, according to Schneider, is covered by small tuberculate hairs, all of which have sense cell connections. Beneath the hair is a large trichogenous cell (fig. 11, *HrCl*), with a large bent nucleus in its base, and having its distal end prolonged into the hollow of the seta (*Hr*). Attached distally to the hair membrane (*HrMb*) is a membrane cell (*MbCl*) which surrounds the neck of the hair cell, and is continued to the basement membrane at one side of the hair cell. Several other hypodermal cells (*b*), belonging to the walls of the tubercle, surround the trichogene and the membrane cell. Since the hairs are renewed with each molt, and are increased in size, the trichogenous cells vary in size and contents according to the period in each instar, becoming large and full before the molt, and shrinking following the molt. New hairs, also, are added with each renewal of the cuticula.

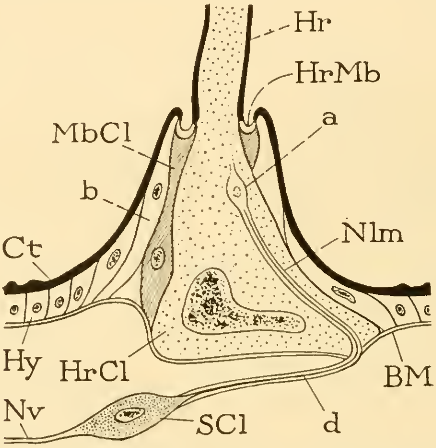

FIG. 11.—Example of the innervation of a larval tactile hair through a subhypodermal sense cell. (Section of a body hair of a cabbage worm, diagrammatic from Schneider, 1923.)

A bipolar sense cell (*SCl*) lies beneath the hypodermis in the immediate neighborhood of each seta, and sends a long, slender distal process (*d*) through the basement membrane (*BM*), along the side of the trichogenous cell, toward the base of the hair. Presumably, the process ends on the base of the hair, but Schneider says that he failed to find its exact termination, though it never penetrates beyond the base of the hair. The process has a subterminal swelling (*a*) which contains a dark nucleus-like body. Whether this body belongs to the cell process, or is a nucleus of the neurilemma investing the latter was not determined, but Schneider points out that the swelling is *not* the sense cell of the organ, though some writers have described it as such.

Other writers, Viallanes (1882), Monti (1893, 1894), Hilton (1902), Zawarzin (1912 *a*), and Orlov (1924), have given essentially the same account of the subhypodermal sense cells in larval insects, but with less detail as to the structure of the sense organs with which they are connected.

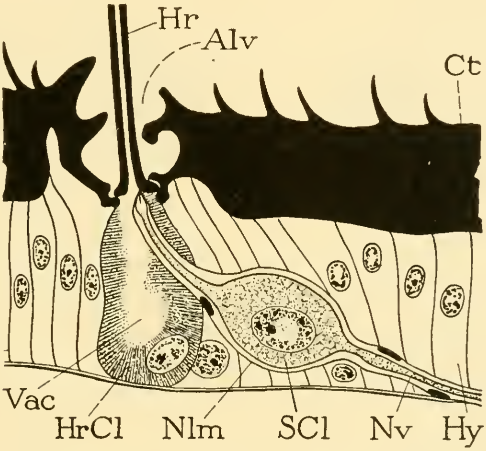

FIG. 12.—Example of a tactile hair innervated through an intrahypodermal sense cell. (Section of a hair on the cercus of an adult cricket, *Gryllus campestris,* diagrammatic from Sihler, 1924.)

Sensory hairs with intrahypodermal sense cells.—The structure of a hair sense organ in which the sense cell lies within the normal hypodermis may be illustrated by an example taken from the work of Sihler (1924) on the sense organs of the cerci of a cricket (*Gryllus campestris*).

The long hairs on the cerci of the cricket are set into deep cup-like alveoli (fig. 12, *Alv*). The lips of each cup project above the surface of the surrounding cuticula as a circular rim, while a horizontal chitinous ring projects from the inner walls of the cup to brace the base of the hair. The hair in these organs is rather solidly inserted into the bottom of the cup and the usual articular membrane is lacking. Beneath the hair is a large trichogenous cell (*HrCl*), with a basal nucleus and its central part occupied by a vacuole (*Vac*) continuous with the hollow of the hair. Sihler does not distinguish in this organ a specific membrane cell, but, as just noted, the alveolar membrane is obliterated by the solid insertion of the hair. Several hypodermal cells, however, surround the trichogene and apparently contribute to the formation of the cup. At the side of the trichogene toward the base of the cercus is the large, oval, intrahypodermal, bipolar sense cell (*SCl*). Its distal process, Sihler says, penetrates the trichogenous cell and ends against the base of the hair. The proximal process (*Nv*) is continued into a sensory nerve trunk after following the basement membrane for some distance toward the base of the cercus. The sense cell and its distal process are invested in a nucleated continuation of the neurilemma of the nerve (*Nlm*).

The structure of the setal sense organ depicted in the above description is typical of that of all the hair-like sense organs of adult insects, (fig. 13 A, B) except that usually two cells are to be distinguished in addition to the sense cell, one of which is the trichogenous cell (*HrCl* or *ECl*), and the other probably the hair membrane cell (*MbCl* or *CCl*).

THE FUNDAMENTAL STRUCTURE OF AN INSECT SENSE ORGAN

A general survey of the structure of insect sense organs shows, in a large number of cases, that a single organ, or a single element of a compound organ, is formed of three cells or the multiples of three cells. We are, therefore, warranted in believing that the foundation structure of most types of insect sense organs consists of three hypodermal cells.

The structure of a simple three-cell sense organ, in which the cuticular part is of the hair type, is shown diagrammatically in figure 13 A. The most conspicuous element in the hypodermal part is the sense cell (*SCl*). Proximally the sense cell is continuous with the nerve (*Nv*), while distally it sends out a long, slender, terminal process (*d*) that goes to the cuticular part of the organ, in the case of a hair organ either attaching to the hair base or to the hair membrane, or penetrating the cavity of the hair. The body of the sense cell and at least the base of its distal process are invested in a thin, nucleated membrane continuous with the neurilemma of the nerve. Lying beside the sense cell, or distal to it, and usually surrounding its distal process, is a second cell, which, on account of its relation to the base of the seta, is clearly the trichogenous cell (*HrCl*), though in the adult organ its protoplasm is often retracted from the hair and from beneath the hair base, leaving here a vacuole (*Vac*) containing the distal process (*d*) of the sense cell. The third cell (*MbCl*) is evidently the hair membrane cell, since its distal part embraces the end of the trichogene and terminates against the hair membrane, when the latter is present.

In many sense organs, the hair membrane cell and the trichogenous cell do not reach to the basement membrane, or the sense cell bulges into the body cavity and comes to lie proximal to the hair cell. The membrane cell, likewise, often lies distal to the body of the hair cell, and thus the three cells may come to be arranged serially along a radial axis, as shown at B of figure 13.

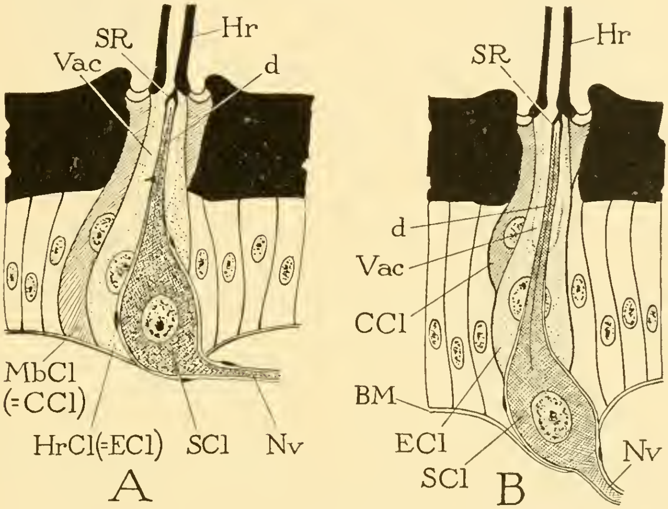

FIG. 13.—Diagrammatic structure of a hair sensillum.

A, showing the apparent origin of a sensillum from the hair membrane cell (*MbCl*), the trichogenous cell (*HrCl*), and a hypodermal sense cell (*SCl*). B, the three cells in axial arrangement, the membrane cell having become the cap cell (*CCl*) of a typical sensillum, and the trichogenous cell the enveloping cell (*ECl*).

A simple sensory complex, comprising the cuticular parts of the sense organ, the hypodermal elements, and the nerve, is known as a *sensillum.* The membrane cell of a sensillum is called the *distal enveloping cell,* or *cap cell* (fig. 13 B, *CCl*), and the trichogenous cell is distinguished as the *basal enveloping cell,* or simply the *enveloping cell* (*ECl*). In some sensilla the single sense cell is replaced by a group of sense cells (figs. 18, 24, *SCls*) ; and some sense organs are compound, each consisting of a group of simple sensilla.

The three cells of a sensillum appear to be partially telescoped one within the other. the neck of the sense cell being contained within the enveloping cell, and the distal part of the latter surrounded by the cap cell. Horizontal sections through some adult sense organs show clearly that each enveloping cell completely encircles the one within it (fig. 24 B, C); but we must believe that this condition is a secondary one brought about by an overlapping of one cell about the other, since all may retain their connections with the cuticula. Berlese (1909) has shown that the cells of a sensillum are entirely separate at an early stage of their development.

CLASSIFICATION OF INSECT SENSE ORGANS

Since so little is known definitely concerning the functions of the various kinds of sense organs possessed by insects, except in the case of the tactile hairs and the eyes, we cannot at present speak of them as organs of smell, organs of taste, organs of hearing, etc. We must therefore, classify them according to their structure. Departing from the typical hair type, the external parts of the sense organs become peg-like or conical; losing the hair form altogether, they are reduced to papillæ or low domes, or they are flattened out to plates or membranes. In still others there is no external part except a pit, a disc, or a nodule of chitin to which the internal parts are attached. In the organs of vision the external parts are simple transparent corneæ or lens-like thickenings of the cuticula.

Most of the sense organs of insects can be grouped, therefore, according to the form of the external cuticular part, though with some the internal structure must be taken into account. Hence, following in part the well-known classification of Schenk (1903), the various kinds of sense organs known in insects will be described in this paper under the headings of *hair organs, campaniform organs, plate organs, chordotonal organs*, the *organ of Johnston*, and the *eyes*. The hair organs include those in which the cuticular part is typically setiform (*sensilla trichodea*), bristle-like (*sensilla chætica*), scale-like (*sensilla squamiforma*), or peg-like or cone-like (*sensilla basiconica*). The campaniform organs include the various sense papillæ, domes and "pores." The plate organs (*sensilla placodea*) are those in which the external part has the form of a thin membranous or chitinous disc or plate. The chordotonal organs and organ of Johnston are internal structures consisting of groups of simple sensilla attached to the cuticula of the body wall. The eyes are the various light-perceiving organs.

THE SENSE CELL

The essential element in an insect sense organ is the sense cell with its nerve connection. The truth of this is attested by the fact that some invertebrate animals possess sense cells in the skin with no accessory structures. The common earthworm, for example, has specialized innervated cells in its hypodermis, which are regarded as being the receptive organs through which the creature receives a stimulus from light suddenly thrown upon its body. Insects are not known to have sense organs of so primitive a nature, though the photoreceptive tissue of eyeless Dipteran larvæ that respond to light has not been specifically determined. The chitinous parts of many insect sense organs, however, are reduced to mere points of the cuticula where the cellular elements are attached.

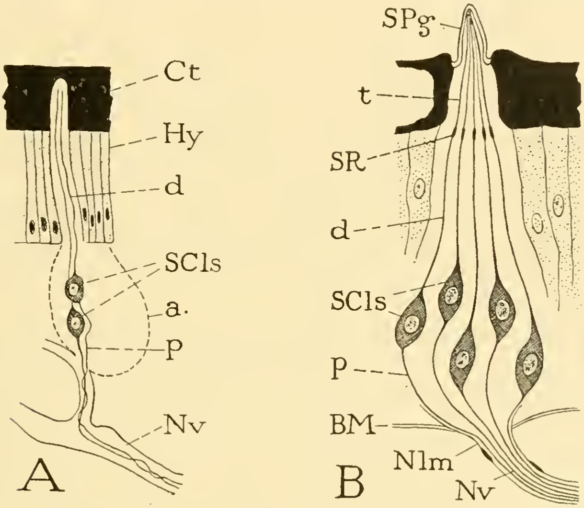

Fig. 14.—Showing the relation of the sense cells of a sensillum to the nerve and to the cuticular part of the sense organ.

A, two sense cells in an organ of the antenna of a wasp, stained by the Golgi method, each cell with a distal process (*d*) to the cuticular part of the organ, and a proximal process (*p*) continuous with a sensory nerve fiber (Vogel, 1923).

B, diagram of a sensillum containing a group of sense cells (*SCls*), the distal processes (*d*) ending in sense rods (*SR*) attached to cuticular part by terminal filaments (*t*), the proximal processes (*p*) continuous with nerve fibers.

The sensory cells in the sense organs of adult insects are probably in all cases specialized hypodermal cells; that this is the usual case, at least, has been amply proven by the observations of many investigators on the development of diverse types of sense organs. Whether the sensory nerve fiber, however, is a product of the sense cell, or the axon of a nerve cell located elsewhere, may be regarded as still an open question, though the evidence, presented in the last section of this paper, appears to favor the second possibility, at least in the case of the antennal sense organs of adult insects. Without conflict with either side of this question, it might be supposed that the primitive sensory apparatus of insects consisted of a specialized innervated hypodermal cell, as in the earthworms; but such a large number of the sense organs of insects suggest by their structure an origin from innervated hairs, that we must give serious consideration to the idea that the hollow cuticular seta was developed first, perhaps as a protective structure, and later became a sense organ through having the end of an innervated cell connected with its base. It, therefore, seems reasonable to suppose that the tactile hairs were the first specific sense organs to be acquired by insects, possibly excepting the eyes, and that from them were developed organs for perceiving chemical stimuli, sound stimuli, or whatever other stimuli are perceptible to insects. On any other basis, it is difficult to account for the uniformity of structure that runs through all types of insect sense organs except the eyes. The extent to which the hair structure can be traced in the various kinds of sense organs will be shown in the following sections of this paper.

The sense cell is, in most cases, easily distinguishable in the sensory complex by its large regular elliptical nucleus, which contains an abundance of chromatin, and by its oval or fusiform bipolar shape, drawn out at one end into the distal process, and continued at the other into a nerve. In many sense organs the sense cell is multiplied, there being from two to many cells (figs. 18, 24, *SCls*), the group sometimes being contained within the limits of the normal hypodermis, sometimes bulging or protruding from it into the body cavity; and sometimes the sense cells of neighboring sensilla form a continuous layer beneath the normal hypodermal cells (fig. 24). In all such cases, however, the sense cells are limited basally by the basement membrane of the body wall. Other sense organs consist of a bundle of sensilla in which there is an equal number of cap cells, enveloping cells, and sense cells.

The work of vom Rath (1896), Vogel (1923), and others appears to demonstrate that a nerve fiber extends into each sense cell from the connected sensory nerve trunk. Vogel says that in the antennal sensilla of wasps (*Polistes, Vespa*) an extremely fine fiber, less than half a micron in diameter, can be traced to the base of the sense cell in specimens stained by the Golgi method, and can be followed in the other direction into the nerve trunk of the organ, leaving thus no doubt of its being a nerve fiber. From the distal end of the sense cell, likewise a fiber somewhat thicker than the basal one can be traced outward to the cuticular part of the organ. Figure 14 A, taken from

Vogel, shows two stained cells of a sensory group with their proximal and distal processes clearly defined. The structure of a sense cell group might, therefore, be represented diagrammatically as at B of the same figure. The findings of those who have used differential staining methods do not substantiate the idea of Berlese (1909) that the nerve end invests the sense cell; but it appears likely that Berlese mistook for nerves the nucleated sheath which is continued over the sense cell and its distal process from the neurilemma of the nerve trunk.

THE RECEPTION OF SENSORY STIMULI

The question now arises whether the specific effect of the stimulus affecting a sense organ depends on the character of the external part, or on the nature of the sense cell itself. It is certain that the cuticular part of a sense organ must be adapted to receiving the specific stimulus to which the organ responds; the outer part of an eye, for example, must transmit light, and an auditory organ must receive sound waves. The receptive part of each sensillum must be so constructed that it will let in its particular class of stimuli and keep out all others. Chemical stimuli could not be supposed to penetrate a thick-walled structure, which, however, if loosely articulated, might respond to purely mechanical stimuli. On the other hand, an organ responsive to stimuli of taste and smell, a chemoreceptor, presupposes that the exposed part of the organ is somehow penetrable by odor or taste substances.

The earlier students of the sense organs of insects commonly assumed that those organs which they believed to be organs of smell and taste had perforations in their cuticular walls which allowed the substances to be perceived to come into direct contact with the ends of the sense cell processes. The presence of slits, pores, or openings of any kind in the outer covering of any insect sense organ, however, has been denied by all recent writers, except McIndoo (1914), and the major part of opinion now favors the idea that a chemoreceptive sense can be possessed only by those organs in which the cuticular walls are thin enough to be penetrated by substances of taste or smell or both.

That osmosis takes place readily through thin layers of the cuticula of insects has been demonstrated; and transudation must be assumed to take place in all glands derived from the ectoderm, the interior surfaces of which are covered by a delicate, imperforate cuticular intima. Eidmann (1922) has specifically shown that both acids and alkalies diffuse through the intestinal walls of the cockroach in from 10 to 15 minutes, though, with the thicker walls of the crop, the results of diffusion are not apparent until nearly 24 hours later. The cuticula of the crop is 5 to 8 microns in thickness, while that of the intestine is but 2 microns thick.

The cuticular walls of insect sense organs are in many cases extremely delicate, frequently not over half a micron in thickness, and in some cases so thin that sections of them do not show a double border under even the highest magnification. It is, therefore, not unreasonable to suppose that they are quickly permeable by substances in solution. Vogel (1923) has noted that the membranous cupola of a sensillum basiconicum of a wasp is colored by hematoxylin stain, and hence is permeable by it. We may believe, therefore, that sense organs in which the walls of the external part are at some point reduced to a thin membrane, half a micron or less in thickness, are organs capable of receiving chemical stimuli. If they are in fact chemoreceptors, then either they must be penetrated directly by odor or taste substances, or a liquid must exude from within them capable of absorbing such substances, thus providing the means of their transmission by osmosis to the ends of the sense cell processes.

The chief objection to the idea that a liquid exudes upon the surfaces of sense organs is the lack of any observations on the presence of such a liquid. Yet, the vacuole which surrounds the distal processes of the sense cells in many organs that have been regarded as chemoreceptive, suggests a possible source of a solvent liquid. Though Berlese's attempt to show that one of the elements of the insect sensillum is always a gland cell has not been generally accepted, it is not unreasonable to suppose that one of the cells might take on a secretive function in certain organs. The cell which contains the vacuole, when a vacuole is present (fig. 13 B, *Vac*), however, is the basal enveloping cell (*ECl*), which is the trichogenous cell (fig. 12, *HrCl*) and not a special gland cell.

What takes place within the sense organ when the latter is penetrated by the stimulating force or substance is entirely unknown, but it seems most probable that there must be produced some chemical change in the substance of the sense cell, which, in turn, acts upon the nerve and causes the latter to transmit a stimulus to the sensory center of the central nervous system. Perhaps every sense cell can be stimulated by a variety of stimuli, that which actually reaches it being normally determined by the nature of the external part of the organ; but the fact that in certain sense organs there is no specialized external part argues in favor of specificity even in the sense cells themselves.

THE SENSE RODS, OR SCOLOPALÆ

The sense cell of the sense organs of adult insects, being a transformed hypodermal cell, lies, during the formative stages, immediately beneath the cuticula. In the organs of vision the sense cells usually become separated from the cuticula during development either by invagination or by delamination; in the other organs the sense cells may retract inward, but they usually remain in connection with the cuticula by chitinous strands of varying length.

In the sensilla trichodea of the simpler types the distal process of the sense cell may remain attached directly to the inner surface of the cuticula of the hair membrane or the hair base (fig. 17 A, *d*). In most of the other sense organs of the hair, plate, campaniform, and chordotonal types, the end of the distal process of the sense cell is more or less withdrawn from the inner surface of the cuticula, but maintains its connection with the latter by means of a special cuticular structure known as the *sense rod,* or *scolopala* (the "Stift" or "Stiftkörperchen" of German writers).

The sense rod usually has the form of a hollow cone, peg, or fusiform rod attached by its apex to the inner surface of the cuticular part of the sense organ. The attachment to the latter may be either direct, or by means of a long filament drawn out from the apex of the rod.

The form and complexity of the sense rods vary much in different organs. In its simplest form, the rod is a mere cap, cone, or bulb *apparently* investing the end of the sense cell process. According to Hochreuther (1912) the sense rod in some of the tactile hairs of *Dytiscus* is a simple arrowhead-shaped peg, attached by its apex to the hair membrane or to the base of the hair. Sihler (1924) says there are two forms of sense rods in the sense organs of the cerci of *Gryllus campestris;* one form (fig. 15 A) has a pear-shaped head and a long cylindrical shaft, the other (B) ends in a club-shaped terminal enlargement. The walls of the rods of each form have ten longitudinal thickenings or ribs (*r, r*), which, however, are not continuous and their separated parts form two or three ribbed zones in the walls of the rods, the positions varying in different organs (A, B, *r, r*). The head of each rod contains a dark-staining *apical body* (*AB*) from which there is continued a fine *axial fiber* (*AxF*) into the body of the sense cell. In the campaniform organs of *Dytiscus marginalis,* Hochreuther (1912) describes a simple club-shaped rod (fig. 15 C) with an apical point inserted into the dome-like external part of the organ (*Do*). There is here no apical body within the rod and the axial fiber (*AxF*) is continuous to its tip. In the campaniform organs on the halteres of Diptera, according to Pflugstaedt (1912), there is a similar sense rod (fig. 15 D, *SR*) attached by a chitinous plate to the under surface of the dome (*Do*). The rod in these organs contains an elongate apical body (*AB*), which is evidently the same structure as that termed the "manubrium" by Janet (1904) in the campaniform organs of ants. Vogel (1911) describes sense rods in the campaniform organs of the wing bases in Lepidoptera, which apparently closely resemble those of the sense organs of the cerci in Orthoptera. Each rod, he says, has a pear-shaped head containing a dark-staining apical body to which is attached the end of an axial fiber from the sense cell, and the rod walls have about ten internal rib-like thickenings.

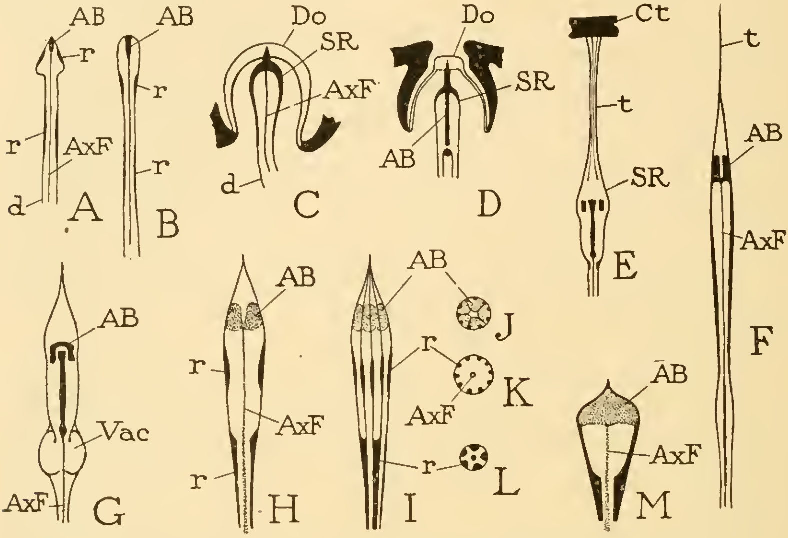

FIG. 15.—Various forms of sense rods, or scolopalæ, in different kinds of sense organs.

A, B, sense rods of tactile hairs of cerci of *Gryllus campestris* (Sihler, 1924). C, sense dome and rod of campaniform organ of *Dytiscus marginalus* (Hochreuther, 1912). D, dorsal scapel campaniform organ and sense rod of halter of *Syrphus* (Pflugstaedt, 1912). E, scolopala of halter of a fly (Pflugstaedt). F, scolopala from chordotonal organ of wing base of a Lepidopteran, *Cheimatobia* (Vogel, 1912). G, scolopala of chordotonal organ of halter of *Syrphus* (Pflugstaedt). H, optical longitudinal section of scolopala of tympanal chordotonal organ of *Acridium ægypticum* (Schwabe, 1906). I, same as H, surface view. J, cross-section through apical body (*AB*). K, cross-section through middle of scolopala. L, cross-section through basal part of scolopala. M, optical longitudinal section of scolopala of chordotonal crest in leg of *Decticus verrucivorus* (Schwabe, 1906).

The sense rods of the chordotonal organs have been carefully studied in many different insects. They are often specifically called *scolopalæ,* but there is no reason for distinguishing scolopalæ from sense rods in general, or for limiting the term to the chordotonal rods. The scolopalæ of one of the chordotonal organs in the base of the halter of Diptera are described by Pflugstaedt (1912) as attached to the cuticula, each by a long terminal fiber (fig. 15 E, *t*) formed by a continuation of the ribs of the scolopala walls. Vogel (1912) finds each rod in the chordotonal organs of the wing bases in Lepidoptera likewise attached to the cuticula by a long terminal filament (fig. 15 F, *t*). In some chordotonal organs there is a vacuole in the sense cell process at the base of the scolopala (fig. 15 G, *Vac*), which is traversed by the axial fiber (*AxF*). This vacuole should not be confused with the vacuole of the basal enveloping cell, which contains the distal process of the sense cell.

The structure of the sense rods in the tympanal chordotonal organs of Orthoptera has been particularly studied by Schwabe (1906). Each scolopala of the sensory body attached to the inner surface of a grasshopper's "ear" (fig. 27 B, *SB*) is a minute hollow rod, about 23 microns in length, fusiform, pointed at the distal end, slightly tapering proximally (fig. 15 H, I). Stained specimens, examined under high magnification, show that the walls of the rod are marked by longitudinal ribs (*r*) formed by thickenings on the inner surface (J, K, L). On the distal two-thirds of the scolopala there are ten ribs, each enlarged at its middle; but proximally the ribs unite in pairs, forming five thicker ridges on the basal third of the rod. The head of the scolopala is occupied by a dark-staining apical body (H, I, J, *AB*) to which is attached the end of the axial fiber (H, *AxF*) from the sense cell. In the rods of the chordotonal organs of Cerambycid larvæ, Hess (1917) finds seven ribs on the basal part that fork to form 14 on the distal part. Vogel (1923 *a*) says that the ribs of the chordotonal rods of the cicada appear to be on the external surfaces of the rods.

In the chordotonal organs, the sense rods are usually some distance removed from the cuticula, being situated in the outer end of the enveloping cell or partially in the base of the elongate cap cell (fig. 26, *SR*). They are usually connected with the cuticula, as we have seen (fig. 15 E, F), by a long terminal filament (*t*) traversing the cap cell, but in some cases the connection appears to be lost. Thus, as noted by Schwabe (1906) in the tympanal organs of the Orthoptera, and by Hess (1917) in the chordotonal organs of Cerambycid larvæ, the terminal fiber, if present, is continued from the apex of the rod only a fourth or a third of the length of the cap cell. Usually, in the tympanal organs of the Orthoptera, according to Schwabe, there is no terminal filament.

In the sensilla of the sensory pegs, cones, plates, and some of the smaller thin-walled hairs, in each of which there is a group of sense cells (figs. 18, 24, *SCls*) with their terminal processes bound together in a bundle or fasciculus (*Fas*), the minute sense rods (*SRs*) are also removed a considerable distance from the cuticula. They are attached to the latter by a long terminal strand (*TS*) composed apparently of the individual terminal filaments (fig. 14 B, *t*) of the sense rods (*SR*).

From a review of the descriptions of the sense rods in the various insect sense organs given by recent investigators, we may conclude that all the rod-like structures are homologous organs. Most investigators believe that the rods are differentiations of the ends of the sense cell processes, and this idea appears to be substantiated by all the known facts bearing on their nature. The appearance and staining properties of the rods suggest that they are weakly chitinous. Vogel says that the scolopalæ of the chordotonal organs in the wing bases of Lepidoptera have the same optical qualities as other thin chitin, and that the inner walls and the ribs stain in eosin and hematoxylin, just as does the inner part of the chitin of hairs and of the body wall. The recent observation by Sihler (1924), however, that the sense rods in immature Orthopteran insects *are shed during a molt* is a most important addition to our knowledge of these heretofore puzzling structures, and, if correct, fixes their status by showing conclusively that they are not only of a cuticular nature, but that they belong to the cuticula of the body wall. Sihler bases his claim of the molting of the sense rods on observations on the sense rods of the tactile hairs of the cerci of an Acridian, *Gomphocerus rufus*. He says that when the exuviæ are separated from the cuticula during a molt, there is usually to be seen attached to the base of each hair of the exuviæ a tubular appendage in which are distinguishable both the head and the ribs of the sense rod as observed in specimens prior to molting (fig. 15, A, B).

If, then, we are to regard the sense rod, or scolopala, as a chitinous product of the end of the sense cell, we must next consider how it may be formed. Sihler and most other recent writers regard the rod as a cuticular sheath (fig. 16 A, *SR*) covering the end of the distal process (*d*) of the sense cell, and attached by its apex either directly, or by means of a terminal stalk or filament, to the cuticula of the body wall. However, from a study of other internal chitinous structures, we are not warranted in assuming that a cuticular process ever grows inward except as an ingrowth from the exterior surrounded by a hypodermal matrix. A muscle "tendon" serves as a good example of a structure produced in this way. As shown by Janet (1907), the long tendon-like stalk to which some insect muscles are attached is produced from a single hypodermal cell. The tendon cell (fig. 16 C, *TndCl*) elongates and its interior secretes a chitinous continuation (*Tnd*) from the outlying cuticula (*Ct*), which finally (B) occupies the entire length of the mature tendon cell and forms at its inner end a funnel-shaped cup holding the end of the muscle (*Mcl*). The tendon is probably to be regarded, theoretically, as a hollow ingrowth of the cuticula, corresponding structurally with the duct of a one-celled gland (fig. 16 E, *Dct*). The important feature to be noted in both these structures, however, is that the hypodermal matrix *surrounds* the cuticular ingrowth.

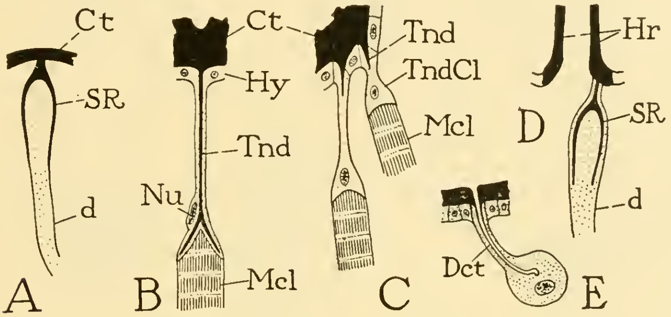

FIG. 16.—Theoretical suggestions of the morphology of the sense rod.

A, sense rod (*SR*) of a campaniform organ of *Dytiscus*, as illustrated by Hochreuther (1912), attached to cuticular part of organ (*Ct*) and ensheathing the end of distal process (*d*) of a sense cell. B, structure of a muscle tendon as illustrated by Janet (1907), the tendon (*Tnd*) is an *intracellular* product continuous with the cuticula (*Ct*). C, early stages in formation of muscle tendons (Janet). D, theoretical relation of a sense rod (*SR*) to distal process (*d*) of a sense cell suggested by comparison with a muscle tendon (B). E, a one-celled gland with intracellular duct.

Applying this principle of the known method of growth of internal cuticular organs to the sense rods, we must suspect that each rod is formed within the distal end of the sense cell process, as shown diagrammatically at D of figure 16, rather than on the outer surface of the process. If produced in the second manner, the rod could not be renewed after a molt and reëstablish its connection with the outer cuticula, especially where the end of the sense cell is retracted from the latter. The parts in question are so minute that the actual facts of construction cannot often be observed. Schwabe (1906) is the only writer who has said definitely that the sense rods lie within the distal part of the sense cell process, though Erhardt (1916) gives figures of the chordotonal organs from the wing base of *Eristalis floreus* in which the scolopalæ are shown distinctly inside the long distal processes of the sense cells.

Eggers (1923) would explain the scolopalæ of the chordotonal organs and of the organ of Johnston as originating from a fibrous differentiation of the terminal part of the sense cell process, a condition which he finds in the sense cells of the primitive organ of Johnston in the antenna of a dragonfly larva. The distal parts of the fibers, Eggers suggests, come together to form the terminal filament of the scolopala, while their proximal parts fuse to form the ribbed walls of the scolopala itself. This explanation, however, leaves us to assume that the fibers are chitinizations of the lateral walls of the sense cell, and, therefore, meets with the same objection above noted, viz., that it violates the rule of similar internal chitinizations being formed otherwise than as a surface deposit, or as a prolongation of the surface deposit within the body of a cell.

THE AXIAL FIBER

An axial fiber (fig. 15 A, C, F, H, and fig. 26, *AxF*) has been observed in all the different groups of insect sense organs, though it has not been shown to exist in every organ. When present, it traverses the distal process of the sense cell from the body of the cell to the sense rod (fig. 26). Its distal end terminates in the apical body (fig. 15 H, *AB*), when the latter is present, or continues to the end of the rod (C) when an apical body is lacking. Proximally, the fiber is usually lost in the body of the sense cell, but Hess (1917) says, in the chordotonal organs of Cerambycid larvæ, it can be traced through the sense cell into the nerve, and Schwabe (1906) claims that it separates within the sense cell into fine fibrils which unite again into a single fiber entering the nerve.

The nature of the axial fiber has not been determined. Some investigators believe that it is the end of the true nerve fiber of the sensillum; others claim that it is of a chitinous texture, though Sihler observes that it is not cast off with the molted rod during ecdysis.

IV. THE HAIR ORGANS

All sense organs in which the cuticular part has the structure of a hair, whether setiform, bristle-like, club-shaped, scale-shaped, cone-shaped, or peg-like, and whether exposed on the surface or sunken into a pit or deeper cavity of the cuticula, may be grouped together as the hair sense organs, since the cuticular part in each is clearly a modified seta. Under this heading we can distinguish *sensilla trichodea* (sense setæ), *sensilla chætica* (sense bristles), *sensilla squamiforma* (sense scales), *sensilla basiconica* (sense cones and pegs), *sensilla cœloconica* (sense pits), *sensilla ampullacea* (sense flasks).

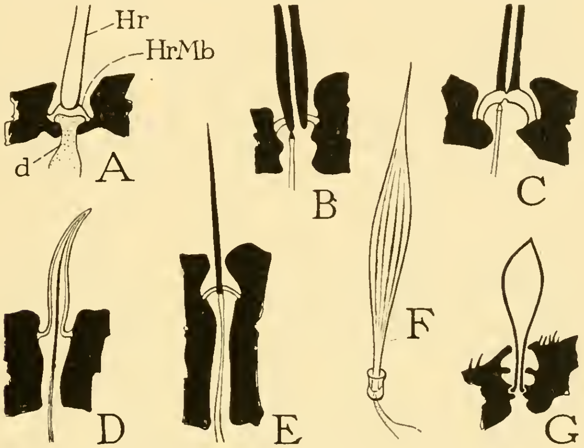

FIG. 17.—Sensory hairs of various forms, and a sensory scale.

A, hair sense organ with distal process of sense cell (*d*) attached directly to articular membrane (adapted from Hochreuther, 1912, sensory hair of *Dytiscus*). B, distal process attached by sense rod to base of hair in sense organ of labium of *Dytiscus* (Hochreuther). C, sense hair with imperforate articular membrane on mandible of *Dytiscus* (Hochreuther). D, thin-walled sensory hair with terminal strand of sense cell processes attached in tip. E, a solid sensory spine on pharyngeal plate of *Dytiscus* (Hochreuther). F, a sensory scale of wing of *Notris verbascella* (Freiling, 1909). G, club-shaped sensory hair of cercus of *Gryllotalpa vulgaris* (Sihler, 1924).

SENSILLA TRICHODEA

The sensitized hair is clearly the most primitive of insect sense organs, excepting possibly those eyes of certain Dipteran larvæ that consist of little else than sensitive hypodermal cells. A sensory hair of the trichodea variety is typically setiform, but there is much variation in length and especially in the thickness and density of the hair walls. The longer, stiffer sensory hairs are probably all organs of touch; they are known as *tactile hairs*. Short hairs with thin transparent walls are usually regarded as organs for receiving stimuli of smell and taste; they are distinguished as *chemoreceptive* hairs.

Tactile hairs are common in all the major groups of the Arthropoda; in insects they occur on most parts of the body and appendages, and in the anterior region of the alimentary canal. The movement of the hair may be supposed to register a more gentle tactile stimulus than would the effect of pressure on the general body surface, especially where the latter is covered by a coating of dense chitin. By means of the sensitive hairs, moreover, the insect can become aware of the approach or nearness of an external object before coming into actual contact with it.

The sensillum of a tactile hair contains usually but one sense cell (fig. 13 B, *SCl*), though some are described and figured as having two or several sense cells. The distal process of the sense cell is attached to the hair membrane or to the base of the hair itself, or perhaps within the cavity of the hair. The attachment may be direct (fig. 17 A), but it is usually by means of a terminal sense rod (B). Some tactile hairs appear to be closed at the base by an imperforate membrane (C).

The supposedly chemoreceptive hairs are short and weakly chitinized, having thin, transparent walls. Each is innervated through a group of sense cells, the terminal strand from which penetrates the cavity of the hair to its tip (fig. 17 D). The sensillum of a chemoreceptive hair, therefore, is identical with that of a chemoreceptive peg (fig. 18) except for the length and shape of the cuticular part. Chemoreceptive hairs are found particularly on the antennæ and the mouth parts.

SENSILLA CHÆTICA

The sense organs classed under this head are separated from the tactile hairs of the trichodea type only by the more spine-like or bristle-like character of the external parts, but the distinction is artificial and unnecessary since the setal organs vary in shape from slender hairs to thick clubs (fig. 17 G). The sensory spines and bristles are usually thick-walled and densely chitinous; some are said to be solid structures (fig. 17 E). Probably most of them are organs of touch.

The organs along the sides of the abdomen in the Nepidæ, consisting of small cavities with a fringe of movable, innervated spines within the respiratory chambers of the young, and of plates associated with the abdominal spiracles covered with a mat of recumbent spines in the adult, probably offer an example of a special use of a tactile spine. These organs have been elaborately described by Baunacke (1912), who believes that they are static in function. Their spines lie horizontally in the plane separating the air in the air space beneath them from surrounding water, and Baunacke, pointing out that a tilting of the body in any direction would alter the plane of the spines, argues that this motion would register the position of the insect in the water.

SENSILLA SQUAMIFORMA

Since scales are but modified hairs, it is not surprising to find that some of them should be innervated in the same manner as the tactile hairs. Sense scales have been described on the wings of Lepidoptera by Guenther (1901), Freiling (1909), and Vogel (1911). Vogel says that innervated scales are found on the wings of all Lepidoptera, even in primitive forms like *Hepialis*. They occur on both sides of the wings, mostly on the veins, and especially on the marginal veins, but they may be present also on the basal parts of the wings wherever there is an internal space sufficiently large to allow a nerve to penetrate.

The sense scales are elongate fusiform in shape, with fewer ribs than the other scales, and each has the distal part drawn out into a long, tapering point (fig. 17 F). The spaces between the internal ridges of a sense scale, Freiling says, are so reduced that the scale is almost a solid structure. Each sensory scale is innervated through a single large sense cell, the distal process of which, according to Vogel, ends in a cone-shaped sense rod attached to the base of the scale. The sense scales are evidently tactile in function.

SENSILLA BASICONICA

Sensory pegs and cones are undoubtedly to be regarded as hairs reduced in size, and there is no sharply dividing line between sensilla trichodea and sensilla basiconica. The character of the external parts and the structure of the internal parts of the peg sensilla, likewise separate these organs into two groups, there being thick-walled or even solid pegs innervated each through a single sense cell, and thin-walled pegs innervated each through a group of sense cells. The former are regarded as receptive to mechanical stimuli, the latter to chemical influences.

Sense pegs and cones have been described on all parts of the body and appendages of various insects, on the epipharynx and hypopharynx, and in the pharyngeal cavity. Many of them are clearly but short hairs of the tactile kind, but the typical pegs, occuring particularly on the antennæ and the mouth parts, are of the chemoreceptive variety. In these the walls of the peg or cone are thin and transparent (fig. 18, *Pg*), some terminating in a membranous cap. The sensillum comprises a large cap cell (*CCl*), a vacuolated enveloping cell (*ECl*), and a compact group of sense cells (*SCls*). The distal processes from the latter form a cylindrical bundle (*Fas*) traversing the vacuole (*Vac*) of the enveloping cell, and attached by a terminal strand (*TS*) in the apex of the peg. In the Hymenoptera, at least, the terminal strand consists apparently of the terminal fibers of the minute sense rods (*SRs*), which latter are here far removed from the external surface.

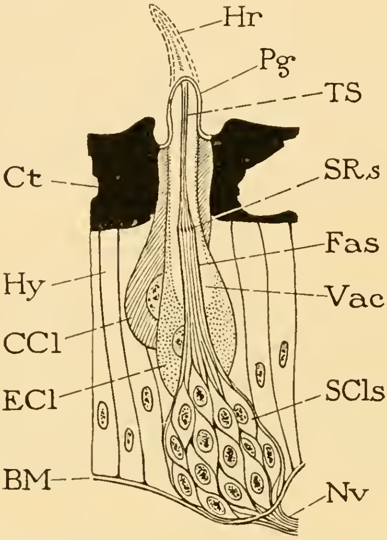

Fig. 18.—Diagrammatic structure of the sensillum of a thin-walled peg (*Pg*) or hair (*Hr*) supposed to be receptive to chemical stimuli.

The distal processes of the sense cells (*SCls*) form a compact fasciculus (*Fas*) ending in a terminal strand (*TS*) of cuticular fibers from the sense rods (*SRs*), attached within tip of external cuticular part; enveloping cell (*ECl*) with vacuole (*Vac*) containing fasciculus and terminal strand.

SENSILLA CŒLOCONICA

Sense organs of this type are simply sensory pegs sunken into shallow cavities of the cuticula (fig. 19 A, B), and again, as with the hairs and exposed pegs, some are thick-walled or solid and innervated each through a single sense cell, while others are thin-walled and innervated each through a group of sense cells. It becomes evident, that a truer classification of both hair and peg sense organs, and one probably more coincident with their function, might be based on the internal structure of the sensillum rather than on the form of the external part, if the state of our knowledge would permit.

Besides the simple pit organs, each with a single peg, there are pits containing each a number of pegs. Organs of this kind occur on the antennæ of some Diptera; those of the housefly are described by Röhler (1906). Some of the cavities contain a single group of from 10 to 20 pegs; others are compound, the cavities being divided into shallow compartments, each with its group of pegs. These organs were called "otocysts" by Graber, but Röhler regards them as olfactory in function. The labial palpus of the cabbage butterfly (*Pieris*) also has at the tip a deep cavity containing many sense pegs.

SENSILLA AMPULLACEA

This term is given to sense organs of the sunken peg type in which the cuticular cavity is deeper and more flask-like (fig. 19 C) than in the typical sensilla cœloconica. In some, the "flask" is far removed from the surface and is connected with the outer cuticula by a long, tubular neck (D). Organs of this kind are known as Forel's flasks. Sensilla ampullacea are particularly characteristic of the antennæ of Hymenoptera. They are usually regarded as organs of smell.

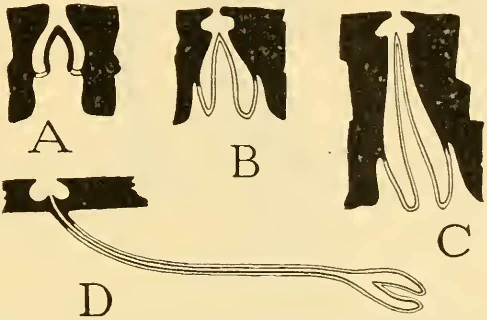

FIG. 19.—The cuticular parts of several varieties of sensilla cœloconica (A, B) and ampullacea (C, D).

A, simple pit peg with thick chitinous walls. B, thin-walled peg more deeply sunken into cuticular cavity. C, a flask-shaped organ. D, a Forel's flask with long tubular neck.

V. THE CAMPANIFORM ORGANS

The sense organs grouped in this class are clearly related to one another structurally. They are all, however, of such simple form and yet vary so much in shape, that they present no feature on which a descriptive or a distinctive name can be based. They have been called *vesicles, organs of Hicks, papillæ, cupola organs, dome organs, umbrella organs, bell organs,* and *sense "pores."* Since the external part commonly has the shape of a thin-walled dome or bell, or suggests that it has been derived from such a form, the name *campani-*

form organs, as used in a general sense by Berlese (1909), is here selected for euphony and because in descriptive value it is equal to any of the others.

The external parts of the campaniform organs are, in most cases, small, rounded, dome-like papillæ or but slightly convex swellings, usually less than 25 microns in diameter; but sometimes they are reduced to minute discs, slightly sunken in the outer surface of the body wall, having the appearance of hair follicles from which the hairs have been removed, though they are usually distinguishable from the circular hair sockets by a more elliptical or oval form.

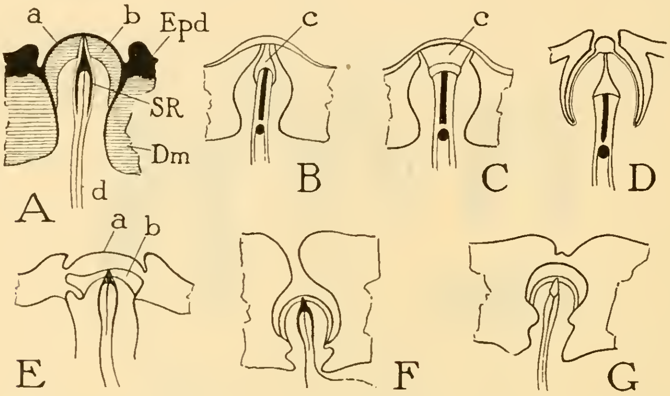

FIG. 20.—Various types of campaniform organs, vertical sections through cuticular parts and ends of sense cell processes with sense rods.

A, Diagrammatic structure of a typical organ: *a,* outer lamella of dome; *b,* inner lamella, the cone or cushion; *d,* distal process of sense cell with axial fiber ending in the sense rod (*SR*).

B, organ from base of halter of *Calliphora* (Pflugstaedt, 1912): *c,* attachment plate of sense cell process. C, longitudinal section of same. D, dorsal scapal organ of halter of *Syrphus* (Pflugstaedt). E, from cercus of *Periplaneta americana* (Sihler, 1924). F, sunken organ on labium of *Dytiscus* (Hochreuther, 1912). G, sunken organ with no apparent external opening, on mandible of *Dytiscus* (Hochreuther).

The dome or disc in typical examples usually consists of a thin, outer, imperforate lamella of dense chitin (fig. 20 A, *a*), and of an inner layer of clear softer chitin (*b*). These two parts probably belong to the epidermal and dermal layers, respectively, of the body wall cuticula (*Epd* and *Dm*). In stained specimens the appearance is sometimes reversed because the softer inner layer, according to most writers, colors more darkly in ordinary staining reagents. The inner layer is the *cushion* (*Polstermasse*) of German writers, the *cone* of McIndoo (1914). Usually it has the form of a cone or an inverted cup or saucer beneath the outer lamella. In many campaniform organs the cone is not present, or at least has not been distinguished by those who have described and figured the organs. When present, it 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 cone is the usual canal in the cuticula, which does not differ from that of the sensory hairs.

The innervation of the campaniform organs is always through a single sense cell (fig. 21, *SCl*). The sense cell is usually large, oval or fusiform; it lies within the hypodermis but may project below the general level of the basement membrane. In some organs the distal process (*d*) appears to end directly on the inner surface of the outer lamella of the dome, but in most of them there is a typical sense rod (*SR*) at the end of the process.

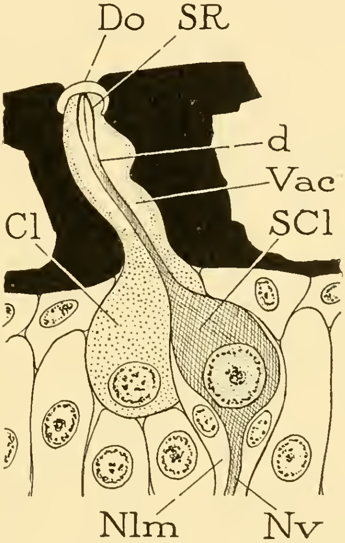

FIG. 21.—Structure of a campaniform sensillum (diagrammatic from Sihler, 1924, organ on cercus of *Periplaneta orientalis*).

Cuticular canal beneath dome occupied by a single cell (*Cl*), apparently the trichogenous cell (fig. 13 B, *ECl*); no cap cell (membrane cell) shown in this organ.

The other cells of the campaniform sensillum have not been definitely identified with those of the hair-bearing sensilla. Erhardt (1916) notes the presence of enveloping cells associated with the sense cell in the campaniform organs of the wing basis of *Chrysopa*. Vogel (1911) finds two enveloping cells in the organs of the wing bases of Lepidoptera, but he says their boundaries are not distinct.

Pflugstaedt (1912) describes and figures a large cell beneath the dome of each organ on the halteres of Diptera; and Sihler (1924) says that the sense cell of the cercal campaniform organs of Orthoptera is always accompanied by a dome-forming cell. The "dome cell" (fig. 21, *Cl*) in its relation to the dome (*Do*) of a campaniform organ corresponds closely with the cap cell of a sensillum placodeum (fig. 24 A, *CCl*) in its relation to the plate (*Pl*); but the two sets of organs are only superficially similar, and the campaniform dome cell, as figured by Sihler in the cockroach (fig. 21, *Cl*), suggests the enveloping, or trichogenous, cell of a hair sensillum (fig. 13 B, *ECl*). The single large cell in the sense organs of the rectum of Lamellicorn beetle larvæ (fig. 22, *Cl*), which appear to be organs of the campaniform type, is described by Orlov (1924) as a gland cell. The question, therefore, as to whether the dome of a campaniform organ represents the reduced hair or the hair membrane of a sensillum trichodeum must be regarded, for the present, as an unsettled one.

It is to be noted that the campaniform organs, having each a single sense cell, fall structurally in the class of the tactile organs of the hair and peg varieties.

The campaniform organs are known to occur on the head, thorax, abdomen, the antennæ, mouth parts, legs, wing bases, cerci and sting of various adult insects in all the principal orders, and they have been found on the larvæ of some species. Their external structure was first described by Hicks (1857, 1859) who called them simply "vesicles." Since then, both the external and the internal structure of the organs, described under various names, have been more closely studied by many other investigators. The distribution of the organs over the various parts of the body and appendages of insects in all the principal orders has been described extensively by McIndoo (1914-1920). The structure of the organs of the wing bases has been particularly studied by Guenther (1901), Freiling (1909), and Erhardt (1916); those of the halteres of Diptera, by Hicks (1857, 1859), Weinland (1891), Pflugstaedt (1912), and McIndoo (1918). Hochreuther (1912) describes the organs on the head, antennæ, mouth parts, and legs of *Dytiscus marginalis,* and Lehr (1914) those on the wing bases of the same species. Sihler (1924) gives an account of the campaniform organs on the cerci of Orthoptera. Janet (1904) describes the organs of ants, and McIndoo (1914) and Trojan (1922) record their presence on the sting of the honeybee.

The shape of the campaniform dome varies in different organs. It may be strongly convex and evenly rounded (fig. 20 A), or its midline may be elevated to form an axial ridge (D); it may again be more or less flattened (B, C, E), or reduced to a minute disc. Its walls may be thick and densely chitinous, membranous, or so thin as to be scarcely perceptible. The dome is sometimes freely exposed on the surface of the body cuticula, but it is often protected by chitinous outgrowths about it (A, E), or by being itself sunken into the cuticula (D, F, G). In the sunken type, the cavity containing the dome may open directly on the surface (D), or by means of a tubular canal (F), while sometimes it appears to be entirely closed (G). In the last case, however, as admitted by both Janet (1904) and Hochreuther (1912), a pore to the exterior might be present, though escaping detection in sections.

The simplest of the campaniform organs are those in which the external part is reduced to a minute circular oval disc, which may be situated at the surface of the body cuticula or sunken into a pit. Those located at the surface or in shallow depressions of the body wall are common on the wing bases, legs, and other parts of many insects. They have been described particularly by McIndoo under the name of " olfactory organs " or " olfactory pores." Simple organs of the sunken variety are described by Erhardt (1916) on the wing bases of dragonflies, each consisting of a delicate, imperforate membrane spanning the floor of a cuticular pit. The cuticular canal beneath the membrane contains the end process of a sense cell and the distal part of an enveloping cell.

Finally, there should be mentioned here the organs found by Orlov (1924) in the posterior part of the alimentary canal of the Lamellicorn larva, *Oryctes*, since these organs apparently belong to the campaniform group. Each consists, according to Orlov, of a delicate, circular chitinous membrane (fig. 22, *a*) which may be slightly convex or concave. Beneath the membrane is a large cell (*Cl*), which Orlov regards as a gland cell, and, beside this, a bipolar sense cell (*SCl*), the distal process of which goes to the center of the membrane. These organs, Orlov says, are similar in structure to sense organs distributed over the body in *Melolontha* larvæ. Other beetle larvæ possess campaniform organs of the more usual type. McIndoo (1918 *a*) describes simple campaniform organs (" olfactory pores ") distributed over the head, antennæ, mouth parts, thorax, and legs of the larva of *Allorhina* (Scarabæidæ), and compound organs on the terminal segments of the antennæ. The compound organs consist of groups of several hundred simple organs situated in thin oval areas, or plates, of the antennal walls.

The function of the campaniform organs is still a subject of speculation. Some writers have suggested that the organs respond to vibratory stimuli, or that they register air pressure. Experiments made by McIndoo (1914) and others appear to indicate that insects are responsive, in a certain degree, to odors by organs other than those of the antennæ, and it is most reasonable to suppose that these organs are the widely spread campaniform organs. McIndoo's claim, however, that the outer membrane of the small disc-like organs is perforated, and allows the distal end of the sense cell process to come into direct contact with the air, has not been verified. All other recent students of the campaniform organs, including Freiling, Vogel, Pflugstaedt, Erhardt, Sihler, state that the outer membrane or the outer lamella of the dome is never traversed by a pore or other opening. The closing membrane, though, may be very thin; Vogel says that the outer lamella of the organs of the wing bases of Lepidoptera is only from 8/10 to 1 micron in thickness. Such organs might be chemoreceptors; but, as already noted, chemoreceptive organs in general are innervated through a group of sense cells, while all campaniform organs have a single sense cell, a feature characteristic of sense organs responding to mechanical stimuli. The outer part of many of the campaniform organs, on the other hand, is so thick as to preclude any idea of a chemical sense in connection with them.

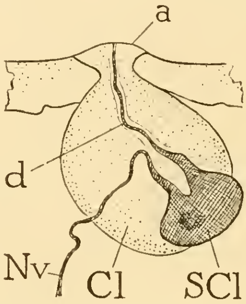

FIG. 22.—A rectal sense organ of larva of *Oryctes* (Orlov, 1924), apparently a simple organ of campaniform type.

a, outer membranous disc; *Cl,* cell beneath disc; *d,* distal process of sense cell (*SCl*); *Nv,* nerve fiber.

VI. THE PLATE ORGANS

The sense organs known as the sensilla placodea, in their typical form, consist of thin chitinous plates, elongate, elliptical, or oval in outline, set over large cavities or pores in the cuticula. They were, therefore, designated "pore plates" by Leydig (1860) and they have since commonly been known by this rather ambiguous name.

The plates of the sensilla placodea often resemble the domes of the sensilla campaniforma (Cf. figs. 23 B, I and 20 E, D), and the plate organs might be supposed to represent an evolutionary stage beyond the campaniform organs in which the dome has been finally flattened to a chitinous plate. A comparison of the internal structure of the two sets of organs (figs. 21 and 24), however, shows that they belong to different series. In each sensillum placodeum there is a group of sense cells (fig. 24, *SCls*), and also a cap cell (*CCl*) and enveloping cell (*ECl*) of typical form and relation to each other and to the sense cells. The external plate (*Pl*), moreover, lies over the cap cell, or hair membrane cell, and is, therefore, evidently the chitinized hair membrane rather than the base of the hair. The plate organs, hence, belong structurally to the chemoreceptive series, while the campaniform organs belong to the tactile series. The campaniform dome is probably the reduced hair; the plate appears to be the chitinized hair membrane. These statements are, of course, tentative and must be tested by a further study of the histology of the organs in question.

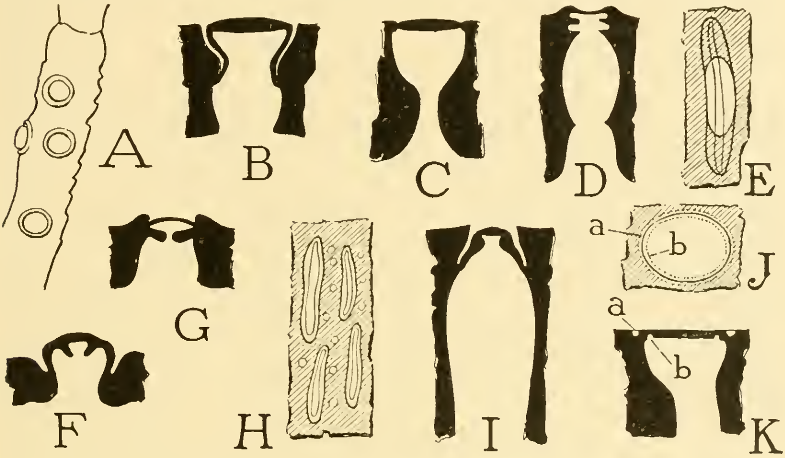

Fig. 23.—Cuticular parts of sensilla placodea in surface view and in section.

A, discs near end of third segment of antenna of grain aphis. B, section of plate on antenna of *Dytiscus* (Hochreuther, 1912). C, same from *Cetonia aurata* (vom Rath, 1888). D, same from *Necrophorus vespillo*. (Ruland, 1888). E, surface view of antennal plate of *Ophion luteus* (Ruland). F, section of antennal plate of *Cynips gallæ tinctoriæ* (Ruland). G, section of antennal plate of *Ophion luteus* (Ruland). H, surface view of antennal plates of *Vespa crabro* (Ruland). I, transverse section of one of same. J, surface view of antennal plate of *Apis mellifera*. K, longitudinal section of same: *a*, outer ring of light chitin; *b*, inner groove.

Plate-like sense organs occur on the antennæ of aphids, Coleoptera, and Hymenoptera, and have been described on the mandibles and the maxillary palpi of *Dytiscus.* They have not been studied with equal care in each of these three groups of insects, and it is possible they are not all homologous structures.

The organs on the antennæ of aphids consist externally of elliptical, oval, or sometimes elongate membranous discs (fig. 23 A). Those present on the insect at hatching are said to persist through all the molts to the mature insect, including both asexual and sexual forms; others appear at the last molt, especially on the winged forms, and are organs of the mature insect only. The internal structure of the organs in the aphids has been but little studied. Flögel (1905) gives a crude figure of a section through one of the discs of *Aphis ribis,* beneath which he shows a mass of sense cells with their distal processes spread over the entire under surface of the membrane. Externally, he says, the membrane is surrounded by a groove, which in turn is encircled by a chitinous ridge. The membrane itself is from 1 to 1-1/2 microns in thickness, the surrounding chitin being 7 microns thick, from which Flögel argues that the membrane is capable of being traversed by a liquid that could absorb odor substances. He believes, therefore, that the antennal organs in aphids have an olfactory function. Organs of a similar external appearance occur also on the legs and wing bases of aphids (Baker, 1917), but it is not certain that the latter are not campaniform organs.

Plate organs have been noted and described in several species of Coleoptera. Vom Rath (1888) says that the antennal lamellæ of *Cetonia aurata* are thickly beset with them ("membrane canals"), and he gives the form of the cuticular parts of one in section as shown at C of figure 23. Ruland (1888) records plate organs on the antennæ of *Necrophorus vespillo,* and figures the chitinous parts as shown at D. Hochreuther (1912) describes plate organs on the antennæ, mandibles, and maxillary palpi of *Dytiscus marginalis* under the name of "chalice-form organs," the term referring to the shape of the cuticular canal beneath the plate in vertical sections (fig. 23 B, C). He says that the plates in *Dytiscus* are extremely small, being from 6 to 8 microns in diameter, and that those of the antennæ number from 4,500 to 5,000. They have the same essential structure (B) as those of the antennæ of Hymenoptera (I, K) except that the margin of each is deeply inflected. The histological elements of the plate sensilla of the Coleoptera have not been well distinguished, though each is innervated through a group of sense cells.

It is in the Hymenoptera that the sensilla placodea are best known and, apparently, best developed. They have been found only on the antennæ in this order. In *Cynips* and *Ophion*, according to Ruland (1888), the plates are greatly elongate in form (fig. 23 E). The outer surface in *Cynips* is slightly elevated above the general surface of the antenna and is surrounded by a deep groove; the under surface presents two longitudinal ridges (F). In *Ophion* (G) the plate is a thin, arched, chitinous membrane, beneath which project two ridges from the walls of the cuticular canal, leaving only an axial slit open between them. In *Vespa crabro* the plates are also elongate and narrow (H), and each is surrounded by a deep furrow, as shown well in a cross-section (I).

In the honeybee the plate organs are closely distributed over the entire inner and ventral surfaces and on the dorsal surface of the distal half of the last eight segments of the flagellum of each antenna. There are about 30,000 on both antennæ of the drone, 5,000 to 6,000 in the worker, and 2,000 to 3,000 in the queen. In the Vespidæ, solitary bees, and bumblebees, according to Schenk (1903), the plate organs are but little more numerous in the males than in the females. Each plate, in the honeybee, is elliptical in shape (fig. 23 J) and from 12 to 14 microns in longest diameter, which is lengthwise on the antenna. The surfaces of the plates are flush with the antennal wall, but each plate is surrounded by a line of clear chitin (*a*) which may be marked by a slight groove in some cases, but is certainly not excavated to form a deep furrow around the plate, as indicated in figures by Ruland (1888), Schenk (1903), and McIndoo (1922). Within the margin of the plate is a second concentric light line (*b*), due to a submarginal groove on the inner surface (K, *b*). The cuticular canal beneath the plate is large but contracted proximally (K), its wall nearest the base of the antenna being approximately vertical while the other slopes inward toward the antennal base.

The inner structure of a plate sensillum in the Hymenoptera is similar to that of the pegs and the thin-walled hairs of the chemoreceptive series (fig. 18). In a plate organ of the honeybee (fig. 24 A) most of the space in the cuticular cavity beneath the plate is occupied by a large cap cell (*CCl*) which projects below the inner surface of the cuticula. On the side toward the base of the antenna the cap cell is perforated by a tubular canal which contains the distal parts of the enveloping cell (A, B, *ECl*) and the terminal strand (*TS*) of the sense cells. The strand expands proximally into the compact, cylindrical bundle or fasciculus (*Fas*) of sense cell processes, which lies in a vacuole (*Vac*) within the enveloping cell. Cross-sections show that there is probably only one enveloping cell to each sensillum (C, *ECl*), though both Vogel (1923) and the present writer in a former work (1925) have shown two. The sensilla lie so close together that, in sections cut vertical to the surface, it is impossible to distinguish the cells of neighboring organs. The sense cells (A, *SCls*) of all the sensilla of the antennal organs of the honeybee form one continuous mass of sensory cells beneath the normal hypodermis, nearly surrounding the lumen of the antenna, being absent only along the outer side where there are no sense organs.

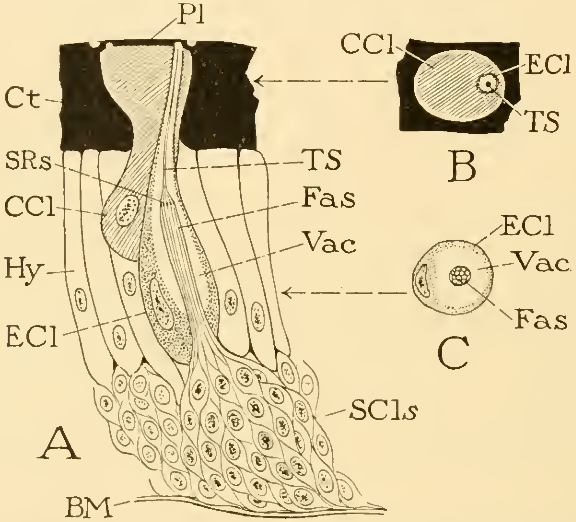

Fig. 24.—Diagrammatic structure of a sensillum placodeum of *Apis mellifera*.

A, vertical longitudinal section. B, cross-section just beneath plate. C, cross-section near base of enveloping cell.

It would be useless to review here all the opinions that have been held concerning the function of the sensilla placodea, since there is little direct evidence connecting any specific sense with these organs. Some writers have regarded them as having an auditory function, others have sought to explain them as organs for perceiving air pressure, and still others have believed that they are organs of smell. Since it seems now pretty well attested that the principal seat of the olfactory sense in bees is located on the antennæ, the most characteristic organs of the antennæ might be supposed to be the organs of smell. Suspicion, therefore, falls upon the plate organs. Yet, these organs would appear to be poorly adapted for the reception of olfactory stimuli. and the responsibility might be shifted to the numerous small, thin-walled hairs which cover the flagella. The plates themselves are about 1.5 microns in thickness, but the surface over the inner groove is not more than half a micron thick. A liquid might, therefore, exude through the groove, spread over the surface of the plate, and absorb odor substances, as some writers have suggested, but, as mentioned before in the case of other supposed olfactory organs, no one has observed the presence of any such liquid.

VII. THE CHORDOTONAL ORGANS

The sensory organs of insects known as the *chordotonal organs* consist of bundles of simple sensilla, each of which comprises a cap cell, an enveloping cell, and a single sense cell. The distal end of the organ is attached to the cuticula of the body wall, but there is no specially differentiated external receptive part, though the point of attachment may be marked by a pit, a thickened disc, or a nodule of chitin. The base of the organ is usually connected with the hypodermis, often by a special ligament. A typical chordotonal organ, therefore, is suspended between two points of the body wall. The organs are frequently associated with enlarged parts of trachæ, or with tracheal sacs, and in some cases with membranous tympana of the body wall.

In form, a chordotonal organ is usually elongate or fusiform (fig. 25); its elements may, however, constitute an oval mass (fig. 27 B, *SB*), they may spread out in the form of a fan (fig. 28, *SgO*), or they may be arranged serially (fig. 28, *TmO*). The cap cell is generally elongate (fig. 26, *CCl*), sometimes attenuate and tapering to the point of attachment (fig. 25), but it may be short and thick (fig. 29 B, *CCl*). The enveloping cell apparently does not reach to the cuticula through the cap cell (fig. 26, *ECl*), but its distal end is buried in the base of the latter. The sense cell is of the usual oval or fusiform shape (*SCl*); its long distal process (*d*), inclosed within the enveloping cell, has a well-developed sense rod, or scolopala (*SR*) at its end. The chordotonal ligament, when present (fig. 25, *d*), is inserted on the bases of the sense cells, and attached distally to the hypodermis at a point opposite the attachment of the cap cells.

The structure of the chordotonal ligament is not well understood. According to Graber (1882), the ligament of the chordotonal organs of the larva of Corethra has the general appearance of a nerve, appearing to be a thin-walled tube filled with a homogeneous granular mass, the membranous walls of which are continuous with the sheath of the nerve. Hess (1917) says the ligament in the organs of Cerambycid larvæ is probably a connective tissue originating from the hypodermis; but Eggers (1920) claims that in the thoracic chordotonal organs of adult Lepidoptera it is composed exclusively of tracheal epithelium. The ligament may be long and slender, or it may be reduced in length or lacking entirely; in the latter case the sense cells of the organ are attached to the hypodermis by a few intervening cells, or they rest upon it directly.

The scolopalæ, or sense rods of the chordotonal organs, have been described in the section treating of the sense rods in general (page 35). In length they vary from a few microns to as much as 23 microns in different organs; some are slender and cylindrical (fig. 15 F, H, I), others are short (E, G) or bulb-like in form (M). The walls are usually ribbed internally (I, K, *r*); the apical body of the head (*AB*) is always conspicuous in stained specimens, and the axial fiber (*AxF*) is attached to it. Often there is no apparent connection between the scolopala and the cuticula of the body wall, but in most organs a distinct terminal fiber (fig. 15, F, fig. 26, *t*) extends from the apex of the scolopala through the cap cell to the cuticula; in a few the fiber appears to end before reaching the cuticula.

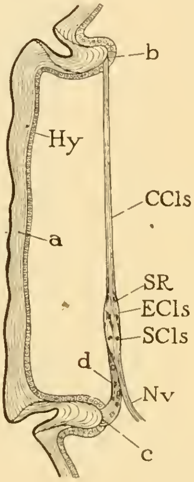

FIG. 25.—Chordotonal organ of larva of *Monohammus confusor*, in horizontal section of a pleural disc of an abdominal segment (Hess, 1917).

a, wall of pleural disc; *b*, attachment of cap cells to infolded cuticula at posterior end of disc; *c*, attachment of chordotonal ligament (*d*) to infolded cuticula at anterior end of disc; *d*, chordotonal ligament.

Scolopalæ were discovered first in the tympanal organs of Orthoptera by von Siebold (1844); they were found next in organs of the wing bases of Coleoptera and Diptera by Leydig (1860). The first concise description, however, of the scolopalæ and of the structure and distribution of the chordotonal organs in insects and in different parts of the insect body was given by Graber (1882) in an extensive paper on the chordotonal organs, which has served as a basis for all subsequent studies of these organs. Graber, however, embraced in his definition of "chordotonal" organs all sense organs "in which there is present a nerve-end structure similar to the well-known 'auditory rod' of the Orthoptera," and he included in his descriptions not only the organs which we now call "chordotonal" but also the campaniform organs of the wing bases.

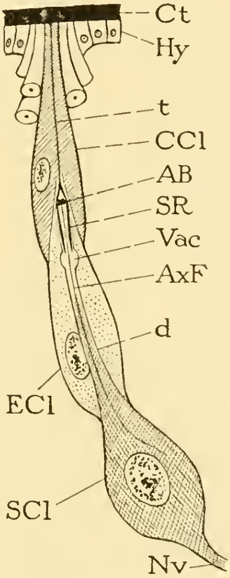

FIG. 26.—Diagrammatic structure of a single sensillum of a chordotonal organ.

Presumably the sense cell (*SCl*) and the enveloping cell (*ECl*) extend to the cuticula, at least in a formative stage, but in the adult organ they appear to end in the base of the cap (*CCl*).

It is clear that the chordotonal organs cannot be defined as "scolopophorous" organs, as is still done by some modern writers, since it is now evident that a scolopala or sense rod of some sort is present in the majority of insect sense organs. The term "chordotonal," however, may be retained inasmuch as it has become well fixed by universal usage, though it carries an auditory implication which probably does not apply to chordotonal organs in general.

Since the time of the earlier writers on the chordotonal organs—von Siebold, Leydig, Graber—our knowledge of these structures has been greatly augmented through the work of many other investigators. Among the latter should be mentioned von Adelung (1892), Herbig (1902), Janet (1904), Schwabe (1906), Berlese (1909), Schön (1911), Vogel (1912), Lehr (1914), Erhardt (1916), Hess (1917), Eggers (1920), and McIndoo (1922); but the student may obtain a complete list of papers on the chordotonal organs from the bibliographical references in the works of these authors.

Chordotonal organs are widely spread in insects, but they have not been recorded in other members of the Arthropoda. In adult insects they occur in the head, the thorax, the abdomen, the antennæ, the legs, and the wing bases; in larvæ they occur mostly along the sides of the abdomen, but have been described also in the labium, in the legs, and even in the tarsi.

The characteristic chordotonal organs of larval insects are those found in the abdomen, where a pair, one organ on each side, occurs in each of the first seven or eight segments. Each organ is stretched longitudinally between points on the anterior and the posterior parts of the lateral wall of the segment, sometimes between infoldings of the cuticula (fig. 25), though usually no external characters mark the site of the organ. The anterior attachment (*c*) is made by the chordotonal ligament (*d*), the posterior one (*b*) by the ends of the cap cells (*CCls*). The chordotonal nerve (*Nv*) turns mesially from the sense cells (*SCls*) to go to the ventral ganglion of the segment. Organs of this type were described by Graber (1882) in aquatic larvæ of Coleoptera, in the caterpillars of *Carpocapsa* and *Tortix,* in larvæ of Diptera (*Corethra, Culex, Simulium, Ptychoptera, Tabanus*), and in the larva of a sawfly (*Nematus*). Hess (1917) gives a particular account of the chordotonal organs of Cerambycid larvæ, showing that the pleural discs along the sides of these insects, on the first eight abdominal segments, mark the points of their attachment, though the presence of chordotonal organs within these discs was first noted by Schiödte (1869).

In adult insects, the chordotonal organs are principally organs of the legs and the wing bases, but they occur also in the head, the antennæ, the thorax, and the abdomen; those connected with the abdominal and leg tympana of Orthoptera are the best known.

The so-called "ear" of the grasshopper, the tympanal chordotonal organ located on the side of the first abdominal segment (fig. 27), is too well known to need a special description here. On the inner surface of the tympanum (B, *Tm*) is a small cellular body

(*SB*) first discovered by Müller (1826), and sometimes known as the organ of Müller, which consists of a mass of scolopophorous sensilla. Some are attached by short thick cap cells to a peg-like invagination of the tympanum (*c*), others by long cap cells to a pear-shaped thickening of the membrane (*a*). The nerve of the organ (*Nv*) goes to the ventral ganglion in the third thoracic segment. Three large air sacs are applied to the inner surface of the tympanum. The large membranous tympanum, set in a cavity of the body wall, suggests an ear drum, and on this suggestion, rather than on concrete evidence, is based the persistent idea that this chordotonal organ of the grasshopper is an organ of hearing, and, by inference the idea that all chordotonal organs have an auditory function.

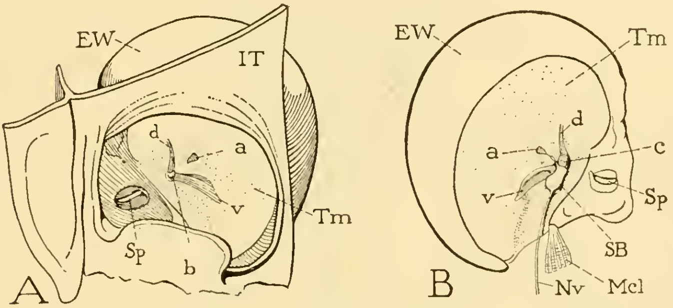

Fig. 27.—The "ear" of a grasshopper (*Dissosteira carolina*).

A, external view of tympanum (*Tm*) on side of first abdominal tergum (*IT*): *a*, pear-shaped thickening of tympanum; *b*, external pit forming peg on inner surface (*B*, *c*); *d*, dorsal supporting arm of internal peg; *EW*, wall of external tympanal cavity; *IT*, lateral part of first abdominal tergum; *Sp*, first abdominal spiracle; *Tm*, membranous tympanum; *v*, ventral arm of internal peg.

B, inner view of tympanum and wall of tympanal cavity; *c*, hollow chitinous peg projecting from tympanum and supporting the sensory body (*SB*); *Mcl*, tensor muscle of tympanum; *Nv*, chordotonal nerve; *SB*, chordotonal sensory body, a branch of which goes to the pear-shaped thickening (*a*). Other letters as on A.

In the fore tibiæ of the Tettigoniidæ (Locustidæ) and the Gryllidæ, there are chordotonal organs also associated with tympana, but not attached to them. The two tympanal areas at the upper end of each tibia lie at the sides of two divisions of the principal leg trachea (fig. 28, *aTr*, *pTr*), one anterior, the other posterior (oriented thus with the leg extended at right angles to the body). In the Tettigoniidæ (figs. 28, 29) the tympana (*aTm*, *pTm*) are covered by folds of the leg wall, forming tympanal cavities (*TC*, *TC*) opening through slits toward the outer surface of the leg (fig. 29, *e*, *e*). In the Gryllidæ the tympana are exposed, but the anterior one is small and more or less rudimentary and is separated from the neighboring trachea by an internal chitinous plate.

In the Tettigoniidæ there are three chordotonal organs in each front tibia (fig. 28). The uppermost (*SgO*) is known as the subgenual organ, since it lies just below the "knee," or femero-tibial articulation.

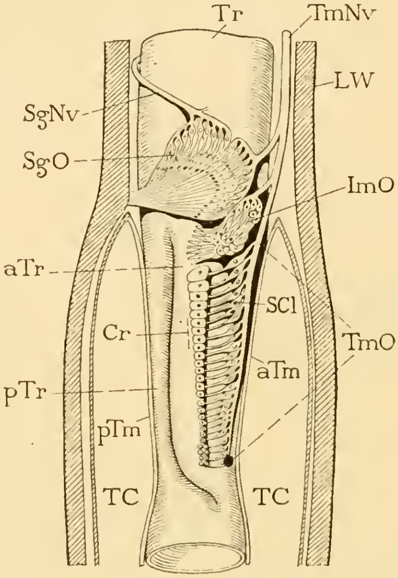

Fig. 28.—Chordotonal organs in the right front tibia of a Tettigoniid (*Decticus verrucivorus*) exposed by removal of outer wall of leg (diagrammatic and simplified from figure by Schwabe, 1906).

aTm, anterior tympanum; *aTr,* anterior tracheal branch; *Cr,* crest of tympanal organ; *ImO,* intermediate organ; *LW,* wall of leg; *pTm,* posterior tympanum; *pTr,* posterior tracheal branch; *SCl,* sense cells of tympanal organ; *SgNv,* subgenual nerve; *SgO,* subgenual organ; *TC, TC,* tympanal cavities opening through slits on exterior of tibia (fig. 29A, *c, c*); *TmNv,* tympanal nerve; *TmO,* tympanal organ; *Tr,* main leg trachea.

The second is termed the intermediate organ (*ImO*) because it lies between the upper ends of the tympana. The third is the tympanal organ (*TmO*) or the so-called "crista acoustica" which forms a crest along the outer surface of the anterior trachea, between the two tympana.

Two separate nerves enter the fore leg, according to Schwabe, from the ventral ganglion of the first thoracic segment. One is the usual leg nerve, the other is a special tympanal nerve. The former follows the ventral wall of the leg and, in the femero-tibial articulation, gives off a sensory branch (fig. 28, *SgNv*) that innervates the upper part of the subgenual organ. The tympanal nerve (*TmNv*) consists entirely of sensory fibers. It follows the anterior wall of the leg and, in the upper part of the tibia, gives off branches to the lower part of the subgenual organ (*SgO*) and to the intermediate organ (*ImO*), while its main trunk ends in fibers to the sense cells of the crest (*TmO*).

The subgenual organ (*SgO*) has the usual chordotonal structure, and is probably the homologue of the chordotonal organ that occurs in a similar position in the legs of some other insects. It is attached by the converging ends of its elongate cap cells to the posterior wall of the leg just above the posterior tympanum. Its sensilla radiate inward and upward, like the ribs of a fan, in cross-section.

The intermediate organ (*ImO*) consists of an irregular mass of sensilla lying at the upper end of the crest on the outer surface of the anterior trachea. Its distal end is attached to the outer wall of the leg by a strand of fibrous and cellular tissue (not shown in the figure).

The tympanal organ (*TmO*) is the organ of particular interest in the Tettigoniid leg, because its sensilla are arranged serially and their outer ends, containing the scolopalæ, form a crest-like ridge (*Cr*) along the outer surface of the anterior trachea (*aTr*), in which the cap cells and scolopalæ decrease in size from above downward. This arrangement, suggesting that the receptive elements are graded to respond to different wave lengths of sound, has strengthened the general belief that the organ has an auditory function.

The sense cells of the tympanal organ lie along the anterior margin of the trachea, in the angle between the latter and the anterior tympanum (figs. 28, 29 A, B, *Scl*) where each receives a fiber from the tympanal nerve trunk (fig. 28, *TmNv*). The distal processes of the sense cells, and the basal parts of the enveloping cells extend posteriorly on the surface of the trachea to its middle where they turn abruptly outward in the crest (*Cr*). The ridge of the crest is formed by the cap cells (fig. 29 B, *CCl*). The crest is covered by a "crest mass" (*a*), which Schwabe (1906) says consists of a fibrous matrix in the meshes of which there is a clear substance and a varying number of scattered cells. Finally, both the crest and the intermediate organ are ensheathed in a delicate membrane (*Mb*) reflected on one side from the inner wall of the anterior tympanum and on the other from the wall of the trachea.

The tympanal chordotonal organ of the Tettigoniidæ appears, at first sight, to differ from all other sense organs in having its cap cells and sense rods directed away from the point of attachment, free from any connection with the body wall. The crest, however, as pointed out by Schwabe, is not distinctly separated from the intermediate organ at its upper end. Both are surrounded by the same membranous sheath, and von Adelung (1892) has shown that there is a cord-like strand of fibrous and cellular tissue that connects the intermediate organ with the outer wall of the leg, where it is inserted upon the cuticula between cells of the hypodermis. It seems probable, therefore, that this strand represents the true origin of these organs in the body wall, and that the position of the crest on the surface of the trachea is a secondary one.

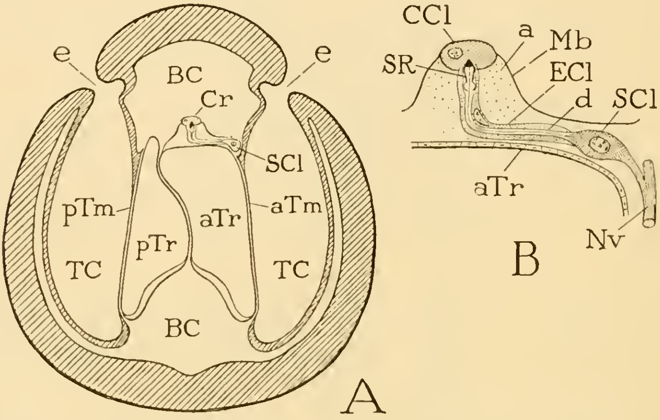

Fig. 29.—Sectional views of tympanal chordotonal organ in front leg of *Decticus verrucivorus.*

A, cross-section of upper end of tibia (simplified from Schwabe, 1906): *BC, BC,* inner cavity of leg; *c, e,* outer openings of tympanal cavities (*TC, TC*); other lettering as in fig. 28. The two tracheal branches (*aTr, pTr*) lie between the tympana (*aTm, pTm*), with chordotonal crest (*Cr*) on outer surface of anterior trachea.

B, diagrammatic cross-section of the crest and a sense cell of the tympanal organ: *a,* "crest mass" inclosing the sensilla; *aTr,* wall of anterior tracheal branch; *CCl,* cap cell; *d,* distal process of sense cell; *ECl,* enveloping cell; *Mb,* membrane covering the crest; *Nv,* tympanal nerve; *SCl,* sense cell; *SR,* sense rod, or scolopala.

In the crickets (Gryllidæ) only two chordotonal organs have been described in the fore tibiæ, a subgenual organ, and one on the trachea corresponding with the crest of the Tettigoniidæ; but the latter is shorter and more fan-shaped than in the katydid species that have been studied. (Herbig, 1902; Berlese, 1909.)

In the Hymenoptera a subgenual chordotonal organ occurs in all the legs of species that have been examined for it, including a sawfly, ants, wasps of the family Vespidæ, Bombus, and the honeybee. (Janet, 1904; Schön, 1911; McIndoo, 1922).

In the wing bases, including the halteres of Diptera, it is now known that chordotonal organs are of frequent occurrence. The studies of Pflugstaedt (1912), Vogel (1912), Lehr (1914) and Erhardt (1916), show that they are present in this location in Odonata, Neuroptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera, but absent in Orthoptera and Hemiptera. Usually, each wing base contains only one or two organs, though Erhardt reports the presence of seven in the base of each front wing of Chrysopa, and six in each hind wing. The distal ends of the wing organs are in all cases attached to the ventral surfaces of the wing bases.

In other parts of the body, chordotonal organs have been described in various situations in different insects: in the head of ants and bees (Janet, 1894, 1911), in the antennæ of *Dytiscus* (Lehr, 1914), in the ventral part of the prothorax of ants (Janet, 1894), in the posterior part of the thorax of many Lepidoptera (Eggers, 1920), and in the first abdominal segment of the cicada (Vogel, 1923 *a*). Judging from the number of chordotonal organs already known in insects, and from the diversity of their positions, it is likely that further studies will show a still wider distribution of them in a greater number of species. It would be surprising, in fact, if they should not be found eventually in most of the species in all orders.

The development of the chordotonal organs in the legs of the honeybee has been studied by Schön (1911). In the worker bee, according to Schön's account, on the eighth day after the laying of the egg, which is the fifth day of the larval stage, there appears in the tibia of the inverted imaginal leg, just below the femero-tibial joint, a small ingrowth of the hypodermis over an invagination of the cuticular wall of the leg. This ingrowth becomes the chordotonal organ. On the ninth and tenth days its cells begin to differentiate, the sense cells being first distinguishable, segregated at the inner end of the mass. From them a short process extends inward which will later unite with the chordotonal branch of the leg nerve. The imaginal bud of the leg is everted on the eleventh day. On the thirteenth day there still remains a remnant of the cuticular invagination; the external opening is finally closed, but the internal part remains as a hollow within the mature organ. On the seventeenth day the organ is completed; on the twenty-first day the young worker emerges from its cell. From this account it is clear that the chordotonal organ is a modification of the body wall, as are all the other sense organs, and that its cells, including the sense cells, are differentiations of the hypodermis.

Concerning the function of the chordotonal organs nothing definite can be said. In the text books the chordotonal organs are presented as "organs of hearing." It is certain, however, that the perception of sound has not been proved to be connected with any of them, and those organs situated within the legs, the wing bases, and various regions of the body where they are affixed to solid parts of the body wall, even though they may be associated with enlarged trachæ, seem poorly adapted for acoustic purposes. On the other hand, the internal position of the organs suggests that they must have some function connected with the workings of internal parts of the body. Following this idea, the discussion of Eggers (1923) on the possible uses of the chordotonal organs leads to conclusions more convincing than any other yet presented bearing on the function of these enigmatical structures peculiar to insects.

Eggers points out that most of the movements made by insects result in rhythms. Especially is this true of the action of the wing mechanism, which sets the whole body into rapid vibration; but also the motions of the antennæ and the legs tend to become rhythmical, while the movements of respiration, the pulsations of the heart, the bodily motions of locomotion in certain aquatic larvæ are all of a rhythmic nature. Since rhythm, then, is such a characteristic feature of muscular activity in insects, it would seem that there should be special organs for registering it and for regulating the action of the muscles that produce it. The chordotonal organs suggest themselves at once as organs adapted for this purpose and as the only organs that could serve in such a capacity. According to this idea, therefore, the chordotonal organs are to be regarded as rhythmometers.

Finally, it is conceivable, as suggested by Eggers, that if a chordotonal organ is connected with a thin membrane of the body wall, or is sufficiently delicate in its construction, it might be responsive to motions of the surrounding medium; *i. e.*, to vibrations of air or water, and hence might act as a receptor of sound waves. Thus, for example, the highly developed organ of Johnston in the antenna of the Culicidæ (fig. 31 B) or the tympanal organs of the Orthoptera may be organs of hearing.

VIII. THE ORGAN OF JOHNSTON

Located in the second segment of the antenna of most insects, the segment commonly distinguished as the pedicel, is the sense organ that has long been known as the organ of Johnston. Structurally it scarcely deserves to be placed in a class by itself, since it appears to be only a simplified chordotonal organ, but inasmuch as it possesses distinctive features and probably has a specific function, there is no particular reason for its demotion.

The organ of Johnston consists of bundles of elongate sensilla forming a cylindrical sheath about the antennal nerve trunks within the pedicel. The distal ends of the sensilla are attached in groups, corresponding with the bundles, to the articular membrane between the second and third segments of the antenna. Usually the points of attachment of the sensilla groups are marked by pits in the membrane, which form a circle at the end of the pedicel. The base of the organ is connected by nerve fibers with the main antennal nerves.

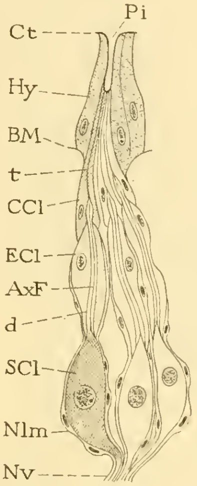

FIG. 30.—Group of sensilla of organ of Johnston of mature pupa of a wasp, *Vespa crabro* (Berlese, 1909).

The organ was described first in the antenna of a mosquito (*Culex*) by Johnston (1855), who gave, however, but a brief account of its structure. Later it was more thoroughly investigated by Child (1894) who found it in ten of the principal orders of insects. More recently the organ named after Johnston has been studied by Berlese (1909) and by Lehr (1914 *a*). The orders of insects in which an organ of Johnston is now known to occur are the Odonata, Orthoptera, Hemiptera, Anopleura, Neuroptera, Coleoptera, Trichoptera, Lepidoptera, Diptera, and Hymenoptera.

The structural details of the organ of Johnston have been less studied than have those of the true chordotonal organs, but there appears to be no radical difference between the two sets of organs.

Berlese (1909) gives a drawing of a group of sensilla from the organ of Johnston of a wasp, *Vespa crabro,* taken from a mature pupa, in which he depicts the usual chordotonal structure (fig. 30), each sensillum being shown to consist of a cap cell (*CCl*), an enveloping cell (*ECl*), and a sense cell (*SCl*). The sense cell has a long neck extending apparently through the enveloping cell into the base of the cap cell, where it ends in a scolopala-like rod attached by a long distal fiber from its apex to a cuticular pit between the second and third antennal segments. Child had noted the presence of rods in the organ of Johnston of the mosquito, but his description and drawing (fig. 31 B) do not show clearly their relation to the sense cells. Lehr describes the organ in the antenna of *Dytiscus marginalis* and his account of the structure of the sensilla agrees essentially with Berlese's figure of that in the wasp. The enveloping cells, according to Lehr, are not as well defined as in a typical chordotonal organ; the scolopalæ are simple fusiform rods, each continued at its apex into a terminal filament attached to the cuticula. Neither writer, however, shows the presence of an apical body in the scolopalæ of the organ of Johnston or ribs in their walls, though each rod is traversed by an axial filament.

An organ of Johnston of a primitive nature is described by Zawarzin (1912) and Eggers (1923) in the antenna of a dragonfly larva. The organ here appears to consist merely of a circle of elongate sense cells in the second antennal segment, the cells being attached by their distal ends to the articular membrane between this segment and the third. According to Eggers there are no enveloping cells present in this organ, and scolopalæ are not differentiated in the sense cells, the distal parts of the latter having a fibrous texture.

In other insects the organ of Johnston varies much in its development. Its bundles of chordotonal-like sensilla usually form a simple cylinder within the pedicel of the antenna, as shown in longitudinal section at A of figure 31. (The details of structure are probably not well illustrated in this figure.) The organ reaches its highest degree of development in the males of the families Chironomidæ and Culicidæ, in which the second segment of the antenna is greatly enlarged. The well-known illustration from Child (fig. 31 B) gives a general idea of the appearance of the organ of Johnston in a longitudinal section through the base of the antenna of a male of *Corethra (Mochlonyx) culiciformis.* The sensilla of the organ are here not attached in the usual way to pits of the articular membrane between the second and third segments; the membrane is chitinized to form a circular plate (*a*) attached to the base of the third segment (*3Scg*), from the outer edge of which 70 to 90 slender chitinous prongs (*b*) radiate into the lumen of the pedicel and carry the distal attachments of the sensilla. The sense cells form a thick peripheral layer in the pedicel (*2Seg*), the distal parts of the sensilla converging toward the supporting arms, while the nerves of the organ diverge from the main antennal trunks (*Nv*) in the first segment (*1Seg*).

The development of the organ of Johnston in *Corethra* is described by Child as follows: Immediately after the last molt of the larva the hypodermis of the second antennal segment forms a fold. growing from before backward, that surrounds the antennal nerve. The outer layer of the fold remains thin, but the inner layer thickens by a multiplication of its cells. The cells of the inner layer then become elongate, but at first are all alike; later they differentiate into sense cells and rod-bearing cells. Nerve fibers from the central nerve axis finally become attached to the bases of the sense cells. This account is probably somewhat crude, but it shows at least that the organ of Johnston is differentiated from the hypodermis as are all other insect sense organs.

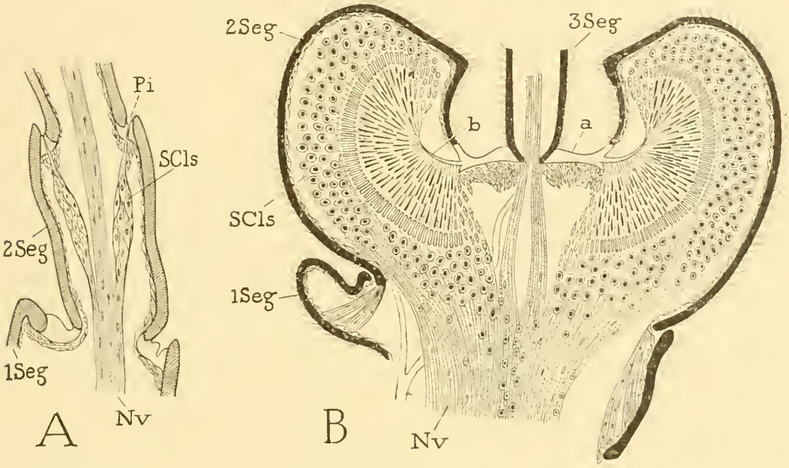

FIG. 31.—The organ of Johnston in simple and complex form (Child, 1894).

A, longitudinal section through base of antenna of *Melolontha vulgaris,* showing two bundles of sense cells (*SCls*) with terminal processes attached to pits (*Pi*) in articular membrane between pedicel (*2Seg*) and third antennal segment.

B, highly developed organ of Johnston in pedicel (*2Seg*) of antenna of *Corethra culiciformis,* longitudinal section. The terminal processes of the sense cells (*SCls*) here attached to prongs (*b*) from circular chitinous plate (*a*) on base of third segment (*3Seg*).

Some writers classify the organ of Johnston as an auditory organ, but there is little evidence in support of the idea that it is a sound receptor in any insect. From its widespread occurrence in insects, however, we may infer that it is an organ of importance, and its constant position suggests that it must have some specific sensory function. Its structure in the Chironomidæ and Culcidæ, especially the union of the supporting plate (fig. 31 B, *a*) with the base of the third antennal segment (*3Seg*), suggests that the organ in these families is an apparatus for registering the movements of the flagellum. It may, therefore, be supposed to be perceptive to slight air motions, but whether to waves of sound or not is still to be questioned.

IX. THE EYES

The word " eye " is used in a general sense for any specific organ that is sensitive to light falling upon it and capable of transmitting the resulting stimulus to the central nervous system. An eye is primarily a light-perceiving organ, or photoreceptor, and it is not to be assumed that all eyes are capable of registering impressions of form, color, or motion in external objects. The effect of the light stimulus on the organism must vary with the structural development of the eye and of the visual centers of the nervous system.

The eyes of insects are usually classified as *simple eyes*, or *ocelli*, and *compound eyes*. The compound eye constitutes a definite type of organ common to insects and crustaceans, and is most probably the primitive eye of these two groups. The ocelli, on the other hand, are a heterogeneous group of photoreceptive organs comprising several distinct kinds of eye structures, which probably either have had separate origins or have followed separate lines of development from a primitive type. Only a brief description of the eyes of insects will be given here, because a complete treatment of the subject would involve a discussion too long for the present paper. A reference to the many valuable works now at hand on the structure of insect eyes must also be omitted. The histology of the eyes is better known than that of other insect sense organs, but still there is much that has not found its way into any general review of the morphology of the visual organs.

The fundamental elements in all the varieties of insect eyes are innervated photoreceptive cells of hypodermal origin. These cells correspond with the sense cells of the other sense organs, and may be designated the sense cells of the ocular sensillum. Associated with them are other cells derived from the hypodermis, but these have so little in common with the enveloping cells of the other sense organs that any theory which would derive an ocular sensillum from that of a sensory hair, as that proposed by Patten (1890), is too far-fetched to be convincing. The number of sense cells in a single eye varies from two cells to many thousand in the different types of insect eyes. All the sense cells of one eye constitute what is generally regarded as the retina of the arthropod eye. The optic lobes of the brain (fig. 4, *OpL*), upon which the compound eyes rest, are parts of the central nervous system and do not contain the precipient elements of the eye, as in vertebrates. Each retina cell is traversed by fibrils which are continuous proximally with the ocular nerve, and which end distally in a definite marginal part of the cell, which part becomes the sensitive area of the cell. This area commonly has the appearance of being vertically striated or formed of a fringe of minute thread-like rods. It is known as the *rhabdomere* because it often combines with the corresponding borders of neighboring cells to form a crystalline visual rod called a *rhabdom*. Retina cells thus grouped about a rhabdom constitute a composite retinal element known as a *retinula*. The retinal cells rest upon the basement membrane, which is perforated by the fibers of the optic nerves.

The same question arises regarding the innervation of the eyes as with the other sense organs; *i. e.,* whether the ocular nerve fibers grow outward and penetrate the retinal cells, or whether they originate in the retinal cells and grow inward to the optic lobes. Some writers are positive in asserting that the second process of growth takes place with the compound eyes, that the growth of the nerves can be followed in the development of the eye from the retinal cells inward to the ganglia of the optic lobes. If this is true, then the hypodermal retinal cells are the cytons of the peripheral ocular nerve fibers.

THE COMPOUND EYES

The well-known lateral compound eyes of Crustacea and Insecta consist, in their typical form, of groups of ocular sensilla or *ommatidia*. The number of ommatidia in a single eye in different insects is usually between a few hundred and 20,000, but in some the number is estimated to be as high as 30,000. In aberrent or degenerate types there are but a few ommatidia or even only one ommatidium.

The outer surface of each ommatidium consists of the cuticular *cornea* (fig. 32 A, B, *Cor*), which is commonly thickened to form a lens. Beneath the cornea of some of the more primitive insects and in crustaceans are two *corneagenous cells* (A, *CorCl*), but in the mature eye of most insects (B) these cells are usually withdrawn from the normal position and from contact with the central part of the cornea. Under the corneagenous cells, or directly beneath the cornea when the corneagenous cells are displaced, are four cells, sometimes called the cells of Semper, that usually unite to form a conical crystalline body (*Cn*) having its apex directed inward. The four component cells are, therefore, usually known as the *cone cells.* Proximal to the cone or the cone cells are the retina cells (*Ret*) of the ommatidium, which typically are slender and elongate, and constitute a retinula with an axial rhabdom (*Rhb*) directly beneath the apex of the cone. The primitive number of retinula cells in each ommatidium is probably eight, but generally one is aborted or crowded away from the axis (D, *a*), leaving seven as the typical number taking part in the formation of the rhabdom. The lower ends of the retinulæ rest upon the basement membrane (*BM*), and the fibers of the optic nerves (*Nv*) entering the optic lobes of the brain penetrate the membrane to end in the ganglia of the lobes.

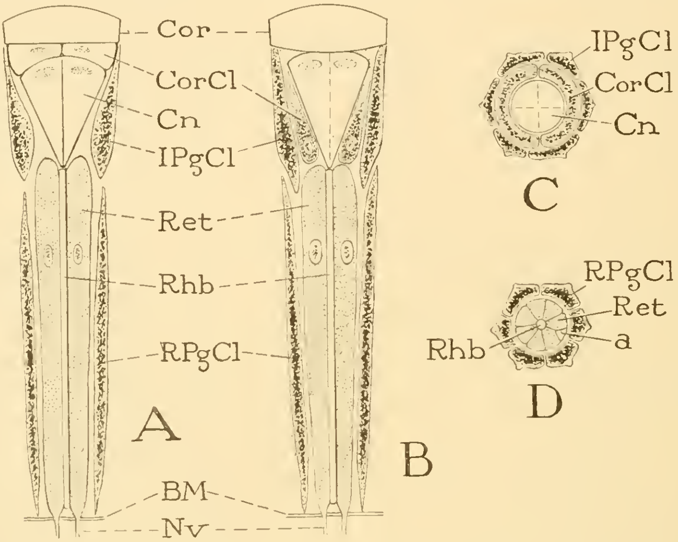

FIG. 32.—Diagrammatic structure of an ommatidium of the compound eye.

A, type of eye in which the corneal cells (*CorCl*) lie immediately beneath the cornea, exemplified by the adult eye of *Machilis* and of many crustaceans and by the immature eye of some insects.

B, type of eye usual in adult insects in which the corneal cells (*CorCl*) have become pigment cells surrounding sides of cone.

C, cross-section of ommatidium through cone, showing the two corneal pigment cells (*CorCl*) surrounding sides of cone.

D, cross-section of ommatidium through retinula, showing rudimentary eighth retinula cell (*a*) at surface of retinula and taking no part in formation of rhabdom (*Rhb*).

The compound eyes are well developed in nearly all adult insects; their absence is to be regarded as due to a degeneration of the organs and not as representing a primitive eyeless condition. In the Collembola, and in Lepisma of the Thysanura, the compound eye does not have the typical form. In the Collembola there are from 1 to 12 small eyes on each side of the head in some species, and in *Lepisma* a group of 12 similar eyes on each side. These eyes have an external resemblance to the scattered lateral ocelli of caterpillars and some other larvæ of the higher insects, and in internal structure they are in some ways also similar to these eyes; but they have other characters that are distinctive of compound eyes. Their structure in general is that of a primitive compound eye with aberrant features, and they are, therefore, probably to be regarded as degenerate ommatidia of compound eyes. This conclusion is strengthened by the fact that in *Machilis,* another member of the Thysanura, the lateral eyes are distinctly of the typical compound eye type (fig. 32 A), and retain the primitive and crustacean character of having the corneagenous cells beneath the lens.

In the compound eye of most other insects the corneagenous cells, as already noted (fig. 32 B, *CorCl*), withdraw from beneath the cornea in the mature stage and take positions at the sides of the cone, where they acquire a deposit of pigment, and become the cells known as the primary pigment cells, or *corneal pigment cells.*

The four cone cells (fig. 32 C, *Cn*), when they form a typical cone, fuse completely; their protoplasm becomes converted into a clear hyaline substance, and their nuclei remain in the outer or basal part of the cone (A, B). Eyes with a cone of this type are designated *eucone* eyes. In some insects, however, especially in the Diptera, the cone cells secrete a transparent substance which forms a conical mass beneath the cornea held between the surrounding pigment cells, but the cone cells remain distinct with their nuclei beneath the vitreous mass. Eyes with an imperfect cone of this kind are distinguished as *pseudocone* eyes. In some of the Diptera, again, the eyes are of an *acone* type, the cone cells remaining distinct without forming a vitreous body of any sort.

The retinulæ cells (fig. 32 A, B, *Ret*) extend from the cone, sometimes embracing its apex, to the basement membrane. In eyes of simpler construction they form one layer of cells, but their arrangement is subject to much variation in the various modifications of the retinular structure in different insects. The nuclei of one or more of the cells may migrate toward the base of the ommatidium, and often the cells themselves become arranged in two layers, sometimes with one cell at the base of the ommatidium and the other seven distal, sometimes with three in a basal layer and four in a distal layer. As already noted, the primitive number of retinula cells appears to be eight; but one is commonly reduced in size and separated from the rhabdom, leaving only seven taking part in the formation of the latter (fig. 32 D), and in such cases, if one of these becomes basal, only six appear in cross-sections through the distal part of the retinula.

The ommatidia are usually separated from one another by cells containing a dark pigment. When this pigment extends through the entire depth of the eye, it serves to isolate optically the individual ommatidia, and to make each a separate receptive element of the eye. The effect of light entering an eye thus divided into isolated tubes must be to give a mosaic image of the exterior, and this is regarded as the usual form of vision with diurnal insects. In the eyes of some nocturnal species, however, it is said that on the decrease of light the pigment condenses between the outer parts of the ommatidia, allowing light rays from any one point to spread over the retinulæ of several ommatidia, thus giving a more effective vision in dim illuminations. Usually but one set of pigment cells is described, besides the corneal pigment cells, but in some eyes there are two sets, a distal one and a proximal one. The distal pigment cells invest the cone and the corneal cells and are conveniently distinguished as the *iris pigment cells* (fig. 32 A, B, C, *IPgCl*). The proximal pigment cells surround and separate the retinulæ and are usually known as the *retinal pigment cells* (A, B, D, *RPgCl*), though they may also embrace the base of the cone. The number of pigment cells of both sets varies much in the eyes of different species of insects. There is some confusion in the names applied by writers to the several sets of pigment cells in the compound eye, including the pigmented corneal cells, due in part to the lack of uniformity in the cells themselves, and in part to the fact that it has not always been recognized by reviewers that the corneagenous cells are the pigment cells immediately investing the cone, except when they retain their primitive subcuticular position.

Compound eyes divided into two parts are common in several orders of insects, and frequently the two parts differ in the internal structure of the ommatidia, probably in accommodation to different ranges of vision or different intensities of light.

THE OCELLI

The various forms of simple eyes of insects have probably been developed independently of one another, and none of them has been proved to have any developmental relation to the compound eyes. Those of most primitive structure occur in the larvæ of the Dipteran families Chironomidæ and Culicidæ, while the ocelli of the Ephemeridæ are perhaps the most highly evolved type. These facts and others indicate that the structure and comparative complexity of the ocelli have no phylogenetic significance, and suggest that ocelli are not the primitive visual organs of insects, but are secondarily acquired organs supplemental to the compound eyes, or substituting for them where the latter have been suppressed.

The ocelli are characterized by their individuality, but they cannot be defined on the basis of a type structure, because they differ so much among one another and have in general no feature that may not be found in ommatidia of compound eyes. They may occur in groups, though a group does not function as a single organ, but a compound eye, as already noted, may degenerate into detached ommatidia. The following six types of simple eyes are to be distinguished:

1. The lateral ocelli of Chironomid and Culicid larvæ.
2. The median ocellus of Collembola.
3. The lateral ocelli of larvæ of insects having a pupal stage, except the eyed larvæ of Diptera and Hymenoptera.
4. The frontal or dorsal ocelli of adult insects and of the young of insects having no pupal stage, except Collembola and Ephemerida, and the lateral eyes of adult fleas.
5. The frontal ocelli of Ephemerida.
6. The lateral ocelli of Tenthredinoidea.

The ocelli of Chironomid and Culicid larvæ are the simplest of all insect eyes and have a striking similarity of structure to the eyes of the Turbellarian worm, *Planaria.* There are two on each side of the head, each eye consisting of a few simple sense cells lying beneath a clear area of the cuticula, with their distal ends in a pigmented cup of the hypodermis. The pigment probably serves to limit the direction of the light rays that may fall upon the sense cells.

A median frontal ocellus similar in structure to that of Dipteran larvæ has been noted in a few species of Collembola. That of *Orchesella* is somewhat more highly evolved than the Dipteran larval eye, and its sense cells have rhabdomere borders. These two groups of insects are so widely separated, however, that it does not seem likely there can be any genetic relationship between the eyes of one and those of the other.

The lateral ocelli of Neuropteran, Coleopteran, and Lepidopteran larvæ consist of an invagination of the hypodermis beneath a lenticular thickening of the cuticula, with the sense cells differentiated at the inner end of the cup and a crystalline body formed as a secretion in the distal part beneath the lens. These eyes occur in a group on each side of the larval head, frequently at the place where the compound eye is to be developed in the pupa, but it has been shown that the larval eyes degenerate without taking any part in the formation of the compound eye, and there appears to be no ground for the idea that the larval ocelli are ommatidia of the adult eye. So far as known to the writer, the roots of the ocellar nerves have not been traced in the larval brain, and until this is done the status of the ocelli probably cannot be decided. In a caterpillar the ocellar nerve trunks arise from the lower parts of the lateral brain lobes, immediately lateral to the antennal nerves, and follow a long semicircular course forward and outward to the ocelli. The optic lobes of the adult are developed from tissues within the larval brain.

The typical frontal or dorsal ocelli of adult insects are without doubt the primitive ocelli of insects since they occur in all the principal orders except the Collembola and Ephemerida. In these ocelli the hypodermal elements become arranged in two horizontal layers, usually by a process of delamination of the cells where the eye is formed. The cells of the outer layer are the corneagenous cells. Generally they secrete a thick biconvex cuticular lens and then become reduced to a thin transparent sheet over the inner layer. The latter consists of the retina cells which become grouped into rhabdom-forming retinulæ. Typically, there are three frontal ocelli, one median and two placed more laterally, but there is evidence in the structure and development of the median eye that it is the product of the fusion of an original pair of eyes. Sometimes the median ocellus is lacking where the others persist. The lateral simple eyes of adult fleas show by their structure that they are ocelli of the frontal type; probably they are the paired frontal ocelli that have moved to the sides of the head in the absence of compound eyes.

The frontal ocelli of adult Ephemeridæ are in certain respects similar to the frontal ocelli of other insects, but they differ from all other insect eyes in having a multicellular hypodermal lens formed apparently by an invagination of the outer surface of the eye.

The large, single, lateral ocellus of the larvæ of sawflies (Tenthredinoidea), finally, is somewhat of an anomaly among insect eyes. In structure it resembles the frontal ocelli of adult insects, but these are eyes that no other larva possesses. On the other hand, it has certain characters that have suggested the idea that it is a prototype of the compound eye, a claim disproved, however, by other investigators. Certainly it has no relation to the lateral eyes of other larvæ, and must be regarded, therefore, either as a primary frontal ocellus persisting in a larval stage and moved to the side of the head, or as an independent development.

POSTSCRIPT

Much has been omitted from the foregoing accounts of the structure of the sense organs and the nervous system of insects that a complete discussion of the subjects involved should contain, though the writer hopes that no recorded information has been overlooked or withheld that would weaken the general statements given, or that might have an important bearing on the matters discussed. Many of our present ideas on insect morphology are still in a controversial stage, and undoubtedly some current generalizations will be found to be based on a too limited knowledge of the facts, considering the great diversity in all the structural parts of insects. The writer, however, who undertakes to present a review of the facts known in any branch of insect anatomy must remember that his offering will be of value chiefly to the student or to the practical entomologist looking for concise information, and who is likely not to be interested in long discussions on subjects still under dispute among specialists.

On the other hand, a reviewer, through his desire to have his subject matter well classified, or to make it appear as complete as possible, may err in presenting it in a form more concise and more definite than is warranted by the facts. This is exemplified in the treatment of insect sense organs as commonly given in entomological texts, where each known group of organs is assigned to a special sense, as is done in text books on human anatomy, while from the writings of specialists it would appear that almost nothing is settled concerning the functions of the insect organs. The condition, however, is not one of chaos. The last twenty-five years has seen a vast increase in our knowledge of insect structure in general, and in particular of the sense organs, but by this very increase of printed information the work of assembling and reviewing it has become a task that can scarcely be done except by one who has all his time to devote to it. We must note with satisfaction, however, the increasing importance being given to morphology by the authors of our present general texts on entomology, and it is clear that the painstaking work of recent students will give to the subject of insect anatomy in the future a higher scientific standing than its adherents have heretofore been able justly to claim in its behalf.

ABBREVIATIONS USED ON THE FIGURES

AB, apical body.
ACy, association cyton.
Alv, alveolus.
AntNv, antennal nerve.
aTm, anterior tympanum.
aTr, anterior trachea.
Axn, axon, or neurite.

BC, body cavity (of leg).
BM, basement membrane.
1Br, protocerebrum.
2Br, deutocerebrum.
3Br, tritocerebrum.
BW, body wall.

CCl, cap cell.
Cl, cell.
Cn, crystalline cone.
CnCl, cone cell.
CœCom, circomœsophageal commissure.
Col, collateral.
1Com, protocerebral commissure.
2Com, deutocerebral commissure.
3Com, tritocerebral commissure.
Cor, cornea.
CorCl, corneagenous cell, or corneal pigment cell.
Cr, crest.
Ct, cuticula.
Cy, cyton (cell body).
CyI, sensory cell of Type I
CyII, sensory cell of Type II.

d, distal process of sense cell.
Dct, duct.
Dm, dermis, endocuticula.
Do, dome.

ECl, enveloping cell.
Ect, ectoderm.
Epd, epidermis, exocuticula.
EW, wall of tympanal cavity.

FrCom, frontal commissure.
FrGng, frontal ganglion.
FrNv, frontal nerve.
Fas, fasciculus of sense cell processes.

GGng, gastric ganglion.
4Gng, fourth head ganglion (mandibular).
5Gng, fifth head ganglion (maxillary).
6Gng, sixth head ganglion (labial).
7Gng, first thoracic ganglion.
GngCls, ganglion cells.

Hr, hair, seta.
HrCl, trichogenous cell.
HrMb, articular membrane of hair.
Hy, hypodermis.

ImO, intermediate organ.
IPgCl, iris pigment cell.
IT, first abdominal tergum.

LbNv, labial nerve.
LCom, longitudinal commissure.
LGng, lateral stomatogastric ganglion.
LmNv, labral nerve.
LW, leg wall.

Mb, membrane.
MbCl, cell of hair membrane.
Mcl, muscle.
MCy, motor cyton.
MdNv, mandibular nerve.
MxNv, maxillary nerve.

Nbl, neuroblast.
NlG, neural groove.
Nlm, neurilemma.
NlR, neural ridge.
Nu, nucleus.
Nv, nerve.

Œ, œsophagus.
ŒGng, œsophageal ganglion.
ONv, ocellar nerve.
OpL, optic lobe.

p, proximal process of sense cell.
Pi, pit.
Pl, sensory plate.
pTm, posterior tympanum.
pTr, posterior trachea.

r, ribs of sense rod.
Ret, retinula cell.
Rhb, rhabdom.
RNv, recurrent nerve.
RPgCl, retinal pigment cell.

SB, sensory body.
SCl, sense cell.
SCls, sense cells.
SCy, sensory cyton.
1Seg, first segment of antenna.
2Seg, second segment of antenna (pedicel).
3Seg, third segment of antenna.
SgNv, subgenual nerve.
SgO, subgenual organ.
SNv, sensory nerve.
SœGng, subœsophageal ganglion.

Sp, spiracle.
SPg, sensory peg.
SpGng, spinal ganglion.
SR, sense rod (scolopala).
SRs, sense rods.

t, terminal filament of sense rod.
TC, tympanal cavity.
Tm, tympanum.
TmNv, tympanal nerve.
TmO, tympanal organ.
Tnd, tendon.
TndCl, tendon-forming cell.
Tr, trachea.
TS, terminal strand.
Tu, tubercle.

Vac, vacuole.

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