

A COMPARATIVE STUDY OF THE STOMODAEAL
NERVOUS SYSTEM OF INSECTS.

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Thesis submitted to the Faculty of the Graduate School
of the University of Maryland in partial
fulfillment of the requirements of the
degree of Doctor of Philosophy

1940

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ABBREVIATIONS USED IN THE FIGURES

A, anterior
Ao, aorta
Ant, antennal

Br, brain
1Br, protocerebrum
2Br, deutocerebrum
3Br, tritocerebrum

CA, corpus allatum
CCd, corpus cardiacum
Coe, circumoesophageal
Com, commissure
Con, connective
Cr, crop

Fr, frontal

G, gastric
Gl, glandular
Gng, ganglion

Ing, ingluvial

L, lateral
Lb, labial
Lm, labral

M, Muscle

Nv, nerve, nervous

O, ocellar
Oc, occipital
OE, oesophagus, oesophageal
Op, optic

P, posterior
Phy, pharynx, pharyngeal
Pmp, pump

R, recurrent

Sl D, salivary duct
Soe, suboesophageal
St, stomodaeum, stomodaeal
Stc, stomacal

Tr, trachea

Vent, ventriculus

INTRODUCTION.

The structure, development, and function of the nervous system of insects have been studied rather extensively. The histology of the brain of various insects has been described in detail. The ventral nerve cord has been the subject of investigation of many workers.

It has been known for a long time that there are three nervous systems in insects: central, peripheral, and stomodaeal. The term, stomodaeal nervous system, is used by Snodgrass (1935) as the name for the system centering in the stomodaeal ganglia and having nerve fibers extending to the stomodaeal part of the alimentary tract. The ganglionic centers arise during embryonic development by an ingrowth from the dorsal wall of the stomodaeum. In the earlier literature the stomodaeal nervous system is usually called the sympathetic nervous system. It was Müller (1828) who first offered the analogy with the sympathetic nervous system of vertebrates. Later workers seemed to prefer the terms visceral, pharyngeal, and stomatogastric. The French workers tend to use the word "stomatogastrique", and the Germans, "Schlundnervensystem". According to Nabert (1913) Straus-Dürckheim referred to the stomodaeal nervous system as the "system nerveux des organes vitaux et ganglion collatéraux ou accessoires du cervau"; Newport (1832) employed the phrase, "nerves of involuntary function". Several other variations are to be found in the literature.

Today the term, stomatogastric, is widely used; but it is not sufficiently inclusive, since various parts of the stomodaeum such as the salivary glands and aorta are innervated by fibers extending from the ganglionic centers of this system. In addition, the alimentary tract is innervated by a system of nerves emanating from the posterior abdominal

ganglion of the ventral nerve chain. Blanchard (1858) objected to the use of the word, sympathetic; and Janet (1899) used the word, stomodaeal.

The variation in number and position of the nerves and ganglia of the stomodaeal nervous system makes it somewhat useless to describe any typical arrangement. There are, however, a few fairly constant features. The ganglia always lie close to the dorsal surface of the fore-gut, and the frontal ganglion is generally present. It is situated on the dorsal wall of the pharynx in front of and slightly below the brain with which it is connected by bilateral connectives, the frontal ganglion connectives. These have been called the arched nerves. One or more frontal nerves may extend anteriorly from the frontal ganglion toward the integument of the clypeus.

Another fairly constant feature is the recurrent nerve which corresponds to the sympathicus of the crayfish figured by Plate (1922). It is the "rucklaufend Nerv" of several German workers, and it is sometimes called the sympathetic, stomatogastric, or gastric nerve, although these names are more often applied to other nerves to be described below.

The recurrent nerve (nervus recurrens) extends posteriorly from the frontal ganglion and, following the dorsal wall of the pharynx and oesophagus, runs under the brain and into the occipital ganglion slightly caudad of the brain. The occipital ganglion has been termed the hypocerebral, the pharyngeal, the oesophageal, the sub-cerebral, and the anterior visceral ganglion by various authors. The word, occipital, should be restricted to the median ganglion which is penetrated anteriorly by the fibers of the recurrent nerve and which often appears as a swelling of the recurrent nerve. The paired nerves extending from the posterior lobes of the brain do not usually connect with the occipital ganglion,

but with the bodies that in the literature are called most frequently the anterior oesophageal or pharyngeal ganglia. These structures, which are usually in close association with the occipital ganglion, are called pharyngeal bodies (corpi faringei) by de Lerma (1933, 1937) and corpora cardiaca by Pflugfelder (1937 A, 1938). These workers conclude from histological evidence that the structures are partly or wholly glandular in nature. There is no experimental proof that a secretion is produced by the corpora cardiaca, nor do we have any idea as to its possible function; nevertheless the term corpora cardiaca seems acceptable and is adopted in the present paper in anticipation of further work along this line and because it is more suitable than many of the older names.¹

The corpora allata are usually located slightly below and posterior to the occipital ganglion with which they are connected by short nerves. The many variations in shape, histology, location and arrangement of these bodies have been described in the excellent paper of Nabert (1913). The glandular nature of these structures, formerly best known as the posterior pharyngeal or oesophageal ganglia, was first suggested by Meinert (1860)², Pawlowa (1895) and by Carrière and Bürger (1897) and confirmed by Heymons (1899), de Sinéty (1899), Janet (1894, 1899) and others through histological and embryological studies. The significant experimental work of Kopec (1922, 1924) established the function of the secretion of the corpora allata. The effects of this secretion on metamorphosis have been the subject of investigation by many workers in the past few years, notably Wigglesworth (1934 A, 1934 B,

¹Pfeiffer (1939) has adopted the term corpora cardiaca.

²This paper, quoted by Holmgren (1904), appears in volume 5 of Naturvidenskabelige og Mathematisk Afhandlinger, a journal unobtainable in the United States.

1939 A), Pflugfelder (1937 A, 1937 B, 1938 A, 1938 B, 1938 C) and Bounhiol (1937, 1938). Summaries of this experimental work are ably supplied by Koller (1938) and Hänstrom (1939).

The oesophageal nerve usually extends posteriorly from the occipital ganglion, and it often ends in the ingluvial ganglion on the posterior wall of the crop. There are usually several short nerves running from the ingluvial ganglion. The oesophageal nerve is often paired, and there may or may not be two ingluvial ganglia. Frequently, where there is a single oesophageal nerve, it simply branches at its posterior extremity, and the ingluvial ganglion is not in evidence. The oesophageal nerve has been called the pharyngeal, the ventricular, the gastric, the stomatogastric, the vagus, and the sympathetic nerve; and it has been referred to as a paired or unpaired continuation of the recurrent nerve. The ingluvial ganglion has been called the vagus, the splanchnic, the visceral, and the stomachic ganglion. The nerves branching from the ingluvial ganglia have been called stomatogastric nerves.

In its more complex form the post-cerebral centers of the stomodaeal nervous system consist of the occipital ganglion and two ingluvial ganglia. Two paired structures are associated with the occipital ganglion: the corpora cardiaca and the corpora allata. Parts of the former are probably nervous tissue. Imms' (1934) concept of two types of systems is based principally on whether the oesophageal (recurrent) nerve is paired or unpaired. This idea was previously set forth by Pawlowa (1895). But there are so many other variations in the pattern of innervation which are of equal significance that any classification is of little value.

The elucidation of the variations in the arrangements of the parts of the stomodaeal nervous system is the primary purpose of this paper. Much of what is presented has been gathered piecemeal from the literature and combined with original observations. The stomodaeal nervous system has been a sort of step-child; our knowledge of it has come incidentally from such sources as investigations of the corpora allata, the histology of the brain, and embryological studies. Unless otherwise indicated, the figures accompanying this paper are from original drawings made from dissections performed under a binocular microscope.

METHODS

The parts of the stomodaeal nervous system are always close to the alimentary tract, and many parts of the latter are often heavily sclerotized. Thus it is nearly impossible to obtain microtome sections unless the various nerves and ganglia are first removed. Attempts to obtain serial sections giving a picture of the entire system were not successful. In some cases the postcerebral nerves and ganglia were removed and sectioned so as to confirm the relationship of the occipital ganglion, the corpora cardiaca, and the corpora allata. This was done in the adult dragonfly, and the cell structure of these bodies was studied. It was found that material fixed in Bouin's fluid or in Carnoy-Lebrun fixative yielded good results. Standard haematoxylin stain was satisfactory, though others were tried. Some specimens were imbedded in celloidin, but they were of little value.

Some material fixed in Bouin's solution was dehydrated and imbedded in the usual way, after which thick sections were made with a razor blade. These sections, which were approximately one millimeter in thickness, were cleared, stained in standard haematoxylin, and preserved in 70% alcohol. They were then dissected under a wide-field binocular. This method made possible a better quality of section than could be obtained without imbedding.

Gross dissection has been the principal means of tracing the nerves and of obtaining a picture of the whole stomodaeal nervous system. The specimens were preserved in 85% alcohol and dissected under a wide-field binocular microscope with a maximum magnification of 30 diameters. Material fixed in Carnoy-Lebrun solution can be satisfactorily used for gross dissections. Occasionally specimens were stained in

toto with methylene blue or with eosin, but this is not necessary if the background of the field is changed from white to black and vice versa, depending upon the nature of the structure under consideration. A more careful study of nerves and ganglia can often be made if they are removed from the specimen and placed in glycerine slightly thinned with alcohol. Such a procedure makes it possible to examine the parts under the compound microscope in which case direct light is usually helpful. A very strong light is needed for any type of gross dissection. A useful dissecting needle was made by inserting a minuten pin in a suitable wooden handle.

Most of the specimens used were collected at Washington's Birthplace, Virginia.

THE STOMODAEAL NERVOUS SYSTEM
OF PROTURA (MYRIENTOMATA) AND COLLEMBOLA.

Berlese (1909) described the frontal ganglion, the recurrent nerve, and the corpora allata in proturans. The ending of the recurrent nerve and the union of the corpora allata with a nerve center are still obscure.

The frontal ganglion and the unpaired corpus allatum of Collembola were observed by Hoffmann (1911). No other information in this group is available.

THE STOMODAEAL NERVOUS SYSTEM OF ORTHOPTERA.

Mention is made of some parts of the stomodaeal nervous system in various Orthoptera by I. F. Brandt (1831); in the oriental cockroach by Newton (1879) and by Koestler (1883); in Blatta by Hofer (1887); in phasmids by Heymons (1899) and by de Sinéty (1899); in the phasmid, Bacillus rossii F. and other Orthoptera by Police (1910); in the phasmid, Dixippus morosus Br., by Giersberg (1928) and by Pflugfelder (1938 A, 1938 C); and in the migratory locust by Roomwal (1937). Most of these papers deal primarily with the nature of the corpora allata. From the papers which are concerned with phasmids, it is possible to obtain a fairly complete picture of the stomodaeal nervous system in these insects. The recurrent nerve unites the frontal ganglion and the occipital (oesophageal) ganglion from which short nerves extend to paired anterior pharyngeal ganglia and posterior pharyngeal ganglia which are without doubt the corpora cardiaca and the corpora allata respectively. There is some disagreement as to the connection of the anterior pharyngeal ganglia with the brain. A median

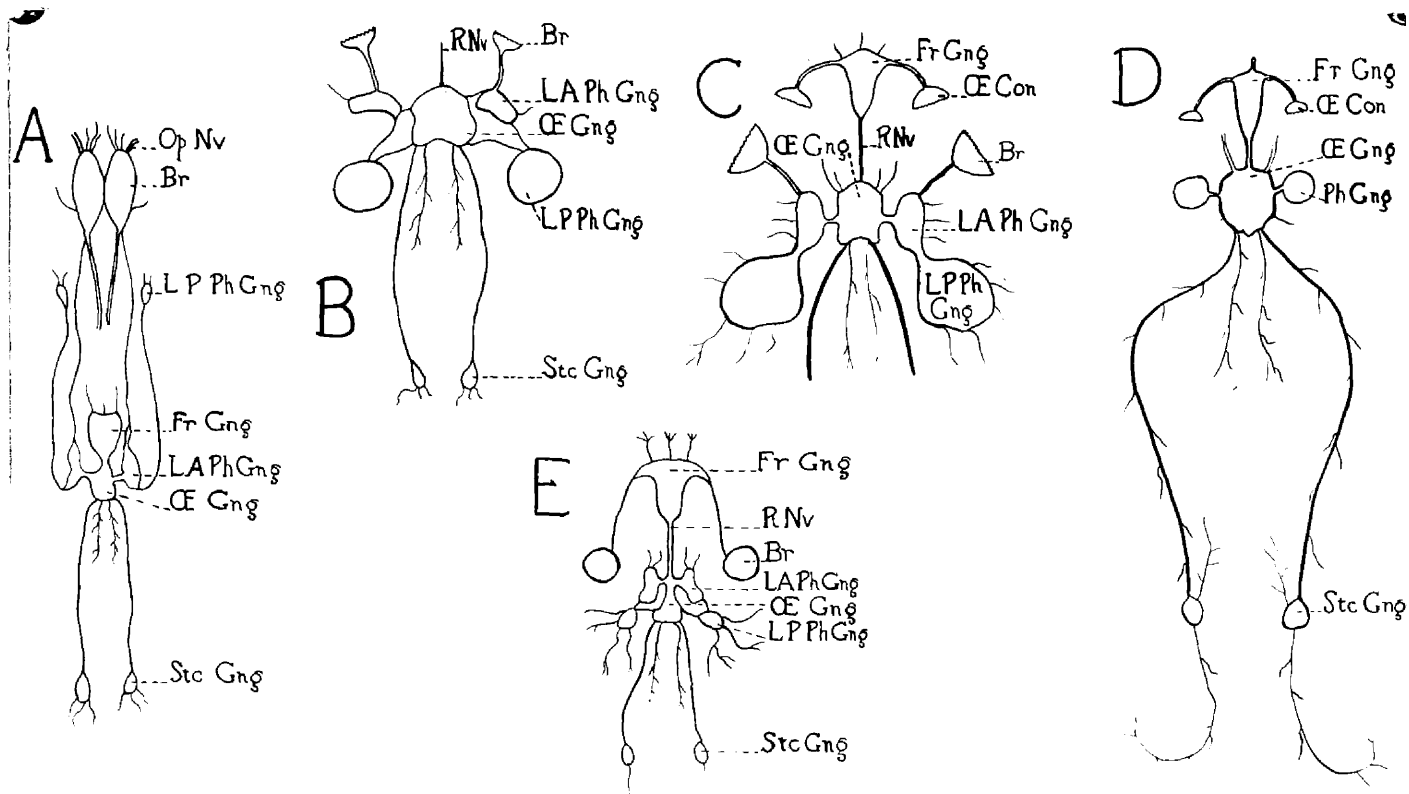


Fig. 1. Stomodaeal Nervous System of Orthoptera; all figures redrawn from Bordas.

- A. *Truxalis unguiculata* Ramb.
- B. *Caloptenus italicus* L.
- C. *Aedipoda coerulescens* L.
- D. *Platyphyllus gigantum* L. or *Pseudophyllanax insularis* Walker
- E. *Schistocerca peregrinum* Oliv.

oesophageal nerve extends posteriorly from the occipital ganglion and ends in an ingluvial (stomachic) ganglion. The picture thus acquired is very like that given by Bordas (1900) for the mantid, Hierodula bioculata Burm. (Fig. 2B).

Pierantoni (1901, 1902) investigated the stomodaeal nervous system in two species of saltatorial Orthoptera (Pachytilus cinerascens and Epacromia thalassina)¹. In them he found the occipital ganglion (median gut ganglion) and the four structures united with it which he termed anterior and median paired ganglia. Extending posteriorly from the occipital ganglion are two pairs of nerves, and the posterior paired ganglia are at the ends of one pair of these oesophageal nerves. The arrangement is similar to that observed by Bordas (1900) in Schistocerca peregrinum Oliv. (Fig. 1E). In both cases the connection of the so-called anterior paired ganglia with the brain is not shown.

Although the work of Bordas (1900) does not take into account the glandular nature of the corpora allata, it is nevertheless of considerable value. It is confined to one order, but this paper contains more detailed information about the stomodaeal nervous system than any other except that of Nabert (1913). Bordas gives figures of the stomodaeal nervous system in acridids, tettigoniids, crickets, roaches, and mantids. Some of these are redrawn in Figures 1, 2A and B, and 5B. The names of the respective parts have been translated literally and retained. The oesophageal connective of Bordas is the circumoesophageal connective of Snodgrass (1935) and others.

¹Pierantoni omitted the authors of these species.

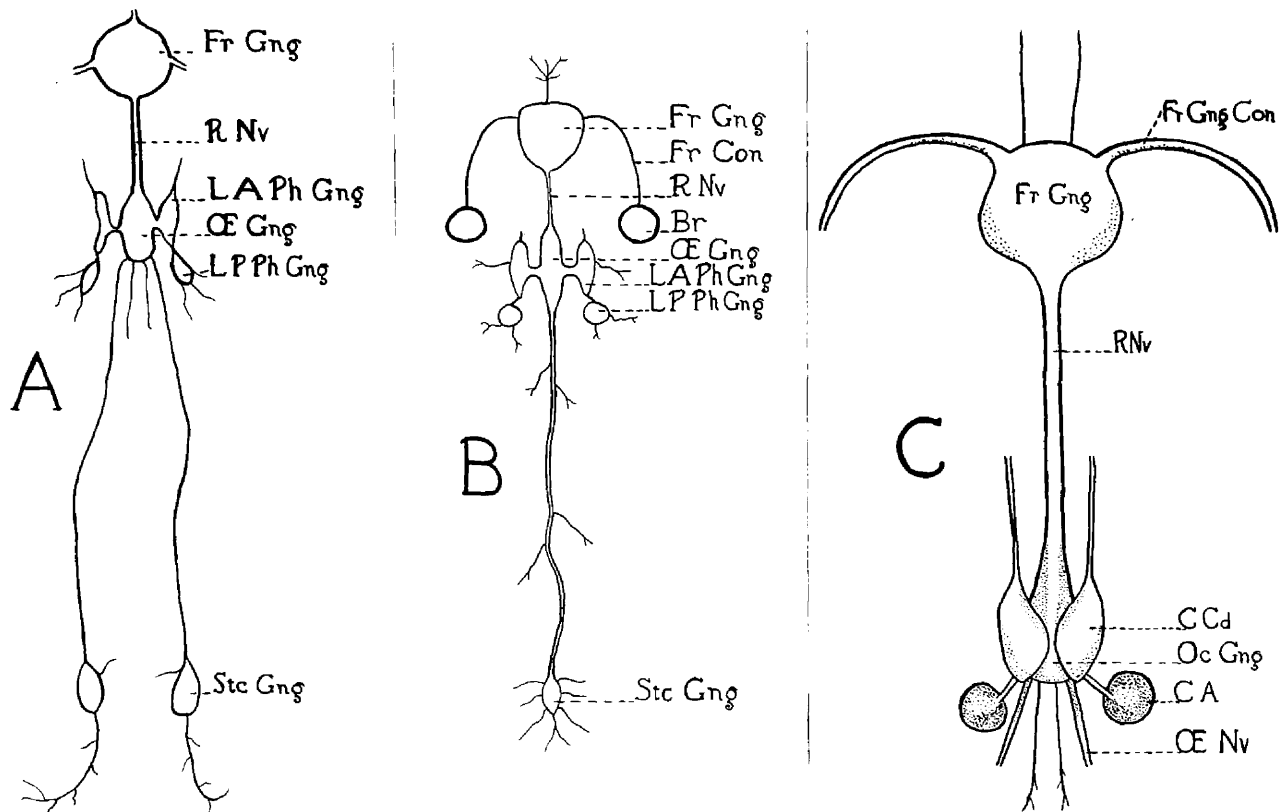


Fig. 2. Stomodaeal Nervous System of Orthoptera.

A. *Gryllus campestris* Latr., redrawn from Bordas.

B. *Hierodula bioculata* Burm., redrawn from Bordas.

C. Anterior Detail of Stomodaeal Nervous System of *Schistocerca americana* (Drury).

Among the acridids it will be seen that there are two pairs of "lateral pharyngeal ganglia" and that the chief variation is in the size, shape, and relative position of these structures and of the "oesophageal ganglion" and the frontal ganglion. In Caloptenus italicus L. (Fig. 1B) the frontal ganglion is present but is not shown. In Aedipoda coerulescens L. (C) the "stomacal ganglia" were not discovered. In Schistocerca peregrinum Oliv. (E) the nerves joining the "lateral anterior pharyngeal ganglia" with the brain were not found.

An investigation of the stomodaeal nervous system of Schistocerca americana (Drury) (Fig. 2C, Fig. 3) has shown that the corpora cardiaca (lateral anterior pharyngeal ganglia) are joined to the protocerebrum by short nerves. These bodies, however, are not connected by separate nerves with the corpora allata (posterior lateral pharyngeal ganglia). There are many similarities in the two grasshoppers. Bordas' figures indicate that the "paired pharyngeal ganglia" are in the same plane with or ventral of the "oesophageal ganglion". In reality the corpora cardiaca are dorsad and the corpora allata are ventrad of the occipital ganglion.

In the katydid, Platyphyllum gigantum L. (Fig. 1D), Bordas assumes that the "lateral anterior oesophageal ganglia" have become fused with the "oesophageal" ganglion. Apparently this is not the case. For dissections of Microcentrum rhombifolium (Saussure) indicated that these bodies are separate. In fact, the entire stomodaeal nervous system in this katydid was found to be so similar to that of the grasshopper that it is not figured.

In the cricket, Gryllus campestris Latr. (Fig. 2A) the frontal ganglion is larger than in acridids and tettigoniids; but if it is assumed that the nerves extending anteriorly from the "lateral anterior

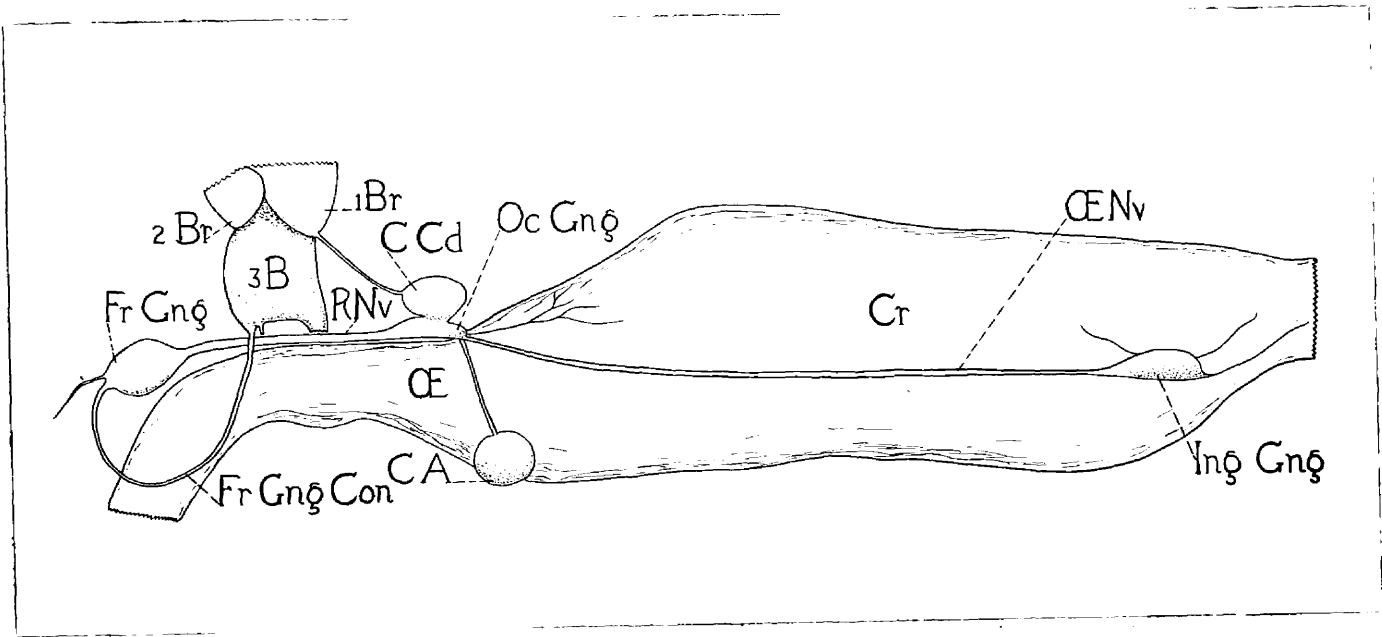


Fig. 3. Lateral View of Stomodaeal Nervous System of Schistocerca americana (Drury).

oesophageal ganglia" unite with the brain, the pattern illustrated by Bordas is otherwise similar in grasshoppers and crickets.

According to Bordas the stomodaeal nervous system of the mantid, Hierodula bioculata Burm. (Fig. 2B), resembles closely that of phasmids, and differs from that of acridids principally with regard to the nerves extending posteriorly from the occipital (oesophageal) ganglion. In mantids and phasmids there is a single oesophageal nerve and a single ingluvial (stomacal) ganglion. In grasshoppers these structures are paired. The union of the "anterior oesophageal ganglion" and the brain in the mantid is obscure.

A diagram of the stomodaeal nervous system of the oriental cockroach, based on the work of Koestler (1883) is given by Miall and Denny (1886). There is no occipital ganglion shown, but in other respects the arrangement is similar to that given by Bordas (1900) for Blabera atropos Stoll. (Fig. 5B). A semischematic drawing of the pharyngeal bodies and the corpora allata of the oriental cockroach is reproduced from the work of de Lerma (1937) in Figure 5C. The paired pharyngeal bodies, which are the lateral anterior pharyngeal ganglia of Bordas, are tickened at their median posterior extremities where they join the recurrent nerve. This area forms the oesophageal ganglion of Bordas. But Bordas shows two nerves extending laterally from this center to the corpora allata (lateral posterior pharyngeal ganglia). These nerves are not present in the American cockroach (Fig. 4). Here the arrangement agrees with that of de Lerma except that the corpora cardiaca (pharyngeal bodies) are placed in a more posterior position, and the occipital ganglion is more distinct. Figure 5C should serve to explain de Lerma's

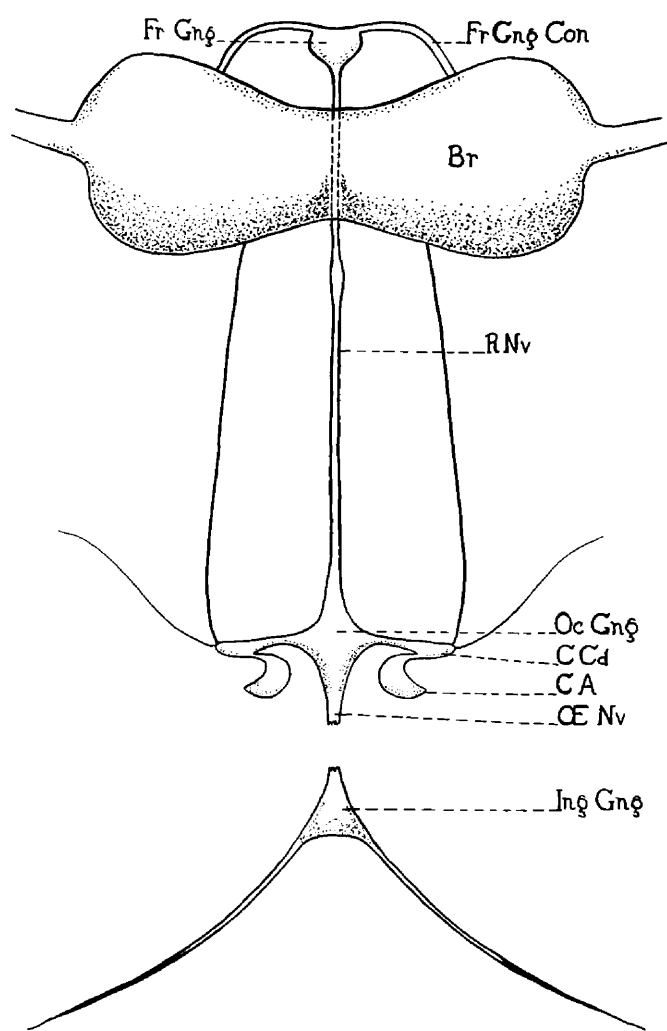


Fig. 4. Stomodaeal Nervous System of Periplaneta americana L.

idea of the secretory function of the "pharyngeal bodies". Experimental work is needed to substantiate his histological evidence.

The corpora cardiaca and corpora allata in many Orthoptera are reported to be somewhat asymmetrical by Bordas (1900) and others.

THE STOMODAEAL NERVOUS SYSTEM OF ODONATA, PLECOPTERA, AND ISOPTERA.

The only mention of any part of the stomodaeal nervous system of Odonata to be found in the literature is that made by Baldus (1924). He figures the frontal ganglion of a dragonfly, but does not show the exact point of union with the brain. Up to the present time, no evidence of the existence of any other ganglia has been given.

In a dragonfly naiad (Fig. 6) the frontal ganglion connectives arise from tritocerebral lobes of the brain which extend anteriorly to the labrum. The recurrent nerve runs back under the brain on the dorsal wall of the pharynx to the occipital ganglion. From this ganglion the corpora cardiaca branch anteriorly and the corpora allata, posteriorly. These five structures are very closely associated with each other. A short nerve connects each corpus cardiacum with the protocerebrum. The median oesophageal nerve runs posteriorly to the ingluvial ganglion which lies on the dorsal wall of the oesophagus where the latter begins to enlarge and form the crop. A nerve from the ingluvial ganglion running posteriorly stops near the hind end of the crop. The corpora cardiaca are slightly dorsad of the occipital ganglion, and the aorta runs between them and stops just behind the brain.

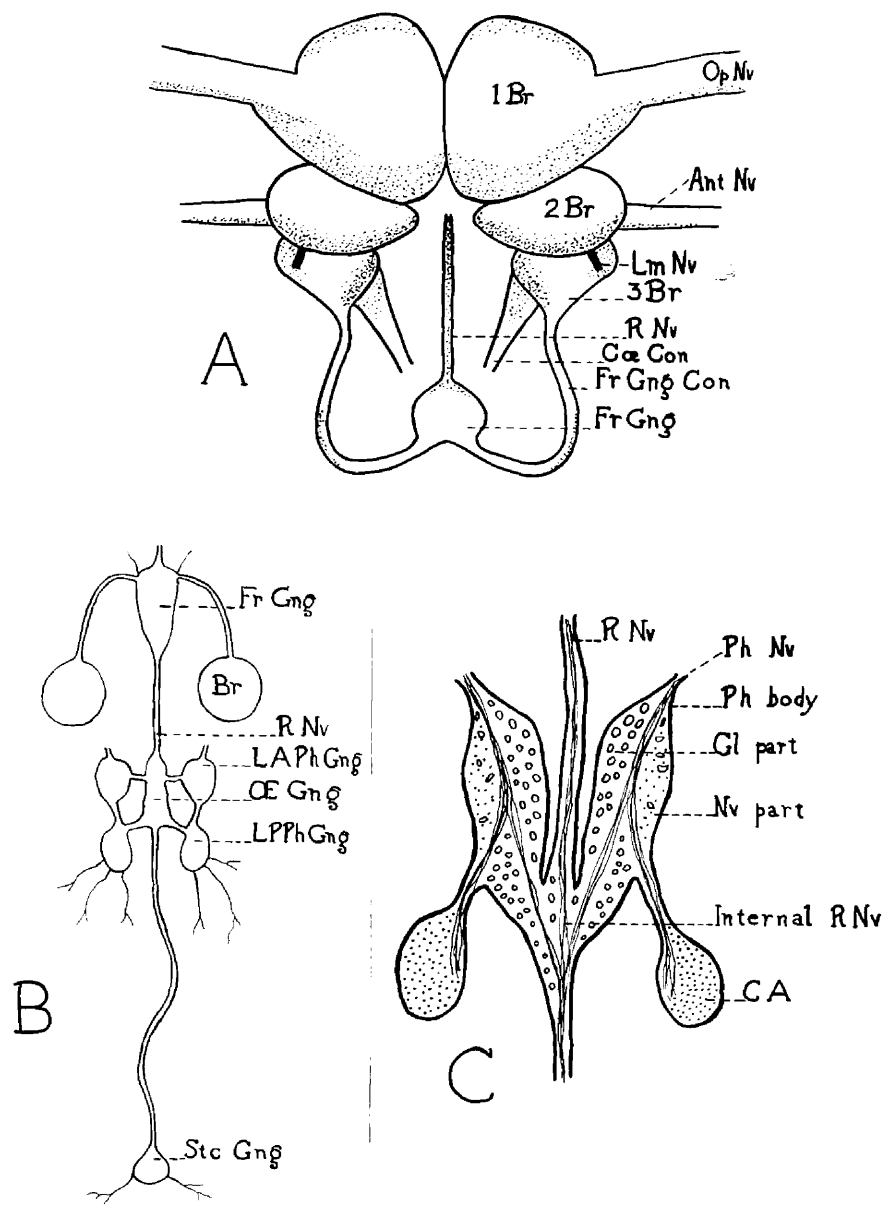


Fig. 5. Stomodaeal Nervous System of Orthoptera.

- A. Frontal view of brain and frontal ganglion of the American roach, *Periplaneta americana* L.
- B. Stomodaeal nervous system of *Blabera atropos* Stoll., redrawn from Bordas.
- C. Pharyngeal bodies and corpora allata of oriental cockroach, *Platta orientalis* L., semi-schematic, redrawn from de Lerma.

In the adult dragonfly (Fig. 7) the frontal ganglion is exceptionally close to the brain and the frontal ganglion connectives are unusually thick. In contrast to their position in the naiad the corpora cardiaca are slightly ventrad of the larger part of the occipital ganglion, and the anterior parts of them are situated under the brain with which they are connected by short, thin nerves. The corpora allata are also located under the brain. They are much farther from the occipital ganglion in the adult than in the naiad. The median oesophageal nerve connects the occipital ganglion with the ingluvial ganglion which is located on the dorsal wall of the anterior part of the crop. The frontal ganglion, the occipital ganglion, and the corpora cardiaca are rather large in the dragonfly as compared with most other insects.

Microtome sections were made of the corpora cardiaca and occipital ganglia of several dragonfly adults. But the results gave no evidence with regard to their glandular nature. All of these structures appear to consist of nervous tissue, but sections of the corpora allata were indicative of their glandular nature.

Nabert (1913) states that in the stone-fly, Perla maxima Scop., the paired corpora allata lie behind the occipital (pharyngeal) ganglion and are connected with it by the "nervus corporis allati". He makes no mention of the recurrent nerve nor of any other parts of the stomodaeal nervous system.

The stomodaeal nervous system of termites was investigated by Holmgren (1896). Nabert (1913), essentially corroborating his findings, states that the "Schlundnervensystem" consists of three structures: the frontal ganglion, the paired "ganglia postcerebralia", and the paired corpora allata. The paired ganglia are said to take their origin from

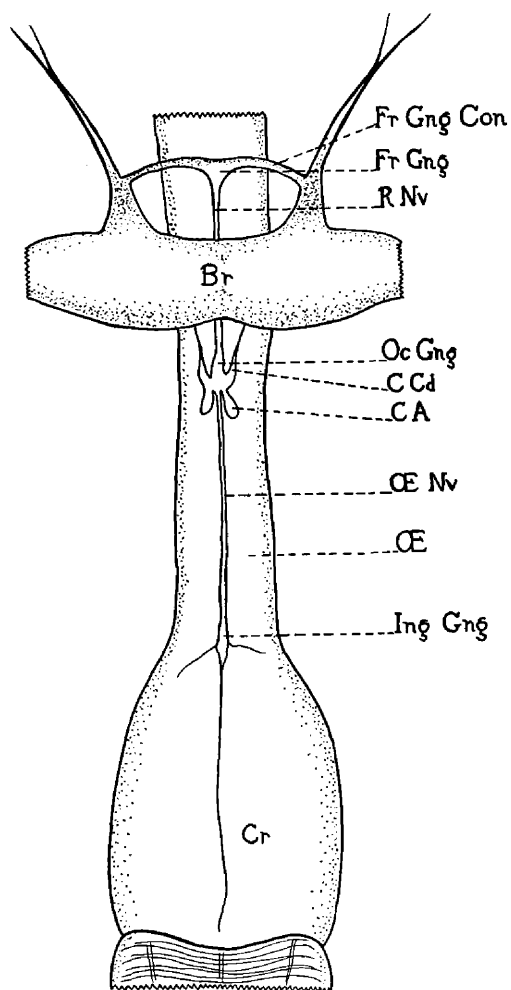


Fig. 6. Stomodaeal Nervous System of a Dragonfly Naiad (unidentified); aorta removed.

the brain, but the recurrent nerve is not mentioned. The embryological studies of Strindberg (1913) do not explain the postcerebral innervation of the stomodaeum, but they show that an occipital ganglion may exist in some species. Thompson (1916) describes an unpaired recurrent nerve extending posteriorly from the frontal ganglion but does not clarify the details of the postcerebral structures.

Imms (1937) illustrates the brain and associated parts of a winged termite. Paired "posterior sympathetic nerves" run posteriorly from the brain into paired "oesophageal sympathetic ganglia" which in turn contact the corpora allata. The recurrent nerve extends posteriorly from the frontal ganglion and ends at a point behind the corpora allata without having any connection with the paired structures. This pattern is unique. In all insects in which the recurrent nerve has been followed to its posterior end there is some degree of consolidation of the recurrent nerve and the corpora cardiaca (oesophageal sympathetic ganglia) or corpora allata. In lepidopterous larvae (Fig. 13) these bodies are unusually far away from the recurrent nerve, but they are connected with it by slender nerves.

According to an investigation of Pflugfelder (1938 B) the corpora cardiaca of several different termites are just above and at the sides of the occipital (hypocerebral) ganglion. The latter is apparently joined to the frontal ganglion by the recurrent nerve.

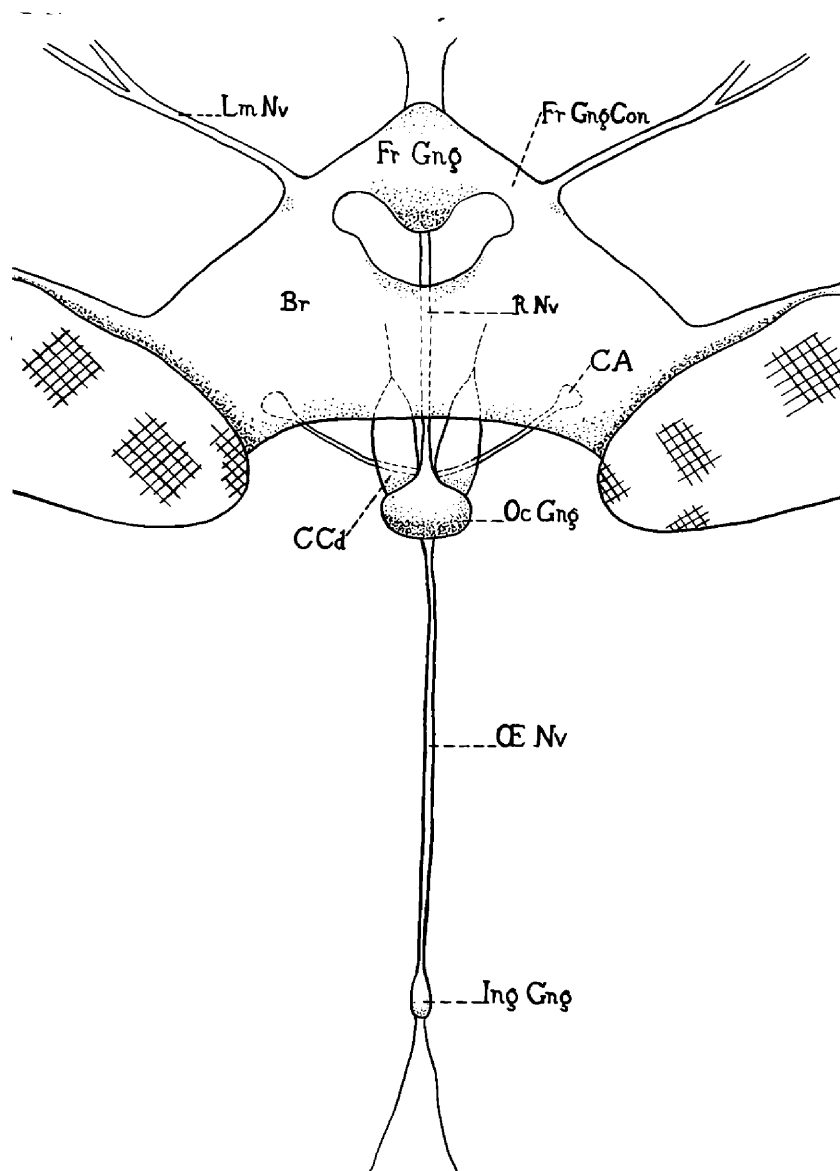


Fig. 7. Stomodaeal Nervous System of *Libellula* sp. (adult); aorta and oesophagus removed.

THE STOMODAEAL NERVOUS SYSTEM OF HOMOPTERA AND HEMIPTERA.

Bugnion (1908) described the stomodaeal nervous system in the lantern-fly, Fulgora. It consists of a frontal ganglion, recurrent nerve, and "anterior and posterior paired visceral ganglia". There is no mention of an occipital ganglion or of ingluvial ganglia. The anterior "visceral ganglia" are supposed to innervate the tracheae, and the posterior "visceral ganglia" are supposed to innervate the heart. This supposition is frequently stated by the older workers for various insects and occasionally it is said that the anterior pair innervates the heart and that the posterior pair innervates the tracheae.

In aphids (Pemphigus) the frontal ganglion is almost directly beneath the brain according to Pflugfelder (1937 A). The corpora allata are apired but are contiguous, and there seems to be no occipital ganglion. The corpora cardiaca are joined by short nerves to the posterior part of the brain and are in contact with the anterior parts of the corpora allata. From the corpora allata there are apparently three nerves which run back over the wall of the foregut. It is possible that these nerves may emanate from the corpora cardiaca instead of the corpora allata.

Pflugfelder also describes the stomodaeal nervous system in a scale insect (Lecanium). Here again the frontal ganglion is beneath the brain. The recurrent nerve, following the stomodaeal wall, swells to form the occipital (hypocerebral) ganglion behind the brain; and continuing along the oesophagus, it stops at a point in front of the midgut. The corpora allata, which are attached to the occipital ganglion, are larger than the brain.

In the cicada (Fig. 8) the frontal ganglion is located just above the stomodaeum near the junction of the latter with the sucking pump. The short recurrent nerve runs under the brain, then bifurcates. The branches run to the paired corpora cardiaca which are irregular in shape and practically surround two of the dilator muscles of the Pharynx. (The attachment of this pair of muscles to the pharynx is omitted in Fig. 8A). Paired oesophageal nerves pass posteriorly from the corpora cardiaca, but there are no ingluvial ganglia. The paired corpora allata are in contact with the posterior ventral parts of the corpora cardiaca. All of these bodies are dorsad of the stomodaeum. Nerves passing from the corpora cardiaca directly to the brain were not found.

In all of the Homoptera which have been studied the corpora allata are distinctly paired, but they are usually very close to each other. In Hemiptera there is only one corpus allatum and it is often somewhat asymmetrical.

Weber (1930) notes the presence in Cimex of the frontal ganglion and two "occipital ganglia" connected to the brain by short nerves and to the frontal ganglion by the recurrent nerve. From these "occipital ganglia" a nerve extends posteriorly along the foregut wall. There is no mention of a corpus allatum. This description was based on unpublished work of Titschack.

A delineation of the stomodaeal nervous system of the coreid Syromastes, is made by Pflugfelder (1937 A). In this bug, the recurrent nerve connects the frontal ganglion and the occipital (hypocerebral) ganglion. Behind the latter in close association with each other are located the corpus cardiacum and the corpus allatum. Their nervous connection is not clearly understood. Paired oesophageal nerves pass

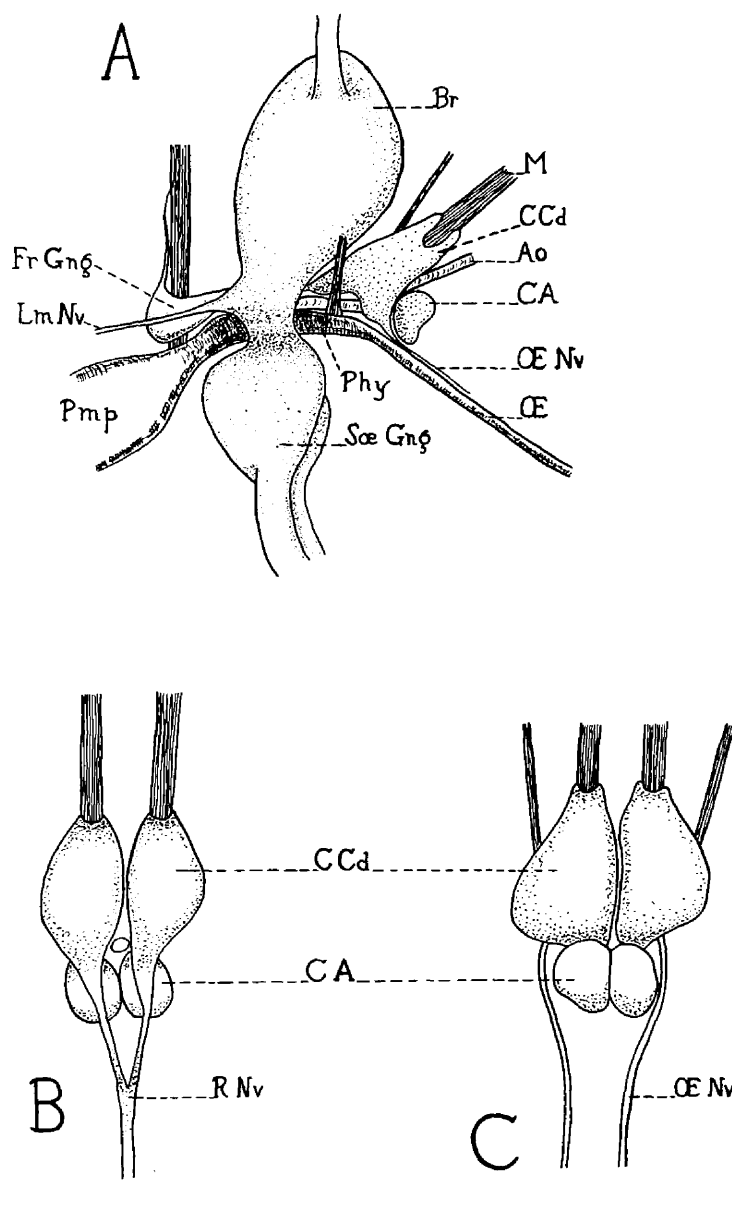


Fig. 8. The Stomodaeal Nervous System of Magicicada septendecim L.

- A. Lateral view; M, dilator muscle, attachment to pharynx not shown.
- B. Frontal view of corpora cardiaca and corpora allata, somewhat diagrammatic.
- C. Posterior view of corpora cardiaca and corpora allata; aorta and oesophagus not shown.

posteriorly from the occipital ganglion, but there are no ingluvial ganglia.

In *Nepa*, according to Graichen (1936), paired connectives extend from the tritocerebrum to the frontal ganglion. A ventral commissure runs around the pharynx from one side of the frontal ganglion to the other; a pair of nerves passes anteriorly from the frontal ganglion to the labrum; and a median dorsal nerve runs to the pharyngeal musculature. The recurrent nerve proceeds posteriorly from the frontal ganglion to the occipital (hypocerebral) ganglion and continues posteriorly from it as an unpaired oesophageal nerve. It soon divides into two branches which traverse the sides of the oesophagus as far as the stomach. There is a pair of "lateral ganglia", each of which is connected with the tritocerebrum by two nerves. Histological evidence of the nervous nature of these lateral ganglia is presented. They are connected with each other by a commissure which apparently does not join the recurrent nerve. The corpora allata are almost fused into a single body, and they lie above the point where the commissure from the lateral ganglia crosses the recurrent nerve.

In the green stink bug, *Nezara*, (Fig. 9) the corpora cardiaca are fused ventrally but are distinctly lobed dorsally. The ventral coalescence of the bodies and their amalgamation with the posterior end of the recurrent nerve apparently form the occipital ganglion. For it is from this plexus that the paired oesophageal nerves originate. They pass under the unpaired corpus allatum which is contiguous with the posterior part of the plexus just described. Its histological structure should be investigated.

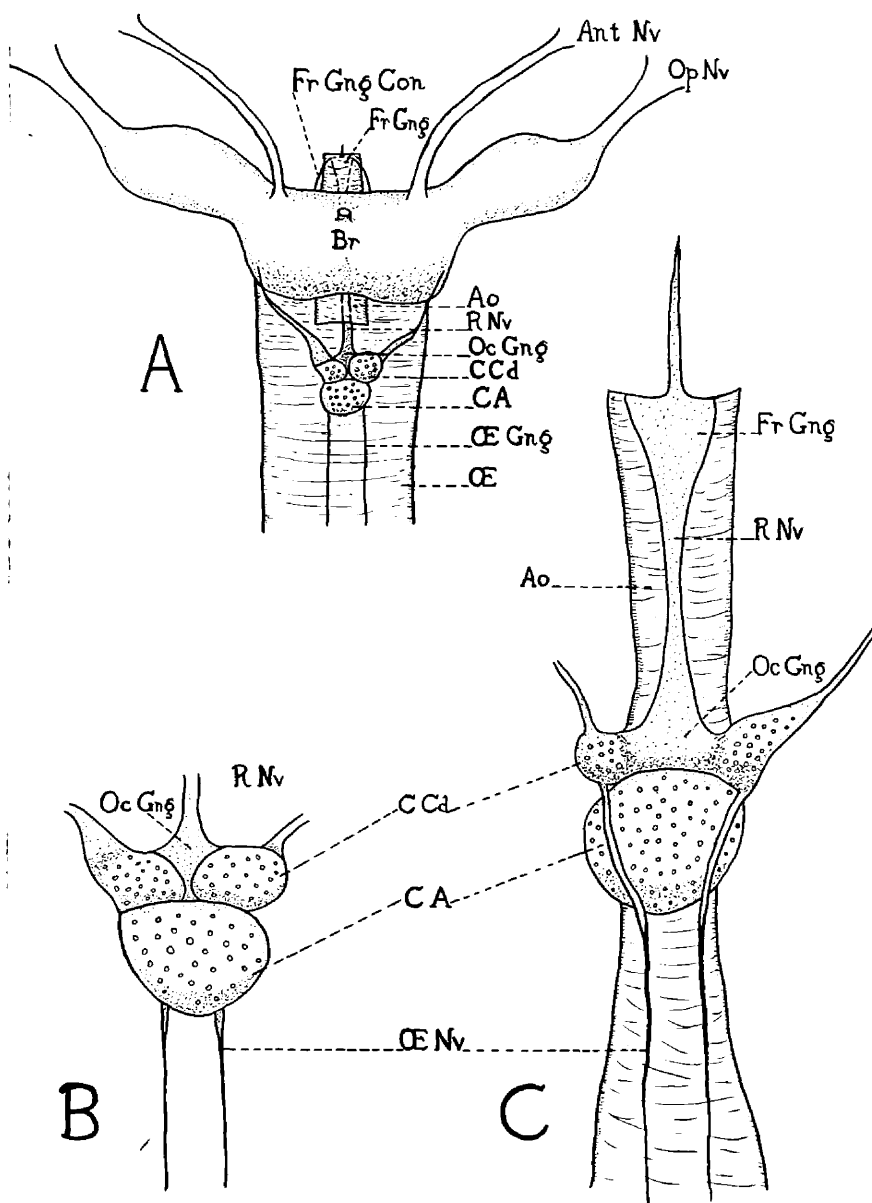


Fig. 9. Stomodaeal Nervous System of Nezara hiliaris Pay.
 A. Dorsal view; aorta partly removed.
 B. Dorsal view, detail of postcerebral structures;
 aorta and oesophagus removed.
 C. Ventral view; oesophagus removed.

In the wheel bug, Arilus (Fig. 10) the postcerebral parts of the stomodaeal nervous system are similar to those of Nezara. There is a fusion of the corpora cardiaca with the occipital ganglion, and the corpus allatum rests on the posterior part of this mass. Numerous specimens of these two bugs were examined, and it is believed that the asymmetry of the corpora cardiaca and corpus allatum is rather constant. This has been observed in Orthoptera, Diptera, and other insects.

THE STOMODAEAL NERVOUS SYSTEM OF COLEOPTERA.

Brandt (1879 C) discovered in beetles the frontal ganglion, the recurrent nerve, one or two pairs of "posterior pharyngeal ganglia," and the "ventricular ganglion." The pharyngeal ganglia were supposed to innervate the heart and tracheae.

The aquatic beetle Dytiscus was studied by Holste (1910) and Korschelt (1924), whose results are essentially the same except for differences in nomenclature. The frontal ganglion sends off nerves anteriorly to the pharyngeal muscles, and these nerves form the "plexus praefrontalis" of Holste. Posteriorly the recurrent nerve passes from the frontal ganglion, swells to form the occipital ganglion under the brain, and continues asymmetrically as the oesophageal nerve to the ingluvial (ventricular) ganglion, which is located on the left wall of the crop near its posterior end. Several short nerves arise from the ingluvial ganglion, and two of these innervate the anterior part of the proventriculus. Along the course of the oesophageal nerve many branching fibers innervate the oesophagus. Immediately behind and below the brain are the paired "ganglia vasis dorsalis" which innervate the dorsal vessel and which are joined to the protocerebrum. The corpora allata

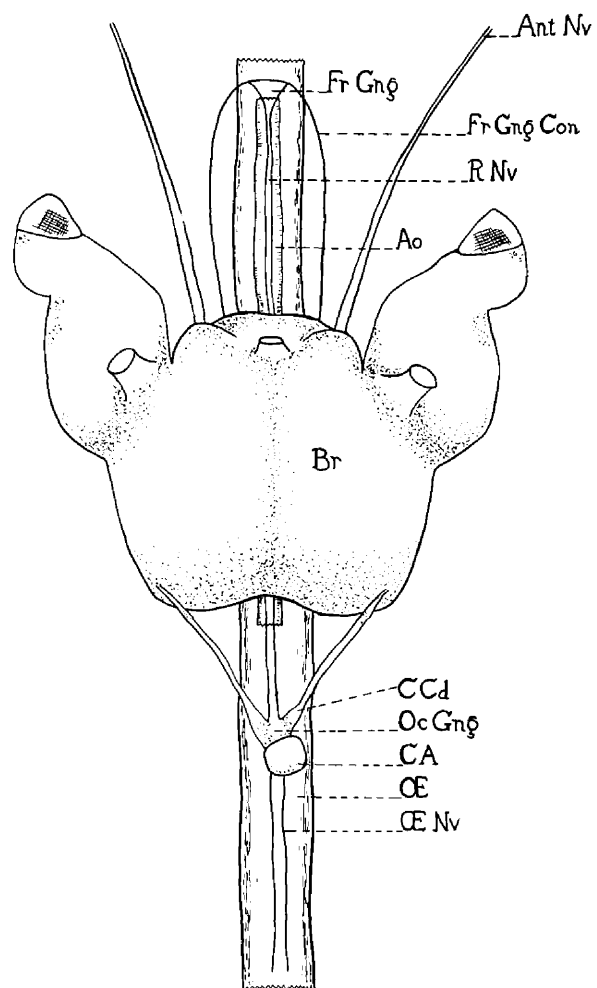


Fig. 10. Stomodaeal Nervous System of Arilus cristatus L.

lie behind the "dorsal vessel ganglia" with which they are united by short, thick fibers. The connections of the "dorsal vessel ganglia" with each other and with the occipital ganglion are not fully understood.

In the scarabaeid Oryctes Mickels (1880) demonstrated the frontal ganglion and the occipital ganglion united by the recurrent nerve. The occipital ganglion, according to this author, sends two nerves to the brain and three pairs of nerves posteriorly along the oesophagus. The endings of these nerves are not shown, and no paired ganglia were observed.

In the same insect (Oryctes) Orlov (1924, 1925) reports the presence of the median occipital (hypocerebral) ganglion from which two nerves run posteriorly to paired "ventricular ganglia." From each of the latter nerves extend posteriorly along the dorsal surface of the oesophagus. A second "ventricular ganglion" appears as a swelling along the course of each median fiber. No mention is made of the corpora allata.

According to Wu (1929) there are two pairs of "lateral oesophageal ganglia" in the "white grub," Osmoderma. These are joined to the brain, but not to the recurrent nerve nor to the occipital ganglion. There are several short nerves branching from each of the aforementioned ganglia, but they were not followed to their endings. The nerves and ganglia were studied histologically, and it is surprising that no mention is made of the corpora allata.

The stomodaeal nervous system of the green June beetle, Cotinis, (Fig. 12A) has one unique feature. The frontal ganglion connectives join the brain at a point between the protocerebrum and the deutocerebrum. In most other insects these connectives arise from the tritocerebrum. In Cotinis the presence of nerve fibers connecting

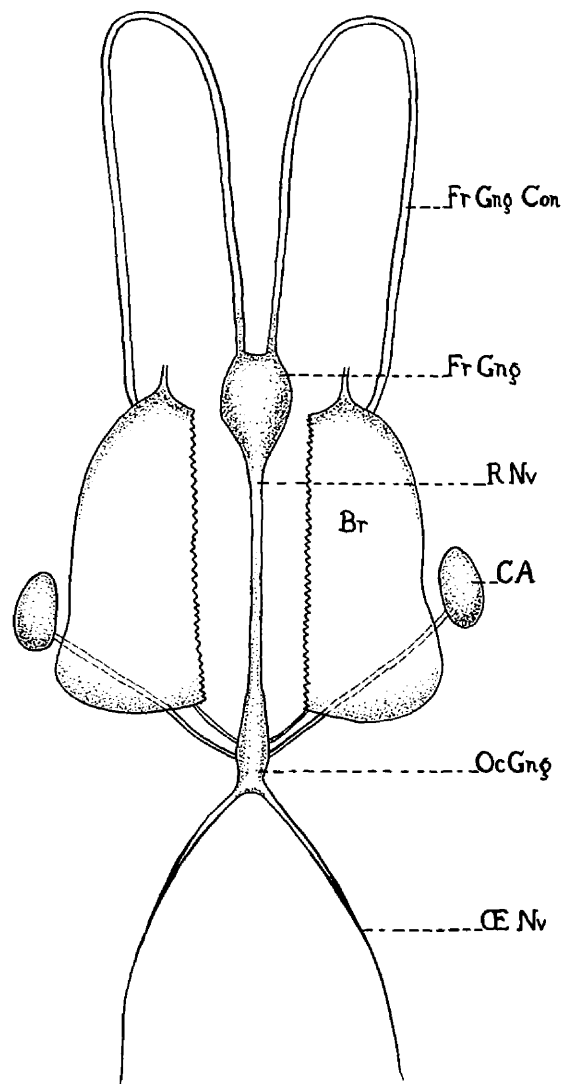


Fig. 11. Stomodaeal Nervous System of the Larva of Passalus cornutus Fab.

the brain and the occipital ganglion has been definitely established. From the occipital ganglion there is a pair of nerves running laterally and posteriorly to the corpora allata, and there is a pair of oesophageal nerves following the dorsal oesophageal wall. The oesophageal nerves send off several short nerves along their course, and each of them terminates by breaking up into four short fibers. The corpora cardiaca were not observed, but it is possible that they have been fused with the occipital ganglion.

In the larva of Passalus (Fig. 11) the general plan of stomodaeal innervation is similar to that in the adult of Cotinis. The frontal ganglion connectives, however, run forward a considerable distance before turning back to the tritocerebrum. The corpora allata are located at the sides of the brain instead of behind it.

THE STOMODAEAL NERVOUS SYSTEM OF NEUROPTERA AND TRICHOPTERA.

A description of the stomodaeal nervous system of Corydalus is given by Hammar (1908). The frontal ganglion is joined to the brain by a fine nerve from its posterior end as well as by the frontal ganglion connectives (arched nerves). The recurrent nerve follows the dorsal wall of the stomodaeum, and swells into a "vagus" ganglion from which paired "stomatogastric" nerves continue down the oesophagus. Three pairs of "lateral sympathetic nerves" spring from the posterior part of the brain. Two of these form many branches and loops, but eventually they end in paired "lateral ganglia." There are several small fibers branching from these. It is interesting to note that there is no connection between the two "lateral ganglia," nor between them and the "vagus" ganglion or recurrent nerve. The corpora allata are not

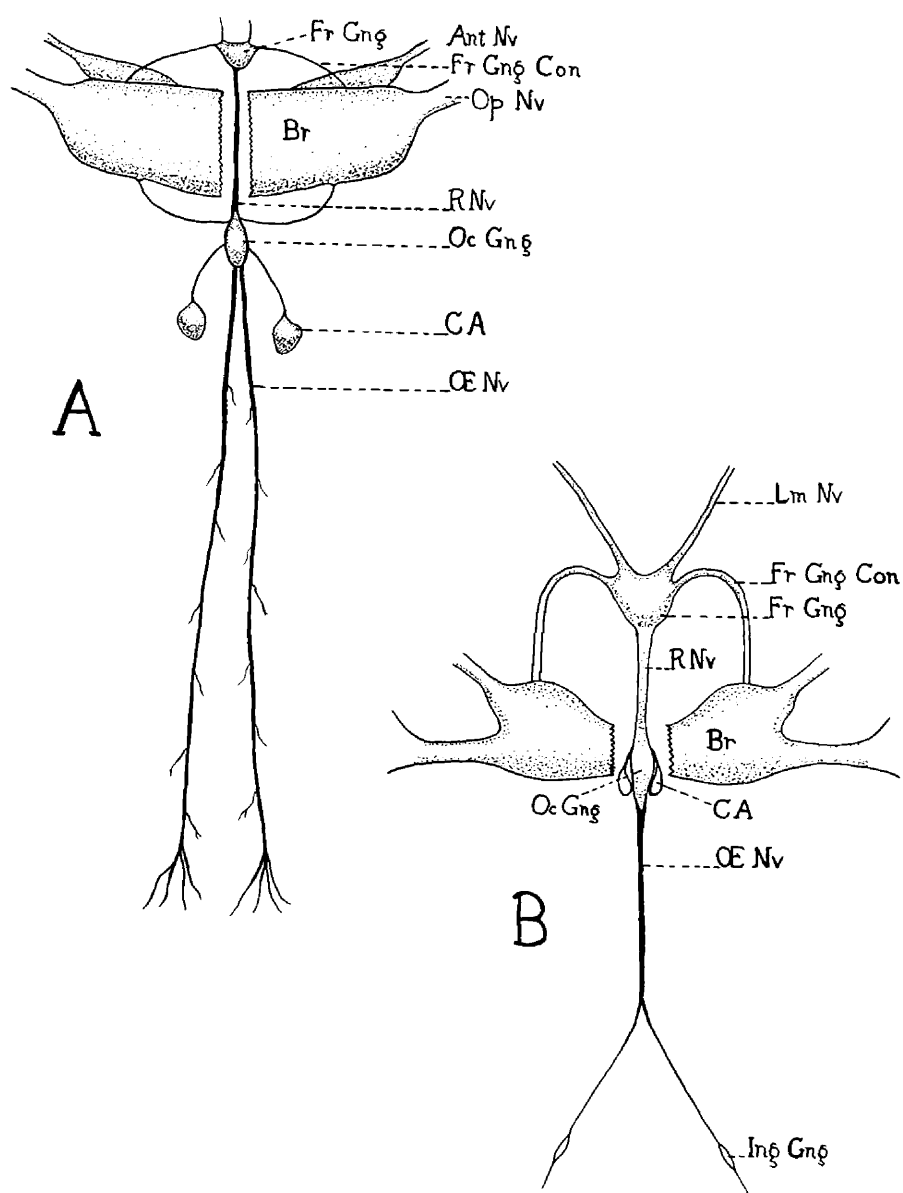


Fig. 12. Stomodaeal Nervous System of Coleoptera and Neuroptera.

A. Cotinis nitida L.

B. Chauliodes pecticornis L.

mentioned. Hammar's work differs somewhat from that of Krauss (1884) who did not locate any lateral ganglia.

In Chauliodes (Fig. 12 B) the stomodaeal nervous system is much simpler. The corpora cardiaca are not distinct. It is possible that they are amalgamated with the occipital ganglion. Two short slender nerves extend from the occipital ganglion to the corpora allata. The corpora allata touch the sides of the occipital ganglion. Nerves joining the occipital ganglion with the brain are apparently absent.

The caddice-fly, Limnophilus, was studied by Branch (1922). The recurrent nerve runs posteriorly from the shield-shaped frontal ganglion along the dorsal wall of the oesophagus and passes on one side of an unnamed median ganglion without being joined to it. From this median ganglion, which is probably the occipital ganglion, a nerve passes posteriorly and unites with the recurrent nerve. How these nerves terminate is not known. Anteriorly from the median ganglion two nerves run to the brain; and laterally two nerves run to two "sympathetic ganglia" which are joined to the brain by still another pair of nerves. The corpora allata are not mentioned.

THE STOMODAEAL NERVOUS SYSTEM OF LEPIDOPTERA.

In the larva of Sphinx ligustri L., according to Newport (1832) there are two pairs of lateral ganglia which are connected to the brain but not to the recurrent nerve. Blanchard (1858) stated that in lepidopterous larvae the lateral anterior ganglia innervate the dorsal vessel and that the lateral posterior ganglia innervate the tracheal trunks of the head. The alimentary tract is innervated by the unpaired part of the "Schlundnervensystem." E. Brandt (1879) established the fact that the lepidopterous larvae as well as adults possess a frontal ganglion and one or two pairs of "pharyngeal ganglia." Cattie (1881) reported that the lateral paired ganglia in lepidopterous larvae are joined to the brain but not to the recurrent nerve. According to Peterson (1912) this is true in the larva of Protoparce. Swaine (1920) investigated the larva of Sthenopis and found that the paired ganglia do join the recurrent nerve. The union of the lateral ganglia and the recurrent nerve in the silkworm was reported by Kuwana (1935) and by Snodgrass (1935).

As far as is known the stomodaeal nervous system of lepidopterous larvae is more complex than that of any other group of insects. An investigation of the larva of Protoparce (Fig. 13) has shown that the so-called anterior lateral ganglia are connected by a nerve to the recurrent nerve. Each of these "ganglia" gives off five nerves; one goes to the recurrent nerve; a second to the brain; a third to the lateral nerve from the brain; a fourth to the mandibular muscles; and a fifth to the corpora allata. The last named nerve has previously been shown to be rather thick; and it is doubtless for this reason that

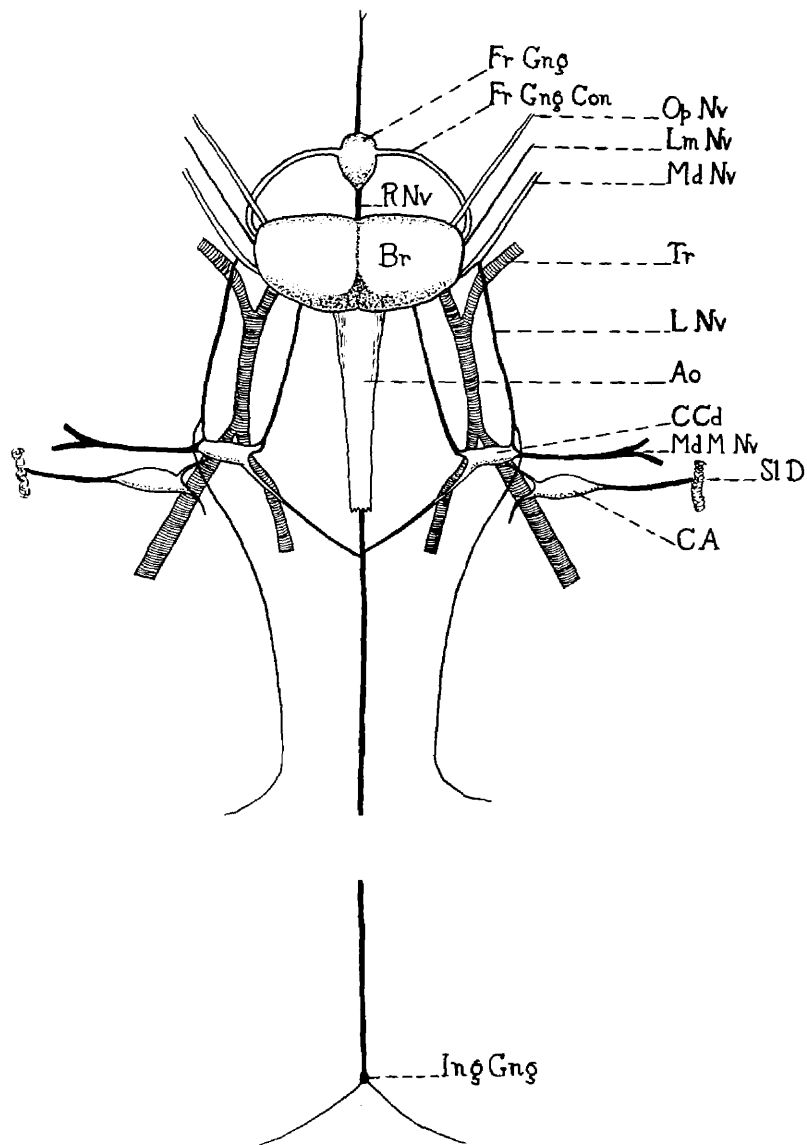


Fig. 13. Stomodaeal Nervous System of the Larva of Protoparce sexta Johanssen.

the corpora allata have not been recognized. These bodies are distinctly separate from the "anterior lateral ganglia." It is felt that the latter structures should be called corpora cardiaca, for they correspond to the corpora cardiaca in other insects in spite of the fact that they are some distance from the recurrent nerve.

The stomodaeal nervous system of the southern army worm moth, Prodenia, (Fig. 14) is quite different from that of lepidopterous larvae. The corpora cardiaca are fused and the median parts of them are joined by the recurrent nerve to form what is probably the occipital ganglion. Two oesophageal nerves extend posteriorly from this mass, part of which is between the ventral parts of the corpora allata. The dorsal parts of the corpora allata are in contact with each other. About halfway down the oesophagus each of the oesophageal nerves sends off a lateral nerve to the salivary glands. Many short nerves branch from the oesophageal nerves to innervate the oesophagus; and the crop, which is a lateral diverticulum, is innervated by branches from them. They end in numerous fine fibers anterior to the ventriculus.

THE STOMODAEAL NERVOUS SYSTEM OF HYMENOPTERA.

I. F. Brandt (1831) illustrated the frontal ganglion and two paired "lateral ganglia" in Bombus, and the paper of E. Brandt (1879 B) contains a figure of the stomodaeal nervous system of Bombus terrestris L. In the mason bee, Chalicodoma, Carrière and Bürger (1897) discovered an occipital ganglion, paired "pharyngeal ganglia", and paired "ganglia allata." In the ant, Myrmica, according to Janet (1899), the recurrent nerve runs posteriorly into an "oesophageal ganglion" from which are sent two oesophageal nerves. Each of these comes in contact with

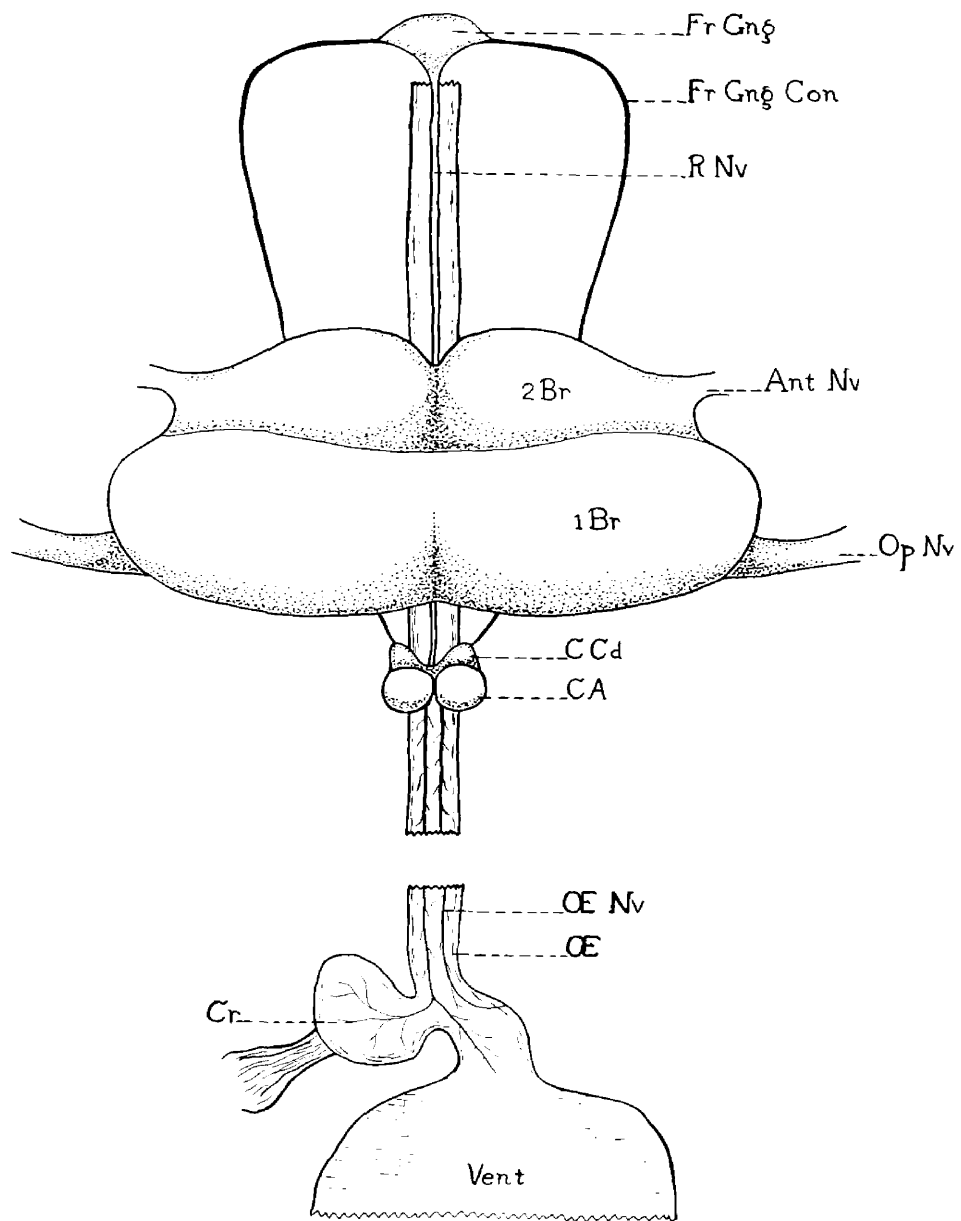


Fig. 14. Stomodaeal nervous system of *Prodenia eridania* Gram. Adult.

a "postcerebral sympathetic ganglion" from which a short nerve passes to one of the corpora allata. Each of the "postcerebral sympathetic ganglia" is joined to the brain by a nerve, but they are not joined to each other. A similar pattern of innervation was found in the ant, Lasius, by Janet (1905). In the honeybee larva according to Nelson (1915, 1924) the recurrent nerve bifurcates near the caudal end of the head, and here are found two cell masses which are interpreted as being pharyngeal ganglia.

In Tremex (Fig. 15) the base of each corpus cardiacum is fused with the recurrent nerve to form what is probably the occipital ganglion from which two oesophageal nerves run posteriorly. The corpora allata are contiguous with the ventral and lateral portions of this plexus. There are no ingluvial ganglia.

In the wasp, Sceliphron, (Fig. 16) a similar condition prevails, but the occipital ganglion is very distinct. It should be noted that the corpora allata are ventrad of the corpora cardiaca and that they are in contact with the occipital ganglion. The paired oesophageal nerves swell into small ingluvial ganglia just before their ends.

In the bumblebee, Bombus pennsylvanicus Degeer, (Fig. 17) there is an interesting fusion of some of the postcerebral parts of the stomodaeal nervous system. Beneath the corpora cardiaca there is a ring around the oesophagus to which the corpora cardiaca and the corpora allata are attached. The recurrent nerve bifurcates just cephalad of this ring and the oesophageal nerves thus formed run under the dorsal part of the ring and continue along the dorsal wall of the alimentary tract to the anterior portion of the ventriculus. Microtome sections are needed to show whether or not the oesophageal nerves actually

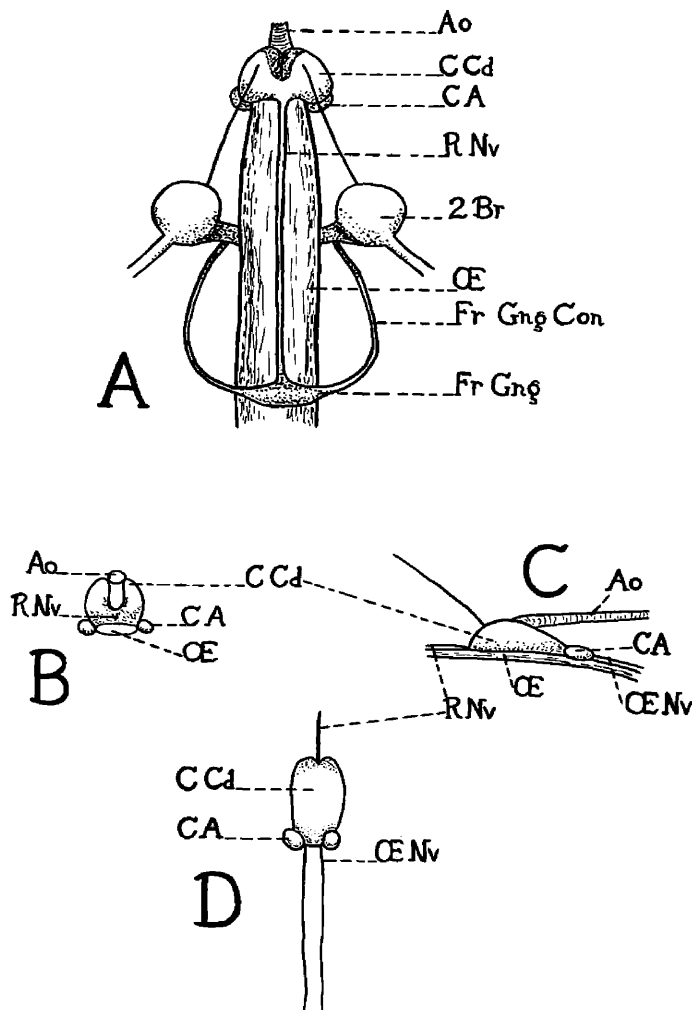


Fig. 15. Stomodaeal Nervous System of Tremex columba L.
 A. Anterior view; protocerebrum removed.
 B. Detail of corpora cardiaca and corpora allata from front, somewhat diagrammatic.
 C. Lateral view of same.
 D. Ventral view of same.

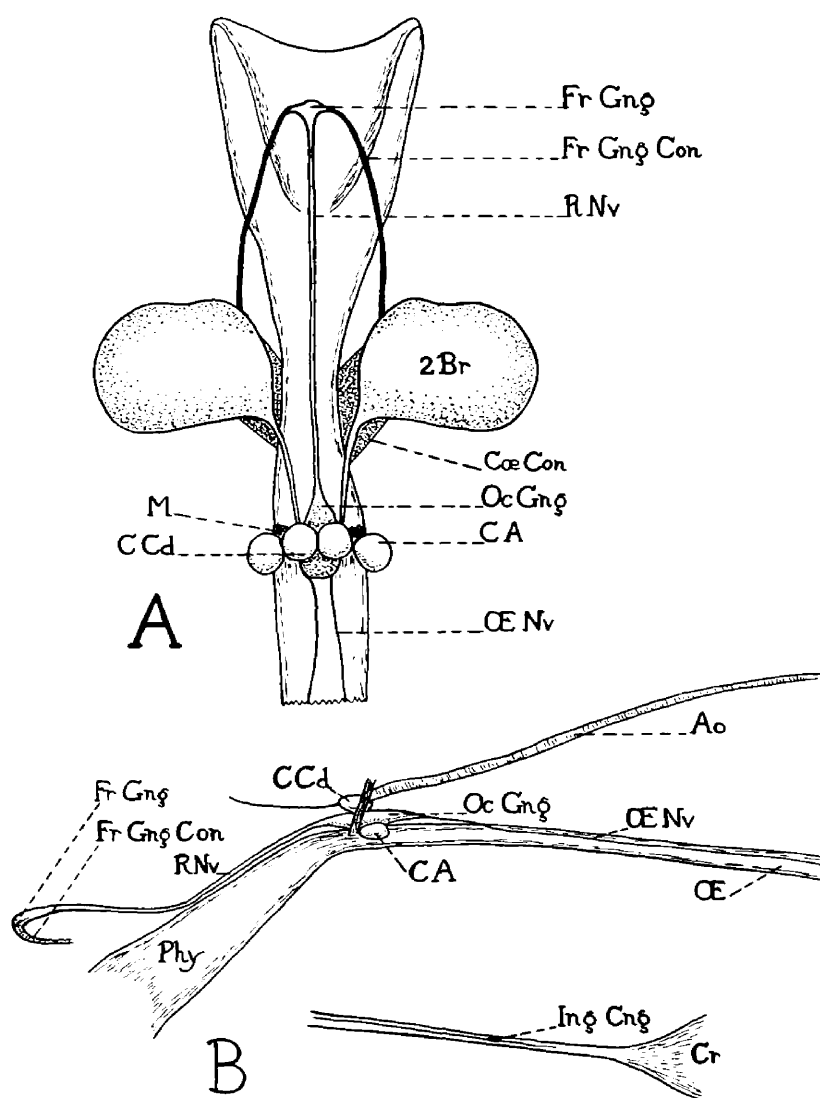


Fig. 16. Stomodaeal Nervous System of Acellularia cerevitarium (Drury).

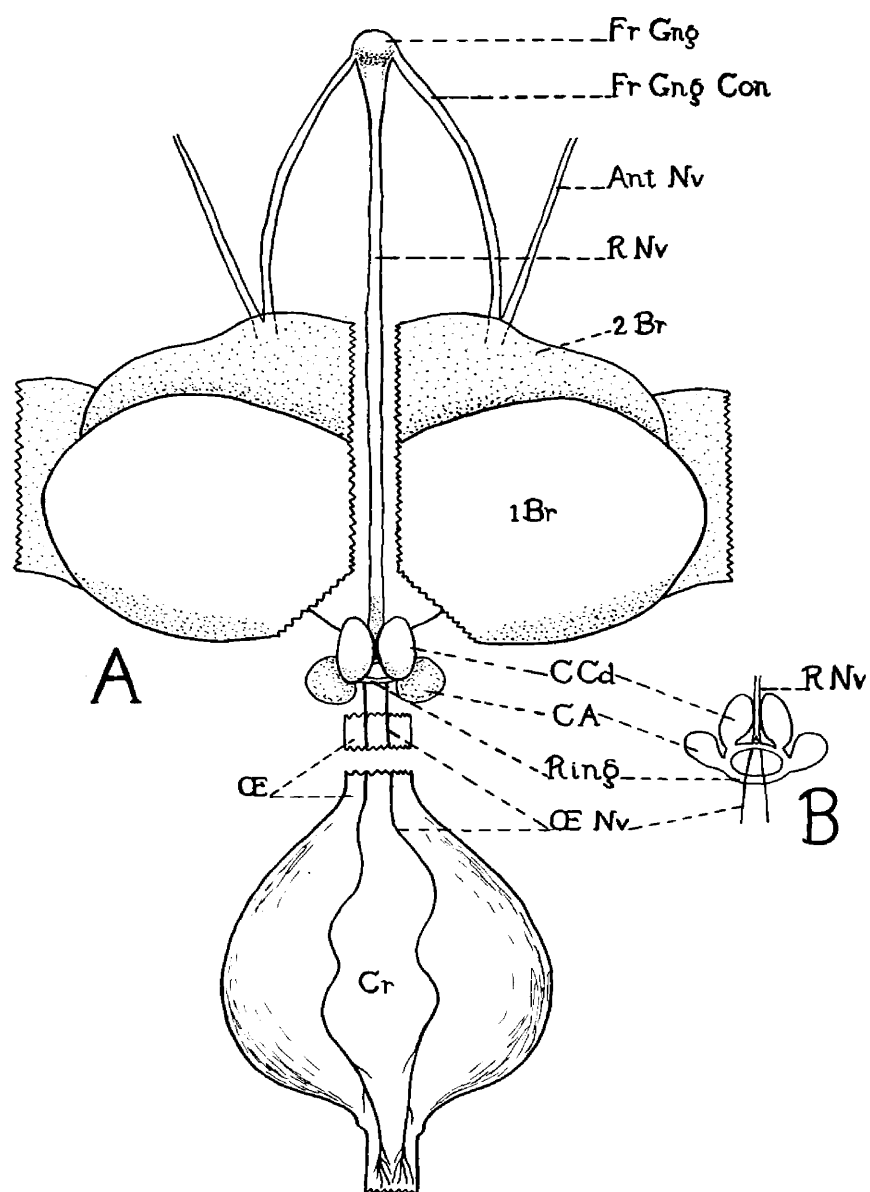


Fig. 17. Stomodaeal Nervous System of *Bombus pennsylvanicus* Degeer.

A. Dorsal view.

B. Ventral view of corpora cardiaca, corpora allata, and ring.

unite with the dorsal half of the ring. The anterior end of the aorta is located between the two corpora cardiaca so that the ventral wall of the aorta is in contact with the ring.

A similar ring was reported by E. Brandt (1879 B) in Bombus terrestris L. The corpora cardiaca (anterior pharyngeal ganglia) are seen to arise from the commissure which encircles the oesophagus. The posterior innervation of the stomodaeum differs slightly in the two species. Brandt reports a continuation of the single recurrent nerve forming a "ventricular ganglion."

THE STOMODAEAL NERVOUS SYSTEM OF DIPTERA.

Brandt (1879) stated that in the stomodaeal nervous system of flies there are two "pharyngeal ganglia" which are doubled to form a stricture. Lowne discovered two median and two paired lateral ganglia in the stomodaeal (splanchnic) nervous system of the blow-fly larva. In the larva of Chironomus, which was studied by Miall and Hammond (1900) and by Holmgren (1904), there is a small occipital (oesophageal) ganglion, and there are a pair of corpora allata and a pair of corpora cardiaca; but the way in which the latter are connected with the brain is not understood. In the larva of Mycetophila the plan of stomodaeal innervation is similar to that of Chironomus according to Holmgren (1907).

Recently Fraenkel (1935), Hadorn (1937), and Burt (1937, 1938) have studied the stomodaeal nervous system incidentally as part of their experimental work on the cause of pupation in various Diptera. The larva of Chironomus was examined by Burt (1937), and his results are somewhat like those of the earlier workers. A more complete explanation is still needed with respect to the nerves connecting the corpora

cardiaca (oesophageal ganglia) with the brain. The nerves which pass posteriorly from the occipital ganglion (hypocerebral ganglion) are called by Burtt recurrent nerves, and to each of these a corpus allatum and a corpus cardiacum (oesophageal ganglion) are attached. From each "recurrent nerve" "a very fine nerve passes to the region of the cerebral commissure and a broader strand of tissue passes forward and is attached to the trachea but does not seem to make any nervous connexion with the brain at this point."

The stomodaeal nervous system of the larva of Tipula has been investigated (Fig. 18) and the description given by Burtt (1937) has been corroborated except for two minor differences. The recurrent nerve bifurcates just in front of the brain instead of behind the brain as reported by Burtt; and no nerve fibers were observed proceeding posteriorly from the corpora allata. There is no occipital ganglion; but the recurrent nerve is rather thick at its point of division, and the paired oesophageal nerves are rather broad at the points where the nerves leading to the corpora cardiaca branch from them.

In the robber fly, Erax, (Fig. 19) the frontal ganglion rests on the anterior wall of a pharyngeal or secondary sucking pump. Dorsally and posteriorly the pharynx has a circular sclerotic plate with a narrow extension to the beginning of the oesophagus. Large muscles are attached to the circular plate; and the recurrent nerve, following the dorsal wall of the pharynx, wends its way between these muscles. Along the extension of the plate the recurrent nerve swells to form an occipital ganglion. At the union of the pharynx and oesophagus, there is a ring of what seems to be nervous tissue around the gut. The recurrent nerve unites with this ring. Posteriorly an oesophageal nerve leaves

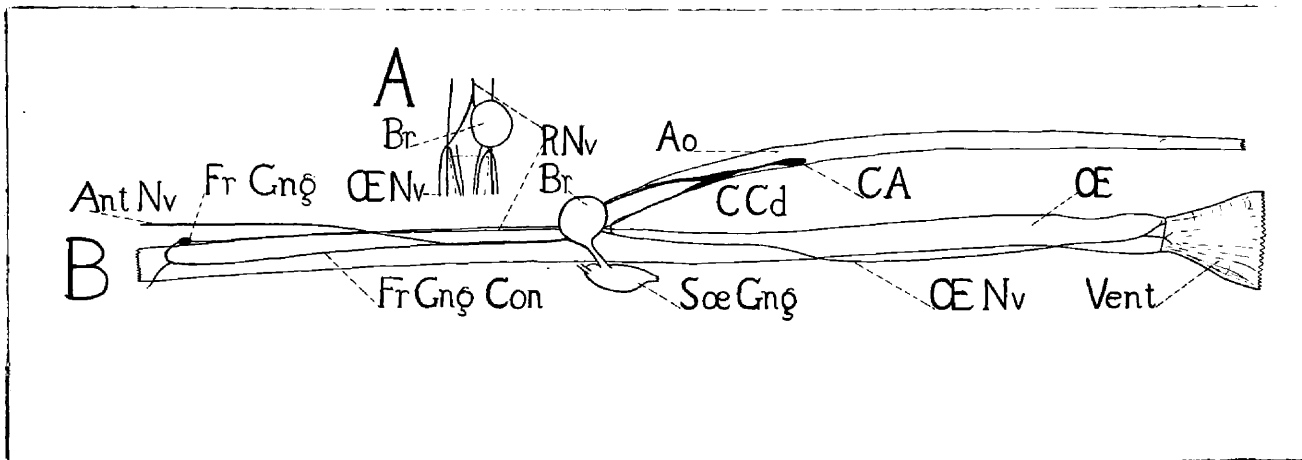


Fig. 18. Stomodaeal Nervous System of Larva of *Tipula abdominalis* Say.

- A. Dorsal view of recurrent nerve and postcerebral nerves; left half of brain removed; broken line represents aorta.
- B. Lateral view.

the ring and passes along the dorsal wall of the oesophagus. Near the end of the oesophagus the nerve bifurcates, but there are no ingluvial ganglia. The frontal ganglion connectives are apparently the only nerves extending from the brain to the stomodaeal system. Whether the ring described above corresponds to the corpora cardiaca or corpora allata is unknown.

The presence of Weismann's ring in some seven genera of cyclorrhaphous Diptera is discussed by Burt (1937). This ring is an irregular mass of cells surrounding the aorta behind the brain, to which it is attached by membranous strands. The ring receives nerves from a median postcerebral ganglion which sends a so-called recurrent nerve posteriorly to a single ingluvial (proventricular) ganglion. In Musca Hewitt (1910) shows an anterior nerve, but no frontal ganglion. In Calliphora the pattern is similar to that in Musca, according to Burt (1937). The "recurrent nerve," proceeding anteriorly from the "proventricular" ganglion, bifurcates; one branch joins the median ganglion, and the other branch runs under the brain to the pharynx. The median ganglion sends two nerves to the brain. It is in intimate contact with Weismann's ring.

Burt believes that the structure of the ring indicates that it represents the fused corpora allata. This view is held by Hadorn (1937) and by DeBach (1937), but Fraenkel (1935) states that there exists no organ in the fly larva which can be homologized with the corpora allata in other insects. Experimental evidence seems to support the conclusion that Weismann's ring secretes a hormone inducing pupation.

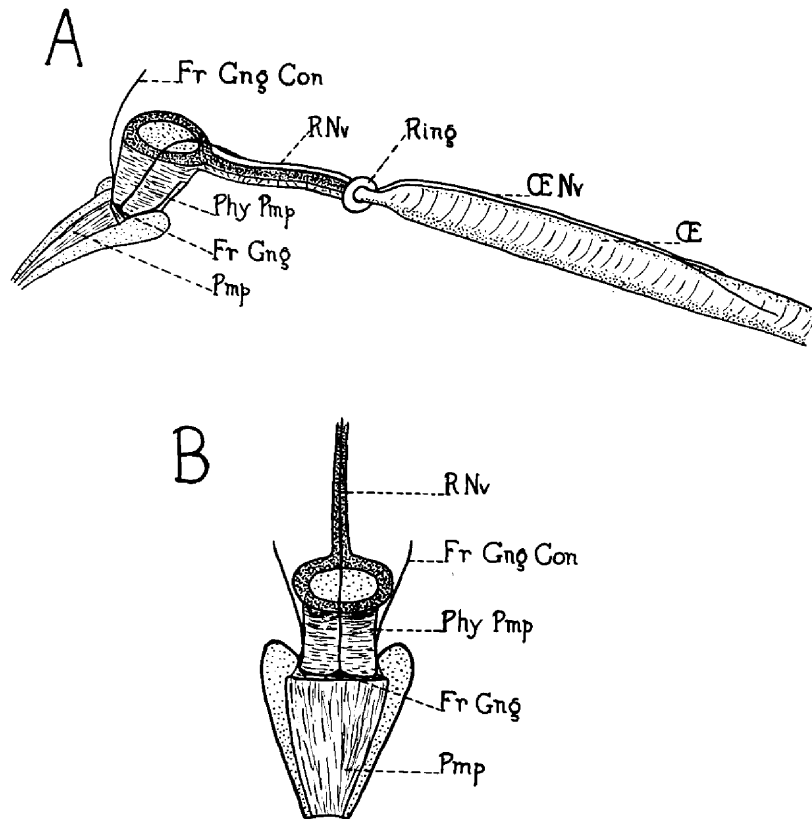


Fig. 19. Stomodaeal Nervous System of *Erax* sp.
 A. Lateral view.
 B. Frontal view.

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