

A STUDY OF THE INTERNAL ANATOMY OF
ACANTHOCEPHALA THOMASI UHLER
(Hemiptera, Coreidae)

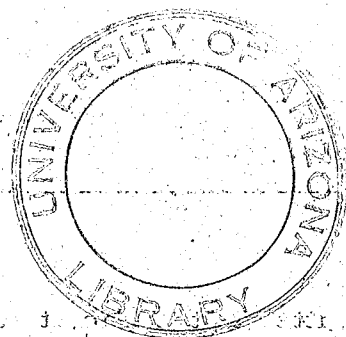
by

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ABBREVIATIONS USED IN FIGURES

AcGl	accessory gland	Ost	ostia
Aed	aedeagus	Ov	ovary
An	anus	Phy	pharynx
AN	abdominal nerve	Pmr	paramere
AntNv	antennal nerve	Ptn Gng	prothoracic ganglion
Ao	aorta	Py	pylorus
bcpX	bursa copulatrix	RGIR	repugnatorial gland reservoir
l Br	protocerebrum	Rect	rectum
Coe Con	circumoesophageal connective	SID	salivary duct
De	ductus ejaculatorius	SIGl	salivary gland
dt	alary muscle	Soe Gng	suboesophageal ganglion
Duc	ductifer	Spt	spermatheca
Enph	endophallus	Spt Gl	spermathecal gland
Gca	gastric caeca	Stp	stapes
Gen Cap	genital capsule	TA	tergal arm
GN	genital nerve	Tes	testis
Ht	heart	Vd	vas deferens
LMS	lateral mesothoracic nerve	1 Vent	first portion of mid-gut
LMt	lateral metathoracic nerve	2 Vent	second portion of mid-gut
LPN	lateral prothoracic nerve	3 Vent	third portion of mid-gut
Mal	malpighian tubule	4 Vent	fourth portion of mid-gut
Odc	oviductus communis	VI	valvula
Odl	oviductus lateralis	VI _f	valvifer
Oe	oesophagus	Vsm	vesicula seminalis
OPdcl	ocellar pedicel		

INTRODUCTION AND LITERATURE REVIEW

This study was undertaken in the hope that it might, in some small way, increase our knowledge of the internal anatomy of the hemipterous insects. Some of the families of this order have been studied quite extensively insofar as reproductive and digestive systems are concerned. The families Miridae and Cimicidae are good examples of this. Other groups, on the contrary, have been the subject of little investigation as is the case in the family Coreidae. Wooley (1949) made a study of the digestive, reproductive, and nervous systems in the box elder bug, Leptocoris trivittatus (Say) (Coreidae). In 1951, he studied the circulatory system of this same insect, and in these two works he has given a fairly detailed description of these systems. He fails to mention anything of the so-called sympathetic nervous system, however.

An excellent work on the nervous system of the large milkweed bug, Oncopeltus fasciatus (Dallas), by Rutschky and Stryjak (1955) proved useful. The nervous system in this member of the family Lygaeidae was found to be very similar to that in the coreid under study.

A comprehensive study of the alimentary canal of the order Hemiptera was made by Elson (1937). The members of the order were

studied in light of their different feeding habits: plant sucking, predaceous, algae-feeding, fungi-feeding, and the blood-sucking insects. The treatment includes general but valuable information for anyone interested in this system.

Several outstanding works on insect genitalia have been done in the past. The reproductive system of the large milkweed bug, Oncopeltus fasciatus (Dallas) was described in great detail by Bonhag and Wick (1953). Both the male and female systems were treated in this excellent work. As was the case with the nervous system, the similarity between the reproductive system of this lygaeid and Acanthocephala is striking. A number of classic works on insect genitalia include those of: Newell (1918), Crampton (1922), Singh-Pruthi (1925), Snodgrass (1933, 1936, 1957), and Michener (1944).

MATERIALS AND METHODS

Specimens used in this study were collected on velvet ash trees, Fraxinus velutina Torr., on the Santa Rita Range Reserve 40 miles south of Tucson, Arizona. Some of the specimens were immediately frozen; the rest were maintained alive in gallon jars with cheesecloth stretched across the top. Vials with cotton plugs provided a source of water. Several different foods were tried over a period of five months. Small mesquite shoots were supplied frequently until they became too dry in late October. The diet was then changed to green beans and summer squash. Finally, only green beans were given to the insects. No attempt was made to correlate type of diet with rate of survival, although some specimens were alive after five months under these conditions. Several were dissected shortly after they had died; often the insects were almost completely desiccated internally with only a trace of the abdominal portion of the alimentary canal recognizable. It was not determined whether the deaths were due to a dietary deficiency, to some abnormality in the rearing conditions, or simply to senility.

From time to time a few of the living insects were preserved in 80 per cent alcohol. Later, these were compared with the specimens

that had been frozen, and the latter seemed to have been much better preserved for internal morphological studies. For the most part, the dissections were made on preserved insects under a stereoscopic dissecting microscope, the specimens being pinned out in a wax-bottomed petri dish under 80 per cent alcohol. Certain structures were removed to a watch glass and placed under alcohol for more detailed study.

Instruments for dissection included No. 3 and No. 5 Dumont watchmaker's forceps and small scissors for separating sclerotized areas. A method for inflating the phallus described by Ashlock (1957) using solutions of alternating osmotic pressures, proved unsuccessful on this insect.

Drawings were made to scale with the use of an ocular grid and squared paper.

THE MALE REPRODUCTIVE SYSTEM

General structure of the abdomen (Figure 1). Dorsally, there are seven distinct abdominal segments preceding the bulbous genital capsule in the male. The eighth abdominal segment is a simple chitinous ring, retracted into the seventh segment when the genitalia are not in use. The genital capsule is the modified ninth abdominal segment housing the phallus and the termination of the alimentary tract or proctiger. The capsule is open dorsally and the parameres and proctiger may be seen lying within the cavity of the capsule. Ventrally only six abdominal segments are clearly visible anterior to the capsule, the first sternite having fused with that of the second.

Testes and ducts (Figure 1). The paired testes are attached to the pleural areas of the fourth abdominal segment by branches from the third abdominal spiracular tracheae. Each testis is dull white tinged with reddish-orange and is composed of seven testicular tubules enclosed in a membranous sheath. Leading posteriorly from each testis is a simple tube of fairly uniform diameter, the vas deferens, which widens posteriorly into a seminal vesicle. Immediately behind this point the two vasa deferentia join, and on the anterior margin of this junction

there is a series of outpocketings representing the accessory glands. The tube continuing posteriorly from the junction of the vasa deferentia is the ejaculatory duct. It is milky white and of uniform diameter, until it widens into the balloon-like erection fluid pump. Within the lumen of the ejaculatory duct lies a structure resembling a bottle brush. A canal runs through the center of this brush, and this is the true sperm tube. Bonhag and Wick state that nothing is known concerning the source of the erection fluid in Oncopeltus and speculate that it might be produced by the epithelium of the erection fluid reservoir. This fluid passes from the reservoir through the ejaculatory duct and into the phallus. The mechanism of the erection process in Oncopeltus is described by Bonhag and Wick (1953). Although these workers described an erection fluid reservoir in Oncopeltus, a comparable structure could not be found in Acanthocephala.

External genitalia (Figures 2, 3). The phallus is composed of two parts, the phallobase and the aedeagus. There is not the typical phallobase and retractible aedeagus-endophallus association commonly described for hemipterous insects. The phallobase typically has a retractible aedeagus attached to its distal end, and within the aedeagus lies the endophallus which is extrusible. In this insect the aedeagus is permanently attached to the phallobase and cannot be extruded, while the endophallus can be forced out of the aedeagus during copulation.

However, within the phallobase there is a complex structure housing part of the endophallus which will be described below.

The phallus is connected to a structure which is a modification of the wall of the genital capsule. This structure is similar to the mechanism described in Oncopeltus by Bonhag and Wick (1953). The stapes is a yoke-like sclerotized area at the anterior margin of the phallobase, when the latter is retracted. The dorso-lateral areas of the stapes articulate with two chitinous bands, phallic arms, which are extensions of the posterior margin of the genital capsule. These articulations are covered by a shield-like plate, the promotor apodeme. A membranous septum separates the phallobase from the abdominal cavity, and in the center of this septum is a sclerotized area known as the ductifer. The sperm tube within the ejaculatory duct passes through an orifice on the upper margin of the stapes and becomes the sinuous, chitinous endophallus just posterior to the stapes.

The erection fluid is admitted to the phallobase through two openings directly beneath the entrance of the sperm duct. Posterior to the stapes is a pair of sclerotized plates, one of which gives rise to the shield of the endophallus. The other lies as a small plate opposite the origin of the aedeagus. The endophallus originates on the posterior face of the stapes and forms two loops before passing into the cork-screw-like aedeagus. Another pair of sclerotized plates form the distal

part of the phallobase, the remainder of the external area of the latter being membranous. The parameres (gonostyli of Bonhag and Wick (1953)) lie well within the cavity of the genital capsule and are connected to the membrane lining the capsule.

THE FEMALE REPRODUCTIVE SYSTEM

General structure of the female abdomen (Figure 4). Nine segments are visible on the dorsal surface of the female abdomen; ventrally six segments are easily distinguished. The first apparent abdominal sternite is actually composed of sternites one and two. Sternite seven bears a transverse slit immediately followed by two large triangular lobes. Segments eight and nine are each represented by a dorsal plate and a pair of paratergites which lie adjacent to the triangular lobes of segment seven. The venter of the eighth segment is represented by a membranous area between the bases of the first valvifers. The ninth venter has invaginated to form the genital chamber. The proctiger, composed of segments ten and eleven, lies within the genital capsule.

Ovaries and ducts (Figure 4). The paired ovaries are connected to the spiracular tracheae of segment three. These tracheae give off a number of branches which envelope and lend some support to the gonads. Each milk-white ovary is composed of seven ovarioles. Apically each ovariole narrows into a terminal filament which together form the suspensory ligament. This is attached anteriorly to the heavily sclerotized cervical ring. From each ovary a simple lateral oviduct passes caudad

to a point in the sixth abdominal segment, where the two fuse. From this point the common oviduct takes the form of a bursa copulatrix. On the dorsal surface of this bursa are found the spermatheca and the paired accessory glands. The former is a sausage-shaped organ with a purplish colored capsule connected to its base. In all specimens examined, this capsule was found associated with the spermatheca, and it is possible that the structure serves as a spermathecal gland. Histological evidence is needed to confirm this point. The duct from the spermatheca opens through the dorsal surface of the bursa. The paired accessory glands are simple tubes of a milky color, so that they are difficult to distinguish from the roof of the bursa. The ducts from these glands pass laterally, then ventrally, to open into the bursa at the base of the second valvifers.

Ovipositor (Figures 5, 6, 7). The large triangular ventral lobes of the seventh abdominal segment are the first valvifers of the ovipositor. If these lobes are spread laterally the bursa and the first valvulae may be seen between them. The first valvulae are joined to the first valvifers anteriorly by thin chitinous bands. The first valvulae are for the most part heavily sclerotized except for a small dorsal membranous area. The second valvulae lie above the first valvulae, their rami being continuous with the second valvifers. The latter are continuous

with an arm from the ninth tergum. The second valvulae are heavily sclerotized except for their membranous apices, which are spinous and modified into hook-like processes. Third valvulae are not present. Snodgrass (1935) claims that the third valvulae are absent also in Anasa tristis but are usually found in other Hemiptera.

THE NERVOUS SYSTEM

Unusual modifications of the characteristic insect nervous system are known to exist among several different orders. This is especially true among some of the Hemiptera. Wooley (1949), for example, found a considerable amount of ganglionic fusion in the brain and ventral nerve cord of the box-elder bug, Leptocoris trivittatus (Say) (Coreidae).

The presumed segmental lobes of the brain have undergone considerable fusion in Acanthocephala (Figure 9). Protocerebrum and, to a less extent, deutocerebrum, are distinctive lobes of the brain which lie in the posterior portion of the head capsule. The tritocerebral lobes have fused completely with deutocerebrum and are no longer recognizable. The lobes of the deutocerebrum, bearing one pair of antennal nerves, lie slightly anterior to the protocerebrum. Optic lobes originate on the antero-dorsal surface of the forebrain. Paired ocellar pedicels arise from the dorsal surface of the protocerebrum. There is no evidence of a single median ocellus. The tritocerebral lobes are presumed to be at the origins of the circumoesophageal connectives. Two pairs of nerves originate on the suboesophageal ganglion; the anterior pair passes forward in the head to innervate the proboscis, the other leads posteriorly into the

cervical region. A single large connective passes from the posterior margin of the suboesophageal ganglion to the prothoracic ganglion (Figure 9). Two pairs of lateral nerves arise from this ganglion. The anterior pair (LPN_1) innervate the prothoracic leg muscles. The second pair (LPN_2) pass caudad to the mesothoracic wing muscles.

A large ganglion lying in the meso- and metathorax terminates the ventral ganglionic chain (Figure 9). This ganglion has been called the central ganglion by Hamilton (1931) and the pterothoracic ganglion by Malouf (1933). Altogether, eight pairs of nerves and a single median nerve originate from this ganglion. The first pair of lateral mesothoracic nerves (LMS_1) arise from the anterior margin and innervate the mesothoracic leg muscles. The second pair of lateral mesothoracic nerves (LMS_2) bifurcate once (a, b), one portion (a) dividing three more times (c, d, e). Nerves a and b innervate mesothoracic leg muscles; c, d, and e innervate mesothoracic wing muscles. The third pair of nerves, the first pair of lateral metathoracic nerves (LMt_1), lead to the metathoracic wing muscles. The fourth pair, second pair of lateral metathoracic nerves (LMt_2), bifurcate once (a, b) while branch a divides again (c). The metathoracic leg muscles receive a and b; the other (c) innervates the reservoir of the metathoracic repugnatorial gland. Four more pairs of nerves (AN_{1-4}) originate nearer the midline and lead to the abdominal viscera. A single median nerve (GN) runs posteriorly

from this central ganglion. It bifurcates once in segment six (GN_1), then passes into segment seven and branches again (GN_2). The first nerve (GN_1) divides once (a, b); branch a leads to the common oviduct, while the other branch (b) innervates the ventro-lateral region of the posterior abdomen. One nerve (GN_2) divides into three branches, a, b, and c. The accessory glands, bursa, and rectum are innervated by nerves a and b; the spermatheca receives the third (c). The other nerve (GN_3) divides twice (a, b, c), the first two branches (a, b) innervating the accessory glands, bursa and rectum; the other (c) passing to the rectum alone.

It was not possible to work out the details of the so-called sympathetic nervous system with the material available. The corpora cardiaca, corpora allata, and frontal ganglion were not found in their expected positions, but this is not surprising in light of the extreme cephalization already noted. Additional material and histological procedures may be necessary to complete this aspect of the nervous system.

THE ALIMENTARY CANAL

The digestive tract and associated structures in Acanthocephala greatly resemble this system as described in other coreids, particularly the squash bug, Anasa tristis (Figure 10). According to Snodgrass (1935) the mesenteron is the functional stomach or ventriculus in insects. Breakey (1936), in his description of the digestive system of the squash bug, subdivided the ventriculus into three regions following the work of Weber (1930). Elson (1937), in his comparative study of the Hemiptera, recognized four areas in the mid-gut or mid-intestine. Wooley (1949), in his study of the box elder bug, restricted the term ventriculus to the first region of the mid-intestine. In this work the terminology of Wooley has been followed for the most part, particularly in regard to the number of subdivisions of the mid-intestine.

This insect possesses typical sucking mouthparts, similar to those described for Leptocoris trivittatus by Wooley (1949). The pharynx lies anterior to the brain as a sclerotized tube with an grooved dorsal surface. Dilator muscles are inserted on the dorsal surface of this tube providing a sucking pump mechanism for the intake of liquid foods. The pharynx passes through the tritocerebral region of the brain as a very

small tube, then into the prothorax as the narrow undifferentiated oesophagus. In the mesothorax, it widens slightly into the ventriculus or stomach proper. The ventriculus, which is sac-like and often greatly distended with liquid food, extends to the fourth abdominal segment, where it becomes differentiated into the second region of the mesenteron. This portion now turns anteriorly to segment three as a narrow tube and then posteriorly again to abdominal segment five. Here, it loops anteriorly to join the larger, tube-like third region. This portion enlarges as it passes anteriorly to the second segment, then narrows appreciably, as it loops caudad again to the sixth segment. At this point the fourth region of the mid-intestine becomes differentiated. This portion of the mid-gut has received a great deal of study by different workers. Gastric caeca are borne on this region as they are by many other hemipterous insects. According to Glasgow (1914) these caeca provide a safe place for the multiplication of the normal bacteria of the alimentary canal. The fourth area of the mid-gut runs transversely in segment six until it meets the pylorus. This region bears two diverticula, each giving rise to two malpighian tubules. These tubules are typical and coil extensively in the abdominal cavity. Posterior to the pylorus (ileum of Wooley (1949)) is the large rectal sac which then narrows into the rectum proper. The latter opens to the outside through the anus which is enveloped by a sclerotized, circular plate (proctiger) formed from the ninth and tenth abdominal segments.

Salivary glands (Figure 11). Elson (1937), in his comparative study of Hemiptera, states that

The salivary glands of phytosuccivorous forms may be differentiated, in a general way, from those of other groups (predaceous, algal and fungus feeders and blood suckers) by their complexity. The principal glands consist of numerous finger-like lobes, variable in size and number. The accessory glands are elongate and tube-like...

The salivary glands in this insect are composed of three finger-like lobes, an oval reservoir, and a large palm-like lobe. The glands lie in the posterior portion of the thorax, one on either side of the dorsal surface of the ventriculus. They are very variable in size and position, lying most often just dorsal to the large, red repugnatorial gland reservoir, but sometimes extending anteriorly into the mesothorax. Two tubules originate on each gland at a point between the circular reservoir and the first finger-like lobe. The anterior tubule, the salivary duct, passes forward through the thorax and into the head capsule, where it enters the salivary syringe. The other tubule, the salivary accessory gland, passes caudad to the posterior margin of the gland, then turns cephalad to undergo a series of loops in the mesothorax. From here it passes caudad to the posterior of the gland, then runs forward all the way into the head, undergoing a distinct increase in diameter as it does so. Looping back from the head it finally terminates blindly just behind the main gland.

THE CIRCULATORY SYSTEM

The dorsal vessel with its supporting muscles is also much simplified in this insect (Figure 12). Snodgrass (1935) defines the aorta as, ". . . the slender part of the dorsal vessel continued forward from the first chamber of the heart into the head." Snodgrass states that the cardiac region may extend as far as the first abdominal segment or even into the thorax. In Acanthocephala, and at least one other coreid, the box elder bug, a reverse trend has taken place.

Four pairs of alary muscles suspend the dorsal vessel from the tergites of the fifth, sixth, and eighth abdominal segments; one pair arise on the bases of the first valvifers which are extensions of segment seven. There appear to be two pairs of ostia, one occurring subterminally in the eighth segment, the other in the seventh segment. These ostia set off the heart or cardiac region of the long dorsal vessel, the true heart then lying in segments seven and eight. One pair of alary muscles originate on the lateral margins of the fifth abdominal tergite and are inserted on the ventral heart wall in segment six. The second pair originate on the lateral margins of the sixth tergite and are inserted on the ventral heart wall in the same segment. Another pair arise on the bases of the first

valvifers and are inserted on the ventral heart wall in segment eight.

The fourth pair arise on the lateral margins of the eighth tergite and are inserted on the ventral heart wall in the seventh segment. Each alary muscle is composed of a small number of loosely anastomosing muscle fibers.

Snodgrass (1935) states that "The diaphragm membranes in some cases are almost entirely absent or but a scant binding between the muscle fibers, consisting of a weblike tissue full of large and small fenestrae." This describes the condition existing in Acanthocephala, for there is no septum separating the perivisceral and pericardial cavities.

The aorta passes anteriorly from its junction with the heart as a tube of fairly uniform diameter. It narrows gradually, as it passes through the thorax continuing through the tritocerebral region of the brain on the dorsal surface of the pharynx. This portion of the pharynx is supported in the body cavity by thin sheets of fat body and connective tissue. The aorta opens into the head cavity anterior to the brain.

DISCUSSION AND CONCLUSIONS

A few hemipterous families have been studied quite extensively in regard to the internal anatomy of their members. Other families, among them the family Coreidae, have received relatively little such attention. This study proposes to throw further light on the internal anatomy of one of the groups that has received less attention in the past, and thus to contribute to our knowledge of the anatomy of the Hemiptera as a whole. The female reproductive system is of the typical hemipterous type, while the male reproductive system exhibits some unusual modifications. These modifications have occurred in groups other than the Coreidae as illustrated by the work of Bonhag and Wick (1953) on Oncopeltus fasciatus (Lygaeidae). A highly specialized fluid pump controls the erection and extrusion of the phallus from the genital capsule. In Acanthocephala this pump mechanism is present, though the ordinarily retractible aedeagus has become fixed to the inner wall of the phallobase, the endophallus still being capable of extrusion from the aedeagus. The digestive system is characteristic of the known plant-sucking hemipterans. There is a sac-like ventriculus, followed by a tubular second and third portions. The third region, however, is often bulbous in other

plant-sucking hemipterans. The fourth portion is also tubular and bears gastric caeca for housing bacteria. According to Elson (1937) these caeca are present on the fourth portion of the mid-intestine of plant-sucking hemipterans but not in such groups as the semi- and fully predaceous hemipterans. Leptocoris trivittatus is generally a plant feeder but may feed on animal fluids occasionally; this insect lacks gastric caeca. Extreme cephalization and fusion have taken place within the central nervous system. Similar modifications have taken place once again in groups other than the coreids. Oncopeltus fasciatus illustrates essentially the same changes in the central nervous system. The three lobes of the brain and the suboesophageal ganglia have merged completely. Cephalization has resulted in a nerve cord containing but two large ganglia in the thorax. The circulatory system shows a reduction in the number of alary muscles and heart chambers. Essig (1942) states that the Hemiptera in general have five-chambered hearts, although the heart in this insect has but one elongated chamber lying in the seventh and eighth abdominal segments. In light of this reduction in number of heart chambers, the aorta can be considered as extending posteriorly from the head into the seventh abdominal segment where it merges with the heart. Other coreids also show a reduction in the number of alary muscles; Leptocoris trivittatus possesses three pairs, while Acanthocephala has four pairs supporting the posterior region of the dorsal vessel. A typical dorsal diaphragm is absent.

SUMMARY

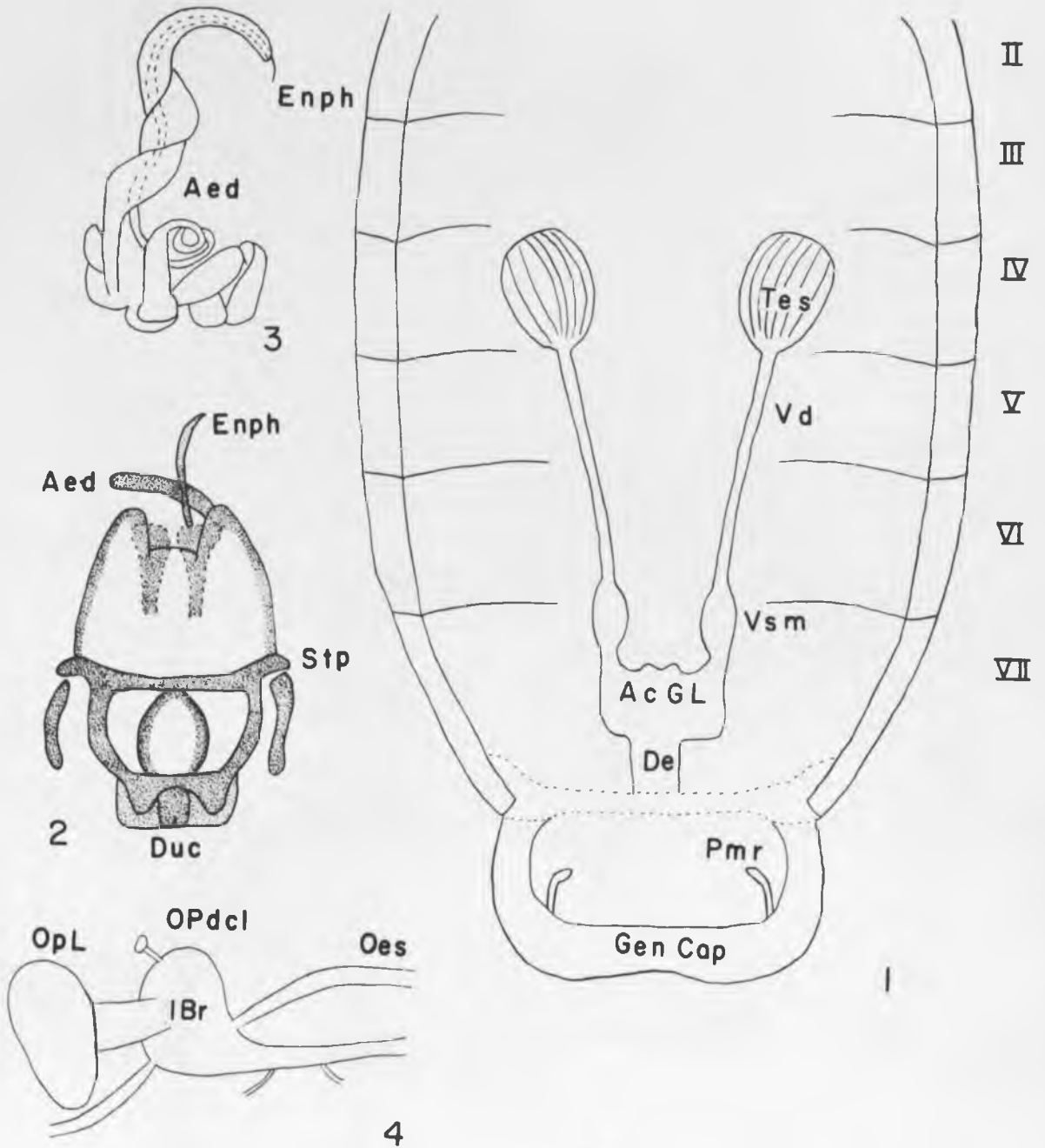
The morphology of the reproductive, nervous, digestive, and circulatory systems of the bug, Acanthocephala, was studied in gross detail. The reproductive system of the female is of the typical hemipterous type, with the exception that third valvulae are absent from the ovipositor. An articulatory apparatus and erection mechanism for the phallus, as described by Bonhag and Wick (1953), are present also in the genitalia of this male. Fusion and cephalization of portions of the central nervous system have occurred. These are shown particularly by the lack of any external evidence of a tritocerebrum and a total of only two thoracic ganglia in the entire ventral nerve cord. The digestive system is typical for the Hemiptera. Gastric caeca are borne on the fourth region of the mid-intestine, which is very characteristic of the plant-sucking members of this order. Although Essig (1942) states that the Hemiptera in general have five-chambered hearts, only one heart chamber is present in the dorsal vessel of Acanthocephala. Four pairs of alary muscles support the dorsal vessel between the fifth and ninth abdominal segments.

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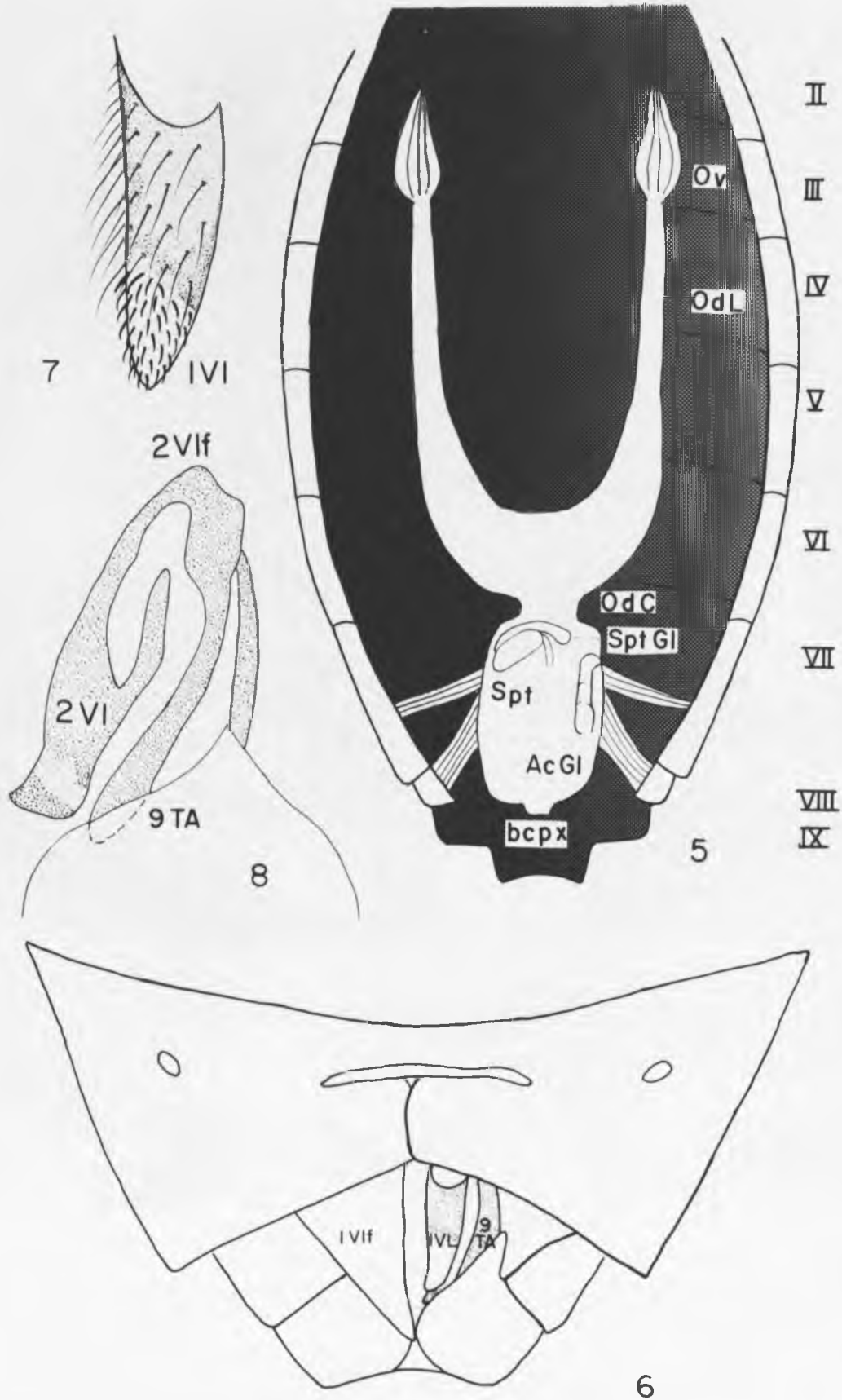
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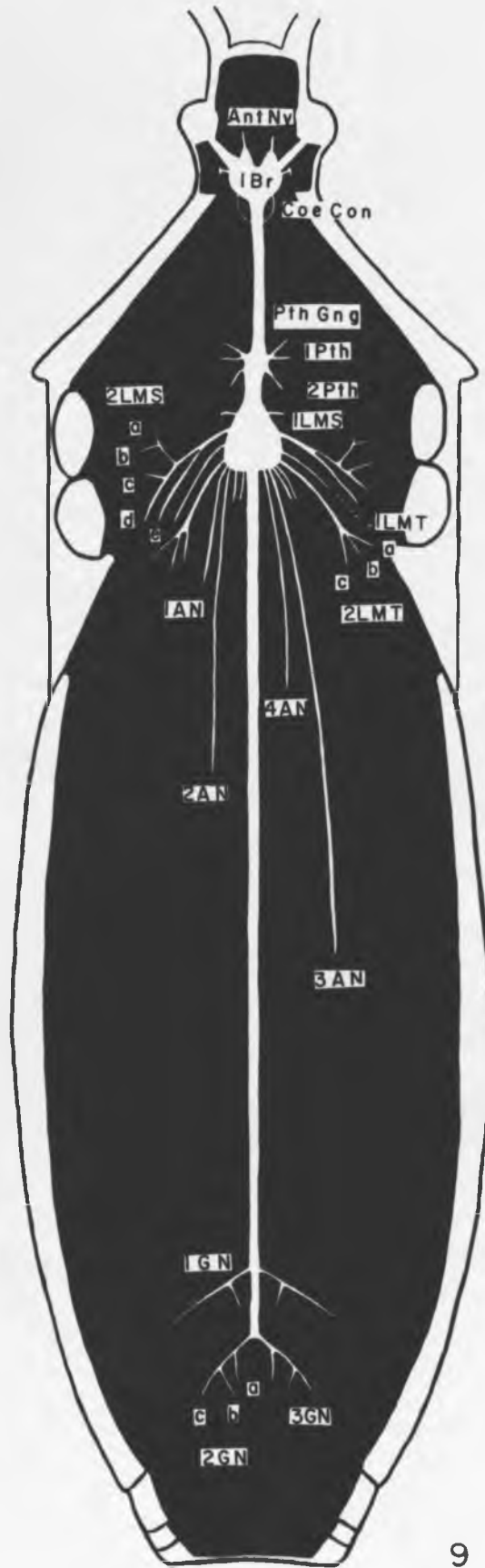
1. Dorsal view of male reproductive system. (x 8)
2. Anterior view of phallus. (x 25)
3. Anterior view of aedeagus and endophallus. (x 20)
4. Left side of brain and suboesophageal ganglion. (x 21)



5. Dorsal view of female reproductive system. (x 8)
6. Ventral view, posterior region of female abdomen with first valvifer removed. (x 11)
7. Dorsal view of first valvula. (x 28)
8. Dorsal view of second valvifer and valvula. (x 36)

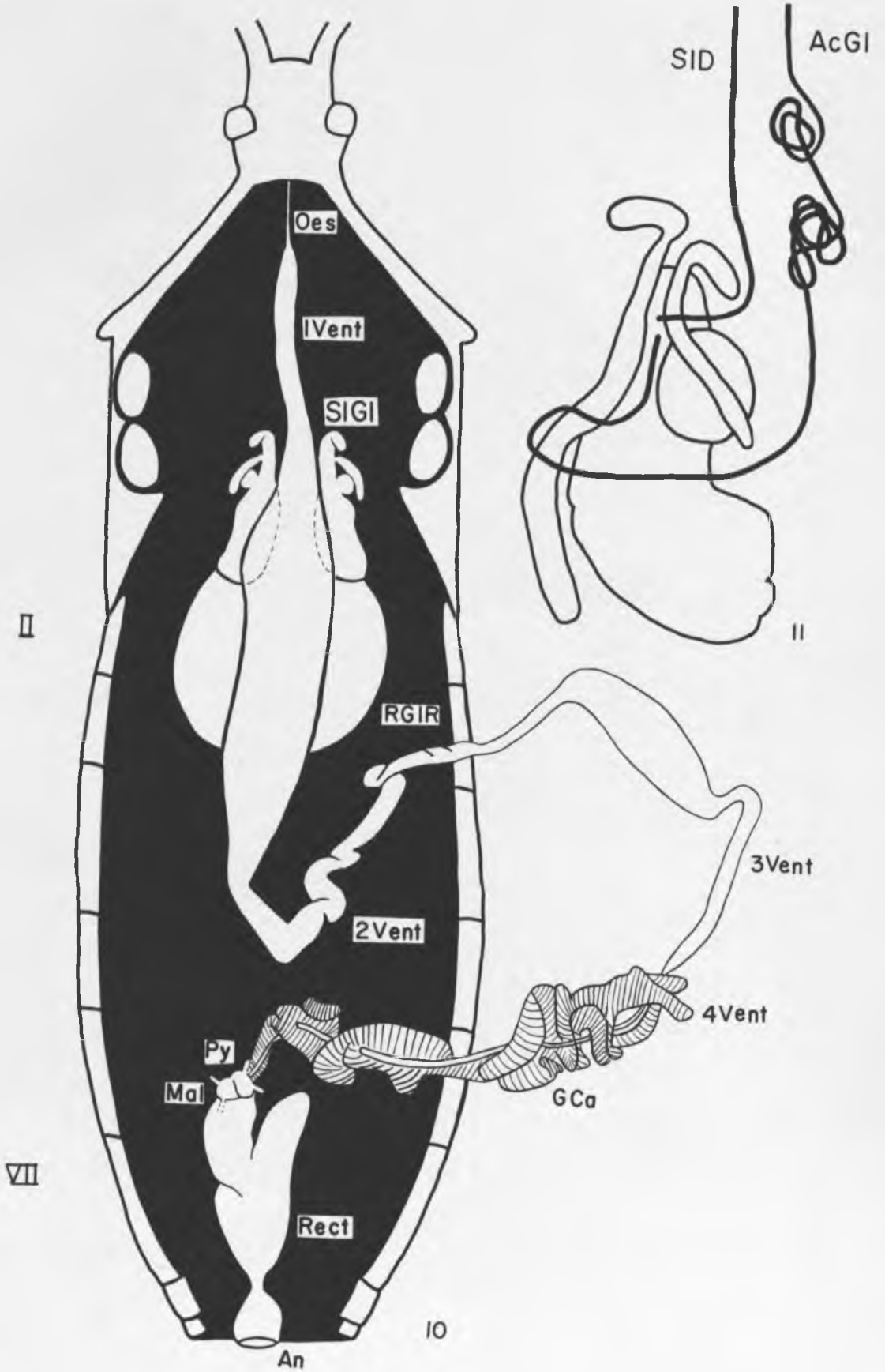


9. Dorsal view of brain and ventral nerve cord. (x 8)



10. Dorsal view of alimentary canal. (x 9)

11. Ventral view of left salivary gland and accessory structures. (x 15)



12. Ventral view of dorsal blood vessel and alary muscles. (x 11)

