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Nervous System of *Triatoma infestans*

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ABSTRACT The anatomy of the adult nervous system of the haematophagous bug *Triatoma infestans* has been studied by means of dissections and histology. The central nervous system comprises three nervous masses: the brain + suboesophageal ganglion, the prothoracic ganglion, and the posterior fused ganglion (meso + metathoracic + abdominal ganglia). The form of the brain is determined by the tubular head and the highly developed muscles of the pharyngeal pump. The prothoracic ganglion is located near the posternum, the posterior ganglionic mass near the mesosternum. A significative variation of the branching pattern of abdominal nerves is reported. The innervations of mouth parts, salivary glands, muscles, retrocerebral complex, spiracles, rectum, reproductive organs, alary muscles, and peripheral nerves are described.

The insect nervous system comprises three portions: (1) the *central nervous system* (CNS), constituted by the brain and the ventral cord, (2) the *peripheral nervous system* (PNS), constituted by sensory and motor fibers innervating peripheral structures, and (c) the *stomodeal nervous system* (SNS), with the frontal ganglion as the more constant element, in addition to the paired hypocerebral ganglia and, sometimes, an ingluvial ganglion. The stomodeal nervous system of insects has a dual function: as the sympathetic innervation of organs and as a site of endocrine activity. The specialized secretory portions of this system are a part of a complex incretory unit known as the *intercerebralis-cardiacum-allatum* system.

The CNS of Heteroptera presents a maximum fusion of the abdominal ganglia. In most Geocorisae (e.g., *Rhodnius spp.*), the suboesophageal and prothoracic ganglia remain independent, whereas the mesothoracic, metathoracic, and abdominal ganglia are fused into one nervous mass. The abdomen is innervated by five pairs of segmental nerves, the median pair being the longer and divided posteriorly in the genital segments.

The SNS comprises the frontal ganglion and commissures, a single recurrent nerve, and a median hypocerebral ganglion. In addition, paired or fused *corpora cardiaca* and *corpora allata* are closely associated with the wall of the dorsal aorta (Horridge, '65).

Among the Reduviidae, *Rhodnius prolixus* is the species most intensively studied in its grossmorphology and histology, and particularly in its physiology. Wigglesworth ('54) based his classical studies on endocrine regulation of moult and metamorphosis in this species. He also conducted research on the histology of the nervous system of *R. prolixus* (Wigglesworth, '53, '59a,b). Additional studies on particular aspects of the nervous system of this species have been published by Kraus ('57), Maddrell ('63, '66), Pinet ('63, '68), Ramirez Perez ('69), Anwyl ('72), Anwyl and Finlayson ('74), and Faruqui ('77).

In contrast to *Rhodnius prolixus, Triatoma infestans* has been relatively neglected, in spite of its importance as the main vector of Chagas disease in South America. The only anatomical studies on the nervous system of this species are those conducted by Barth ('52, '54, '75). The aim of this work is to establish a morphological basis for future work on the neurobiology of *T. infestans*, an insect of considerable medical importance.

MATERIALS AND METHODS

Adult specimens of both sexes of *Triatoma infestans* were reared in the laboratory at 30°C, 70% relative humidity, and fed on citrated sheep blood using an artificial feeder (Núñez and Segura, '87; Núñez and Lazzari, '90). The nervous system was studied both

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by means of dissections and by histological preparations to reveal fine details of the dissected structures and trace the nerves.

Dissection

The animals were anesthetized by chilling them on ice and then included in paraffin wax in a Petri dish. Dissections were performed under a stereoscopic microscope with the specimen immersed in insect saline solution (Barth, '58). Muscles and nerves were drawn with the aid of a camera lucida.

Three staining methods were used to examine the musculature and its innervation. (1) The head capsule and the body were opened and the overlying tissues cleared away. In order to make the nerves stand out from the muscular and fatty tissue in the dissections, a few drops of Delafield's hematoxylin were introduced into the area to be studied, by means of a fine pipette. The large nerves and ganglia appeared light blue, fine nerves dark blue, and muscular tissue purple. (2) Methylene blue solution 0.5% (0.5–0.8 ml) was injected into the dorsal vessel of the live insect through a microsyringe. The dissection was made between 1.0 and 1.5 hr after the initial injection, under saline solution. The nervous tissue appeared dark blue, muscular tissue light blue, and tracheae unstained. (3) Methylene blue was injected following Zawarzin's method for intra vitam staining (Plotnikova and Nevmyvaka, '80).

Histology

The entire body of adult insects was sectioned for histological study. The insects were fixed by injecting aqueous Bouin's solution into the body cavity immediately after moulting while the exoskeleton was still soft, to facilitate sectioning. The preparations were slowly dehydrated in a series of decreasing ethanol dilutions and then were infiltrated with butyl alcohol + paraffin wax for ~ 2 weeks (de la Serna de Esteban, pers. comm.). Transverse and sagittal serial sections were cut at 8 μm and then stained with Delafield's hematoxylin-xylidine ponceau-aniline blue. Reconstructions were made from serial sections examined microscopically.

Nerve roots leaving the ganglia were numbered, starting from the anterior ones. Muscles were named according to Ramirez Perez ('69).

RESULTS

Central and peripheral nervous system

The CNS of *Triatoma infestans,* like that of other Hemiptera, shows a high degree of fusion of the ganglia. It consists of four main ganglionic masses: **brain, suboesophageal ganglion, prothoracic ganglion**, and **posterior ganglion** (Figs. 1–3). The latter is formed by the fusion of the mesothoracic, metathoracic, and abdominal ganglia. The brain and suboesophageal ganglion are closely connected by short, thick **circumoesophageal connectives** and thus appear externally as a single mass. A pair of long, thick **interganglionic connectives** run from the suboesophageal ganglion to the prothoracic one and from the prothoracic to the posterior ganglion. These ganglia are clearly separated from each other, and their connectives fuse medially. The tubular form of the head and the pharyngeal pump musculature affect the position of the brain and suboesophageal ganglion, which are confined to the posterior region of the cephalic capsule. The prothoracic ganglion (PG, Fig. 1) is located near the prosternum, and the posterior ganglionic mass near the mesosternum (PoG, Fig. 1).

Brain

The brain consists predominantly of the **protocerebrum** and the **optic lobes** (P, OL, Fig. 3). The latter are voluminous, being separated from the central protocerebral lobes by a slight constriction. The **deuto-** and **tritocerebrum** are covered dorsally by the large protocerebral lobes. The **ocellar nerves** (OcN, Figs. 2, 3) extend from the central surface of the protocerebrum to the ocelli. One *tegumentary nerve* and two thin *corpora cardiaca nerves* (TN, NCC I, NCC II, Fig. 2, 5) run from the back of each protocerebral lobe.

The *deutocerebrum* (D, Fig. 4) is much smaller than the protocerebrum. It lies laterally and ventrally to the brain, below the protocerebrum, and appears externally as a pair of swellings on each side. From the anterior portion of each deutocerebral lobe, a thick *antennal nerve* arises (AN, Figs. 1, 2, 4). This is one of the most conspicuous nerves of the brain; it runs antero-laterally, passing between the elevator and depressor muscles of the antenna and their tendons (M1, M2, Te, Fig. 2). In this region the antennal nerve sends three slender nerves (Fig. 2), two to the above mentioned muscles and one to the depressor muscle and the tegument. The latter runs to the near antennal base and innervates the tegument of this region (TN, Fig. 2). The other two bifurcate near to their bases and innervate the depressor and elevator muscles of the antenna (Fig. 2). Slightly before the eye, the antennal nerve bifurcates into a thick and a very thin branches (Figs. 2, 4). At the antennal base, the bigger branch divides into two equal branches. All three branches run into the antenna.

The tritocerebrum (T, Fig. 4) is very small. It lies medial to the deutocerebrum on each side of the gut, but there is no clear separation between the two brain regions externally. Its location can be roughly estimated by the point of origin of the *frontolabral nerves* (FLN). These short, thick nerves soon divide into the short, medially directed *frontal nerves* (FrN) and the long, slender, anteriorly directed *labral nerves* (LrN, Figs. 1, 2, 4). The frontal nerves join over the midline of the oesophagus in the *frontal ganglion* (FG, Fig. 4). From the anterior portion of the latter, a *median frontal nerve* arises (MFrN, Figs. 1, 4). The ganglion narrows posteriorly into a nerve trunk, the *recurrent nerve* (RN, Figs. 4, 5). The frontal ganglion is, therefore, the connection between the CNS and the stomodeal nervous system, and is itself the center of the latter. The labral nerve runs ventrally to the clypeous-labral region of the head. The mandibular protractor muscle (M3, Fig. 2) is innervated by a nerve branching off from this nerve. The median frontal nerve runs between the voluminous pharyngeal dilatory muscles (M9, Fig. 2) and sends branches to them.

Suboesophageal ganglion

The boundary between the brain and the suboesophageal ganglion (SG, Figs. 1–4) is marked externally by the protocerebral lobes

Abbreviations

Ao	aorta	M22	mesopleurum-trochanteral muscle
AbN	abdominal nerve (I-V)	M23	metascutum-coxal muscle
AbSp	abdominal spiracle	M24	metapleurum-trochantinal muscle
AN	antennal nerve	M25	metapleurum-coxal muscle
AoN	aortic nerve	M26	metapleurum-trochanteral muscle
Ap	apodeme	M27	metafurcum-trochanteral muscle
AT	adipose tissue	M28	metasternum-abdominal muscle
B	brain	M29	metafurcum-abdominal muscle
BFw	base of the forewing	M30	metapleurum-abdominal muscle
BHw	base of the hindwing	M31	aliform muscle
Bmd	base of mandibular stylet	MdS	mandibular stylet
Bmx	base of maxillary stylet	MFrN	median frontal nerve
CA	*corpus allatum*	MsN	mesothoracic nerve (I–III)
CC	*corpora cardiaca*	MT	Malpighian tubules
Co	connective	MtN	metathoracic nerve (I–III)
Cx	coxa	MxS	maxillary stylet
D	deutocerebrum	NCC I	*nervi corpora cardiacci I*
DV	dorsal vessel	NCC II	*nervi corpora cardiacci II*
E	eye	NCC III	*nervi corpora cardiacci III*
FG	frontal ganglion	NCP	*nervus capitis protoracicus*
FLN	fronto-labral nerve	Oc	ocelli
FrN	frontal nerve	OcN	ocellar nerve
HG	hypocerebral ganglion	Oe	oesophagus
LbN	labial nerve	OeN	oesophageal nerve
LrN	labral nerve	OL	optic lobe
M1	antennal elevator muscle	P	protocerebrum
M2	antennal depressor muscle	PG	prothoracic ganglion
M3	mandibular protractor muscle	Ph	pharynx
M4	mandibular retractor muscle	Pm	promesenteron
M5	dorsal oesophagus dilator muscle	PN	prothoracic nerve (I–VI)
M6	ventral oesophagus dilator muscle	PoG	posterior ganglion
M7	maxillary retractor muscle	R	abdominal nerve rami (I–VII)
M8	maxillary protractor muscle	RN	recurrent nerve
M9	pharynx dilator muscle	RS	rectal sac
M10	tergum-sternum-abdominal muscle	SD	salivary duct
M11	pronotum-trochantinal muscle	SF	suspensory filament
M12	posterolateral pronotum-coxal muscle	SG	suboesophageal ganglion
M13	anterior and posterior pronotum-coxal muscle	SN	stylet's nerve
		St	sternite
M14	pronotum-trochantinal muscle	SvG	salivary gland
M15	prosternum-mesosternal muscle	SvGN	salivary glands nerve
M16	mesoscutum-trochantinal muscle	T	tritocerebrum
M17	mesopleurum-coxal muscle	Te	tendon
M18	mesofurcum-trochanteral muscle	Tg	tergum
M19	mesofurcum-pleural muscle	ThSp	thoracic spiracle
M20	mesoscutellum-coxal muscle	TN	tegumentary nerve
M21	mesosternum-phragmaticum muscle	Tr	trachea

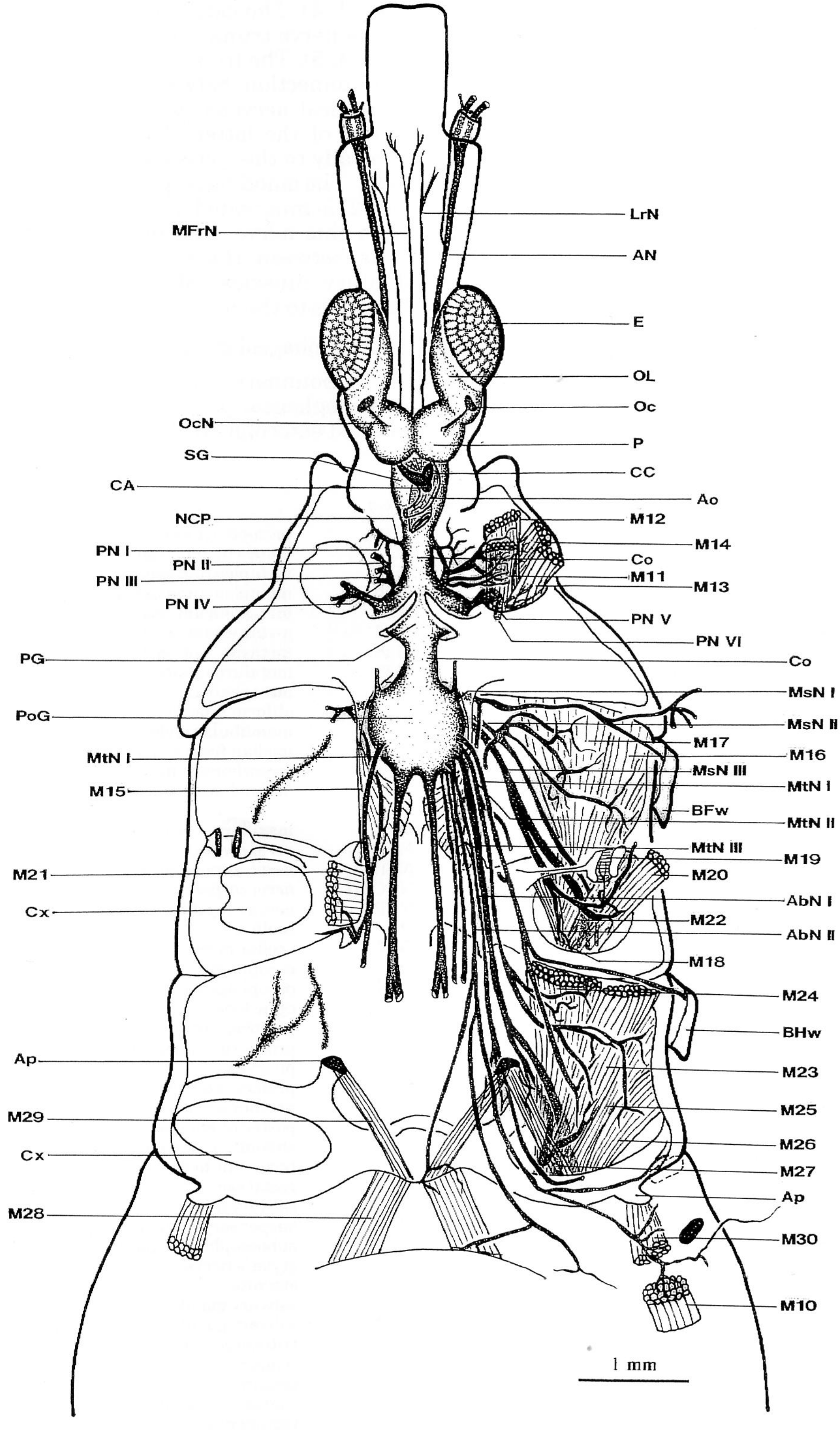

Fig. 1. *Triatoma infestans.* Dorsal view of the CNS and peripheral nerves. Ventral and legs muscles and their innervation are shown.

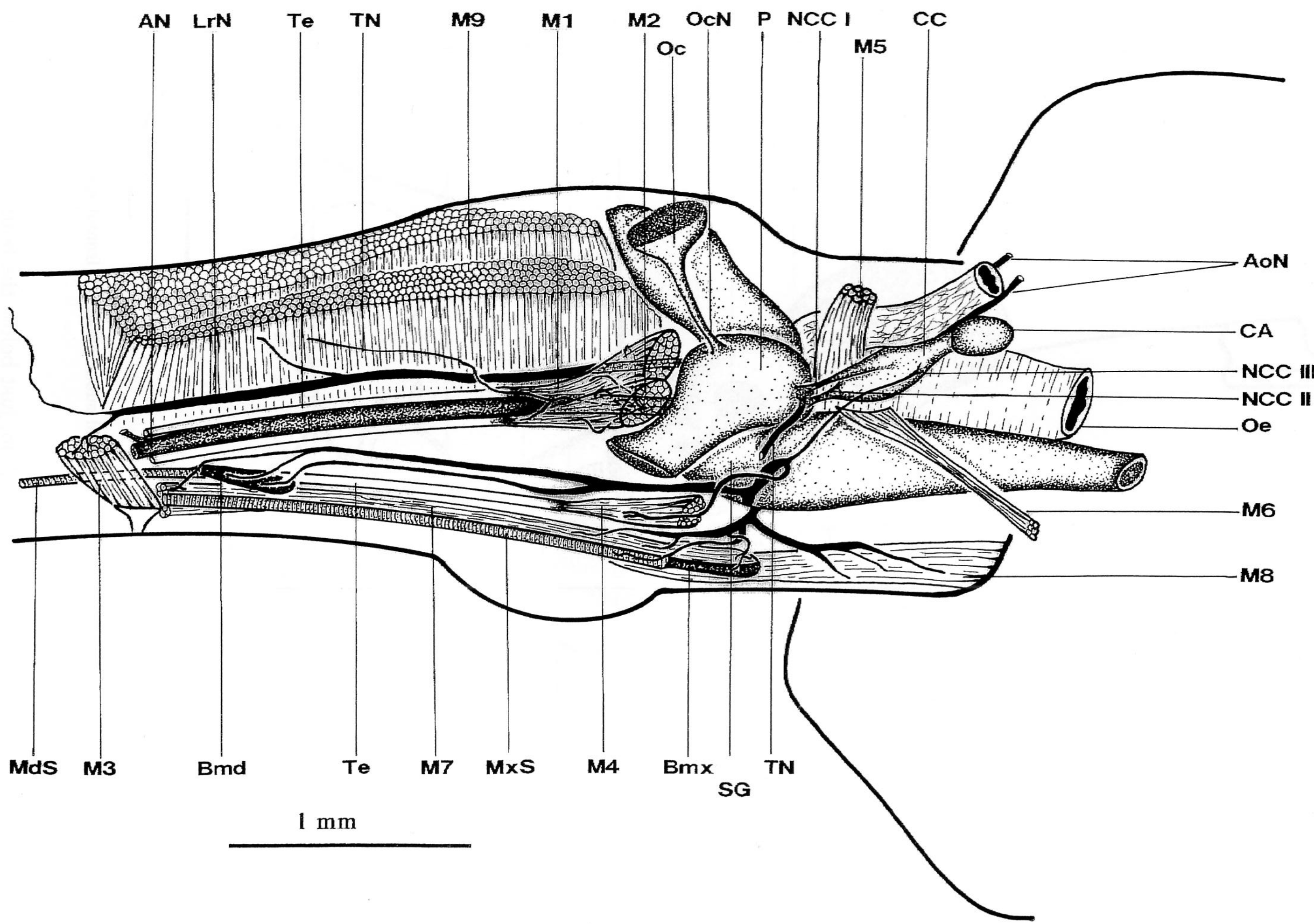

Fig. 2. *Triatoma infestans*. Lateral view of the cephalic nervous system. Muscles of mouth parts and pharyngeal pump, as well as the retrocerebral complex, are depicted.

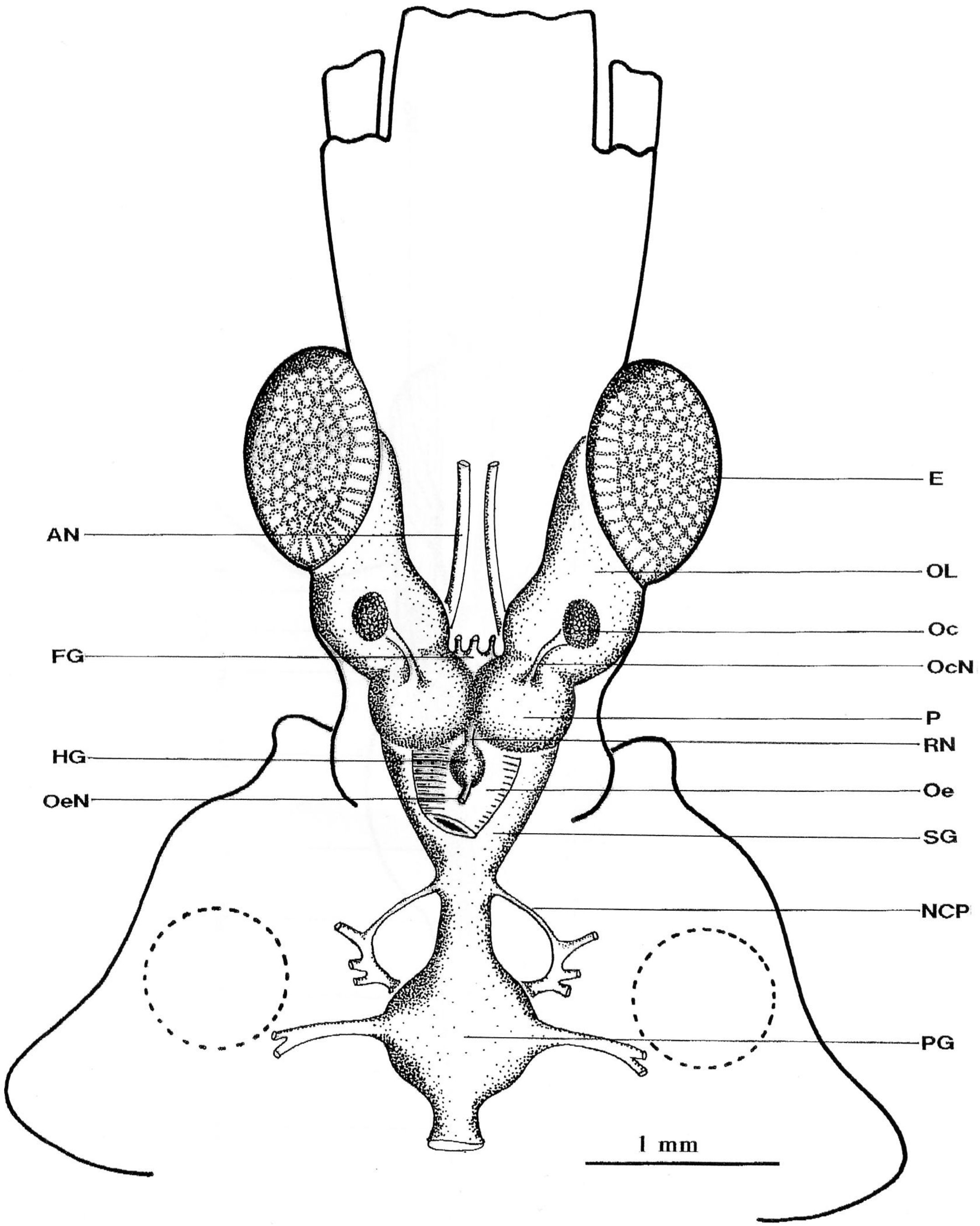

Fig. 3. *Triatoma infestans.* Dorsal view of the brain and suboesophageal, frontal and hypocerebral ganglia, as seen after removing the aorta.

dorsally and the deutocerebral lobes ventrally. The circumoesophageal connectives are apparent only histologically. From the anterolateral region of the suboesophageal ganglion, just below the boundary between this ganglion and the brain, the nerves to the muscles of the stylets originate. The *mandibular* and *maxillary nerves* originate in

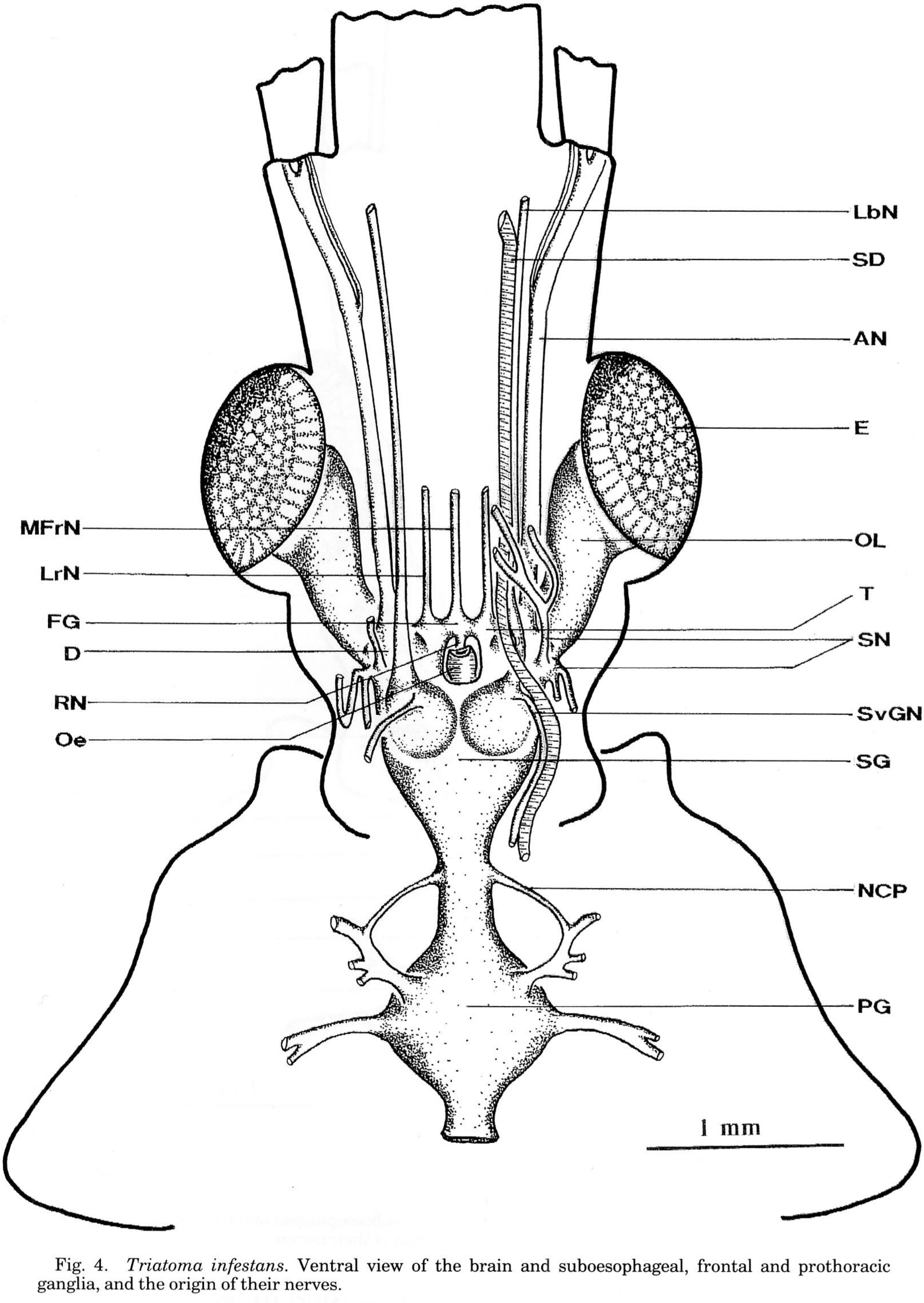

Fig. 4. *Triatoma infestans*. Ventral view of the brain and suboesophageal, frontal and prothoracic ganglia, and the origin of their nerves.

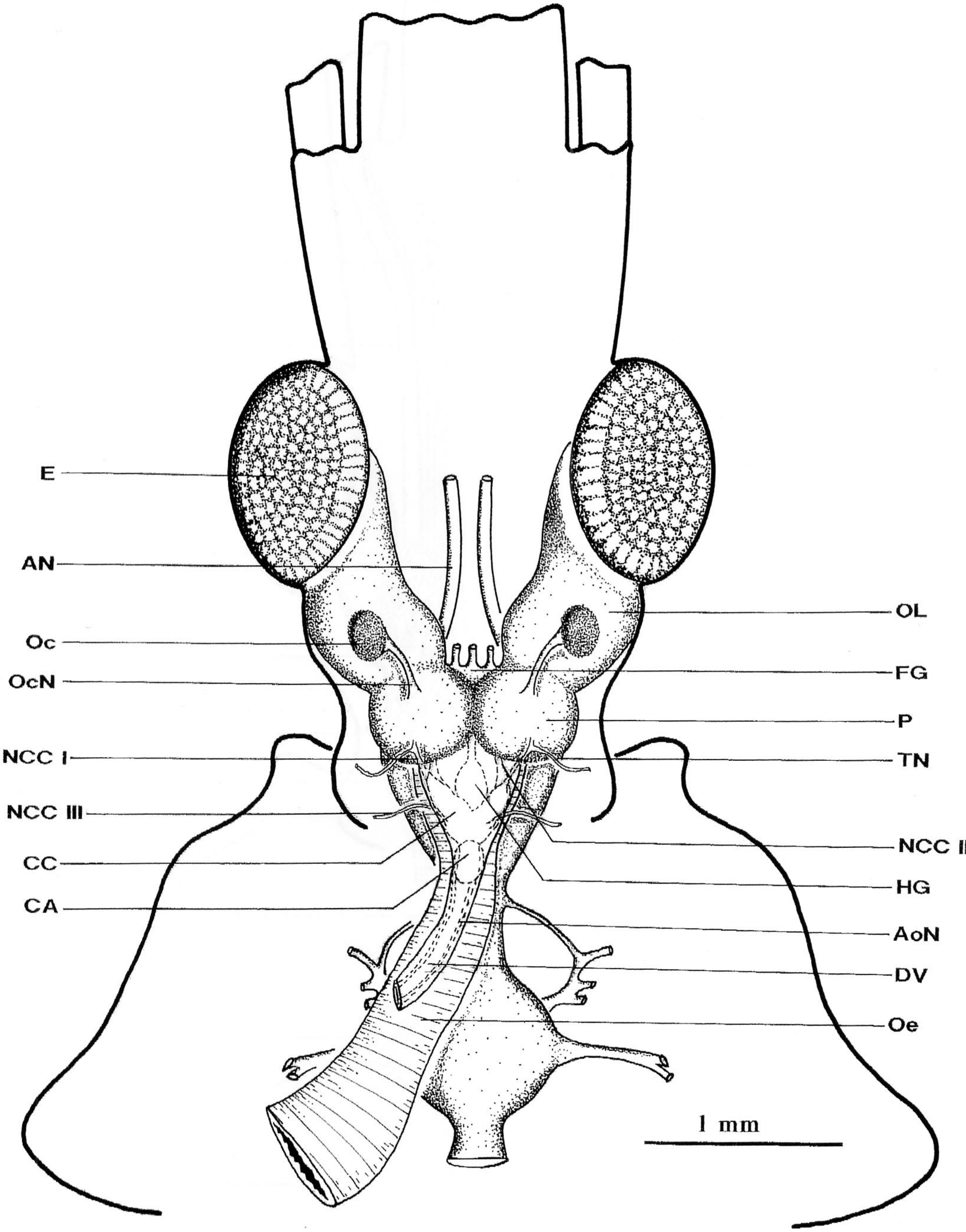

Fig. 5. *Triatoma infestans.* Dorsal view of the brain and suboesophageal and frontal ganglia, retrocerebral complex and prothoracic ganglionic mass, and the origin of their nerves.

two principal trunks, one slightly anterior to the other (Figs. 2, 4). The anterior trunk is a composite nerve with three branches. The first branch is slender and goes to the *corpora cardiaca* (NCC III, Figs. 2, 5). The second branch innervates the retractor mandibular muscle (M4, Fig. 2). The third branch bifurcates; one ramus goes to the base of the mandibular stylet (Bmd, Fig. 2), and the other bifurcates again sending branch to the mandible and another to the distal region of the maxillar protractor muscle (M8, Fig. 2). The posterior trunk also divides into three rami. The first and second branches innervate the retractor maxillar muscle (M7, Fig. 2). The third one divides into three rami; one innervates the base of the maxillary stylet (Bmx, Fig. 2), another sprouts over the stylet sheath, and the remaining one innervates the proximal region of the maxillar protractor muscle (M8, Fig. 2).

A pair of thick, conspicuous *labial nerves* (LbN, Fig. 4) arise from the ventral surface of the suboesophageal ganglion lobes and run ventrally into the labium. These nerves run very close together with the salivary duct (SD, Fig. 4). A very slender nerve arises ventrally from the base of the labial nerve and runs posteriorly to join the salivary duct, innervating (in the thorax) the salivary glands (SvGN, Fig. 4).

Prothoracic ganglion

The prothoracic ganglion (PG, Figs. 1, 3, 4) is joined anteriorly to the suboesophageal ganglion. The longitudinal connectives between them are fused medially (Co, Fig. 1). A *head-prothoracic nerve* arises from these connectives and joins the prothoracic nerve I (NCP, Figs. 1, 3, 4). From each side of the ganglion originate two nerves, one of which divides into four and the other into two branches.

The **prothoracic nerve I** (PN I, Fig. 1) bifurcates into two nerves; one of them joins the head-prothoracic nerve, and the other one sends branches to supply the muscles moving the head.

The **prothoracic nerve II** (PN II, Fig. 1) sends branches postero-laterally to innervate the promotor and rotor muscles of the forelegs, pronotocoxal (M12, Fig. 1) and pronototrochantinal (M14, Fig. 1).

The **prothoracic nerves III** and **IV** (PN III, PN IV, Fig. 1) innervate the depressor muscle of the trochanter (pronototrochanteral) (M11, Fig. 1).

The **prothoracic nerve V** (PN V, Fig. 1) and **prothoracic nerve VI** (PN VI, Fig. 1) branch off close to the common base. The prothoracic nerve V is slender and innervates the rotor muscles of the leg (anterior and posterior pronotocoxal muscles) (M13, Fig. 1). The prothoracic nerve VI is thick and enters into the coxal cavity.

Posterior ganglion

The posterior ganglion is larger and more elongate than the prothoracic one (PoG, Figs. 1, 6). It represents the fused mesothoracic, metathoracic, and abdominal ganglia, and gives rise to three groups of nerves. The first and second groups have three pairs of nerves that innervate the meso- and metathorax, respectively. The third group has five pairs of nerves that supply the abdominal segments.

Mesothoracic nerves

In the antero-lateral region from each side of the posterior ganglion, arise the **mesothoracic nerve I** (MsN, Fig. 1). At its base, it divides into two branches; one branch goes to the prothorax (*head-mesothoracic nerve*), whereas the other originates two nerves. The first nerve runs posteriorly and innervates the protractor muscle of the thorax, the prosternum mesosternal muscle (M15, Fig. 1), and thereafter joins the metathoracic nerve I (MtN I, Fig. 1). The second nerve originates two branches. The anterior branch innervates the dorso-longitudinal and dorso-ventral muscles, depressor and elevator of the forewing, respectively. The posterior branch runs into the base of the forewing and innervates the muscles of the region of the axillary sclerites (BFw, Fig. 1).

The **mesothoracic nerve II** arises posteriorly to the mesothoracic nerve I (MsN II, Fig. 1). This nerve divides into five main branches. Three branches innervate the rotor of the coxa and promotor of the leg muscle (mesoscutum trochantinal) (M16, Fig. 1), one goes into the coxal cavity, and the remaining sprouts ventrally through the adipose tissue.

The **mesothoracic nerve III** (MsN III, Fig. 1) is the thickest of the three nerves of the mesothorax, and it originates one anterior and one posterior nerve. The anterior nerve is thicker than the posterior one. It runs into the leg and bifurcates before going into the coxal cavity. The posterior nerve is slender and divides into two branches. One of these branches innervates the depressor muscles of the trochanter, mesofurco trochanteral and mesopleuro trochanteral (M18, M22, Fig. 1). The other branch divides innervating the dorso-ventral and the dorso-longitudinal muscles, the mesofurco pleural that accounts for the pleural position during flight and the mesoscutellum coxal, rotor of the coxa (M19, M20, Fig. 1).

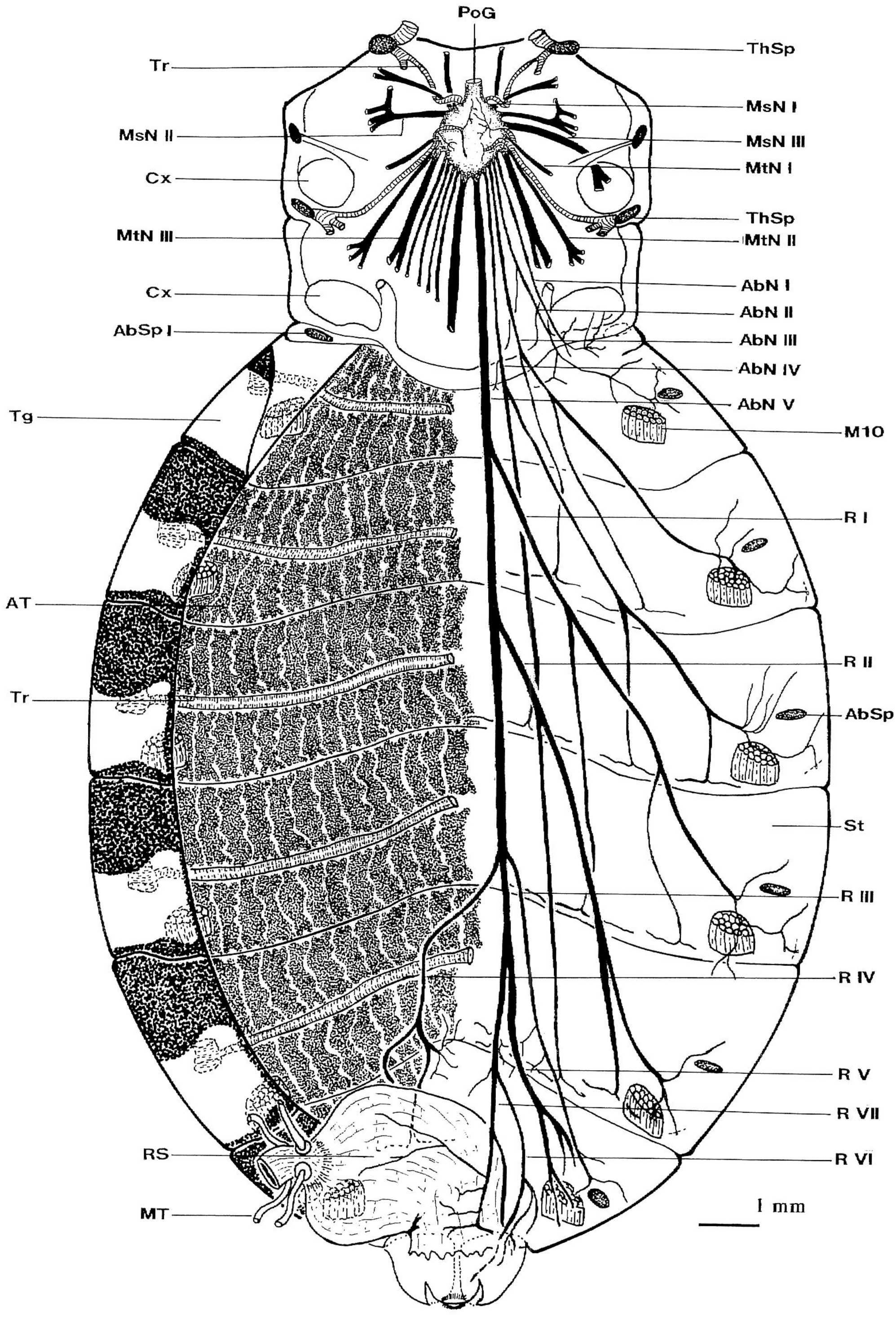

Fig. 6. *Triatoma infestans*. Dorsal view of the posterior fused ganglion (meso + metathoracic + abdominal ganglia). The innervations of the abdominal segments and rectum are shown.

Metathoracic nerves

The **metathoracic nerve I** (MtN I, Fig. 1) arises latero-dorsally from the ganglion. This nerve is slender, and it originates three main branches along its way. The first branch joins the mesothoracic nerve I and innervates the prosternum mesosternal and mesosternum phragmal muscles (M15, M21, Fig. 1). The second branch goes into the base of the hindwing, innervating the muscles of the axillary sclerites (BHw, Fig. 1). The third branch innervates the rotor muscle of the coxa, metascutum coxal (M23, Fig. 1).

The **metathoracic nerve II** (MtN II, Fig. 1) is slender also and arises laterally from the ganglion. This nerve originates two main rami. One of these sprouts ventrally through the adipose tissue. The other branch bifurcates, innervating the upper ramus of the muscle rotor of the coxa and promotor of the leg, metapleuro trochantinal (M24, Fig. 1). The lower ramus innervates the muscle rotor of the coxa (metascutum coxal), the muscle rotor of the coxa and promotor of the leg (metapleuro coxal), and the muscle depressor of the trochanter, metapleuro trochanteral (M23, M25, M26, Fig. 1).

The **metathoracic nerve III** (MtN III, Fig. 1) is thicker than the two preceding nerves. It runs to the metathorax and divides, originating one thick nerve that goes into the coxal cavity and one slight nerve. This last nerve innervates the muscle depressor of the trochanter, metafurco trochanteral (M27, Fig. 1) and runs to supply the rotor of the coxa muscle, metascutum coxal (M23, Fig. 1).

Abdominal nerves

The abdomen is supplied by five pairs of nerves, which come off from the posterior ganglion. The first four pairs are relatively fine, whereas the most medial fifth pair is fairly stout.

The **abdominal nerve I** (AbN I, Fig. 1) arises laterodorsally from the posterior ganglion. It extends posteriorly as far as the region of the metathoracic apodeme (Ap, Fig. 1), sending one ventral and one dorsal branch. The ventral branch innervates the muscle extensor of the abdomen, metafurco abdominal (M29, Fig. 1), which extends from the metathoracic apodeme to the antero-medial margin of the first abdominal sternum. The dorsal branch innervates the retractor muscle of the abdomen, postmetascutellum abdominal, which emerges at the postmetascutellum and inserts posteriorly on the first abdominal tergum.

The abdominal nerves II, III, and IV (AbN II, AbN III, AbN IV, Figs. 1, 6) come off very close together from the posterolateral part of the posterior ganglion. They innervate the second, third, and fourth abdominal segments, respectively.

The **abdominal nerve II** (AbN II, Figs. 1, 6) divides into three branches. The first branch innervates the muscle retractor of the abdomen, metasternum abdominal (M28, Fig. 1), which arises on the posterior margin of the metasternum and inserts on the anterior margin of the third abdominal sternum. The second branch bifurcates into two nerves; one nerve supplies the lower part of the metasternum abdominal muscle, and the other one branches on the second abdominal sternum under adipose tissue. The third branch divides into several rami. One ramus innervates the metapleuro abdominal muscle (M30, Fig. 1), which arises on the posterolateral apodeme of the metapleura and inserts on the second abdominal sternum; some other rami go to the tergo sternal muscle (M10, Figs. 1, 6) of the second abdominal segment, which arises laterally on the tergum and inserts on the sternum of the same segment. The remaining rami run dorsally surrounding the spiracle.

The **abdominal nerve III** (AbN III, Fig. 6) divides into three rami. The first two rami branch on the third abdominal sternum under adipose tissue. The remaining ramus branches on the tergo-sternal muscle of the fourth segment and runs dorsally surrounding the spiracle (see Fig. 8).

The **abdominal nerve IV** (AbN IV, Fig. 6) resembles the abdominal nerve III in its branching pattern and in the muscles it innervates. It sends three rami to the fourth sternum and branches under adipose tissue. Its fourth branch innervates the tergo-sternal muscle and runs dorsally surrounding the spiracle.

The fifth and following abdominal segment are supplied by branches of the median **abdominal nerve V** (AbN V, Fig. 6). It innervates the reproductive organs and the rectal sac, as well as the musculature of the terminal abdominal segments. The branching of this large, paired nerve shows considerable individual variation (see Fig. 9). Its size and the fact that it supplies several segments suggest that AbN V originates from the fusion of several abdominal nerves that have become fused. The first and second branches of the AbN V innervate the fifth and sixth abdominal segments, respectively (R I, R II, Fig. 6). These two branches resemble those of abdominal nerves III and IV, and both bifurcate into three nerves. The first two nerves branch under the adipose tissue of their respective segments. The third branch innervates the tergo-sternal muscles and turns dorsally surrounding the spiracle. In the fifth and sixth segments, the last dorsal ramus branches into the aliform muscles (M31, see Fig. 8). The aliform muscles arise on the tergum and insert on the dorsal vessel, forming the dorsal diaphragm in the sixth and seventh segments. The third branch of the AbN V innervates the seventh abdominal segment (R III, Fig. 6). The fourth branch of the AbN V innervates the muscles of the female's vagina and the male's copulatory apparatus (R IV, Fig. 6). The fifth branch of the same nerve bifurcates into two branches (R V, Fig. 6). Its upper branch innervates the duct of the male's accessory glands, whereas the other branch innervates the muscles of the male's genitalia and the female's ovipositor. The sixth branch of the AbN V supplies the anal muscles (R VI, Fig. 6). The seventh branch of the AbN V innervates the rectal sac (R VII, Fig. 6).

Stomodeal nervous system

The stomodeal nervous system consists of the **frontal** and the **hypocerebral ganglia** (FG, HG, Figs. 3–5). The **frontal ganglion,** which is connected to the tritocerebrum by two thick *frontal nerves,* lies anterior to the brain and dorsal to the gut. From the anterodorsal part of the ganglion, the *median frontal nerve* (MFrN, Figs. 1, 4) extends forward along the midline, above the pharyngeal pump; it innervates the pharyngeal dilatory muscles (M9, Fig. 2). The *recurrent nerve* (RN, Figs. 3–5) runs from the posterior part of the frontal ganglion toward the rear and passes between the brain and the suboesophageal ganglion, dorsal to the gut. Just before emerging posterior to the brain (central protocerebral lobes), below the aorta, the nerve becomes flat and broad. The flattened, broad part of the recurrent nerve ends as the hypocerebral ganglion, which was almost unnoticeable in unstained dissections. Its presence and form could be determined by dyeing this area. In the presence of a few drops of Delafield's hematoxylin or methylene blue, a group of cell bodies forming a plexus over the dorsal wall of the oesophagus become apparent. Histological preparations clearly revealed that this ganglion is closely associated with the *corpora cardiaca* dorsally.

A single medial *oesophageal nerve* (OeN, Fig. 3) runs posteriorly from the hypocerebral ganglion. This nerve extends over the dorsal muscular band of the oesophagus to the promesenteron. It runs between the salivary glands and sends branches to them (SvG, Fig. 7). The three pairs of salivary glands lie in the thorax on each side of the promesenteron. Therefore, they have double innervation, from the CNS through the salivary nerve and from the SNS through the oesophageal nerve.

The two oval *corpora cardiaca* are free anteriorly but fused posteriorly (CC, Figs. 2, 5). They lie just behind the brain, under the point where the aorta originates and becomes closely associated with its wall. The fused end of the *corpora cardiaca* joins the hypocerebral ganglion ventrally and the *corpus allatum* (CA, Figs. 2, 5) posteriorly. The latter is a single oval gland and together with the *corpora cardiaca* appears as a single structure.

The hypocerebral ganglion, the *corpora cardiaca,* the *corpus allatum,* and their nerves form the so-called *retrocerebral complex.* The latter joins the brain by two pairs of nerves, which arise from the back of the protocerebrum. The external upper nerve joins the anterior end of the *corpora cardiaca* (NCC I, Figs. 2, 5). The internal inferior nerve unites with the medial area of the last one (NCC III, Figs. 2, 5). From the latero-medial region of these corpora, a slender nerve (NCC III, Figs. 2, 5) extends anteriorly and joins the anterior trunk of the stylets nerves, very close to the place where they enter the suboesophageal ganglion. From the anterior extreme of the *corpora cardiaca,* two aortic nerves arise (AoN, Figs. 2, 5, 8). They form a longitudinal nerve on each side of the dorsal vessel and ramify on the aliform muscles (M31, Fig. 8) from the fifth and sixth abdominal segments.

DISCUSSION

The CNS in *Triatoma infestans,* as in other insects, is composed of the brain or supraoesophageal ganglion, the suboesophageal ganglion, and thoracic and abdominal ganglia. So far, some information on the anatomy of different parts of the brain and tracts linking them is available (Barth, '52, '75). However, for our study we lacked any detailed descriptions of the cephalic neuroanatomy, and almost nothing was known

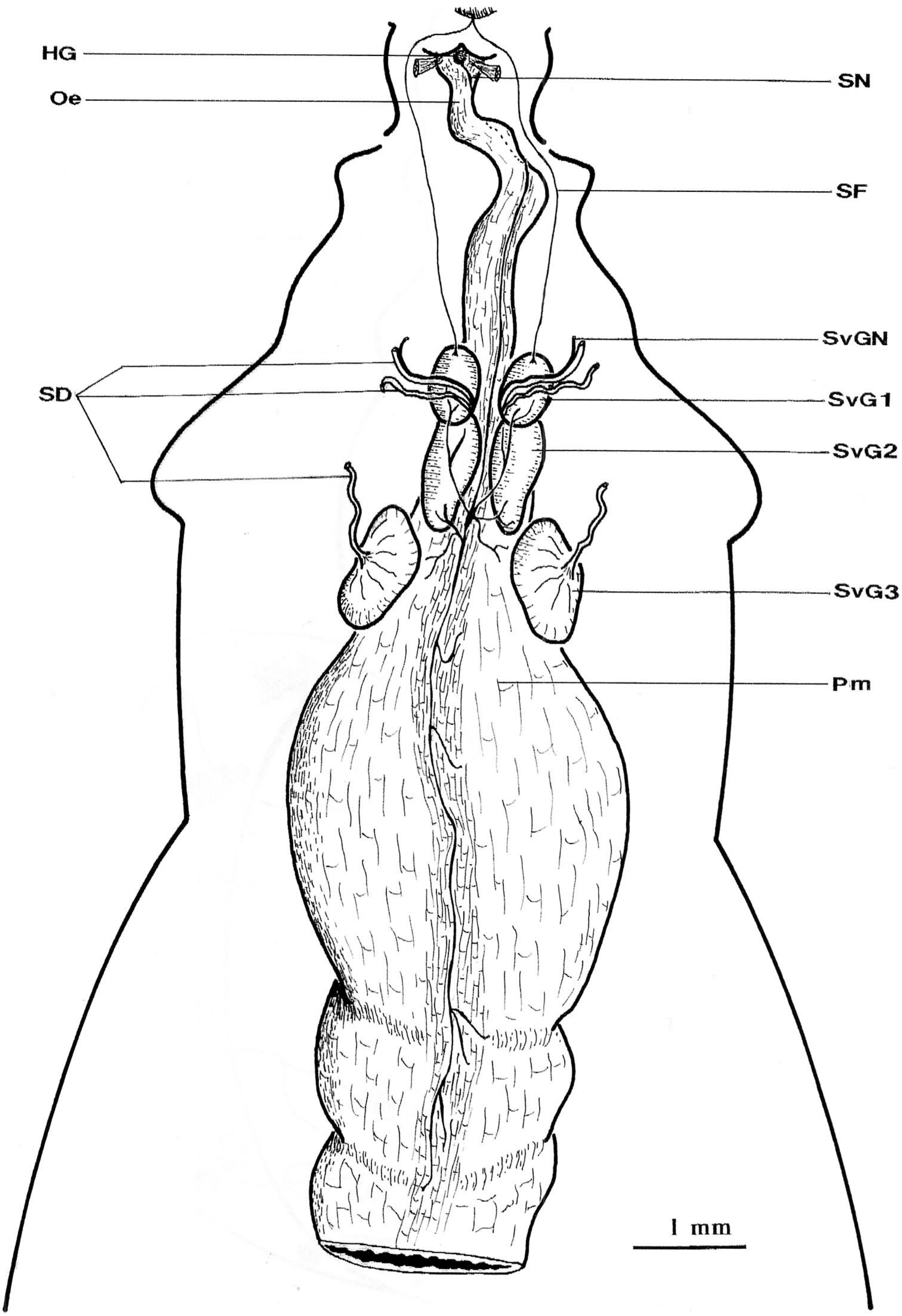

Fig. 7. *Triatoma infestans*. Dorsal view of the stomodeal nervous system. The hypocerebral ganglion, the oesophagic nerve and the innervation of the crop (promesenteron) and salivary glands are depicted.

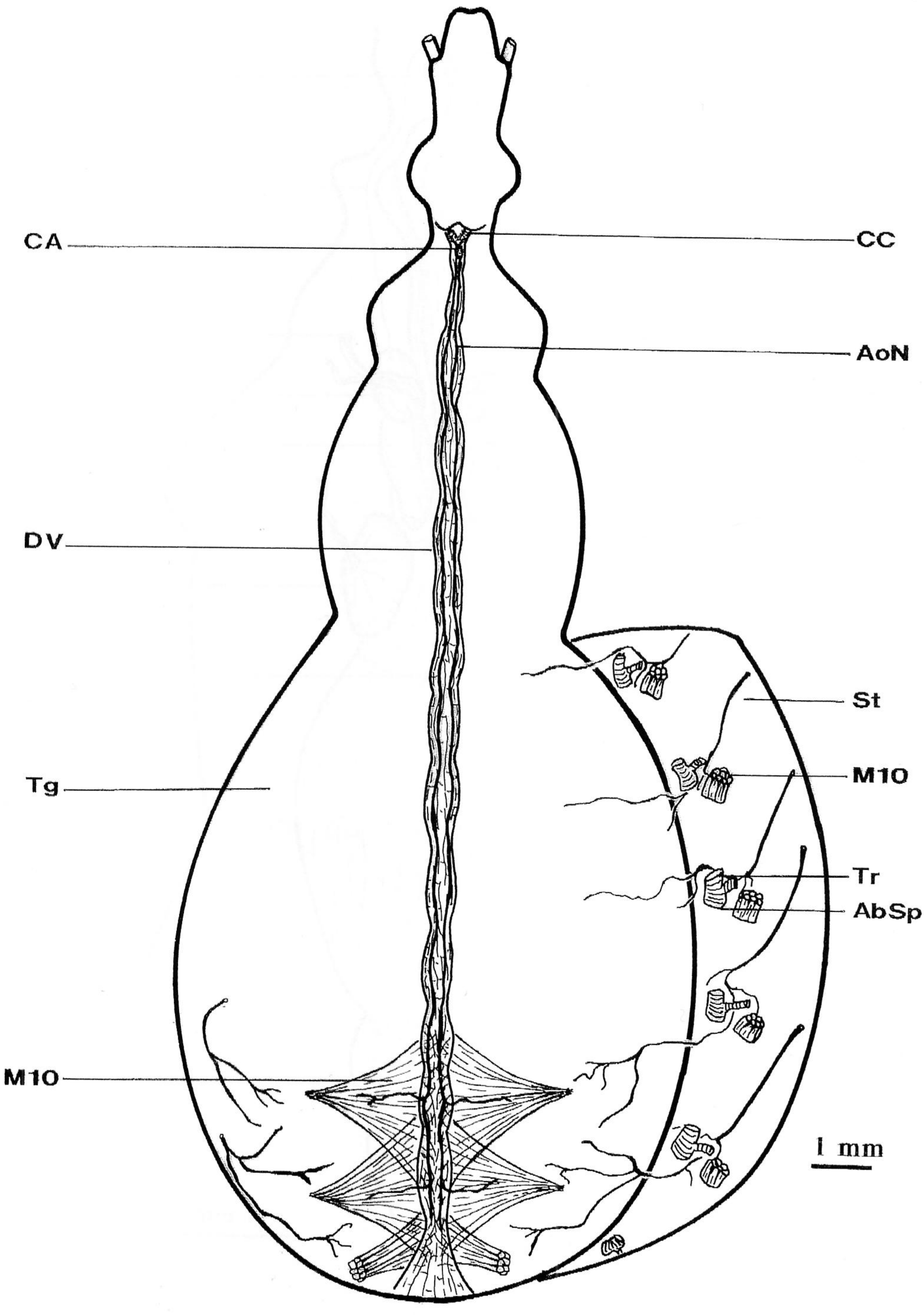

Fig. 8. *Triatoma infestans*. Dorsal view of the aorta, alary muscles, and spiracles showing their innervation.

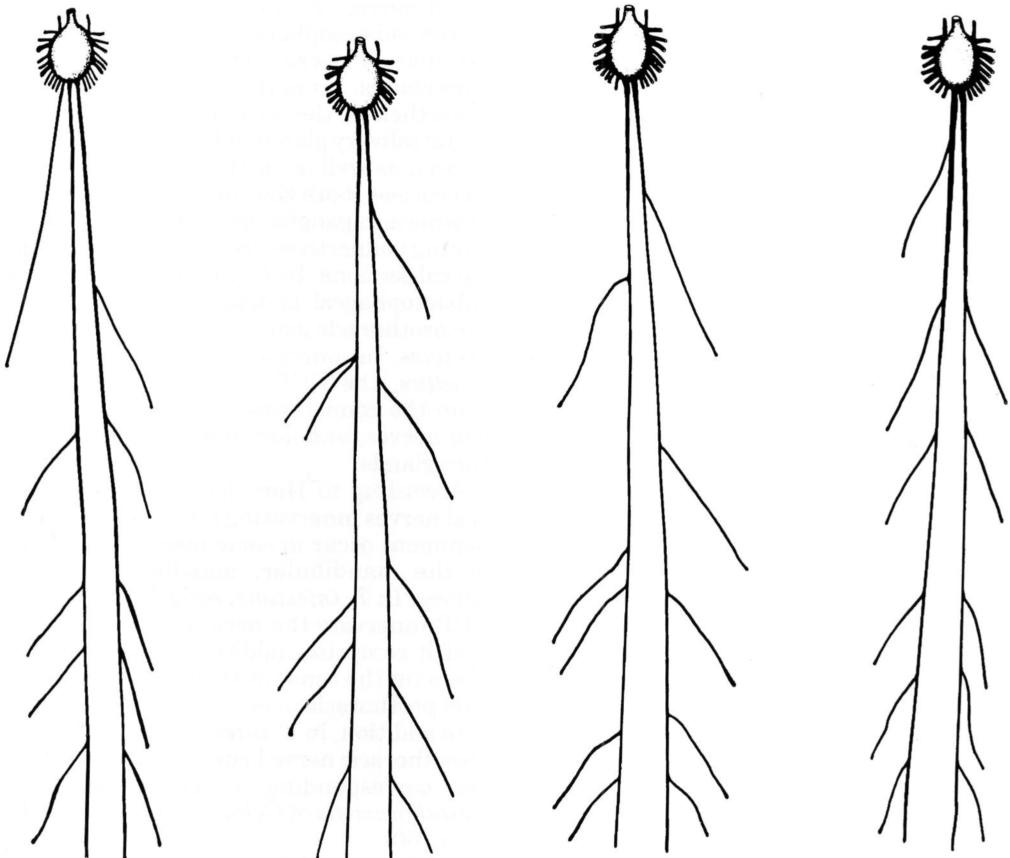

Fig. 9. *Triatoma infestans.* Branching of abdominal nerve V in four different individuals illustrating individual variations.

about the neuroanatomical features of the suboesophageal ganglion and the other ganglia of the ventral nerve cord. The ventral cord of this species exhibits a high grade of fusion. The posterior ganglion is formed by the fusion of the mesothoracic, metathoracic, and abdominal ganglia. As far as these features are concerned, the observations here presented for *T. infestans* are in general agreement with those of other workers, and no unusual conditions have been noted. A similar arrangement was described for *Rhodnius prolixus* by Wigglesworth ('59b) and Ramirez Perez ('69).

The morphology and location of the brain in *Triatoma* are related to the tubular and elongate shape of the head. This form determines the shift of the brain to the posterior part of the cephalic capsule, and the extreme shortness of connectives among the brain and the frontal and suboesophageal ganglia accounts for consolidating all three ganglia into a tight structure. The fusion of the brain and the suboesophageal ganglion is found in bugs, bees and flies, whereas crickets and locust have long circumoesophageal connectives separating the brain from the suboesophageal ganglion.

Most of the brain of *T. infestans* corresponds to the protocerebrum, which covers the smaller deuto- and tritocerebrum located ventrally (Barth, '75). Protocerebral nerves are principally those of the compound eyes and ocelli. However, other nerves leave the protocerebrum, i.e., NCCI, NCCII, and tegumentary nerves. According to Horridge ('65), the tegumentary nerves originate in the tritocerebral area and run dorsally before they emerge. Strictly speaking, they should not be considered as protocerebral nerves. *Corpora cardiaca* nerves actually belong to the protocerebrum, because they originate there as tracts and emerge on the posterior part of the brain.

A pair of thick antennal nerves originate in the deutocerebrum. From their basis arises a tegumentary nerve (*nervus tegumentarius primus*), similar to that found by Parsons ('60) in *Gelastocoris,* whose existence in Triatominae was not reported previously.

The labral nerves give origin to a nerve innervating the protractor muscles of the mandibles. In *Corixa, Gelastocoris,* and *Oncopeltus* a similar innervation of these muscles was found (Benwitz, '56; Johannson, '57; Parsons, '60). In addition, Johannson ('57) recognized in *Oncopeltus* the presence of nerve fibers innervating the mandibular protractor muscles, arising from the circumoesophageal connectives, and he found other fibers innervating the labral region, arising from the tritocerebrum.

The anterior nervous trunk arising from the suboesophageal ganglion is a composite one and divides into three branches. The thinnest branch is related to the *corpus cardiacum* in the way described by Cazal ('48). One of the other two branches bifurcates and one of these innervates the basis of the mandibular stylet, having apparently a sensory role (Bernard, '74). The posterior nervous trunk arising from the suboesophageal ganglion is also formed by three branches. A ramification innervates the basis of the maxillary stylet in the above described manner and another the stylet shield, having a probable sensory function. Pinet ('63) described in *Rhodnius prolixus* an innervation pattern of the stylets similar to that here described for *T. infestans.*

From the suboesophageal ganglion arises, in addition, the labial nerve. The innervation of the salivary glands is accomplished in *T. infestans,* as in Phasmodea, Blattodea and *Oncopeltus,* by a nerve emerging from the basis of the labial nerve and running in close association to the salivary channel, as described by Barth ('76).

Parsons ('60) described in *Gelastocoris oculatus* a *nervus capitis prothoracicus* (NCP) arising from the lateral surface of the suboesophageal ganglion, dorsal to the labial nerves. It runs posteriorly to join the first prothoracic nerve. Johannson ('57) described in *Oncopeltus* a similar nerve, the "salivary gland nerve," running from the lateral part of the suboesophageal ganglion to the first prothoracic nerve and innervating the salivary glands. From the work of Parsons ('60), nevertheless, the NCP does not appear to go to the salivary glands of *G. oculatus.* In *Gelastocoris,* as well as in Hydrocorisae and some Geocorisae, both the suboesophageal and the prothoracic ganglia are widely fused and the joining connectives are only evident in histological sections. In *T. infestans,* however, the suboesophageal ganglion is associated with the prothoracic ganglion by conspicuous connectives. In contrast to *Gelastocoris* and *Oncopeltus,* the NCP of *T. infestans* emerges from the connectives, far away from the labial nerves, and does not innervate the salivary glands.

According to Horridge ('65), suboesophageal nerves innervating the neck muscles and tegument occur in some insects, additionally to the mandibular, maxillary, and labial nerves. In *T. infestans,* some branches of the NCP innervate the neck muscles, indicating that it comprises additional suboesophageal fibers (in the sense of Horridge, '65), and not only prothoracic ones.

In addition, in *T. infestans,* a branch of the mesothoracic nerve I runs toward the prothorax, corresponding to the *nervus capitis-mesothoracicus* of *Gelastocoris oculatus* (Parsons, '60).

The larva of *T. infestans* possesses ventral intersegmental abdominal muscles, but these muscles are absent in the adult. The innervation of these larval muscles is provided in *Rhodnius prolixus* by mixed fibers, both motor and neurosecretory (Maddrell, '63, '66; Anwyl and Finlayson, '74). Some fibers go through the muscles innervating the ventral epidermis (Anwyl and Finlayson, '74). These nerves do not disappear in the imaginal stage, as the muscles do, retaining their neurosecretory function. On the basis of these facts, a similar neurosecretory function can also be postulated for the nerves running below the abdominal adipose tissue of the adult *T. infestans.*

We observed in *T. infestans* that the branching pattern of the AbN V is different in different individuals. The same fact was noted by Atkins and Chapman ('57) in *Dendroctonus pseudotsugae* (Scolytidae, Coleoptera) and in *Gelastocoris* by Parsons ('60). The former authors interpreted these variations as a possible consequence of the fusion of the ganglia.

The stomodeal nervous system of *T. infestans* comprises the frontal and the hypocerebral ganglia. The diffuse hypocerebral ganglion is included in the dorsal wall of the oesophagus and dorsally joined to the *corpora cardiaca.* A similar arrangement was also reported for *Nezara* and *Arilus* (Bickley, '42) and in Gimnocerata (Cazal, '48). From this ganglion arises a unique oesophageal nerve, innervating the gut and the salivary glands. These organs, therefore, receive a double innervation, from both the CNS and the SNS.

The retrocerebral complex, formed by the hypocerebral ganglion, the *corpora cardiaca,* and the *corpus allatum,* is related with the CNS by the NCC I and NCC II, arising from the protocerebrum, and by the NCC III arising from the suboesophageal ganglion. The oesophageal ventral dilator muscle is innervated by a branch from the NCC III. Parsons ('60) described a different innervation pattern in *Gelastocoris.* In this species he found a *nervus tritocerebralis,* which is absent in *Triatoma infestans.*

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