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RESEARCH ARTICLE

GENERAL ANATOMY AND HISTOLOGY OF THE NERVOUS SYSTEM IN *ACHATINA FULICA*

MALEEYA KRUATRACHUE[a], E. SUCHART UPATHAM[a], VIYADA SEEHABUTR[b], JITTIPAN CHAVADEJ[b], PRAPEE SRETARUGSA[b], AND PRASERT SOBHON[b]

[a]*Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand.*
[b]*Department of Anatomy, Faculty of Science, Mahidol University, Bangkok 10400, Thailand.*

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ABSTRACT

The nervous system of Achatina fulica *is composed of 13 ganglia : a pair of buccal ganglia, a pair of cerebral ganglia, a pair of pleural ganglia, a pair of parietal ganglia, a pair of pedal ganglia, a pair of tentacular ganglia and a single visceral ganglion. All ganglia give rise to many nerve branches which supply the snail body. They are surrounded by two layers of connective tissues: the thick outer layer and the thin inner layer connective tissue. Within the ganglia, there are nerve cells or ganglionic cells of four sizes: (1) the small cells which have the diameter of <20 microns, (2) the medium-sized cells which have the diameter of 20 - 39 microns, (3) the large cells which have the diameter of 40 - 99 microns, and (4) the giant cells which have the diameter of > 100 microns. In addition, there are masses of very small cells or globuli cells which have the diameter of 5 - 7 microns in the cerebral ganglia and the tentacular ganglia. Furthermore, in the cerebral ganglia, there is a group of neurosecretory cells which are characterized by a round heterochromatic nucleus and a large vacuole. Similarly, neurosecretory cells or collar cells were found around the finger-like projections of tentacular ganglion. These cells contain small round nuclei and their cytoplasm is full of granules and droplets.*

INTRODUCTION

Achatina fulica, the giant African snail, belongs to the Order Stylommatophora. The nervous system of stylommatophoran snails consists of six pairs of ganglia: cerebral ganglia, buccal ganglia, pleural ganglia, parietal ganglia, pedal ganglia, tentacular ganglia, and a single visceral ganglion[1]. The anatomy of the nervous system of *Helix aspersa* had been extensively studied[2].

The cerebral ganglia are often called the brain[1]. They lie dorsally to the esophagus and are connected by a short intercerebral commissure. In stylommatophoran snails, the cerebral ganglion can be divided into three parts, a procerebrum, mesocerebrum and metacerebrum such as in *H. aspersa*[3] , *H. pomatia*[4] and *Arion ater*[5].

The tentacular ganglion can be found in *H. aspersa*[2] and *A. ater*[5,6]. It is divided into many finger-like projections which in term break down into individual nerve fibers which terminate in small sensory endings between epidermal cells of the tip of tentacles[5]. There is a tentacular nerve connecting between the procerebrum of cerebral ganglia and the tentacular ganglion[1].

The histology of ganglia in the nervous system in the stylommatophoran snails had been studied in *H. pomatia*[7-10] , *A. ater*[5], *Limax maximus*[10]. The neurons in the ganglia are arranged with their cell bodies peripherally and their axons running centrally into the neuropil[2].

There are several methods to identify the types of neurons in the nervous system of the stylommatophoran snails. Nabias[7] classified the neurons in *H. pomatia* into three types according to the cell size : (a) the globuli cells with a diameter of 8 microns, (b) the medium-sized cells with a diameter of 20 or more microns, and (c) the giant cells with a diameter of 132 or more microns. Kunze[8] and Kandel and Tauc[9] classified the giant cells of *H. pomatia* to have a diameter of more than 100 microns.

Smith[5] classified neurons in the central nervous system of *A. ater* into four sizes. The size range of the cells in each ganglion is not equal. They are small cells, medium cells, large cells and giant cells. In the parietal ganglion of *A. ater*, there are small cells with diameter of 20-30 microns, medium cells with diameter of 30-50 microns, large cells with diameter of 50-95 microns and giant cells with diameter of 100-290 microns. In the pedal ganglion, there are small cells with diameter of 15-30 microns, medium cells with diameter of 30-50 microns, large cells with diameter of 50-80 microns and giant cells with diameter of 100-150 microns.

Pentreath *et al.*[10] classified the neurons on the basis of morphology of the cell and its nucleus. They concluded that the giant cells of *H. pomatia* and *L. maximus* were similar to those described in other gastropod species. They are large cells containing irregular-shaped nucleus[11,12].

The occurrence of neurosecretory cells in pulmonate snails was first reported by Gabe[13]. On the basis of stainability of neurosecretory cells to different histochemical methods, such as classical staining methods using chrome-hematoxylin phloxine[14] and paraldehyde-fuchsin[15], various types of neurosecretory cells could be distinguished. The blue-black colored or deep-purple colored cell of chrome-hematoxylin and paraldehyde-fuchsin, respectively, is regarded to be the "Gomori - positive cell". The other type of neurosecretory cells is "Gomori-negative cell" which appears red in the chrome-hematoxylin phloxine method[16-18].

There have been several reports on general anatomy and histology of the nervous system in various species of stylommatophoran snails. However, the detailed study on anatomy and histology of the nervous system of *A. fulica* is still unclear. Hence, the aims of the present study is (1) to study the anatomy and morphology of the ganglia and nerve connections, (2) to study the histology of ganglia and the pattern of distribution of neurons in each ganglion, and (3) to identify the presence of neurosecretory cells in the ganglia by using two special staining methods, chrome-hematoxylin phloxine and paraldehyde-funchsin.

MATERIALS AND METHODS

Anatomical study

The mature snails, *A. fulica* were collected from the wild during the rainy season. Snails with the shell length of 6-7 cm or the weight of 25-30 g were used in the experiment. After the snails were anesthesized with 1% nembutal for 30 min, they were sacrificed and their shells were removed. Dissections were made by placing the snails in enamel pans in each of which a layer of paraffin had been poured. Specimens were secured to this base with entomologistsû needles. Most of the dissections were made under a stereomicroscope, with the specimen in 70% alcohol. Anatomical drawings were made with the aid of a camera lucida.

Histological study

The mature snails, *A. fulica*, were anesthesized with 1% nembutal for 30 min. Then, they were sacrificed and all the ganglia such as buccal ganglia, cerebral ganglia and subesophageal ganglionic mass were dissected out. The optic tentacles in the region of tentacular ganglia were cut off. All the ganglia and the optic tentacles were fixed immediately in Bouin's fluid for 5-7 hours. The specimens were then dehydrated through a graded series of ethanol (50%, 70%, 80%, 90%, 95% and 100%). After infiltration with dioxane, the specimens were embedded in paraffin and sectioned serially at 6 microns thickness with an A.O. rotary microtome. Then, all the serial sections were stained with hematoxylin and eosin. Measurement of the size of the ganglionic cells was done by using ocular grid.

In addition, two special staining methods, chrome-hematoxylin phoxine[14] and paraldehyde-fuchsin[15] were employed to localize the neurosecretory cells in all the ganglia and optic tentacles.

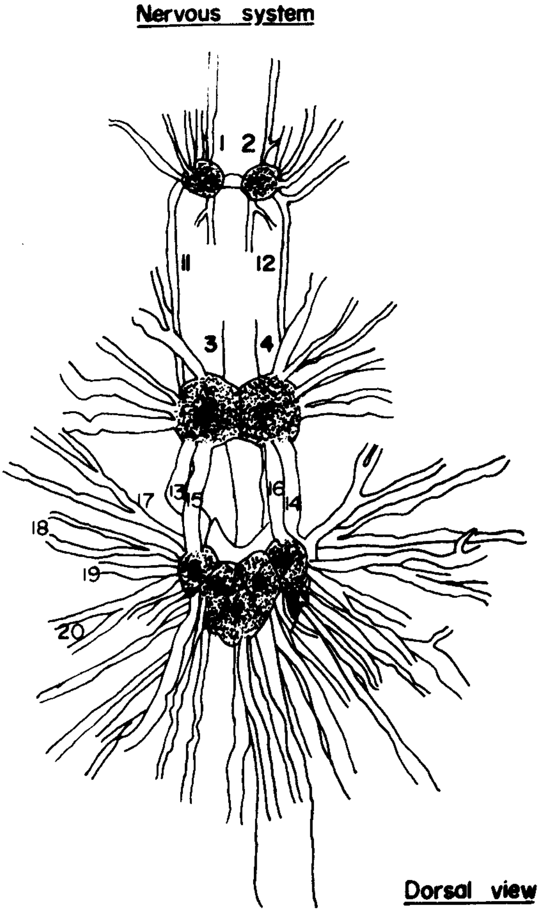
RESULTS

Anatomical study

The nervous system of *A. fulica* consists of 13 ganglia : a pair of buccal ganglia, a pair of cerebral ganglia, a pair of pleural ganglia, a pair of parietal ganglia, a pair of pedal ganglia, a pair of tentacular ganglia and a single visceral ganglion.

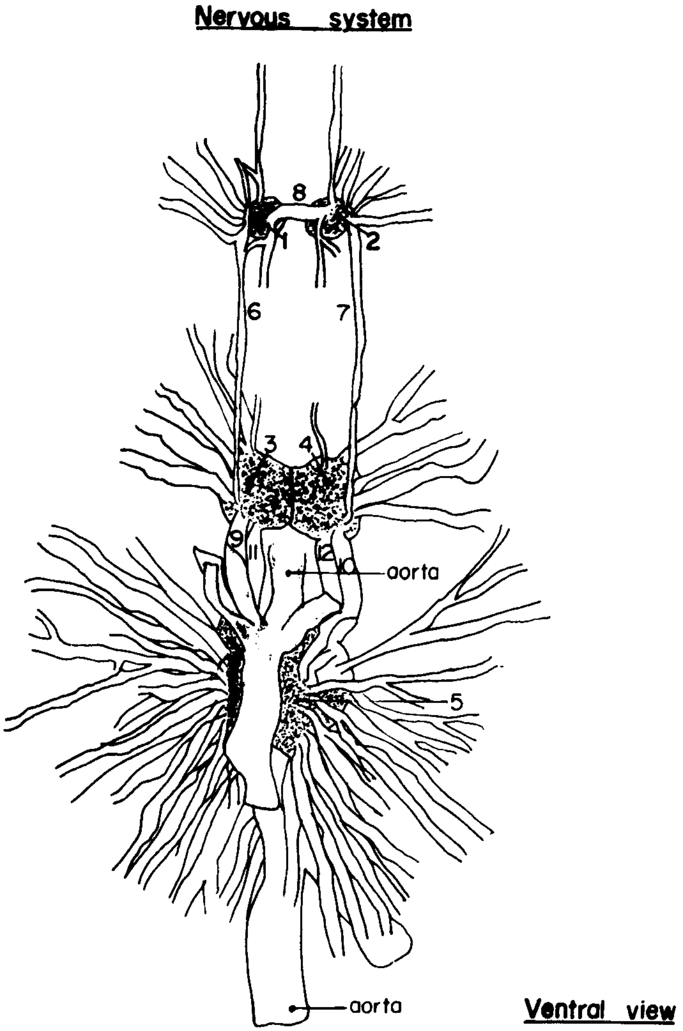
Figures 1 and 2 show the dorsal and ventral views of the nervous system. From the dorsal view, a pair of buccal ganglia lies by the side of esophagus. They are connected with the cerebral ganglia by the cerebral - buccal commissure.

The subesophageal ganglionic mass lies underneath the esophagus and is connected with the cerebral ganglia by the cerebral - pleural and cerebral - pedal commissures (Figs. 1,2).



1. Left buccal ganglia.
2. Right buccal ganglia.
3. Left cerebral ganglia.
4. Right cerebral ganglia.
5. Left pleural ganglia.
6. Left parietal ganglia.
7. Visceral (abdominal) ganglia.
8. Right parietal ganglia.
9. Right pleural ganglia.
10. Pedal ganglia.
11. Cerebral—buccal commissure.
12. Cerebral-buccal commissure.
13. Cerebral—pedal commissure.
14. Cerebral—pedal commissure.
15. Cerebral—pleural commissure.
16. Cerebral—pleural commissure.
17. Nerve to anterior body.
18. Nerve to muscle.
19. Nerve to posterior body.
20. Nerve to anterior body and muscle.

Fig. 1 Dorsal view of the nervous system of *Achatina fulica*.



1. Right buccal ganglia.
2. Left buccal ganglia.
3. Right cerebral ganglia.
4. Left cerebral ganglia.
5. Pedal ganglia.
6. Cerebral–buccal commissure.
7. Cerebral–buccal commissure.
8. Buccal commissure.
9. Cerebral–pedal commissure.
10. Cerebral–pedal commissure.
11. Cerebral–pleural commissure.
12. Cerebral–pleural commissure.

Fig. 2 Ventral view of the nervous system of *Achatina fulica*.

Buccal ganglia

The buccal ganglia lie upon various parts of the buccal mass, under the esophagus and anterior to the cerebral ganglia (Figs. 1,2). They are joined by the interbuccal commissure which occurs on the dorsal surface of the buccal mass immediately beneath the esophagus where the esophagus enters the buccal mass (Fig. 3A).

Fig. 3A reveals the dorsal view of the buccal ganglia which give rise to the nerves from the dorso-anterior sides of the ganglia. These nerves innervate muscles of the mouth and radula. The salivary gland nerves arise from the dorso-median sides of the ganglia and innervate the salivary glands. The pharyngeal nerves originate from the lateral sides of the ganglia and innervate the pharyngeal walls and muscles. At the latero - caudal sides, there are cerebral - buccal commissures.

Cerebral ganglia

The cerebral ganglia lie bilaterally upon the esophagus, posterior to the buccal ganglia. The cerebral ganglia are connected with each other by very short intercerebral commissure.

The cerebral ganglia give rise to the tentacular nerves and the optic nerves (Fig. 3B). These are sensory nerves, receiving impulses from the posterior tentacles and the eyes, respectively, and carrying the impulses to the cerebral ganglia. At the lateral sides of the ganglia arise the external peritentacular nerves, the external labial nerves and the medial labial nerves (Fig.3B). The external peritentacular nerves innervate the skin of the optic tentacles and the external and medial labial nerves innervate the muscles of the buccal mass. Furthermore, at the postero-lateral sides, arise the cerebral - pedal commissure and at the postero-medial sides, arise the cerebral - pleural and cerebral - pedal commissures (Fig. 3B).

Subesophageal ganglionic mass

The subesophageal ganglionic mass is a mass of nervous tissue which lies under the esophagus and columellar muscle. It is composed of seven ganglia : two pleural ganglia, two parietal ganglia, two pedal ganglia and a single visceral ganglion (Fig. 3C).

Pleural ganglia The pleural ganglia are situated between the cerebral and parietal ganglia (Fig. 3C). They are the two extreme lateral lobes of the pleuro-parieto-visceral ganglionic mass. The pleural ganglia are also fused over a large area with the pedal ganglia. There are no nerves that emerge from the pleural ganglia.

Parietal ganglia The two parietal ganglia are similar, though the right one is slightly larger than the left. They are situated between the pleural ganglia and a single visceral ganglion (Fig. 3C).

The left parietal ganglion gives rise to three pallial nerves whereas the right parietal ganglion gives rise to two pallial nerves (Fig. 3C). The nerves from the left parietal ganglion innervate the mantle skirt and muscles. They emerge from the dorso-lateral sides of the parietal ganglion. The other nerves from the left parietal ganglion are the nerve to muscle

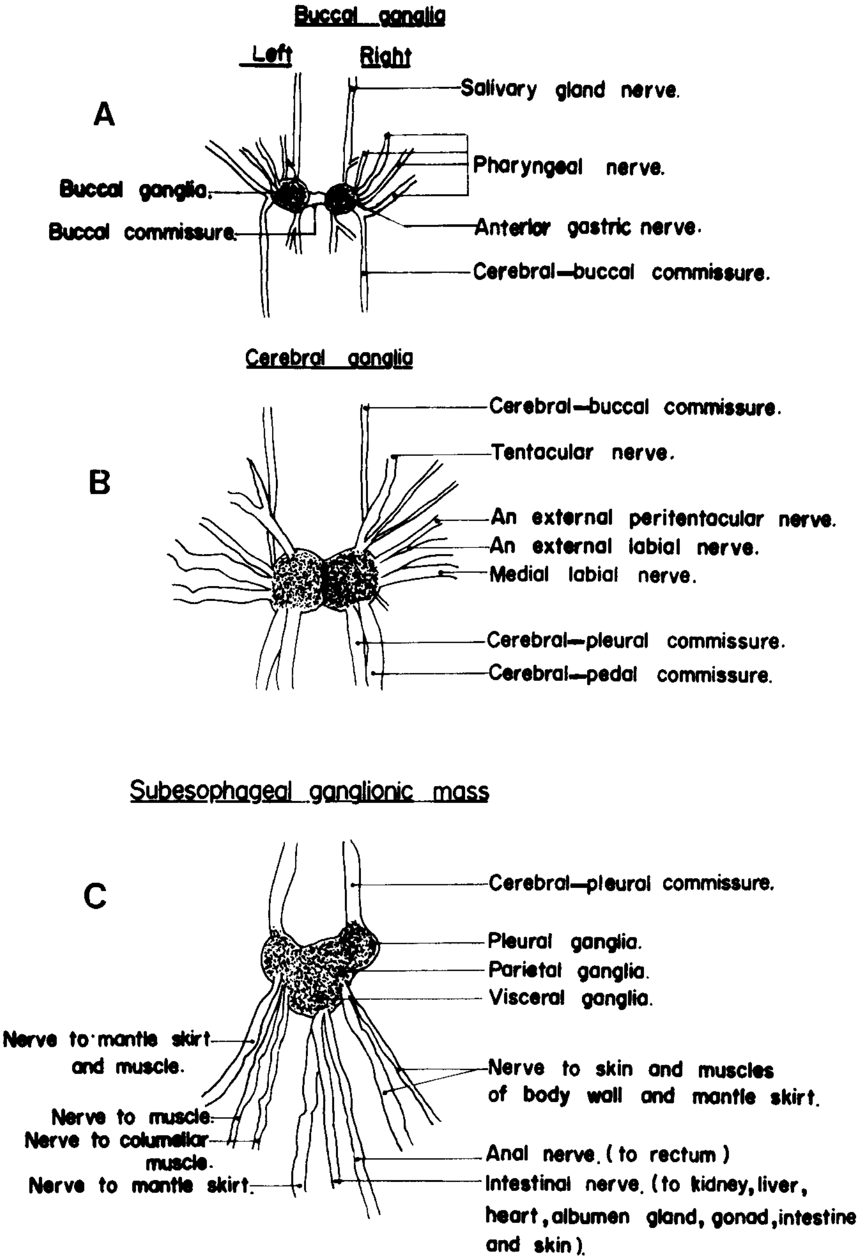


Fig. 3 Dorsal view showing:

A. Buccal ganglia with their nerves.

B. Cerebral ganglia with their nerves.

C. Subesophageal ganglionic mass consisting of pleural,parietal and visceral ganglia and their nerves.

and the nerve to columellar muscle. They emerge from the dorso-lateral side of the ganglion and are below the nerves to mantle skirt and muscle. The right parietal ganglion gives rise to two pallial nerves which innervate skin and muscles of body wall and mantle skirt. They originate from the dorso-posterior side of the ganglion.

Visceral ganglion. The visceral ganglion is a single ganglion, situating in the middle part of the pleuro-parieto-visceral ganglionic mass. Each lateral side of the visceral ganglion is connected with the parietal ganglia with a very short commissure.

There are three peripheral nerves that emerge from the visceral ganglion (Fig. 3C) : (a) the main visceral nerve or intestinal nerve which is the most dorsal of the three nerves leaving the ganglion, running posteriorly and innervating kidney, liver, heart, albumen gland, gonad, intestine and skin, (b) the anal nerve to supply the rectum and (c) the posterior pallial nerve which emerges immediately beneath the visceral nerve and runs to supply the mantle skirt.

Pedal ganglia. The pedal ganglia are situated ventrally to the pleuro-parieto-visceral ganglionic mass and are composed of two large oval pedal ganglia (Fig. 4). They are joined to each other by the short interpedal commissure. There are many nerves that originate from the pedal ganglia, such as, the antero-lateral nerves which originate from the antero-lateral side of the pedal ganglia and innervate the lateral and middle body walls and penis, the posterior nerves which emerge beneath the anterior parietal nerves and innervate the posterior body wall (Fig. 4).

Optic tentacles.

The optic tentacles are the large upper pair of tentacles carrying the eyes and the large digitated tentacular ganglia. The eye is innervated by the thin optic nerves from the cerebral ganglia. Running by the side of this, though completely separated from it, is the much larger tentacular nerve which terminates just below the eye in the large digitated tentacular ganglion.

Histological study

All the ganglia in the nervous system of *A. fulica* are covered with two layers of connective tissues, the condensed inner layer and the loosely-arranged outer layer. The observation on histology of all the ganglia reveals that the nerve cells or ganglionic cells in the ganglia can be classified into five types according to size and shape of the cells, shape of the nucleus and chromatin distribution in the nucleus. They are :

1. The globuli cells, characterized by small size (5-7 microns in diameter), paucity of cytoplasm and abundance of chromatin in the nuclei which are proportionally large compared to the cells.

2. The small cells, characterized by round cells with the diameter of 15-18 microns, containing round nuclei with evenly distributed patches of chromatin.

3. The medium cells, characterized by round or oval cells with the diameter of 20-39 microns, containing round or oval nuclei with evenly distributed patches of chromatin.

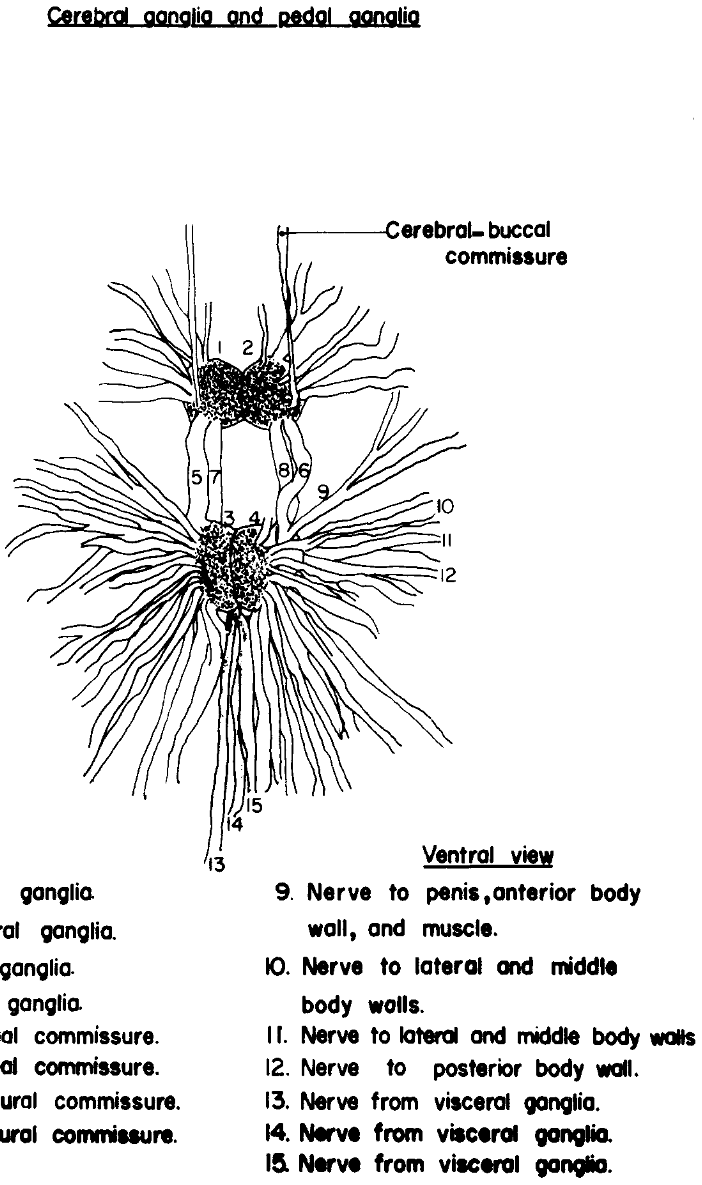


Fig. 4 Ventral view of cerebral ganglia and pedal ganglia connected by cerebral-pedal commissure. Pedal ganglia are part of subesophageal ganglionic mass.

4. The large cells, characterized by round or oval cells with the diameter of 40-99 microns, containing round or oval nuclei similar to those in the medium cells.

5. The giant cells, characterized by prodigious size (>100 microns in diameter), abundance of cytoplasm, and paucity of chromatin in the irregular-shaped nuclei.

Buccal ganglia

In the buccal ganglia, the neurons are arranged peripherally around the neuropil (Fig. 5A). There are four giant cells with a mean diameter of 114 ± 2.02 microns and large cells with the diameter of 79 ± 3.09 microns(Tables 1,2) which are separated from the smaller cells (Fig. 5A). On the contrary, the smaller cells usually form a group of nerve cells. The giant cells of the buccal ganglia contain an irregular heterochromatic nucleus (Fig. 5A). The medium cells and the small cells with the mean diameters of 33 ± 1.22 and 15 ± 0.91 microns, respectively, could be observed (Table 1).

Cerebral ganglia

The cerebral ganglion can be divided into three parts: the procerebrum, mesocerebrum and metacerebrum (Fig. 5B). The procerebrum is separated from the mesocerebrum by a septum. The cells in the procerebrum send the axons into the central part of the cerebral ganglia. Most of the neurons in the procerebrum are globuli cells with the mean diameter of 5 ± 0.92 microns with prominent nuclei (Fig. 6A).

Furthermore, in the cerebral ganglia of *A. fulica* especially in the procerebrum, there is a group of neurosecretory cells with a mean diameter of 25 ± 5.34 microns lying against the perineurium. The typical characteristic of these neurosecretory cells is the large vacuole in the cytoplasm (Fig. 6A). The round heterochromatic nucleus with its conspicuous nucleolus is pushed to one pole of the cell by this vacuole.

The mesocerebrum is the antero-medial part of the cerebral ganglion (Fig. 7A). The typical characteristic of this part is the presence of giant cells with a mean diameter of 136 to 209 microns. The giant cell contains irregular heterochromatic nucleus with a small part of cytoplasm (Fig. 6B). It is observed that the giant cells are clearly separated from the group of smaller cells. In addition, there are some large cells, medium cells and small cells which are formed in clusters (Figs. 7B,7C).

The metacerebrum is the posterior part of the cerebral ganglion. The giant cells in this part have the diameter in the range of 150 to 179 microns. In addition, there are a few large cells, numerous medium and small cells. Similar to the mesocerebrum, the neurons in this part usually are formed in clusters, except for the solitary giant cells.

The cerebral ganglia contain eight giant cells (Table 2) which have a large irregular heterochromatic nucleus (Fig. 6B). However, the smaller neurons contain nuclei which are round or oval in shape with one or two conspicuous nucleoli (Figs. 7B,7C). The mean diameter of the giant cells in the cerebral ganglia is 164 ± 6.86 microns, of the large cells 75 ± 4.64 microns, of the medium cellls 31 ± 1.77 microns and of the small cells 15 ± 0.83 microns (Table 1).

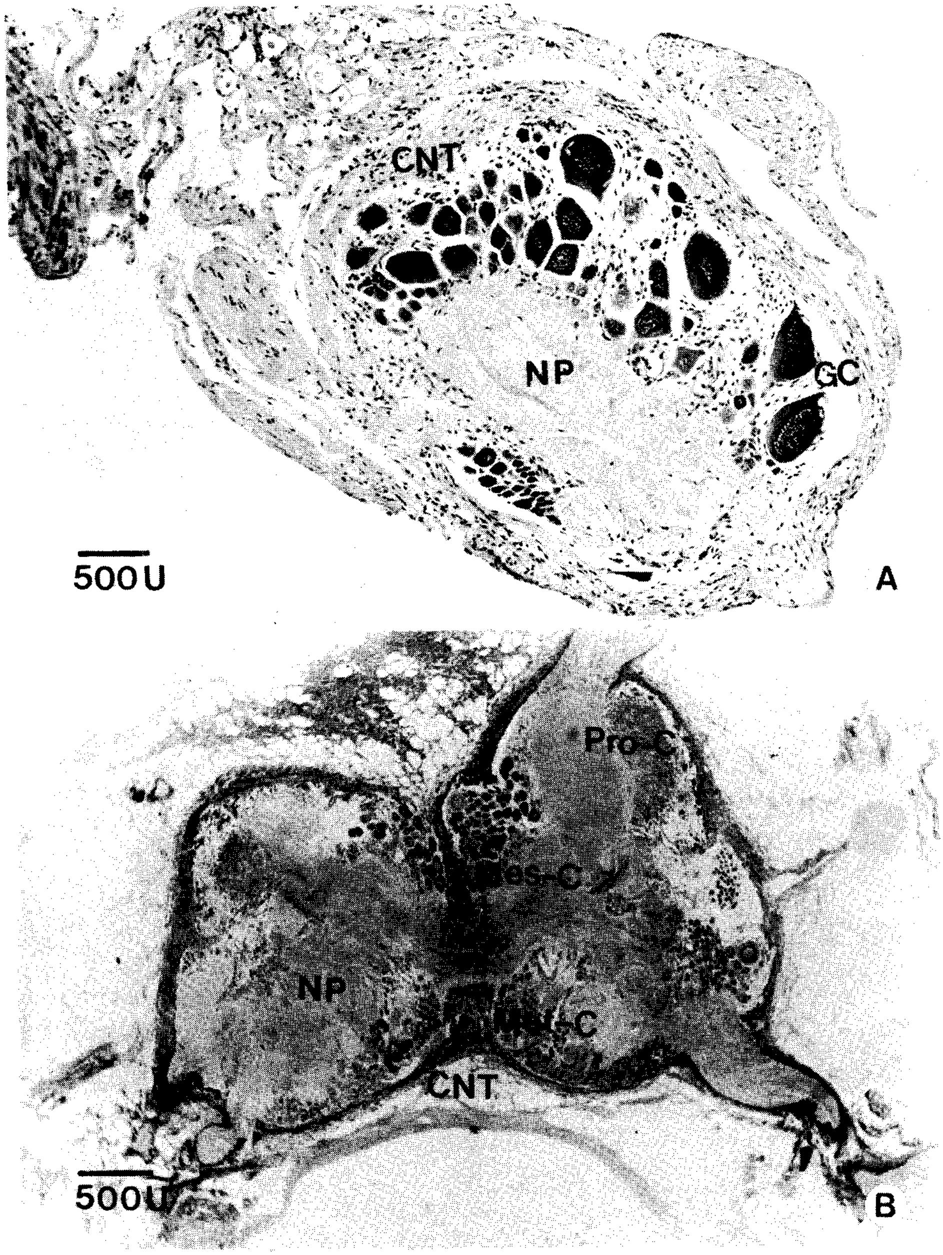


Fig. 5 Photomicrographs of longitudinal section of buccal and cerebral ganglia.

A. Buccal ganglion with its giant nerve cells (GC) which are usually located at the periphery. CNT = connective tissue, NP = neuropil.

B. Cerebral ganglia covered by two layers of connective tissues (CNT) and can be divided into three parts: procerebrum (Pro-C), mesocerebrum (Mes-C) and metacerebrum (Met-C). NP = neuropil.

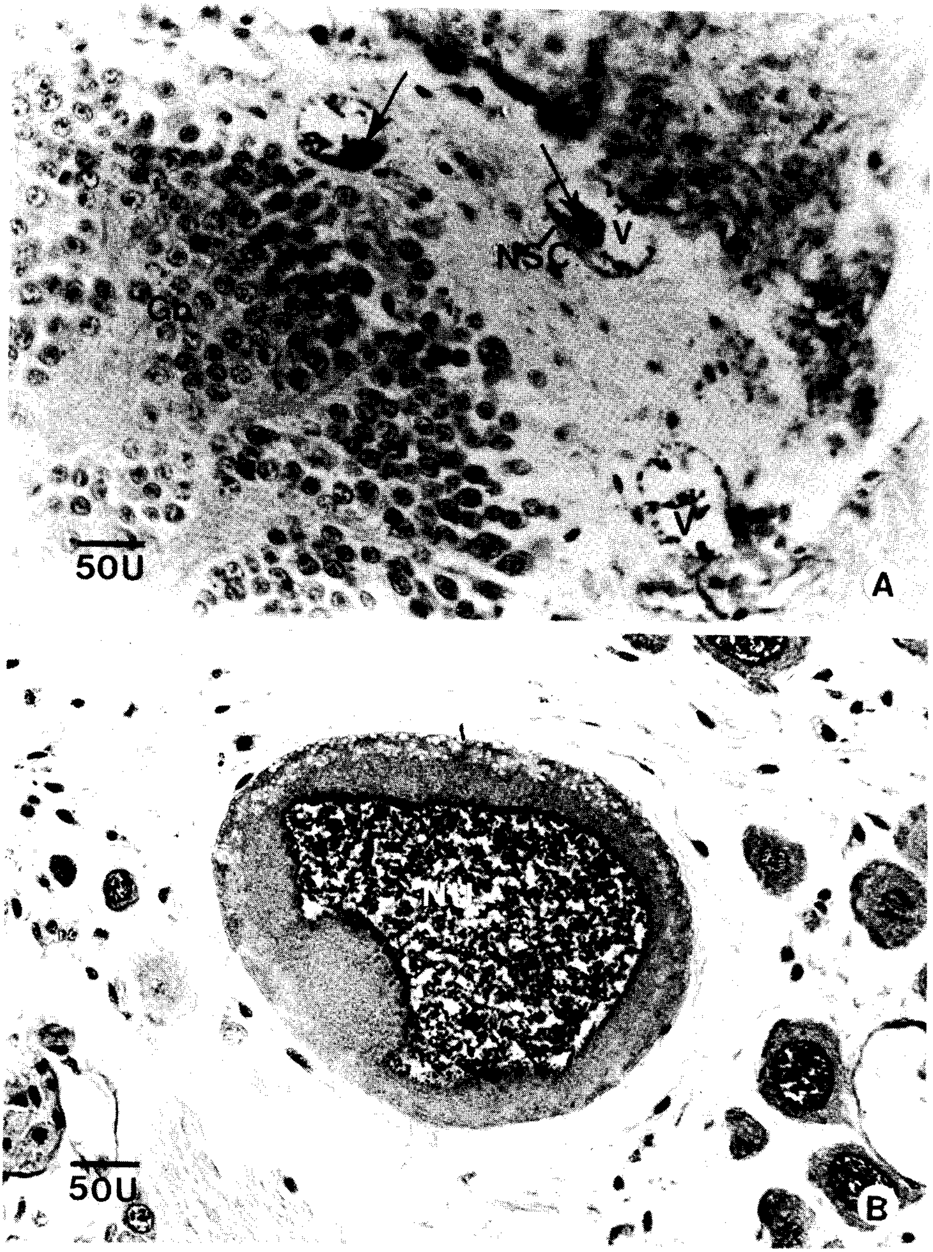


Fig. 6 A. Typical characteristics of procerebrum of cerebral ganglia are the mass of globuli cells (Gb) and neurosecretory cells (NSC) containing large vacuoles (V) and round to oval nuclei (arrows).

B. High magnification of giant nerve cell of cerebral ganglia with irregular nucleus (NU).

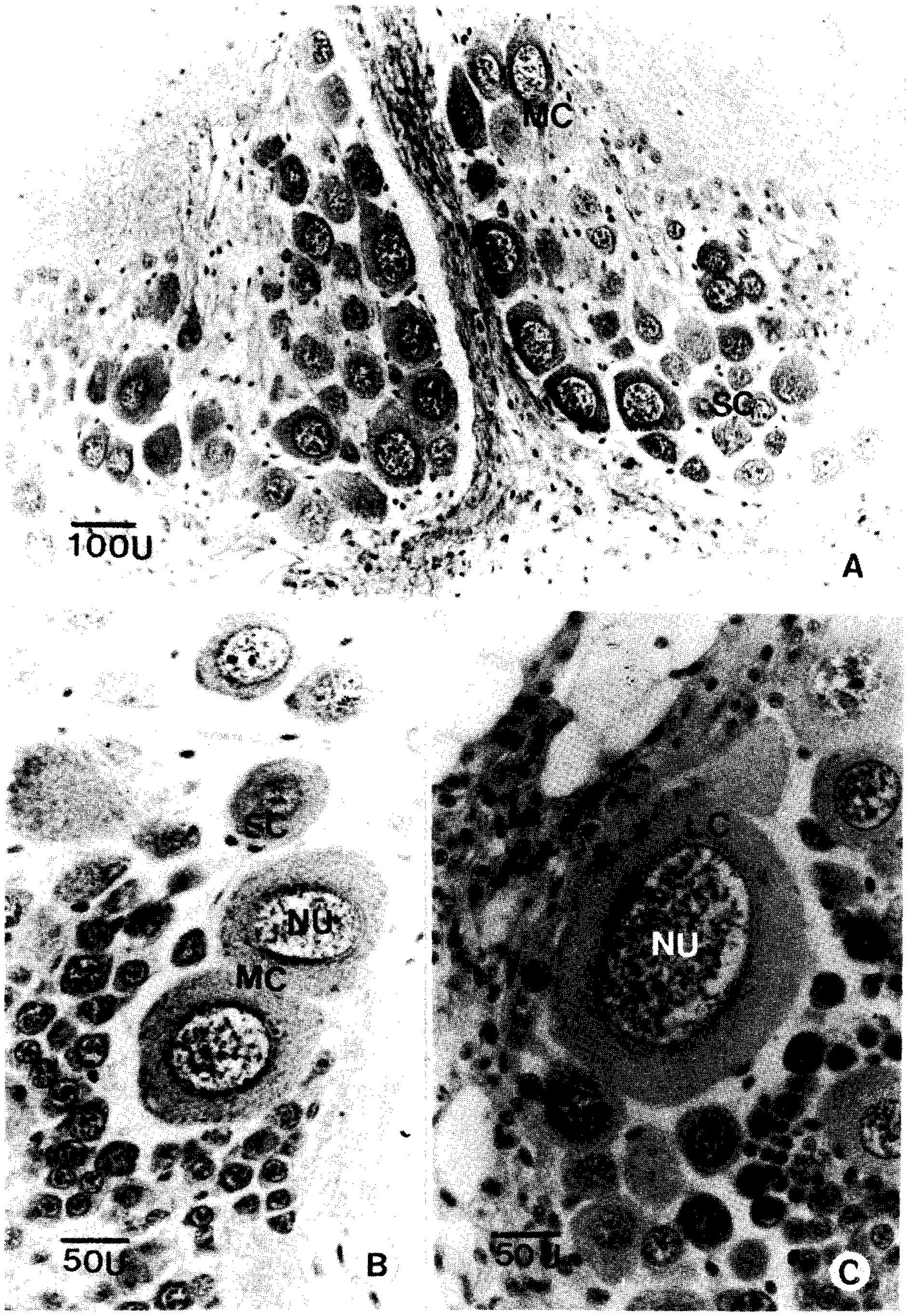


Fig. 7 A. Mesocerebrum of cerebral ganglia showing clusters of small (SC) and medium (MC) nerve cells.
B. High magnification of medium (MC) and small nerve cells (SC) with round nuclei (NU).
C. High magnification of large nerve cell (LC) with oval nucleus (NU).

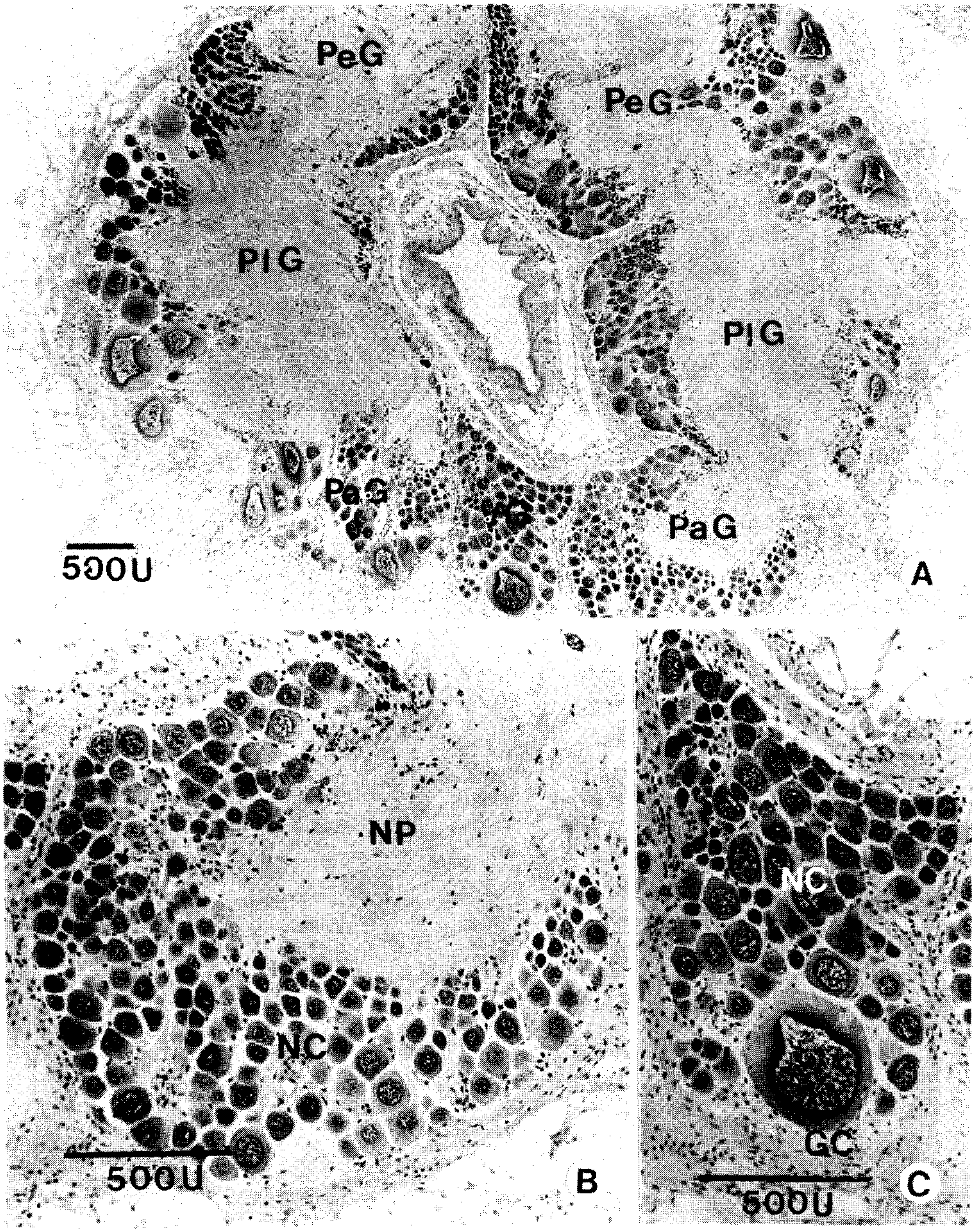


Fig. 8 Photomicrographs of longitudinal section of subesophageal ganglionic mass.

A. Subesophageal ganglionic mass consisting of a pair of pedal (PeG), pleural (PlG), parietal ganglia (PaG), and a single visceral ganglion (VG).

B. Parietal ganglion with mass of nerve cells (NC). NP = neuropil.

C. Visceral ganglion showing group of nerve cells (NC) and giant cell (GC).

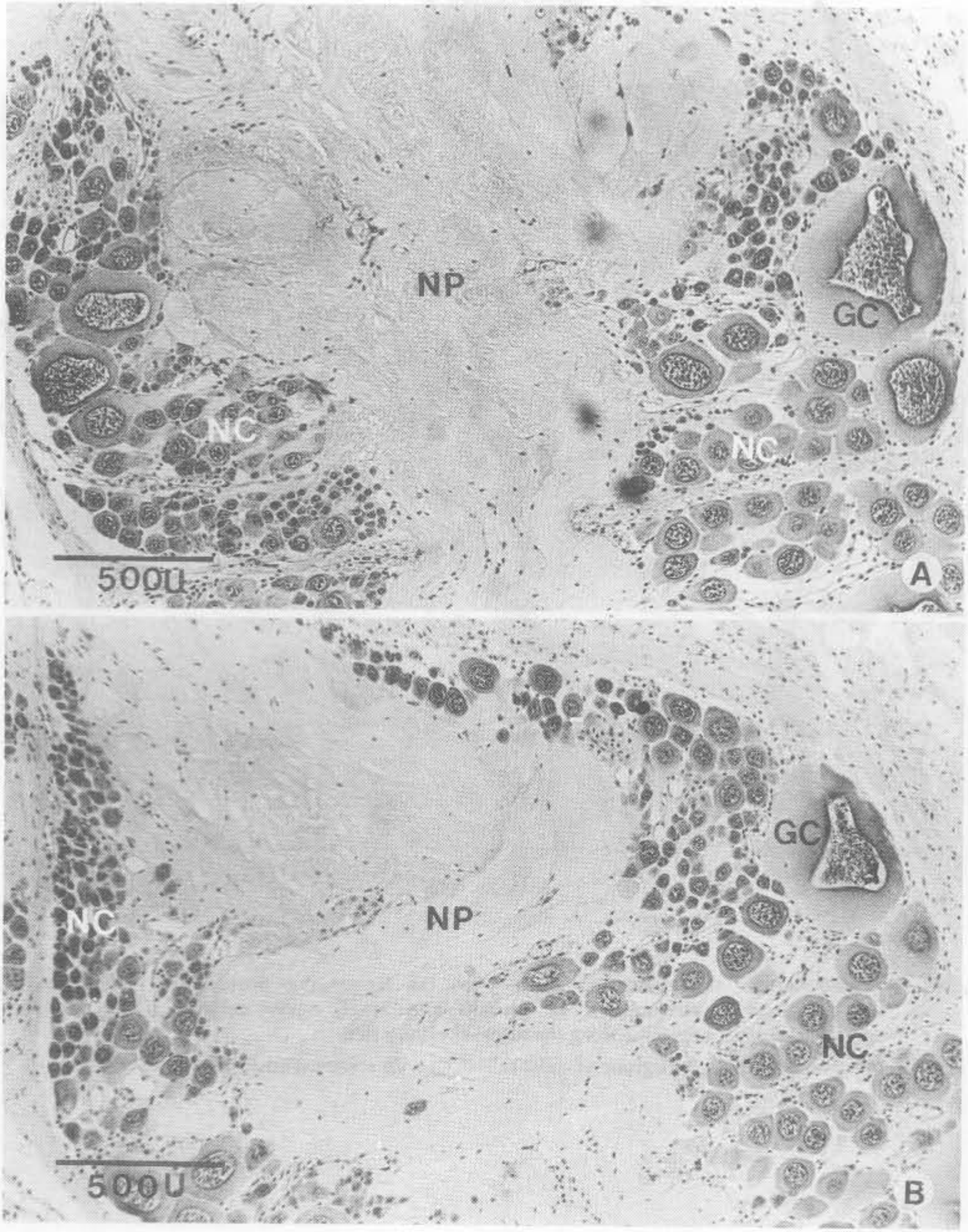


Fig. 9 A. Pleural ganglion showing giant nerve cells (GC) and groups of nerve cells (NC). NP = neuropil.
B. Pedal ganglion showing giant cell (GC) and groups of nerve cells (NC). NP = neuropil.

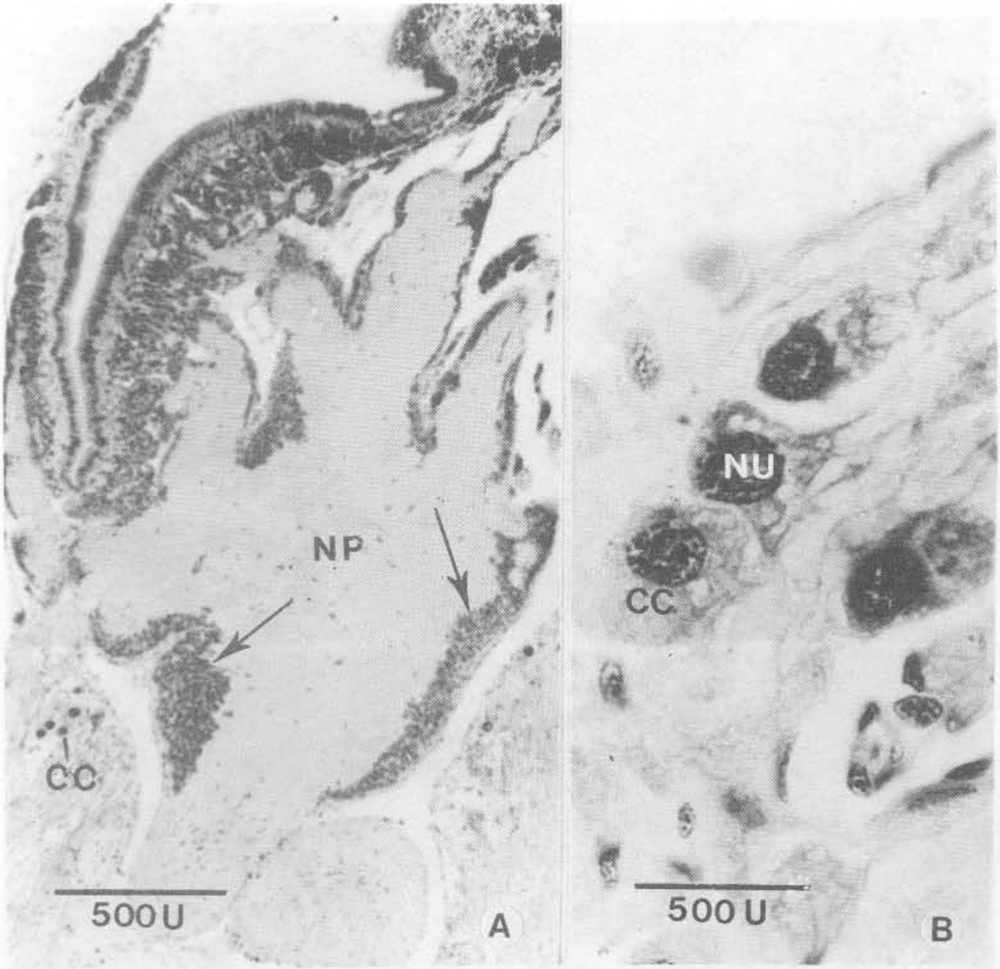


Fig. 10 A. Hand-shaped tentacular ganglion with its finger-like projections. Neuropil (NP) of ganglion is surrounded by globuli and small nerve cells (arrows). Note the presence of collar cells (CC) along the finger-like projection.

B. High magnification of a group of collar cells (CC) with spherical nuclei (NU).

TABLE 1. The average size of nerve cells in each ganglion of *Achatina fulica*.

Ganglia	Type of nerve cell	Cell Diameter (μm) X ± S.E.
Buccal	Giant	114 ± 2.02
	Large	79 ± 3.09
	Medium	33 ± 1.22
	Small	15 ± 0.91
Cerebral	Giant	164 ± 6.86
	Large	75 ± 4.64
	Medium	31 ± 1.77
	Small	15 ± 0.83
	Globuli	5 ± 0.92
	Neurosecretory	25 ± 5.34
Parietal	Giant	155 ± 10.36
	Large	79 ± 3.97
	Medium	31 ± 1.35
	Small	16 ± 0.68
Visceral	Giant	173 ± 8.25
	Large	87 ± 2.21
	Medium	32 ± 2.17
	Small	15 ± 0.67
Pleural	Giant	147 ± 13.73
	Large	45 ± 1.26
	Medium	25 ± 0.74
	Small	15 ± 0.69
Pedal	Giant	178 ± 9.36
	Large	81 ± 3.72
	Medium	31 ± 1.41
	Small	16 ± 0.71
Tentacular	Collar	25 ± 6.5
	Small	16 ± 3.2
	Globuli	5 ± 2.7

TABLE 2. The number of giant nerve cells in each ganglion of *Achatina fulica.*

Ganglia	Nos. of Giant Nerve Cell
Buccal	4
Cerebral	8
Parietal	14
Visceral	6
Pleural	4
Pedal	16
Tentacular	–

Subesophageal ganglionic mass

All the ganglia in the subesophageal ganglionic mass are separated from each other by a septum (Fig. 8A).

Parietal ganglia. There are a large number of large cells and 14 giant cells in the parietal ganglia (Table 2). They are usually found at the anterior and posterior portions of the ganglia, and these cells are isolated from smaller cells or nearby cells (Fig. 8B). Similar to the other ganglia, the medium cells and the small cells usually form a cluster that can be observed. The sizes of the giant cells, the large cells, the medium cells and the small cells are 155 ±_10.36, 79 ± 3.97, 31 ±1.35 and 16 ± 0.68 microns, respectively (Table 1).

Visceral ganglion. In the viscereal ganglion, there are neurons of many sizes, from very small cells with the diameter of 15 microns to very large cells with the diameter of 173 microns (Fig. 8C). The locations of the large cells and the small cells can be distinguished. The large cells and the giant cells are found in the anterior and posterior portions; occasionally they form a group of cells. In contrast, the group of small cells are found on the lateral and central portions or scattered in the ganglion. The small cells are observed to line the lateral border of the ganglion. There are six giant cells in the visceral ganglion (Table 2). The large cells and the giant cells send their axons into the mass of neuropil. The mean diameters of the giant cells, the large cells, the medium cells and the small cells are 173 ± 8.25, 87 ± 2.21, 32 ± 2.17 and 15 ± 0.67 microns, respectively (Table 1).

Pleural ganglia. It can be observed that most of the neurons in the pleural ganglia are rather small and form a mass of cells (Fig. 9A). The nerve axons from the pleural ganglionic cells are collected into a mass of neuropil and form a nerve tract into the parietal ganglion. Most of the neurons in the pleural ganglia are medium cells and small cells which have a mean diameter of 25 ± 0.74 and 15 ± 0.69 microns, respectively (Table 1). A few large cells with a mean diameter of 45 ± 1.26 microns and four giant cells with a mean diameter of 147 ± 13.73 microns are observed (Tables 1,2). The giant cells in the pleural ganglia are similar to those in the other ganglia. They are isolated from the nearby cells in the lateral part of the pleural ganglion, and have a large irregular-shaped heterochromatic nucleus with many conspicuous nucleoli (Fig. 9A).

Pedal ganglia. Since the pedal ganglia are larger than the other ganglia in the nervous system of A. fulica, they contain a large amount of nerve cells and also numerous large cells and giant cells. There are 16 giant cells in the pedal ganglia (Table 2). The large cells and giant cells are usually located at the antero-lateral, postero - lateral and medial portions of each pedal ganglion (Fig. 9B). The medium cells and small cells are the main components of the ganglia, forming masses of nerve cells filling the pedal ganglia. The largest giant neuron is found in the pedal ganglia. The mean diameters of the giant cells, the large cells, the medium cells and the small cells are 178 ± 9.36, 81 ± 3.72, 31 ± 1.41 and 16 ± 0.71 microns, respectively (Table 1).

Tentacular ganglia

The optic tentacle of *A. fulica* consists of two essential structures, the eye and the tentacular ganglion. The hand-shaped tentacular ganglion lies at the base of the optic tentacle and has very dense neuropil (Fig. 10A). The tentacular ganglion which sends out the finger - like projections, can be divided into two parts: the proximal part and the distal part. The end of these finger-like projections or the distal part of the ganglion is covered with sensory epithelium. The center of the ganglion is occupied by neuropil. Along the periphery of the ganglion lie small dense globuli cells which have the mean diameter of 5 ± 2.7 microns (Table 1) and are formed in clusters (Fig. 10A). Small nerve cells with the mean diameter of 16 ± 3.2 microns (Table 1) are found to be intermingled with globuli cells. In addition, there is another type of cells which are neurosecretory or collar cells with a mean diameter of 25 ± 6.5 microns (Table 1). These cells are arranged singly or in groups around the finger-like projections of tentacular ganglion (Fig. 10A). They contain round and heterochromatic nuclei and their cytoplasm is devoid of large vacuoles (Fig. 10B).

DISCUSSION

The anatomy of nervous system of the land snail, *A. fulica* is similar to that of stylommatophoran snails, *H. pomatia*[10,19-21] *H. aspersa*[2,22-25] *A. ater*[26] and *Archachatina marginata*[27]. The nomenclature of all the ganglia in *A. fulica* corresponds to that of the ganglia in *H. aspersa*[2].

The buccal ganglia, which are found in the buccal mass, give rise to the nerves that innervate the salivary glands, the mouth and the muscle of the buccal mass. It may be suggested that the neurons in the buccal ganglia control the eating movement of *A. fulica*. This observation is confirmed by the experiment of Goldschmeding[28] on the buccal ganglia of *Lymnaea stagnalis*. He found that the buccal ganglia had motor neurons that controlled the eating movement cycle. Benjamin *et al.*[29,30] also found that the motor neurons in the buccal ganglia of *L. stagnalis* were the feeding rhythm generator and controlled the feeding system.

The cerebral ganglia in *A. fulica* are connected with the buccal ganglia. It may be suggested that the cerebral ganglia have a role in the activity of neurons in the buccal ganglia. This idea is confirmed by McCrohan[31] . He found that the neurons in the ventral lobes of the cerebral ganglia in *L. stagnalis* controlled the movement of lip musculature during feeding. In addition, McCrohan *et al.*[32] also found that the serotonergic cerebral giant cells in the cerebral ganglia of *L. stagnalis* could initiate the rhythmic feeding movements. McCrohan and Benjamin[33] reported that the cerebral giant cells of *L. stagnalis* made excitatory synaptic connections with the buccal motor neurons and affected the frequency and occurrence of the feeding rhythm.

The subesophageal ganglionic mass is situated in the foot region. The peripheral nerves of this ganglionic mass are distributed in the region of visceral mass and foot. Hence, the main functions of this ganglionic mass may be concerned with controlling the activity of the visceral organs and the locomotion of snails. This idea is confirmed by the experiment of Vehovszky and Elekes[21]. They found that the intestinal nerve from the visceral ganglion of *H. pomatia* controlled the visceral functions. Postma[34] and Postma and De Jong[35] suggested that the foot musculature in *H. pomatia* was controlled by the activator and inhibitor centers in the pedal ganglia and these centers were controlled by the cerebral ganglia.

The tentacular ganglion of *A. fulica* is found in the optic tentacle, lying against the eye. This ganglion is also found in the other stylommatophoran snails, such as *A. ater*[26], *H. aspersa*[2], and *A. marginata*[27]. The tentacular ganglion is not present in the basommatophoran snails, *L. stagnalis*[1]. Cook[36] reported that the optic tentacles of *Limax pseudoflavus* were concerned with the detection and identification of trails since they possessed optic, olfactory and tactile senses. The tentacles of all pulmonate gastropods are important sensory structures which are necessary for locomotor orientation to odor sources[37,38]. The tentacular ganglion is composed of sensory nerve cells. The ganglion is located in the optic tentacle which is the organ of chemoreception [37-40].

The histology of the ganglia in the nervous system of *A. fulica* is quite similar to that of *H. aspersa*, *H. pomatia* and *A. ater*. The histological structure of the buccal ganglia of *A. fulica* is similar to that of *H. pomatia* in the pattern of distribution of neurons[8]. There are 3-4 giant neurons in the buccal ganglia of *A. fulica*. In *H. pomatia*, there are three giant neurons with a diameter of 100-200 microns in the lateral lobe of the buccal ganglion and dorsal to the origin of the second pharyngeal nerve[8,41,42]. The main axons of these neurons enter the second pharyngeal nerve. The functional significance of these cells may be a transfer of information from pharyngeal feeding activities to the kidney [43].

The histological structure of the cerebral ganglia in *A. fulica* is similar to that of *H. aspersa*[44] and *H. pomatia*[8]. They contain a mass of globuli cells in the procerebrum and neurons of many sizes in the mesocerebrum and metacerebrum, although the sizes of the cells are not the same. The cerebral ganglia of *A. fulica* are composed of many neurons in the size range of 8-164 microns. There are four giant cells with a diameter of 164 microns in the cerebral ganglia of *A. fulica*. The cerebral ganglia of *H. pomatia* have two giant cells with a diameter of 200 microns[8]. These giant cells are similar to the giant cells in other gastropods[1,2,19]. They are defined by the size and shape of the cells and their nuclei, and the location in the ganglia[10-12].

The subesophageal ganglionic mass is composed of seven ganglia. This ganglion is much larger than the cerebral and buccal ganglia. However, the pattern of distribution of neurons in these ganglia is quite similar. The giant cells in the subesophageal ganglionic mass, similar to those in the cerebral and buccal ganglia, are identified by their position, the cell size and their irregular-shaped nuclei. Although the pairs of buccal ganglia, cerebral ganglia and a pair of pedal ganglia in the subesophageal ganglionic mass are symmetrical, the right and left parietal and the visceral ganglia are not constructed symmetrically. The right parietal ganglion is much larger than the left one. This situation is also found in *H. pomatia*[19].

There are more than 30 giant cells altogelher in the subesophageal ganglionic mass. Most of them are found in the pedal ganglia. The largest giant cell with a diameter of 178 microns can be found in the pedal ganglia since the pedal ganglia are the largest ganglia of the subesophageal ganglionic mass. In *H. pomatia*, there are many giant cells with a diameter of 200 or more microns in the subesophageal ganglionic mass[19]. The giant cells on the latero-ventral surface of the right pedal ganglion in *H. pomatia* send the axons to innervate the penis retractor muscle[20]. In addition, the distribution of the giant cells in the subesophageal ganglionic mass in *A. fulica* is quite similar to that in *H. aspersa*[2]. Moreover, it was found that the giant cells in parietal ganglia and visceral ganglion of *Euhadra congenita hickonis*, Japanese domestic snail, sent the axons to innervate the mantle and visceral organs, respectively[45].

The histological structure of the tentacular ganglion in *A. fulica* is similar to that in *H. aspersa*[6] and *A. ater*[26]. The diameter of the neurons in the tentacular ganglia of *A. fulica* is 8 - 15 microns. In *A. ater*, the diameter of the neurons is 10 - 25 microns[26]. In *A. fulica*, the pattern of distribution of neurons in the tentacular ganglia is different from that in the previous ganglia. There are no medium cells, large cells and giant cells in the tentacular ganglia.

In the stylommatophoran snails, the neurosecretory cells were reported to be present in the cerebral, buccal, parietal, pleural ganglia and optic tentacles of *A. ater*[26], in the buccal ganglia of *Succinea putris*[46], in the cerebral ganglia and optic tentacles of *H. aspersa*[6,47] and in the optic tentacles of *A. marginata*[27], *Arion subfucus* and *L. maximus*[48] and *Milax* spp.[49].

There is only one group of neurosecretory cells located in the procerebrum of the cerebral ganglia of *A. fulica*. However, there are many groups of cells around the finger-like processes of the tentacular ganglion. These cells gave positive reaction with chrome-hematoxylin phloxine and paraldehyde-fuchsin. Moreover, these cells are surrounded by connective tissue. From the position and stainability of these cells, it may be concluded that they are the collar cells, similar to those in the other species of stylommatophoran snails, i.e. *A. ater*[26], *A. subfucus* and *L. maximus*[48], *Milax* spp.[49] and *H. aspersa*[6].

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บทคัดย่อ

ระบบประสาทของหอยทากยักษ์ *Achatina fulica* ประกอบด้วยปมประสาท 13 อัน ได้แก่ ปมประสาทบิวคัล 1 คู่ ปมประสาทเซรีบรัล 1 คู่ ปมประสาทพลูรัล 1 คู่ ปมประสาทพาไรเอทัล 1 คู่ ปมประสาทพีดัล 1 คู่ ปมประสาทเทนแทคิวล่าร์ 1 คู่ และปมประสาทวิสเซอรัล ปมประสาททั้งหมดเชื่อมติดกันด้วยเส้นประสาท และส่งแขนงประสาทออกไปควบคุมการทำงานของอวัยวะต่าง ๆ ปมประสาทมีเนื้อเยื่อเกี่ยวพันหุ้มสองชั้น ภายในปมประสาทมีเซลล์ประสาทมากมาย ซึ่งอาจจะแบ่งตามขนาดได้เป็นสี่ขนาด คือ เซลล์ประสาทขนาดใหญ่มาก (>100 ไมครอน) เซลล์ประสาทขนาดใหญ่ (40-99 ไมครอน) เซลล์ประสาทขนาดกลาง (20-39 ไมครอน) และเซลล์ประสาทขนาดเล็ก (< 20 ไมครอน) นอกจากนั้น ยังพบเซลล์ประสาทขนาดเล็กมาก เรียก เซลล์โกลบิวไล (5-7 ไมครอน) ปรากฏอยู่ในปมประสาทเซรีบรัลและปมประสาทเทนแทคิวล่าร์ จากการย้อมเซลล์ประสาทของหอยทากยักษ์ด้วยสีโครเมี่ยม-ฮีมาทอกไซลีนและฟลอกซิน และสีพาราดีไฮด์-ฟิวซิน ภายในปมประสาทเซรีบรัลจะมีเซลล์นิวโรเซครีทอรี่ (20-30 ไมครอน) ซึ่งมีนิวเคลียสกลมและแวคิวโอลขนาดใหญ่ และภายนอกปมประสาทเทนแทคิวล่าร์ ก็มีเซลล์นิวโรเซครีทอรีหรือเซลล์คอลล่าร์ ซึ่งมีขนาดใกล้เคียงกัน แต่ไม่มีแวคิวโอล มีนิวเคลียสกลม และไซโทพลาสซึมข้น