Applied Microscopy
Korean Society of Microscopy

pISSN 2287-5123 · eISSN 2287-4445
http://dx.doi.org/10.9729/AM.2013.43.2.65

Microstructural Organization of the Central Nervous System in the Orb-Web Spider *Araneus ventricosus* (Araneae: Araneidae)

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Received April 27, 2013
Revised May 17, 2013
Accepted June 7, 2013

Although the geometrical difference in body position between web-building and wandering spiders could affect the organization of their central nervous system (CNS), however most of our informations about spider's CNS are dependent on those revealed from the wandering spiders. Therefore, this paper describes microstructural organizations of the CNS in the geometric orb-web spider *Araneus ventricosus*. Similarly to other wandering spiders, the CNS of *A. ventricosus* is also consisted of a dorsal supraesophageal ganglion and a ventral subesophageal mass. The supraesophageal ganglia are fused together and made up of a large sized nerve cell clusters, whereas the subesophageal ganglia are made up of the foremost part of the ventral nerve cord. It has been revealed that the only nerve arising from the supraesophageal mass was the optic nerve which connected with four pairs of eyes, whereas a pair of pedipalpal and four pairs of appendage nerves including abdominal nerve pairs were arisen from the subesophageal nerve mass. Fibrous masses are highly organized into longitudinal and transverse tracts, and are only consisted of processes of neurons and the terminal ramnifications of peripheral sensory neurons. In addition, central fibrous mass of both the brain and the subesophageal mass are totally devoid of nerve cell bodies.

Key Words: Spiders, Central nervous system, Microstructure, *Araneus ventricosus*

INTRODUCTION

Since the organization of the arthropod central nervous system (CNS) is related to the body segment and to the degree of development of segmental appendages and sense organs (Goodman et al., 1981; Weygoldt, 1985), the arachnid CNS is concentrated in the cephalothorax and a brain is formed by fusion of the ganglia for the head segments (Palmgren, 1980). However, there are unique characteristics in spider's nervous system, not shared by insects and crustaceans (Babu, 1985; Weygoldt,1985). Arachnids are distinguished from insects by the fact they have eight legs and have no antennae or wings. Their body is organized into two segments called the cephalothorax and the abdomen by the fusion of the head and the thorax (Foelix, 1996; Barth, 2002).

Although the segmentation of the arachnid brain is still a topic of discussion (Weygoldt, 1985), it is generally accepted that the supraesophageal ganglion (brain) consists of a protocerebrum and tritocerebrum and the brain encircles the esophagus (Strausfeld & Barth, 1993; Strausfeld et al., 1993). All the ganglia of all segments behind the esophagus are fused, so that the cephalothorax is largely filled with nervous tissue and there are no ganglia in the abdomen (Ruppert et al., 2004). In addition, there are many interneurons (Friedel & Barth, 1997) which linking the sensory input to the motor output (Milde & Seyfarth, 1988; Gronenberg, 1989, 1990; Schmid & Duncker, 1993; Albert et al., 2001), and well developed cross-commissures which connecting the both sides of the subesophageal ganglia (Babu & Barth, 1984).

Research has shown that these and other characteristic features are reflected by the structure of their CNS (Ruppert et al., 2004). Since spiders do not have antennae or abdominal appendages except for spinnerets, the nervous system for controlling the appendages are concentrated on the

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cephalothorax, and the absence of antennae implies the absence of a deutocerebrum as found in crustaceans and insects (Gullan & Cranston, 2010). Following Babu's fine work concerning the CNS of arachnids (Babu, 1975), several other workers (Babu & Barth, 1984; Babu, 1985; Weygoldt, 1985; Weltzien & Barth, 1991; Hwang & Moon, 2003; Hill, 2006) have reported detailed observations on this area of research. However, previous researches on the spider's CNS are mostly concentrated on those of the wandering spiders, and those of the web spiders have been nearly neglected. Therefore, most of our knowledges of spider's CNS are solely dependent on those revealed from the wandering spiders, *Cupiennius* (Babu & Barth, 1984; Babu, 1985) and *Phidippus* (Hill, 2006).

The orb-weaver spiders of the family Araneidae are among the best-known group of spiders including more than 2,800 species in over 160 genera. It is the 3rd largest spider family world-wide (Coddington & Levi, 1991). Most araneid spiders are excellent web-builders to capture their preys, and their webs are vertical. There are conspicuous differences in geometrical body position between web-building spiders and wandering spiders because the web spiders usually hang with their head downward. Recent studies have demonstrated that behavior differences could affect the changes in brain structure (Mattson et al., 2001), and there are evidences that geometry difference in spider could affect the structure of brain. Thus, in order to understand the structure of spider's CNS more precisely, it is necessary to learn more about from the web-building spiders. To begin filling this gap, we have examined the microstructural organization of the CNS in the spider, *Araneus ventricosus*, one species of common orb-weaving spiders.

MATERIALS AND METHODS

The orb-web spiders, *A. ventricosus* (Araneae: Araneidae) were collected in a local area near the Cheonan campus of Dankook University, Chungcheongnam-do, Korea. Adult spiders were maintained under ambient conditions with natural lighting in enclosures comprising a wooden frame with glass panels on the front and back. They were fed insect larvae and water daily.

Eight females and five male specimens were anesthetized with

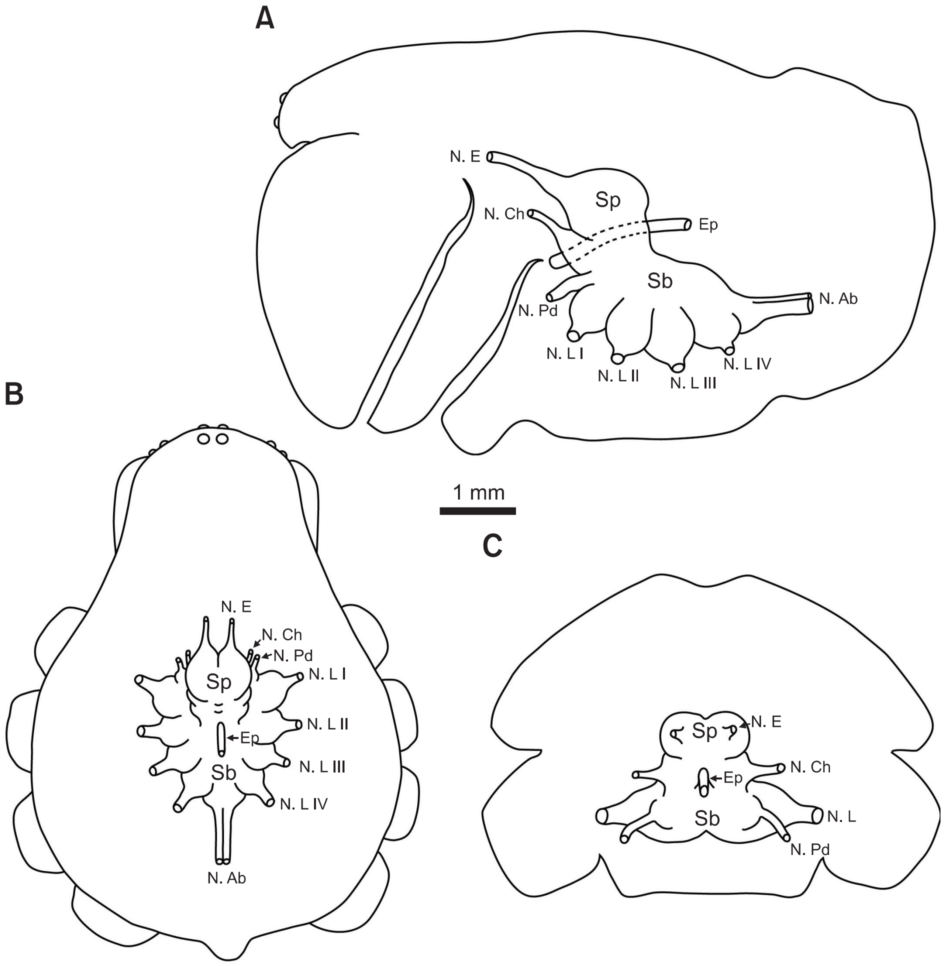

Fig. 1. Diagram of the central nervous system within the cephalothorax of the orb-web spider, *Araneus ventricosus*. (A) Lateral view, (B) dorsal view, (C) front view. Ep, esophagus; N. Ab, abdominal nerve; N. Ch, cheliceral nerve; N. E, nerve of eyes; N. L, N. LI, N. LII, N. LIII, N. LIV, nerve of the legs; N. Pd, nerve of the pedipalp; Sb, subesophageal nerve mass; Sp, supraesophageal ganglion.

CO_2 and dissected under a dissecting light microscope in a drop of spider Ringer's solution consisting of 160 mM NaCl, 7.5 mM KCl, 4 mM $CaCl_2$, 1 mM $MgCl_2$, 4 mM $NaHCO_3$, 20 mM glucose, pH 7.4 (Groome et al., 1991). The specimens for histologic preparation were fixed in alcoholic Bouin's solution consisting of 150 mL of 80% ethanol, 15 mL of formaldehyde, and 1 g of picric acid. Following fixation, they were dehydrated in gradient series of ethanol from 30 to 100% for 60 min at each concentration, with one repeat at 100%.

After dehydration, the specimens were transferred to xylene for clearing, and they were embedded with Paraplast Embedding Medium (Fisher Scientific Co., Pittsburgh, PA, USA) immediately. The sections were cut with a thickness of approximately 5 μm using a microtome (Reichert-Jung, Histocut 820-II) and they were stained with hematoxylin and eosin solutions. Most specimens were photographed using Zeiss Axiophot Microscope (Carl Zeiss, Jena, Germany) coupled with Motic Digital Imaging System (Motic Instruments Inc., Richmond, BC, Canada).

RESULTS

The CNS of the orb-web spiders, *A. ventricosus* is located entirely within the cephalothorax, and is largely filled with simple mass of nervous tissues (Fig. 1). At a sagittal plane, this nerve mass can be divided into the upper spherical supraesophageal ganglion and the lower star-shaped subesophageal ganglion, and they are joined with circumesophageal connectives. A number of nerves arise from these ganglia and spread out to the body, making up the peripheral nervous system (PNS) of this spider (Fig. 1A, Fig. 2A and B). At a frontal plane, the CNS is made up of two relatively simple ganglia: anterior small supraesophageal ganglion and posterior extensive subesophageal ganglion. These nerve clusters are connected with the nerves leading to various muscles and sensory organs (Fig. 1B, Fig. 2C and D).

At a transverse plane, the brain of this spider is composed of a protocerebral and tritocerebral ganglion, whereas the subesophageal mass is located underneath the brain and made up of the foremost part of the ventral nerve cord. The ganglia of this part are fused together and made up of a large sized nerve mass. At a vicinity of the CNS, several organs such

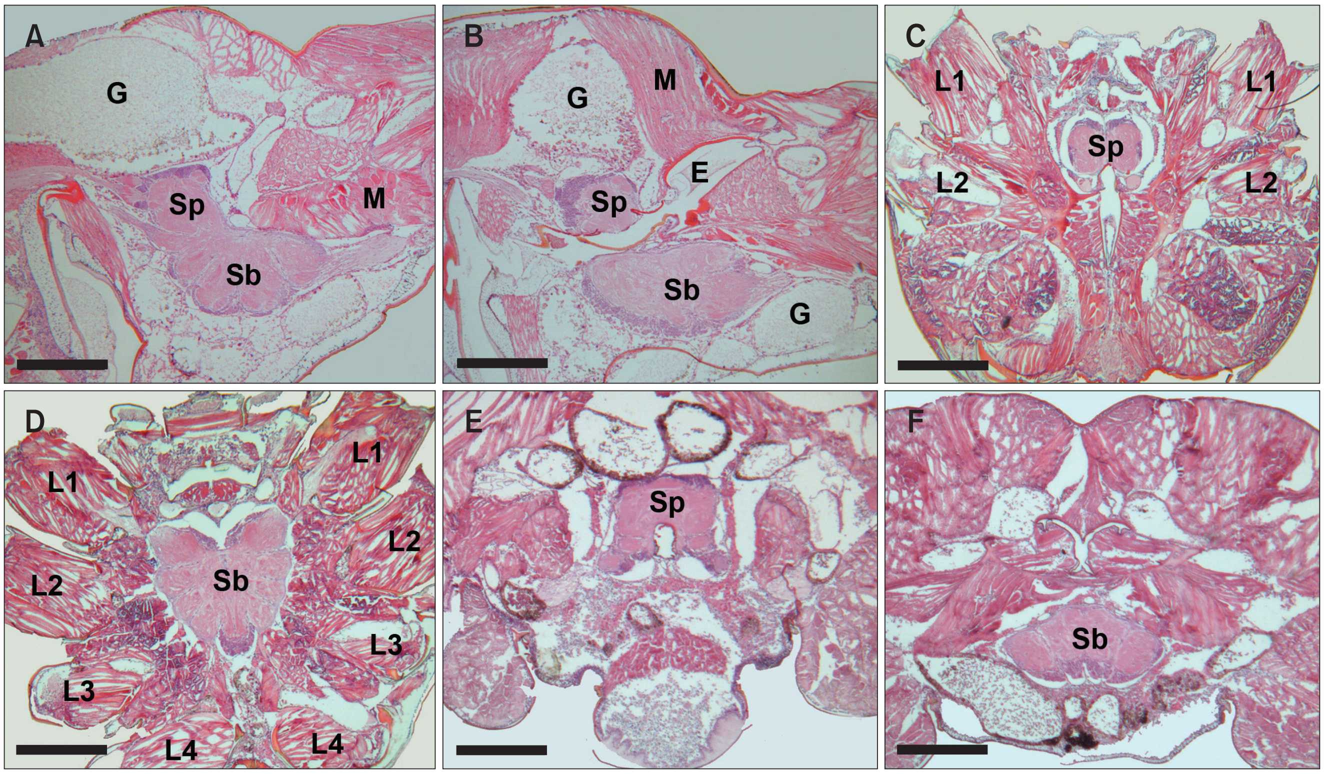

Fig. 2. The central nervous system of the spider *Araneus ventricosus* is filled with simple mass of nervous tissues within the cephalothorax. (A, B) At sagittal planes, this nerve mass can be divided into the upper supraesophageal ganglion (Sp) and the lower subesophageal ganglion (Sb). (C, D) At frontal planes, the nerve clusters which connected with the nerves leading to various muscles of limbs (L1-L4) and sensory organs are seen. (E, F) At transverse planes, nerve masses are fused together and forming a dorsal supraesophageal ganglion and a ventral subesophageal nerve mass. G, digestive diverticula of midgut; M, muscles; E, esophagus. All scale bars=1 mm.

as a part of the intestinal tract, a pair of poison glands, an extensive musculature, the pharynx and the sucking stomach are also observed (Fig. 1C, Fig. 2E and F).

In *A. ventricosus*, the only nerves arising from the protocerebrum are the optic nerves which connected with eight eyes (Fig. 3A). These optic nerves are composed of more than four pairs of neuropile masses which arising from the dorsal part of the protocerebrum (Fig. 3B). Among the four pairs of eyes arranged in two rows, the neuropiles of the optic nerves which connect from the protocerebrum to the principle eyes are the most thick and abundant. The neuropiles of the optic nerves originated from the principle eyes are the most thick and abundant (Fig. 3C).

These eyes have two masses of optic neuropiles of visual ganglionic cells on each side of the brain and are interconnected with the central body. In addition, the optic lobes in the anterior part of the protocerebrum are composed of several distinct neuropile masses, each surrounded by the type B cells. The second optic mass of the lateral eyes is also interconnected with the central body through a well-formed large optic tract (Fig. 3D).

Although, the supraesophageal ganglion is very simple and is restricted to a small area comparing to subesophageal ganglion, the distribution of the neuronal complex is more complicated than that of subesophageal ganglion. In the supraesophageal ganglion the cells are packed in the frontal, dorsal, and lateral regions, but are absent from the posterior region. The dorsal part of supraesophageal ganglion has a quite condensed cell body compared with other parts of CNS (Fig. 4A). The cell bodies of the CNS in spider are arranged in the periphery, whereas the central parts of the ganglia are fibrous (Fig. 4B and C). On the basis of microstructural characteristics two basic types of small cells are observed: the globuli cells (type-A cells) and the numerous type-B cells. Each globuli cell has a large nucleus and poorly stained cytoplasm, whereas cytoplasm of the type-B cell is clear and the nucleus has granular chromatin (Fig. 4C and D).

The central fibrous mass of the CNS is totally devoid of nerve

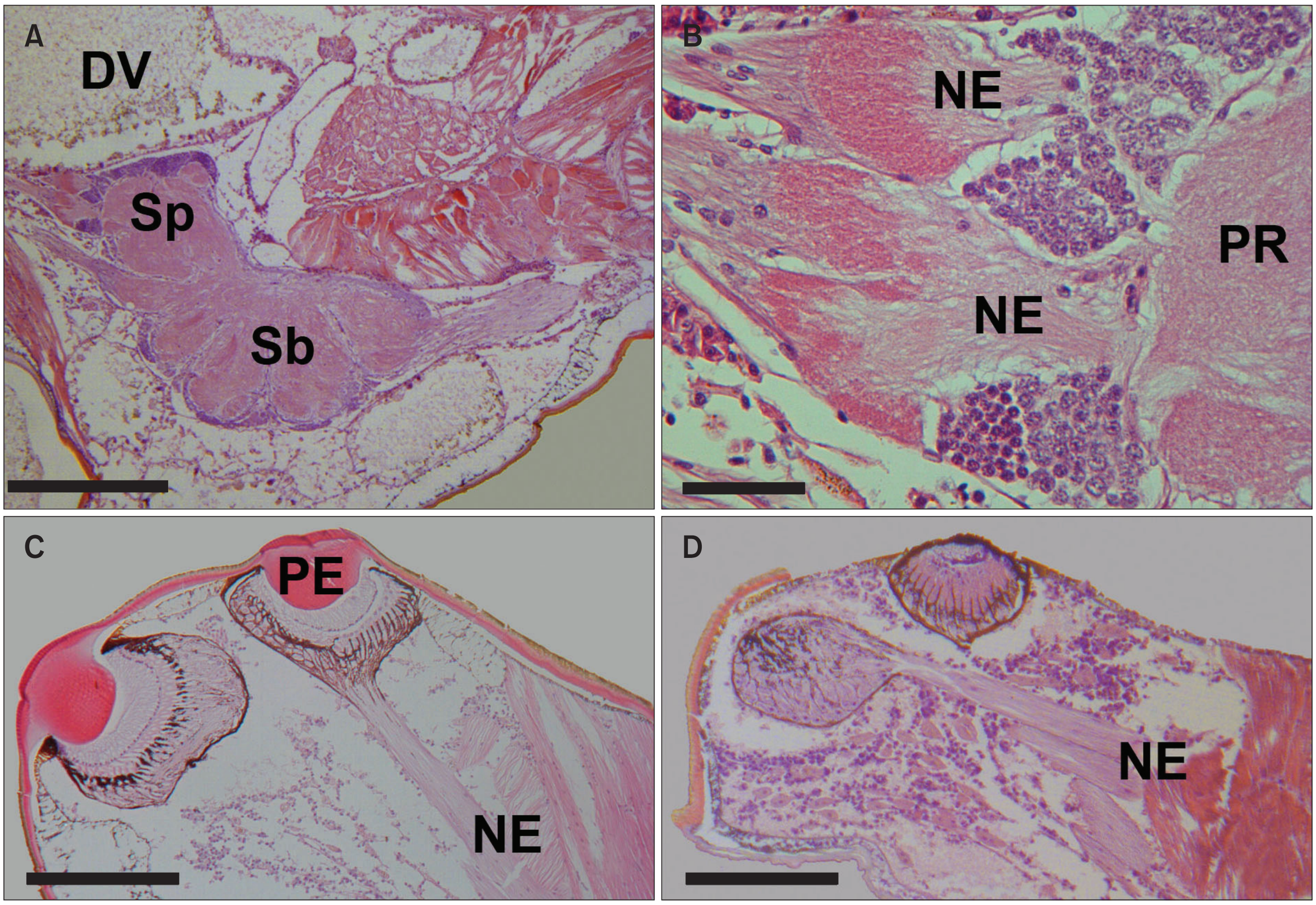

Fig. 3. (A) In *Araneus ventricosus*, the only nerves arising from the protocerebrum are the optic nerves. (B) These optic nerves are composed of neuropile masses (NE) which arising from the dorsal part of the protocerebrum (PR). (C, D) Among the four pairs of eyes, the neuropiles of the principle eyes (PE) are the most thick and abundant. DV, digestive diverticula of midgut; Sb, subesophageal nerve mass; Sp, supraesophageal ganglion. Scale bars=1 mm (A), 500 μm (C, D) and 100 μm (B).

cell bodies, instead it consists only of processes of neurons and the terminal ramnification of peripheral sensory neurons (Fig. 5A and B). In the supraesophageal ganglia, fibrous mass is highly organized into longitudinal and transverse tracts. However, the areas of synaptic contacts in the protocerebrum are differentiated into special structured neuropile masses such as the optic ganglia and the central body, as well as the dense fine fibrous neuropile regions of other ganglia (Fig. 5C-E). In *A. ventricosus*, the central body appeared as a complex of highly condensed neurons and is enclosed by its own membrane which comparted with supraesophageal ganglion. Even though the central body is occupied only a small region, it is covered by layer of cell bodies on its dorsal and posterior sides (Fig. 5F). In addition, the upper part of supraesophageal ganglion has a numerous cell bodies of type-A cells (Fig. 5G).

The subesophageal ganglion lies ventrally, and is located below the esophagus. All the ganglia of all segments behind the esophagus are fused, so that the cephalothorax is largely filled with nervous tissue (Fig. 6A). Since the subesophageal nerve mass has the feature of appendage ganglion, it has many tracts of sensory and motor neurons (Fig. 6B). They get tangled one another, and then some bundles of neuron of each appendage ganglia are mixed, so they make up the dense CNS (Fig. 6C). The nerve mass of this subesophageal region is distributed underneath the supraesophageal ganglion and made up of the foremost part of the ventral nerve cord (Fig. 6D). In *A. ventricosus*, a pair of pedipalpal and four pairs of appendage nerves including several pairs of abdominal nerves arise from this subesophageal nerve mass (Fig. 6E and F).

In *A. ventricosus*, the cell bodies of the neurons are found mostly on the surface of the CNS and many axons penetrate into the CNS. The CNS is covered by lots of muscles and a

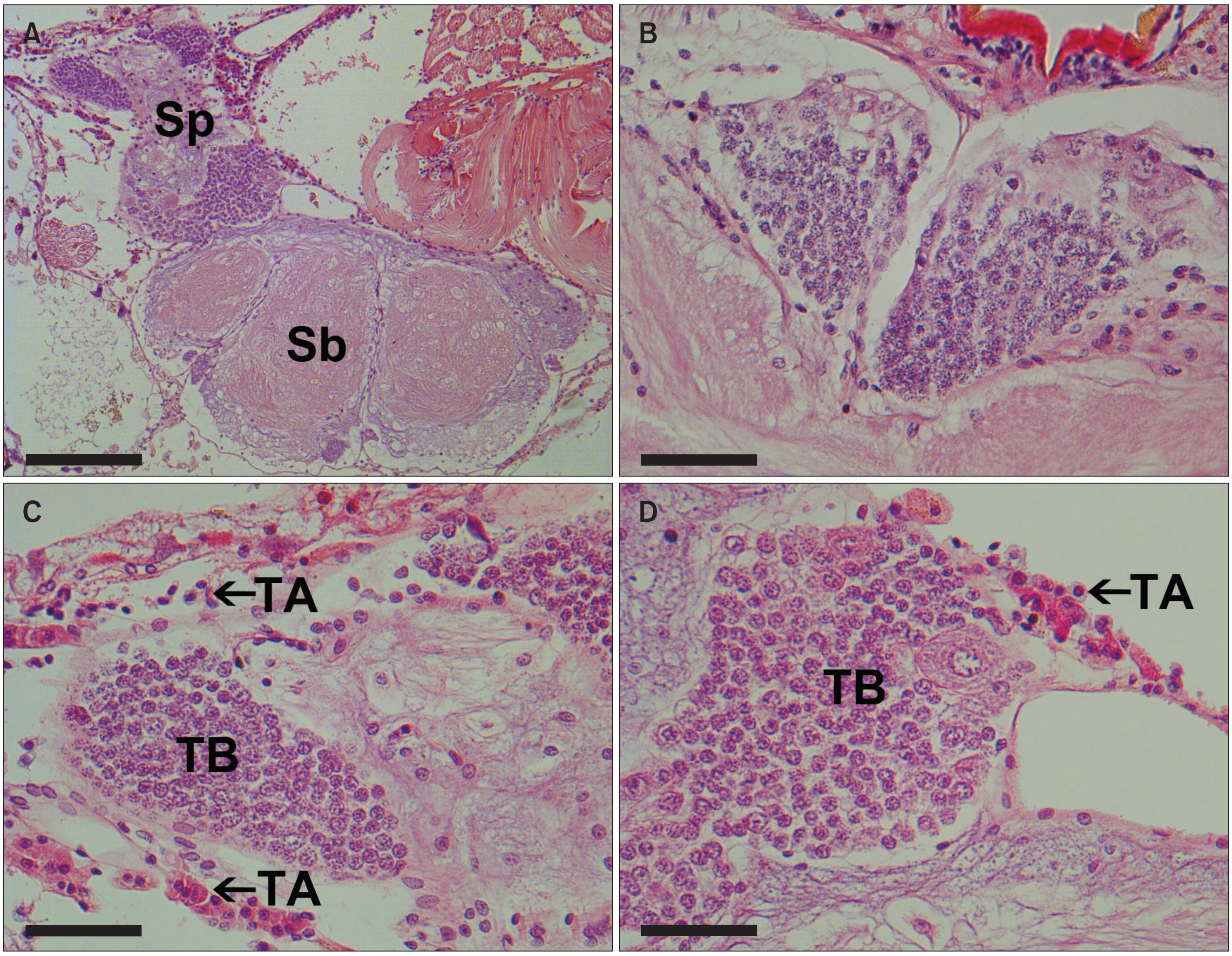

Fig. 4. (A, B) The supraesophageal ganglion (Sp) has a quite condensed cell body compared with other parts of central nervous system, and the cells are packed in the frontal, dorsal, and lateral regions. (C, D) The cell bodies of the protocerebrum are arranged in the periphery, and basically composed of two types of cells: the type-A cells (TA) and numerous type-B cells (TB). Sb, subesophageal nerve mass. Scale bars=500 μm (A) and 100 μm (B-D).

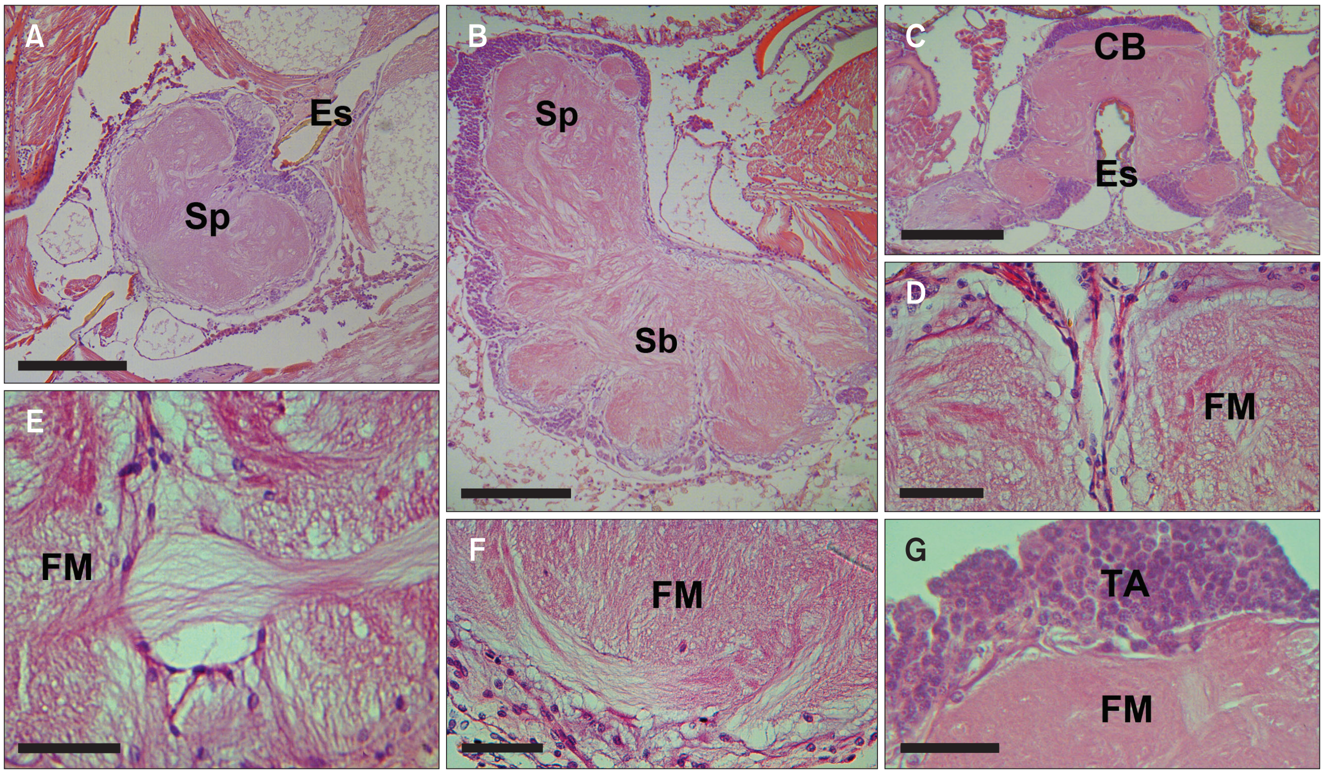

Fig. 5. (A-C) The central body (CB) is covered by layer of lots of cell bodies on its dorsal and posterior sides. The central body appeared as a complex of highly condensed neurons and is comparted with supraesophageal ganglion (Sp). Frontal (A), sagittal (B), and transverse section (C). (D-F) The central fibrous mass of the central nervous system is consists of processes of neurons and the terminal arborizations of peripheral sensory neurons. In the supraesophageal ganglia, fibrous mass (FM) is highly organized into longitudinal and transverse tracts. (G) The upper part of the central body is covered by a numerous cell bodies of type-A cells (TA). Sb, subesophageal nerve mass; Es, esophagus. Scale bars=500 μm (A-C), 100 μm (D-G).

connective tissue layer. At the lower frontal plane, we could identify the subesophageal nerve mass which consists of several individual ganglia. It presents a unified structure integrated by connections between these ganglia, which are observed as well-formed longitudinal and transverse tracts of neurons (Fig. 7A). At the sagittal plane, the subesophageal nerve mass can be divided into two main tracts, on the basis of direction and diameter of the fibers. The dorsal tracts are relatively larger and contain larger diameter of fibers arising from each ganglion, on the other hand, the ventral tracts contain smaller fibers, respectively (Fig. 7B).

The ventral part of subesophageal ganglion has condensed cell bodies compared with other parts of CNS. The cell bodies are basically arranged in the periphery, whereas the central parts of the ganglia are totally fibrous. These fibrous masses are totally devoid of nerve cell bodies, instead they consisted of processes of neurons and the terminal ramnifications of peripheral neurons (Fig. 7C and D). The basic composite cells of this area are similar to those observed in supraesophageal ganglion. They are made up of the type-A cells and the type-B cells. The type-A cell has a chromatin-rich nucleus, and poorly stained cytoplasm, whereas the type-B cell has a granular chromatin and clear cytoplasm. In addition, the largest cells known as motor or interneuronal functions are prominently distributed in all ganglia except for the protocerebral area (Fig. 7E and F).

DISCUSSION

The organization of the arthropod CNS is related to the body segment and to the degree of development of segmental appendages and sense organs (Goodman et al., 1981; Weygoldt, 1985). In the most primitive insect there is one pair of ganglia per body segment, but in most of the higher insects some of abdominal ganglia have been lost (Gullan & Cranston, 2010). Since the arachnids are distinguished from insects by the fact they have eight legs and have no antennae or wings, the spider's CNS is made up of two relatively simple ganglia, or nerve cell clusters, connected to nerves leading to various muscles and sensory systems (Babu, 1985; Weygoldt, 1985). Moreover, by the fusion of the head and the thorax, their body is organized into two segments called the cephalothorax and the abdomen (Foelix, 1996; Barth, 2002). Although the ganglia of the abdomen and the posterior part

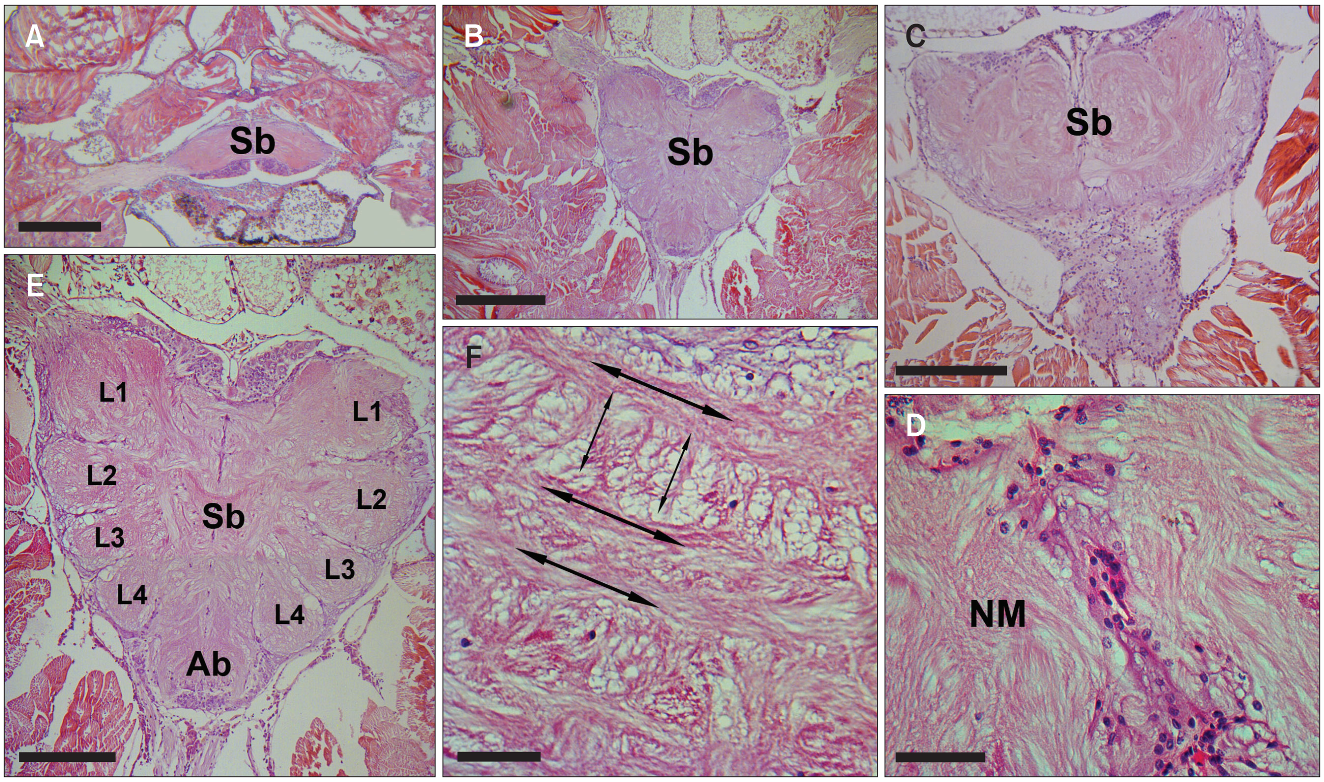

Fig. 6. (A, B) The subesophageal ganglion (Sb) lies ventrally, and is located below the esophagus. All the ganglia behind the esophagus (NM) are fused, and the cephalothorax is filled with nervous tissue. (C, D) The nerve mass of this subesophageal region is distributed underneath the supraesophageal ganglion and made up of the foremost part of the ventral nerve cord. (E) The subesophageal nerve mass has the feature of appendage ganglion, thus four pairs of appendage nerves (L1-L4) including abdominal nerves (Ab) arisen from this nerve mass. (F) It has many tracts of sensory and motor neurons which composed of longitudinal (large arrows) and transverse tracts (small arrows). Scale bars=1 mm (A, B), 500 μm (C, E) and 100 μm (D, F), respectively.

of the cephalothorax in the primitive Mesothelae spiders still remain unfused (Coddington & Levi, 1991), the ganglia of the CNS are fused together and made up of a large-sized nerve mass in most Opisthothelae spiders (Babu & Barth, 1984). Thus, all the ganglia behind the esophagus are fused, so that the cephalothorax is largely filled with nervous tissue and there are no ganglia in the abdomen (Ruppert et al., 2004). In *A. ventricosus*, the supraesophageal ganglion is fused together and made up of a large sized nerve mass. In addition, the subesophageal nerve mass is also fused together with the ventral nerve cord and forming subesophageal ganglia in this spider.

The CNS of spider is not enough to be regarded as a brain because its function and structure are somewhat insufficient. But it can be considered as a brain in a way as it is complex of more highly diffused neuron when compared with that of other arthropods (Babu, 1985; Foelix, 1996). Previous work has shown that the most special feature of the araneid CNS is the perforated structure by the esophageal tract (Babu, 1985; Foelix, 1996; Hwang & Moon, 2003). We could observe the CNS is located in the lower part of cephalothorax, and is separated into two regions by the presence of esophagus. As a part of alimentary canal, the esophagus traverses the CNS horizontally and dividing it into a supraesophageal and a subesophageal ganglia. However, there's no morphological evidence to divide the CNS of this spider as the left and the right brain with the name of hemisphere as seen in the brains of vertebral animals.

It has been noted by Babu & Barth (1984) that the brain (or the supraesophageal ganglion) of the spider is made up of a protocerebral and tritocerebral ganglion, and the brain only receives information from the eyes via the optic nerve. Even though the arrangement pattern is different from one family to another (Blest et al., 1990), two kinds of the optic nerves which composed of the median optic nerves arising from the dorsal part and the lateral optic nerves from the ventral part of the protocerebrum have been reported (Babu, 1985; Foelix, 1996; Barth, 2002). Here, we could identify the only nerve arising from the protocerebrum is the optic nerve which composed of more than four pairs of neuropile masses in *A. ventricosus*. Although it has been known that the eyes of web-building spiders are primitive and can detect little more than light and dark (Land, 1985; Mueller & Labhart, 2010), but this orb-web spider also have well-organized neuropile masses,

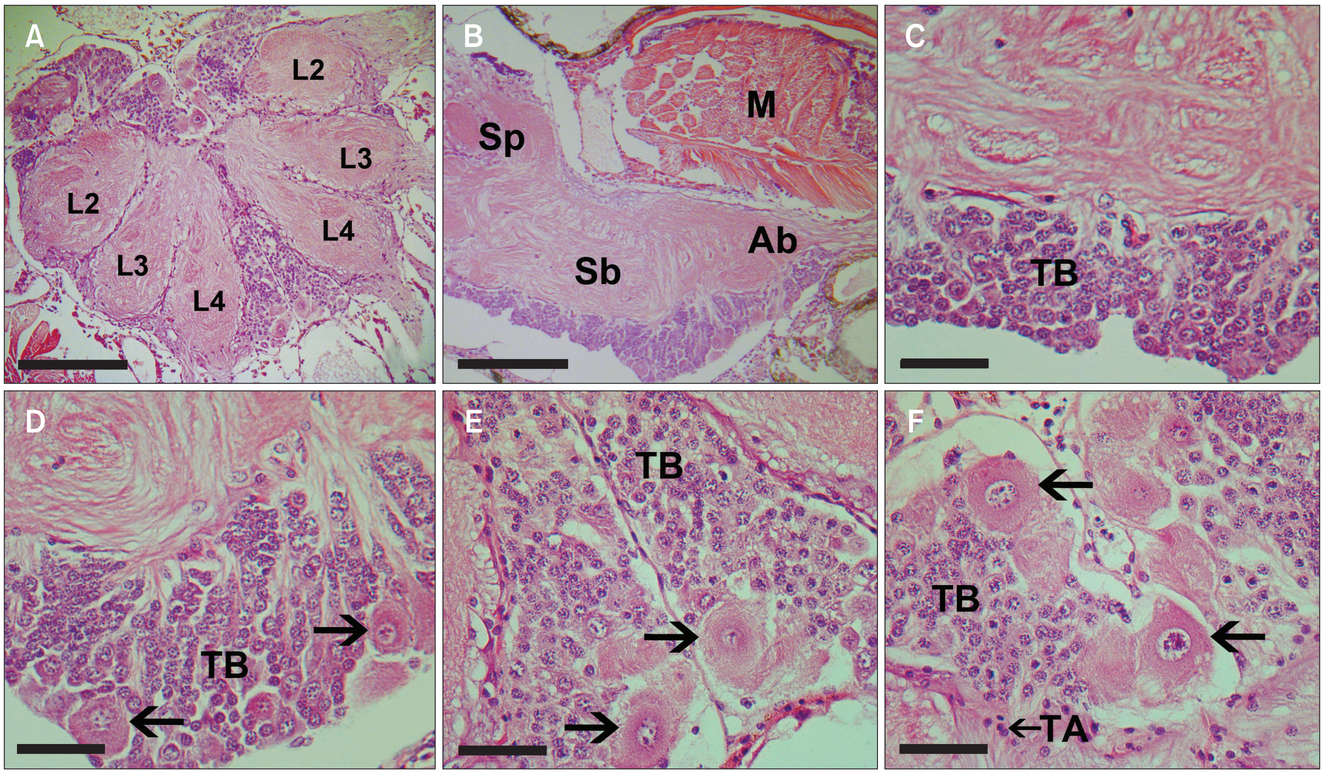

Fig. 7. (A) At frontal plane, the subesophageal nerve mass (Sb) can be divided into appendage ganglia (L2-L4) and abdominal ganglia (Ab). The cell bodies are located on the surface of the central nervous system (CNS) and many axons penetrate into the CNS. (B) The ventral part of subesophageal ganglion has more condensed cell bodies comparing with other parts. (C, D) The cell bodies are basically arranged in the periphery, whereas the central parts of the ganglia are totally fibrous. (E, F) The basic composite cells are made up of numerous type-B cells (TB). In addition, the largest cells (arrows) known as motor or interneuronal functions are also observed. M: muscle, Sp: supraesophageal ganglion, TA, type-A cells. Scale bars=500 μm (A, B), 100 μm (C-F).

and the principle eyes have the most thick and abundant neuropiles comparing to other optic nerves connected with the lateral eyes.

Previous research concerning the analysis of the post-embryonic development has demonstrated that the number of neurons in *Argiope* spider's CNS remains the same at all stages of growth (Babu, 1985). It is generally accepted because most of nerve cells do not undergo cell division once fully formed. However, total cephalothoracic nerve mass is increases 24-fold in volume from the first instar to the adult stage mainly due to an increase in cell volume and the number of glial cells. Thus, most of the neural growth is due to the growth of fibrous mass, and this phenomenon includes increase in fiber size and ramification and number of incoming sensory fibers (Babu, 1975; Babu & Barth, 1984).

In *A. ventricosus*, fibrous masses are highly organized into the central parts of the ganglia, but the cells in all ganglia are arranged in the periphery and are packed in the frontal, dorsal, and lateral regions. According to Babu (1985), the condensed structure of the dorsal region considered as main memorial area in spider's CNS, and the frontal and lateral region are related to the function of eyes, chelicera and fang.

In arachnids the important and complex neuropile masses are located in the protocerebrum, and a common feature among arachnids is the presence of a compactly arranged mass of cells in the protocerebrum (Strausfeld & Barth, 1993; Strausfeld et al., 1993). Our microscopic observations also reveal that the central body appeared as a complex of highly condensed neurons. These cells give off fine parallel bundles of axons. Following Millot's observation (Millot, 1949) that the central body is a control center of programmed behavior in spiders, Hill (2006) has demonstrated recently that the upper lobe appears to handle sensory information, while the lower lobe may be largely a coordinating center for motor functions.

Anatomically, the central body of the insect is situated at the central region of the CNS (Bernstein & Bernstein, 1969; Weiss, 1974), however the central body of this orb-web spider is isolated at the rear of the protocerebrum. Witt et al. (1968) and Weltzien & Barth (1991) noted the large extent of the central body in orb weavers and termed it as a coordinating center. Other isolated studies have also recognized it as an important association center between the visual centers and the subesophageal ganglia (Satija & Grewal, 1970; Hill, 2006).

In addition, Barth (2002) also described the central body as either a visual center based on its interconnection with other visual centers in *Cupiennius* spider or an additional integration function based on its interconnection with other regions of the CNS.

The subesophageal nerve mass is located underneath the brain and is subdivided into a single pair of pedipalpal ganglia and four pairs of appendage ganglia which play a important role to controling the movement of their pedipalps and respective legs. Although the subesophageal ganglion consists of several appendage ganglia, it has a unified structure integrated by connection one another (Babu & Barth, 1984). Thus, fusion of subesophageal ganglia is major characteristic of arachnids, and the degree of this fusion varies in different orders.

It has been reported that this estimated number of the nerve mass is 9 ganglia in Scorpionidea, 10 in Solifugida, 12 in Uropygida, 16 in Araneae and 17 in Amblypygida (Babu, 1985). In *A. ventricosus*, we could observe a pair of pedipalpal and four pairs of appendage ganglia which arise from this subesophageal ganglionic mass. In addition, all of the abdominal nerves also arise from this subesophageal mass, however the exact number of the abdominal nerves is still difficult to ascertain mainly because of the extreme fusion of the posterior neuromeres. Babu & Barth (1984) traced seven major paired longitudinal tracts of the subesophageal ganglia in *Cupiennius*, and Hill (2006) also reported at least seven pairs of fused abdominal neuromeres in the jumping spider, *Phidippus*.

The neuronal structure of the subesophageal nerve mass is first proposed by Hanstrom (1923) using the Golgi preparation that the subesophageal mass is traversed by several pairs of longitudinal tracts. By introducing intracellular dye injections and electrophysiological recordings, Weiss (1972) and Bowerman & Burrows (1980) have presented evidences for this area of research. In *A. ventricosus*, we could observe two main tracts within the subesophageal nerve mass according to direction and diameter of each composite fiber. Our microstructural observation have shown that the axons of nerve cells around the ganglia are arranged into bundles, and they are linked one another by their neurons to establish a structural pathway able to combine the informations originated from the different areas.

CONCLUSIONS

The CNS of the orb-web building spider *A. ventricosus* is made up of two compact nerve cell clusters which consist of a dorsal brain or supraesophageal ganglion and a subesophageal mass. A number of nerves arise from these ganglia and spread out to various muscles and sensory systems, making up the PNS. The ganglia of a supraesophageal part are fused together and made up of a large sized nerve mass, whereas the subesophageal mass is located underneath the brain and made up of the foremost part of the ventral nerve cord. In *A. ventricosus*, the optic nerves which connected with four pairs of eyes arise from the supraesophageal mass, whereas a pair of pedipalpal and four pairs of appendage nerves including several pairs of abdominal nerves arise from the subesophageal nerve mass. Central fibrous mass of both the brain and the subesophageal mass are totally devoid of nerve cell bodies. The fibrous mass is highly organized into longitudinal and transverse tracts, and is only consisted of processes of neurons and the terminal ramnifications of peripheral sensory neurons. Synaptic contacts are occurring in the central fibrous core, but they are not found in the cellular cortex. In addition, thin layer of the neural lamella tissue which covering externally the CNS were observed below the cephalothoracic nerve mass. Comparing the CNS ganglia with those of wandering spiders in most respects, remarkable differences can be detected in the protocerebral area known as an important association center for web building behavior.

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