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Nervous System of *Parhyale hawaiensis* Dana (Crustacea: Amphipoda)

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The nervous system of *P. hawaiensis* consists of the anterodorsal brain, ventral chain of ganglia and a series of sensory and motor nerves. The brain and the ventral cord including the suboesophageal ganglion form the central nervous system. Originating from definite regions of the central nervous system are the peripheral nerves which supply the various organs of the body.

Key Words: *Parhyale hawaiensis*, **Nervous system, Brain, Suboesophageal ganglion, Ventral nerve cord**

Introduction

Studies on the nervous system of amphipods are comparatively few. Claus' (1879) monumental work on the nervous system of *Phronima* is the most detailed description available. Abraham (1930) and Wetzel (1935) published detailed descriptions of the nerves of the various appendages of *G. pulex* and Caprella respectively. Alexandrowicz (1954) described the nerves innervating the heart and the associated structures in *Marinogammarus marinus*. Some of the other studies on the general anatomy of the nervous system are those of Hilton (1917), Cussans (1904), Hanstrom (1928, 1947) and Schmitz (1967). Bullock and Horridge (1965) in describing the structure and physiology of the invertebrate nervous system, touched only briefly upon the nervous system of amphipods. The present paper deals with the ventral nerve cord and the peripheral nervous system, including those of the brain of *Parhyale hawaiensis* in some detail.

Material and Methods

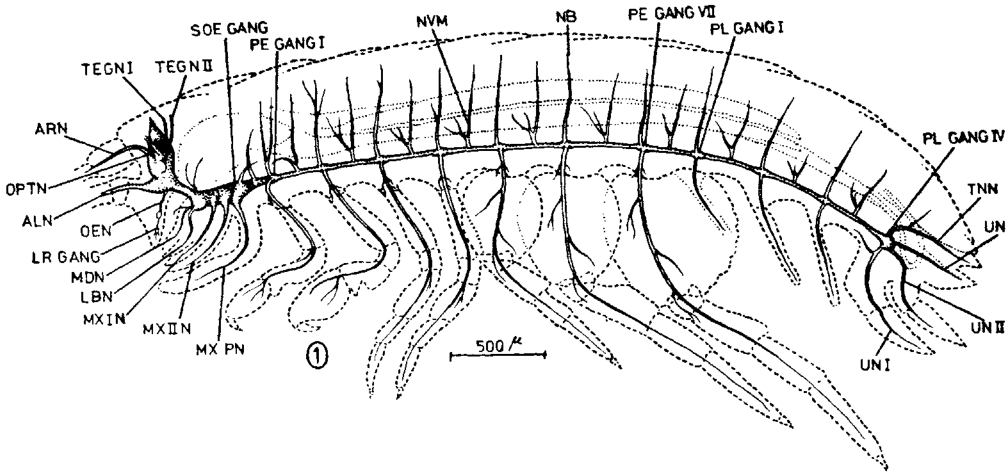
The nervous system was studied with the help of gross dissections and serial sections. For dissecting, the specimens were cut along the longitudinal axis slightly the right or left of the median line. Dissection was done in specimens fixed in 10% formalin or aqueous Bouin. The fixed material was washed in water and dissected in lactic acid or glycerine. These preparations helped to study the peripheral nerves up to their more conspicuous branches. For histological study material was fixed in Heidenhain's Susa, Carnoy's fluid, Bouin's fluid and Zenker's fluid. Material fixed in the last two fixatives gave the best results. Heidenhain's Azan, Herris' Haematoxylin and Phloxin were used for staining.

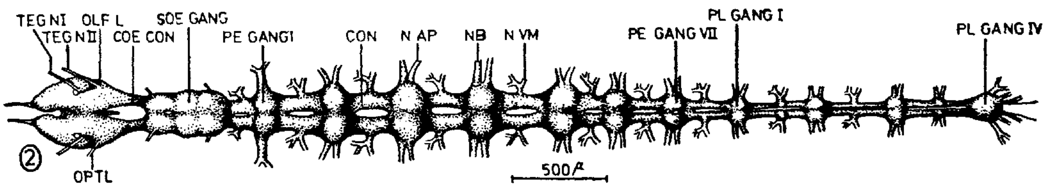
Observations

The nervous system of *Parhyale hawaiensis* consists of the antero-dorsal brain, ventral chain of ganglia and a series of sensory and motor nerves (figures 1, 2). The brain and the ventral cord including the suboesophageal ganglion, form the central nervous system. Originating from definite regions of the central nervous system are the peripheral nerves which link the various organs of the body.

Circumoesophageal Connectives

The dorsal brain is connected to the suboesophageal ganglia by a pair of connectives known as circumoesophageal connectives (figure 2; COE CON). These connectives are solid masses of nerve fibres originating from the postero-





Figures 1 & 2. *1*, Lateral view of the nervous system; *2*, Dorsal view of the central nervous system

Abbreviations

ALN, antennal nerve; **ARN**, antennular nerve; **COE CON**, circumoesophageal connective; **COM**, commissure; **CON**, connective; **GN**, giant neuron; **LBN**, labial nerve; **LR GANG**, labral ganglion; **MDN**, mandibular nerve; **MXIN**, **MXIIN**, maxillary nerves; **MXPN**, maxillipedal nerve; **N**, nucleus; **NAP**, nerve to the appendage; **NB**, nerve to the body wall; **NEU**, neurilemma; **NO**, nucleolus; **NP**, neuropile; **NVM**, nerves to the visceral organs and the lateral body muscles; **OEN**, oesophageal nerve; **OE GANG**, oesophageal ganglion; **OLF L**, olfactory lobe; **ON**, ordinary neuron; **OPTL**, optic lobe; **OPTN**, optic nerve; **PE GANGI**, **PE GANG VII** peraeonic ganglia; **PL GANGI**, PL GANGIV pleonic ganglia; **PLL**, protocerebral lobe; **PN**, peripheral nerve; **SOE GANG**, suboesophageal ganglion; **TEGNI**, **TEGN II**, tegumental nerves.

ventral part of the tritocerebrum, rather submedially. They curve obliquely downwards embracing the oesophagus and join the suboesophageal ganglion on its antero-dorsal part.

The outer surface of the circumoesophageal connectives is covered by nerve cells, two to five cell thick (figure 6). These cells are of the same size and in structure similar to the peripheral cells of the brain. The inner surface of the connectives is devoid of these cells. Situated almost at the centre of the connectives is a giant cell (figure 6; GN) with highly granular cytoplasm. Its cytoplasm stains light blue with Azan. The giant cell has a centrally placed oval nucleus, about $8 \times 12\ \mu$. Its karioplasm does not take Azan or Harris' Haematoxylin but the chromatin stains red with Azan and black with Harris' Haematoxylin. A prominent deeply staining nucleolus deep stain is present. A pair of similar cells is seen in the third thoracic ganglia also.

The nerve fibres forming the connectives run parallel and do not form neuropiles. The circumoesophageal connectives of *P. hawaiensis* do not supply nerves to any part of the body as they do in *Phronima*, in which the nerves to the mouthparts originate from the connectives close to the ventral side of the brain (Calman 1909).

The Ventral Cord

The ventral nerve cord is situated close to the ventral body wall and its surface is almost fully bathed by the blood in the sternal sinus. It is kept in position by the various peripheral nerves, which get distributed in the adjacent somatic muscles and the ventral body wall, and also by the surrounding connective tissue.

The ventral cord is composed of a series of ganglia or neuromeres joined together by longitudinal connectives (figure 2). The neuromeres in crustaceans show various degrees of fusion but in *P. hawaiensis* the first four neuromeres form the suboesophageal ganglion (figure 2; SOE GANG) following which there are seven peraeonic ganglia and four abdominal ganglia. Neuromeres are composed of nerve cells, neuropiles and nerves.

Structure of the Ganglia

The ganglia of the ventral cord are covered by a sheath which consists of an inner layer of cells called the perilemma and an outer noncellular layer, the neurilemma. The cells of the ganglia vary in size and structure. Most of them are small with deep staining chromatin and very little of cytoplasm (figure 5; ON). Scattered among these cells are a few larger ones, varying in size and with a large quantity of granular cytoplasm (figures 5, 7). The body of the ganglia is demarcated into an outer rind and an

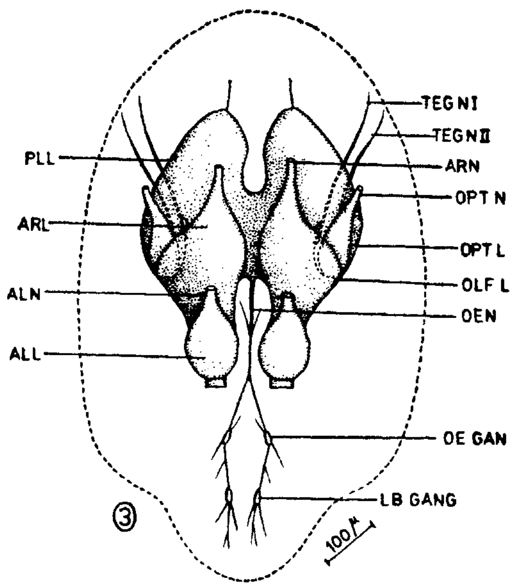


Figure 3 Anterior view of the brain and the nerves originating from it

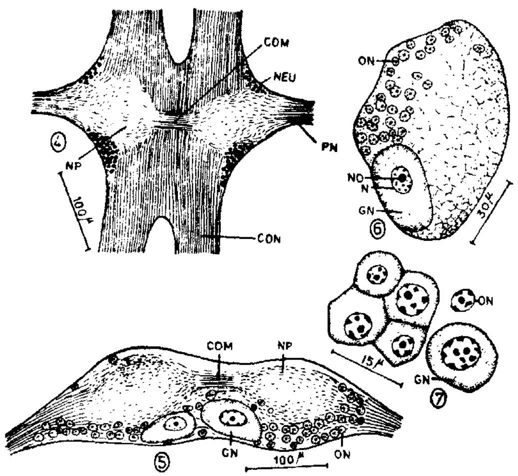


Figure 4–7. *4,* Frontal section of the first peraeonic ganglion; *5,* TS of the third thoracic ganglion; *6,* T S of the circumoesophageal connective; *7,* Neurons of the last abdominal ganglion

inner core. The former is composed entirely of nerve cells and the latter of nerve fibres devoid of nerve cells. However, on the dorsal surface the ganglia are devoid of nerve cells. In the disposition of the rind and the structure of the cells that compose it the different ganglia show wide variation.

In *P. hawaiensis* the two ganglia of each pair are differentially fused. In peraeonic ganglia one to seven the paired neuropiles are connected by a commissure (figures 4, 5; COM). However, in pleonic ganglia one to four the fusion of the components has advanced still further so that the two neuropiles instead of being connected by a commissure are united by a median neuropile, the three neuropiles forming a very compact unit. Though some of the ganglia have lost their paired nature externally, the median constriction and the paired nature of the neuropiles within clearly indicate the paired origin.

The anterior four ganglia of the ventral chain are fused together to form the suboesophageal mass. It is somewhat rectangular in dorsal view (figure 2; SOE GANG) and lies ventral to the cardiac stomach. The first, the mandibular ganglion, is represented by a pair of large neuropiles fused along the median line. The neuropiles project downwards to a great extent and from their tip originate the mandibular nerves. The mandibular ganglion is followed by the comparatively small maxillary ganglion. These two pairs of ganglia remain rather apart and are connected by a pair of connectives leaving a central foramen through which the retractor muscle of the labium passes to the median ligament of the subgastric cephalic apodemes. The third ganglion, the second maxillary, is still smaller than the first maxillary. The fourth pair, the maxillipedal, is very large and has large downwardly directed ventral lobes. Of the four pairs of ganglia forming the suboesophageal mass, the last three are more or less completely fused and hence have lost their connectives while the connectives between the first two are retained. However, median vertical longitudinal sections indicate the presence of vertical ridges of what appears to be perilemma between the last three pairs of ganglia which are the remnants of the original perilemma. All these facts clearly show that the suboesophageal mass in *P. hawaiensis* is formed by the fusion of four pairs of ganglia. Even among amphipods there is variation in the number of pairs of ganglia that fuse to form the suboesophageal ganglion. Thus *Caprella* (Mayer 1882) and *G.L. lacustris* (Schmitz 1967) possess 4 pairs each while *Phronima* and *Hyperia* (Claus 1879) possess 6 each.

Considerable variation in the formation of the suboesophageal ganglion is noticed within peracarida. In general, four pairs of ganglia go to form the suboesophageal mass in isopods. In *Oniscus* (Walker 1935) there are only three pairs, because the maxillipedal pair is distinct and is counted as the first thoracic ganglion. Among mysids, three pairs form the suboesophageal mass except in *Boreomysis* where all the ganglia are distinct (Sars 1867) (vide Bullock & Horridge 1965).

According to Weygoldt (1958), the first pair of neuromeres or the mandibular neuromeres of *G.P. pulex* embryologically originates as part of the brain just posterior to the tritocerebrum, but in the adult migrates to form part of the suboesophageal mass.

In *P. hawaiensis* nerves originating from the suboesophageal ganglion innervate the oral appendages, and also part of the proventriculus (figure 1). From the antero-ventral part of the mandibular ganglion arise 2 pairs of nerves, an outer and an inner. The inner mainly innervates the mandibles (MDN) but a few fine branches go to the anterior portion of the oesophagus. The outer, which is stouter than the inner, goes to the labium (LBN). The next three pairs of nerves go to the maxillules (MXIN), maxillae (MXIIN) and maxillipeds (MXPN) respectively. All the four pairs of nerves going to the oral appendages are very stout. A pair of comparatively slender nerves originating from the dorsal side of the 4th ganglion innervates the ventral portion of the pyloric stomach.

In most amphipods there are seven distinct peraeonic ganglia. All the seven are clear in *P. hawaiensis*. The first peraeonic ganglion is connected to the suboesophageal mass by short connectives. In other words this ganglion is placed very close to the suboesophageal mass. In this connection it may be mentioned that Hanstrom (1928) considered the first peraeonic ganglion of Gammaridea as being almost fully incorporated into the suboesophageal mass.

The second to the fifth peraeonic ganglia in *P. hawaiensis* are identical and larger than the rest. Nevertheless there is no difference in the basic structure of these ganglia which has been described above. All are bilobed indicating that they are formed by the fusion of pairs of ganglia.

The third peraeonic ganglion however differs from the rest in having a pair of giant cells situated submedially on the ventral side and more towards the anterior part (figure 5). These are exactly similar to the giant cells observed in the circumoesophageal connectives.

The pleonic ganglia are roughly similar in size and almost spherical in shape. All the ganglia except the 4th give off peripheral nerves from the ventral side. Some of the neurons of the last abdominal ganglia are large with granular cytoplasm (figure 7).

Fusion of segments has taken place mostly at the hind end of the body among amphipods. Consequently there is a reduction in the number of the pleonic ganglia. While *G.L. lacustris* (Schmitz 1967) has six ganglia, *G. pulex* (Cussans 1904) and *P. hawaiensis* have only four each. Caprellidea represents the extreme case where all the pleonic ganglia are fused into a single mass situated in the penultimate peraeonic somite (Calman 1909).

Two pairs of nerves originate from every ganglion except the first peraeonic and last pleonic. The first peraeonic ganglion gives rise to a single pair of nerves (figure 2; PE GANGI). Each nerve runs laterally at first for a short distance and then divides into dorsal and ventral branches. The dorsal branch, where it turns upwards, gives off a branch to the ventro-lateral somatic muscles. The main stouter branch runs upwards and innervates the lateral somatic muscles. The main ventral branch runs anteriad and enters the first gnathopod. In the case of all the other peraeonic ganglia, the anterior nerves bend upwards and innervate the lateral body wall and the somatic muscles. The posterior nerves run outwards and then downwards and enter the coxal segments.

In segments 2–6 the posterior nerves after entering the coxae give off a branch to the branchia. In the female yet another branch is given off to the oostegites in segments 2 to 5.

Each of the first three pairs of pleonic ganglia gives off two pairs of nerves as the peraeonic ganglia do. But the 4th abdominal ganglion, which is by no means larger than the other pleonic ganglia, gives rise to four pairs of nerves. The first pair originates from the ventral side and goes to the first pair of uropods. A second pair originating from the postero-lateral margins enters the second pair of uropods and a third pair from the hind margin supplies the third pair of uropods. The fourth pair originates from the posterior submarginal dorsal part and terminates in the telson after giving off small nerves to the wall of the hindgut.

From the interganglionic connectives both in the peraeonic and pleonic portions originates a pair of distinct nerves. They cannot be clearly traced to any particular organ but are obviously distributed in the ventral body musculature and visceral organs. Frontal sections appear to indicate that these nerves are supplied with fibres from both the adjacent ganglia.

Nerves Arising from the Brain

Arising from the protocerebrum are paired optic nerves and a pair of tegumental nerves. The optic nerves are stout and originate from the optic lobes and innervating the compound eyes (figure 3; OPTN). The first pair of tegumental nerves is rather slender and arises from the postero-lateral surface of the accessory lobes (figure 1; TEGNI). They run upwards just behind the optic lobes and reach the roof of the cephalic sheild. They terminate subcutaneously in very fine branches.

From the deutocerebrum arise a pair of antennular nerves (figure 1, ARN). The stout antennular nerves originate from the antennular lobes, run dorsalwards and finally enter the antennules as compact masses of fibres. In the second peduncular segment of the antennule each nerve expands and gets invested in a thick layer of nerve cells. These cells are identical with the neurons of the brain in size, structure and also in staining properties. The antennular nerve supplies fine branches to the muscles of the antennule and the different sensory outgrowths.

A pair of antennal nerves, a pair of tegumental nerves (second pair) and a median ventral nerve arise from the tritocerebrum. The antennal nerves arise from the tip of the antennal lobes, (figure 1; ALN) run forwards and enter the antennae. Like the antennular nerve the antennal nerve also enlarges in the third peduncular segment and gets ensheathed in nerve cells. The nerve bifurcates and the two branches run up to the tip of the flagellum giving off fine branches in each flagellar segment. The tegumental nerves (figure 1; TEGNII) originate from the posterolateral portion of the tritocerebrum, run upwards just behind the olfactory lobes and terminate in fine branches below the cephalic shield, just ventral to the termination of the protocerebral tegumental nerves.

A slender nerve (figure 3; OEN) arises from the ventro-median part of the tritocerebrum. It runs forwards and bifurcates above the oesophagus. The two branches swell into ganglia (figure 3; OE GANG) just behind the base of the labrum. From the ganglia arise a few branches which innervate the oesophageal muscles. A main nerve from each of these ganglia runs forwards and enters the labrum, and inside the labrum expands into a terminal ganglion, the labral ganglion (figure 3; LB GANG), Fine branches from this ganglion get distributed inside the labrum.

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