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# The Eyestalk Neurosecretory Cell Types in the Freshwater Prawn *Palaemon paucidens*. I. A Light Microscopical Study

By

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(With 2 Text-figures, 2 Tables and 2 Plates)

Since Enami's classical work (1951) on cytological features of the neurosecretory cells in the optic ganglia and other central nervous system in the crabs *Sesarma*, several investigators have described the "neurosecretory" cells in diverse decapod species (Durand, 1956; Miyawaki, 1956; Matsumoto, 1958; Potter, 1958; Lake, 1970), and some of them have gone farther to relate certain types of the cells to some physiological phenomena in animals (Durand, 1956, 1960). However, there are controversies about exact number of neurosecretory cell types present in decapod eyestalks.

The sinus gland, a neurohormonal storage organ composed primarily of swollen axon terminals from these neurosecretory cells of the optic ganglia, is well accepted as the center for storage and release of a number of neurohormones, including molt-inhibiting hormone, ovary-inhibiting hormone, hyperglycemic hormone, salt and water balance regulating hormones, chromatophorotropins and retinal pigment hormones. In the blue crab *Callinectes sapidus* five morphologically different types of neurosecretory granules have been found in the sinus gland (Andrews *et al.*, 1971). Therefore, if we assume that one type of neurosecretory granules represents one neurohormone, that one cell type produces only one neurohormone, and that all the neurosecretory cells that send their axon terminals to the sinus gland are located in the eyestalk, there must be no less than five different types of neurosecretory cells in optic ganglia. At present, however, no information is available on which type of cell is responsible for synthesis of what kind of neurohormone.

It would be most important to know cytological details of each neurosecretory cell type before we can assume its physiological significance. The present investigation deals with a cytological classification of the optic ganglia neurosecretory cells in the freshwater prawn, *Palaemon paucidens*, at the light microscopical level.

## Materials and Methods

For this study, adult prawns *Palaemon paucidens* of both sexes were collected at a lake in the vicinity of Sapporo. They were brought to the laboratory and stocked in aerated aquaria. The water was changed fortnightly and the animals were fed with small cut pieces of boiled fish paste once or twice a week.

Distribution of the neurosecretory cell groups on the surface of optic ganglia was examined by the vital staining method as follows. The eyestalks were cut off with a pair of Wecker's scissors, their exoskeletons were removed while being immersed in van Harreveld's solution (van Harreveld, 1936), and then the optic ganglia were carefully separated from the surrounding tissues and put into the saline containing a few drops of 0.2% methylene blue and glycerine. After five minutes these materials were observed under the binocular dissecting microscope in renewed saline.

For histological study of the neurosecretory cells, only the prawns which are in intermolt stage (stage C) (Kamiguchi, 1968) were selected. Eyestalks were cut off and fixed in Bouin's fluid for a few days. After their exoskeletons were removed in 70% alcohol they were embedded in paraffin, cut at 6–8  $\mu$  in thickness, and stained with the following staining methods: 1) Delafield's hematoxylin-eosin, 2) Mallory's triple stain, 3) Heidenhain's Azan, 4) Gomori's chrome-hematoxylin phloxine (CHP) (Gomori, 1941), 5) Gabe's aldehyde fuchsin (AF) (Gabe, 1953).

## Observations

### 1. Gross anatomy

In the eyestalk of *Palaemon paucidens* the optic ganglia consist of four parts enclosed by a thin connective tissue sheath: the *lamina ganglionaris*, *medulla externa*, *medulla interna*, *medulla terminalis*. These ganglia are connected by the bundles of axons (Fig. 1).

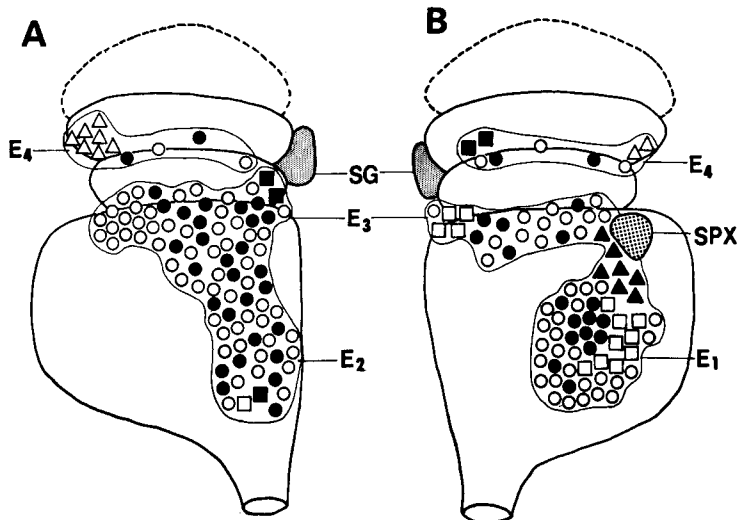
The sinus gland is located in the dorso-lateral portion of the axonal connection between the medulla externa and the medulla interna (Text-fig. 1) and is supplied by a distinct nerve tract from the medulla terminalis ganglionic x-organ (MTGX) (Fig. 2). Innervation from other groups of neurosecretory cells is indistinctive.

The sensory pore x-organ (SPX), situated in the ventral portion of the medulla terminalis (Text-fig. 1B), contains several onion bodies. Many nerve fibers from this organ terminate in the sensory pore where the cuticle is apparently thinner than in other portion of the eyestalk (Fig. 3).

### 2. The neurosecretory cell groups

Four cell groups made up mainly of non-ordinary, possibly neurosecretory, neurons take place in the eyestalk of this prawn. The distribution of these cell groups, which were denoted as  $E_1$ ,  $E_2$ ,  $E_3$  and  $E_4$  for convenience' sake, is shown in Text-fig. 1.

There occur two cell groups,  $E_1$  and  $E_2$ , in the medulla terminalis. Group  $E_1$ , corresponding to the MTGX, is located at the ventral part of the medulla terminalis (Fig. 4) and is connected with group  $E_3$  at its distal portion where the SPX is developed.



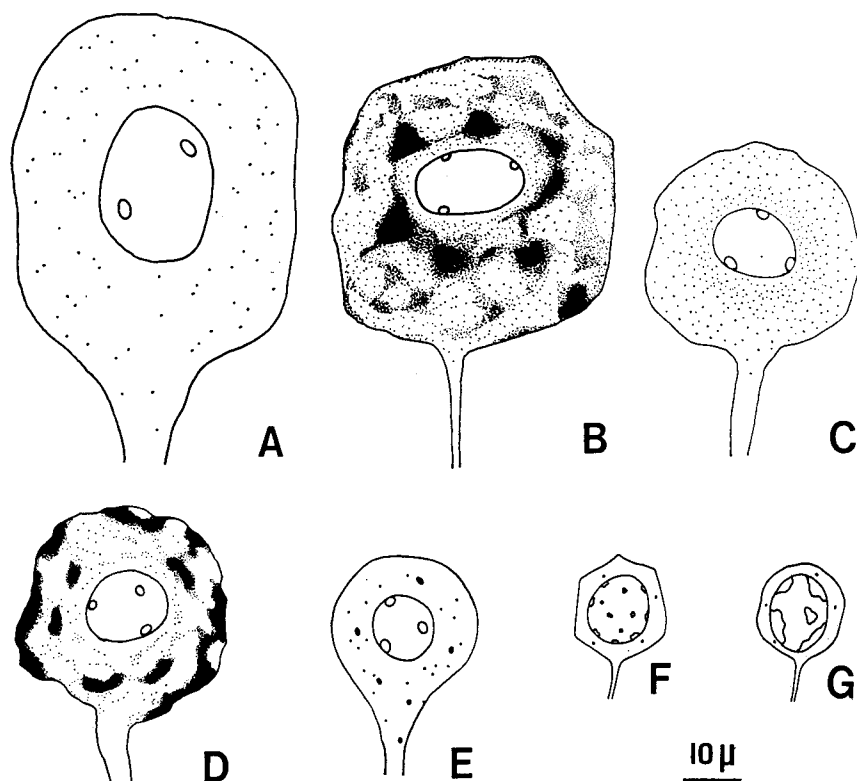
Text-fig. 1. Diagrammatic representation of the optic ganglia from the right eyestalk of a prawn, *Palaemon paucidens*, indicating the distribution of four groups ( $E_1$ - $E_4$ ) of possibly neurosecretory cells. A, dorsal view; B, ventral view. SG, sinus gland; SPX, sensory pore x-organ; ■, Type-I cell; △, Type-II cell; □, Type-III cell; ●, Type-IV cell; ▲, Type-V cell; ○, Type-VI cell.

Group  $E_2$  occupies the dorsal base of the medulla terminalis and is connected with group  $E_3$  at the proximal part of the medulla terminalis. Group  $E_3$ , situated between the medulla interna and the medulla terminalis, is equivalent to the medulla interna ganglionic x-organ (MIGX). The remaining group  $E_4$  is located on the medulla externa. There the possibly neurosecretory cells are more or less loosely dispersed throughout the surface of medulla externa except in its antero-dorsal portion where many cells are seen to form a compact mass, the medulla externa ganglionic x-organ (MEGX).

### 3. The types of neurosecretory cells

In the present investigation, the cell types were classified mainly on the basis of the following criteria: (1) size and outline of the cell, (2) size and stainability of the nucleus, (3) staining properties of the cytoplasm, and (4) staining properties and appearance of the secretory products.

Six cell types other than the ordinary neurons were identified in the optic ganglia of the prawn. For convenience' sake, hereafter they will be referred to as Type-I, Type-II, Type-III, Type-IV, Type-V and Type-VI cells in order of cell size (Text-fig. 1).



Text-fig. 2. Diagrams of six types of possibly neurosecretory neurons as shown in AF-stained preparations of the optic ganglia of the freshwater prawn, *Palaemon pavidus*. A, Type-I cell; B, Type-II cell; C and D, Type-III cells; E, Type-IV cell; F, Type-V cell; G, Type-VI cell.

#### *Type-I cell*

The Type-I cells are very small in number, roughly from 5 to 7 per an eyestalk, and are found in the cell groups  $E_2$ ,  $E_3$  and  $E_4$ . The cell is large in size (ranging  $40\text{--}60\ \mu$ , or  $51\ \mu$  on an average, in diameter), and is pear-shaped in outline. It has a large round nucleus ( $20\ \mu$  in mean diameter) with two or three distinct nucleoli. Its homogeneous cytoplasm shows a weak affinity to aniline blue, and contains small numbers of aldehyde fuchsin (AF)-positive granules dispersed throughout the cytoplasm (Text-fig. 2A).

#### *Type-II cell*

Type-II cells are found only in the cell group  $E_4$ . They count approximately

ten, forming a cluster at the antero-lateral part of the medulla externa. The cell is relatively large in size (ranging 42–56  $\mu$ , or 48  $\mu$  on an average, in diameter) and is polygonal in its outline. It has an oblong nucleus (about 14  $\mu$  long) with two or three nucleoli. The cytoplasm is stained with azo-carmin, acid fuchsin and orange G. The CH-positive materials are seen in the phloxine-positive cytoplasm (Fig. 6). Also AF-positive matters are observed in the cytoplasm (Text-fig. 2B).

#### *Type-III cell*

The cells are rather irregular in shape and their large nucleus (15  $\mu$  in mean diameter) contains three or four nucleoli. With Mallory's triple stain, the cytoplasm stains blue at periphery and orange at perinuclear region. In the CHP-stained preparations, masses of CH-positive materials are noticed in peripheral cytoplasm (Figs. 7 and 8). With AF stain, in some cells the stained materials are seen as numerous fine granules that are scattered throughout the cytoplasm (Text-fig. 2C), whereas in others they occur as aggregated masses in the cytoplasm (Text-fig. 2D). Different degrees of affinity to AF are seen among these masses. Two subtype cells are discernible of the Type-III cells by their different size and distribution. Type-IIIa cells are found in the MTGX or the cell group E<sub>1</sub>, whereas Type-IIIb cells are seen in the cell groups E<sub>2</sub> and E<sub>3</sub>. The former cells, measuring 27–35  $\mu$  in diameter (31  $\mu$  in average), are significantly smaller than the latter cells which are 32–44  $\mu$  in diameter (38  $\mu$  in average).

#### *Type-IV cell*

Type-IV cells are present in all of the four cell groups, and those in group E<sub>1</sub> form a cluster (Fig. 9) whereas in other sites they are dispersed among other cell types. At the light microscopical level, it cannot be decided if they belong to different cell types. The cells are round, medium-sized (ranging 14–30  $\mu$ , or 24  $\mu$  on an average, in diameter) and monopolar. The large round nucleus (13  $\mu$  in mean diameter) has three or four distinct nucleoli. The cytoplasm is stained blue and orange with Mallory's triple stain. With CHP stain no masses of stained materials are observed, but there are rare cases in which a few dark blue granules are seen on purple background (Figs. 9 and 10). With AF stain, moderate amounts of granules are seen (Text-fig. 2E).

#### *Type-V cell*

These cells are distributed in group E<sub>1</sub>, being in contact with the SPX. They are small (ranging 14–18  $\mu$ , or 16  $\mu$  on an average, in diameter) and have a poor cytoplasm. The round nucleus (11  $\mu$  in mean diameter) contains several small chromatin pieces but no distinct nucleolus (Fig. 11). The cytoplasm stains blue or orange with Mallory's triple stain and contains a few AF-positive granules (Text-fig. 2F).

*Type-VI cell*

The cells are assembled in group E<sub>2</sub>, although they are always found in all the cell groups. They are small (ranging 12–16  $\mu$ , or 15  $\mu$  on an average, in diameter), round and monopolar. In the nucleus, 13  $\mu$  in diameter, nucleolus is not visible (Fig. 12). Nuclear contents are agglutinated in an irregular shape in some cells (Fig. 13, arrows). Several AF-positive granules are observed in poor cytoplasm (Text-fig. 2G).

Size and staining properties of these six cell types are summarized in Table 1.

Table 1. Size and staining properties of six types of neurosecretory cells located in the optic ganglia of the freshwater prawn, *Palaemon paucidens*.

Cell type		Cell diameter on an average ( $\mu$ )	Staining			
			CHP	AF	Azan	Mallory's triple stain
Type I	Cytoplasm	51	bluish gray	—*	purple	yellowish brown
	Secretory materials		dark blue	+		
	Nucleus		bluish gray	—	purple	yellowish brown
Type II	Cytoplasm	48	pink	—	red	red or orange
	Secretory materials		dark blue	+		
	Nucleus		gray	—	red	orange
Type III	Cytoplasm	31 <sup>a)</sup> and 38 <sup>b)</sup>	bluish gray	—	purple	blue <sup>1)</sup> and orange <sup>2)</sup>
	Secretory materials		dark blue	+		
	Nucleus		dark purple	—	bluish purple	maroon
Type IV	Cytoplasm	24	purple	—	dark purple	blue or orange
	Secretory materials		dark blue	+		
	Nucleus		purple	—	purple	maroon
Type V	Cytoplasm	16	bluish gray	—	purple	blue
	Secretory materials		—	+		
	Nucleus		bluish gray	—	purple	blue or orange
Type VI	Cytoplasm	15	bluish gray	—	purple	blue
	Secretory materials		—	+		
	Nucleus		bluish gray	—	purple	blue or orange

\*+, positive; —, negative. <sup>a)</sup>subtype-IIIa cell; <sup>b)</sup>subtype-IIIb cell. <sup>1)</sup>peripheral region;

<sup>2)</sup>perinuclear region.

#### 4. *The sinus gland*

At least five kinds of axon terminals are distinguishable in the sinus gland with different staining techniques.

First, with CHP stain two kinds of axon terminals, pink and gray ones, are found. The pink terminals are much more abundant than the gray ones. Both terminals take place at random in all parts of the sinus gland.

Second, with AF stain two kinds of axon terminals are recognized, the AF-positive and the AF-negative ones, the former being more abundant than the latter. Roughly by the manner of their arrangement three regions are distinguished in the sinus gland: the region consisted exclusively of AF-positive terminals, the region of only AF-negative terminals, and the region consisted of both terminals (Fig. 14).

Third, with Mallory's triple stain there are observed three kinds of axon terminals, blue, orange and grayish green ones. Some of the blue terminals may be derived from Type-III cells, if we assume that their peripheral region which also stains blue with Mallory's triple stain represents accumulation of the secretory products.

Fourth, with azan method five kinds of axon terminals are identified tinctorially, blue, red, vermillion, orange and purple ones. Most part of the sinus gland consists of these terminals arranged at random, and only in certain areas these terminals make an appearance in group, respectively (Fig. 15). By the similarity of their staining properties, it may be suggested that the red terminals are the axonal endings of Type-II cells. The origin of other types of terminals is still unknown.

Correlation among these axon terminals as identified by different staining methods remains to be elucidated in future.

### Discussion

In spite of abundant literatures on the neurosecretion in crustaceans, the classification of neurosecretory cells has been incomplete and even the exact number of cell types identified in optic ganglia is not always agreed among investigators. The present study has shown that there are at least six different types of non-ordinary, possibly secretory, nerve cells in the eyestalk of *Palaemon*, four of them constituting the MTGX. The sinus gland, on the other hand, has been shown to be constituted of at least five kinds of axon terminals.

Some relationships are pointed out between our results in *Palaemon* and those obtained by previous investigators in other species.

Our Type-I cell in *Palaemon* is apparently comparable to Matsumoto's  $\epsilon$ -cell in five species of crabs (Matsumoto, 1958), judging from its size, cytoplasmic properties and distribution, whereas the Type-II cell seems to correspond to Miyawaki's "giant cell" in the crab *Telmessus* (Miyawaki, 1956), Matsumoto's  $\alpha$ -cell (Matsumoto, 1958), and Lake's "large cell" in the crab *Paragrapsus* (Lake,



1970). The fact that the *Palaemon* Type-II cell is confined to the medulla externa coincides with Matsumoto's description of his  $\alpha$ -cell.

The MTGX of *Palaemon* is mainly composed of two kinds of medium-sized, possibly neurosecretory, cells, Type-III and Type-IV cells. Obviously the Type-III cell is homologous to Durand's Type 1 cell in *Orconectes* (Durand, 1956) and is very similar to Matsumoto's  $\beta$ -cell. On the other hand, the Type-IV cell of *Palaemon* may be comparable to Durand's Type 2 and Type 3 cells. Durand distinguished his Type 2 and Type 3 cells by their different appearance of the vacuoles and the secretory granules, besides the fact that the former gather to make up a cluster at proximal part of the MTGX. In *Palaemon*, most Type-IV cells take place dispersedly on other ganglia, although some assemble to form a similar cluster of cells in the MTGX. Moreover, no distinct histological difference has been noticed between the cluster-forming Type-IV cells and other Type-IV cells in this investigation. Although Durand was of the opinion that his Type 2 cell was homologous to Enami's  $\beta$ -cell, it is unlikely the case because Durand's description of his Type 2 cells is so different from Enami's semidiagrammatic representation of his  $\beta$ -cells (Fig. 10 of Enami's paper, 1951). Rather the  $\beta$ -cell seems to be comparable to Durand's Type 1 cell of *Orconectes* and the Type-III cell of *Palaemon*. It should be noted that Durand, examining the change of the secretory activity of his Type 2 cell during the molting cycle, found the parallelism between these two metabolic events and concluded that the molt-inhibiting hormone (MIH) is produced by the Type 2 cells. For the purpose of re-examination of his conclusion the cluster-forming Type-IV cells of *Palaemon* were investigated during the molting cycle. Contrary to expectation, however, no distinct change has been observed, so that further studies are needed in order to determine the site of origin, other than the Type-IV cells, of MIH in this species.

The homologous cell to our Type-V cells has never been mentioned before by other investigators. They are present near the SPX, the position where in the crabs Matsumoto's  $\delta$ -cells occur. The *Palaemon* Type-V cells possess conspicuous axons, whereas the  $\delta$ -cells do not. Also, difference in staining property is noticed of the cytoplasm of these two cells. Presence of colloidal substances around the  $\delta$ -cells suggests that they are homologous to the *Paratya* "onion body cells" (Lake and Ong, 1972). The Type-VI cell, the smallest among the six cell types, probably corresponds to Enami's  $\gamma$ -cell, Durand's Type 4 cell, Miyawaki's Da Fano cell, Matsumoto's  $\gamma$ -cell and Lake's "small cell". Relationship among these cell types described by different authors in several decapods is summarized in Table 2.

Neurosecretory cells are generally characterized by their large size and a large nucleus. In *Palaemon*, the Type-I, -II, -III and -IV cells, measuring 51  $\mu$ , 48  $\mu$ , 35  $\mu$  and 24  $\mu$  on an average, respectively, are much larger in size than the ordinary neurons (10  $\mu$ ), whereas the Type-V (16  $\mu$ ) and Type-VI (15  $\mu$ ) cells are not. However, some established neurosecretory cells in some teleost urophysis have been found to be very small (about 4-9  $\mu$  in diameter) (Romeu, 1962), so that the cell size cannot necessarily be relied upon as a definite criterion for identification of

Table 2. The neurosecretory cell types of the optic ganglia described by different investigators in several decapods.

<i>Palaemon paucidens</i> (present paper)	<i>Sesarma</i> sp. (Enami, 1951)	<i>Orconectes</i> <i>virilis</i> (Durand, 1956)	<i>Telmessus</i> <i>cheiragonus</i> (Miyawaki, 1956)	<i>Chionoecetes</i> <i>opilio</i> (Matsumoto, 1958)	<i>Paragrapsus</i> <i>gaimardii</i> (Lake, 1970)
Type-I cell Type-II cell Type-III cell Type-IV cell Type-V cell Type-VI cell	$\beta$ -cell $\alpha$ -cell(?) $\gamma$ -cell	Type 1 cell Type 2 cell Type 3 cell Type 4 cell	giant cell giant cell giant cell Da Fano cell	$\varepsilon$ -cell $\alpha$ -cell $\beta$ -cell B-cell(?) $\gamma$ -cell	large cell large cell medium oval cell small cell

the neurosecretory cell. Whether our Type-V and -VI cells are secretory in nature is not determined in the present study.

The cytoplasmic inclusions which are stained with chrome-hematoxylin or aldehyde fuchsin have been regarded as one of the criteria to distinguish a neurosecretory cell from a non-secretory one, and "if evidence of a secretory cycle can be adduced, --- then it is possible to conclude that such neurons are *probably*, but not necessarily, neurosecretory" (Bern, 1962). All the six cell types that have been identified in the eyestalks of *Palaemon* are found to have AF-positive materials in the cytoplasm, and four types of cells (Type-I, -II, -III and -IV cells) CH-positive materials, although their "secretory" cycle at the light microscopical level was not established. Morphologically, the presence of electron dense granules or vesicles between 500 and 3,000Å in diameter is thought as "probably one of the best criteria for a neuron that has become neurosecretory" (Jenkin, 1970, p. 19). Although electron dense granules or vesicles in axon terminals of the eyestalks have been studied by several investigators (Bunt and Ashby, 1967; Meusy, 1968; Andrews *et al.*, 1971), at present little or no information is available on ultrastructure of such cytoplasmic inclusions located in perikaryon of such neurosecretory cells. Electron microscope studies are in progress along this line.

### Summary

1. The classification of eyestalk neurosecretory cells was performed in adult male and female freshwater prawns *Palaemon paucidens* at the light microscopical level.
2. Four cell groups ( $E_1$ - $E_4$ ) take place attached to the optic ganglia. The group  $E_1$  corresponds to the medulla terminalis ganglionic x-organ (MTGX).
3. Six types of cells other than ordinary neurons are identified histologically in the intermolt animals. All of these cells contain AF (aldehyde fuchsin)-positive materials and four of them (Type-I, -II, -III and -IV cells) possess CH (chrome-hematoxylin)-positive materials. The MTGX consists of four types of possibly

neurosecretory cells (Type-III, -IV, -V and -VI cells).

4. At least five types of axon terminals are distinguishable tinctorially in the sinus gland, and some types of terminals make an appearance in groups.

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### Explanation of Plates XXXII-XXXIII

Fig. 1. Longitudinal section of the left eyestalk through four optic ganglia: LG, lamina ganglionaris; ME, medulla externa; MI, medulla interna; and MT, medulla terminalis. OP, optic lobe peduncle. CHP.  $\times 55$ .

Fig. 2. Sagittal section through the optic ganglia, showing conspicuous nerve tracts that terminate at the sinus gland. SG, sinus gland; NT, nerve tract. Hematoxylin-eosin.  $\times 175$ .

Fig. 3. The sensory pore x-organ (SPX) is shown to contain several onion bodies (arrows). Hematoxylin-eosin.  $\times 400$ .

Fig. 4. Histological section through the MTGX, showing that it is composed of many possibly neurosecretory cells. CHP.  $\times 300$ .

Fig. 5. A Type-I cell situated in the midst of many ordinary, possibly non-secretory, nerve cells. CHP.  $\times 750$ .

Fig. 6. Type-II cells containing the masses of CH-positive materials. CHP.  $\times 750$ .

Fig. 7. Type-IIIa cells possessing the irregularly-outlined CH-positive materials. CHP.  $\times 750$ .

Fig. 8. Type-IIIb cells that are distributed in cell group  $E_3$ . CHP.  $\times 750$ .

Fig. 9. The cluster of Type-IV cells in the MTGX. CHP.  $\times 750$ .

Fig. 10. Type-IV cells distributed in cell group  $E_3$ . CHP.  $\times 750$ .

Fig. 11. Type-V cells with a relatively poor cytoplasm. CHP.  $\times 750$ .

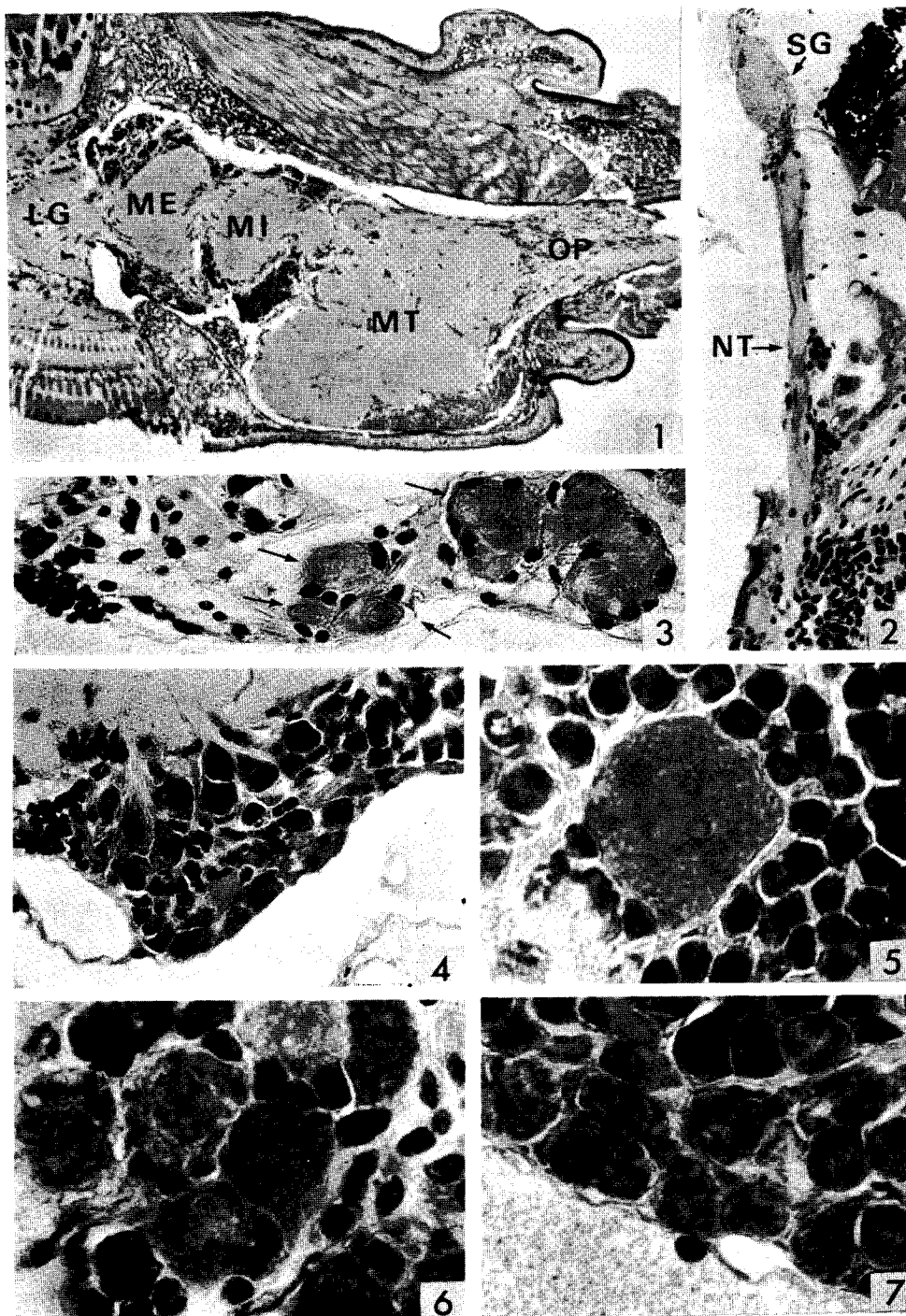
Fig. 12. A mass of Type-VI cells present in cell group  $E_3$ . CHP.  $\times 750$ .

Fig. 13. Type-VI cells in group  $E_2$ . Some cells have their nuclear contents aggregated in the center (arrows). CHP.  $\times 750$ .

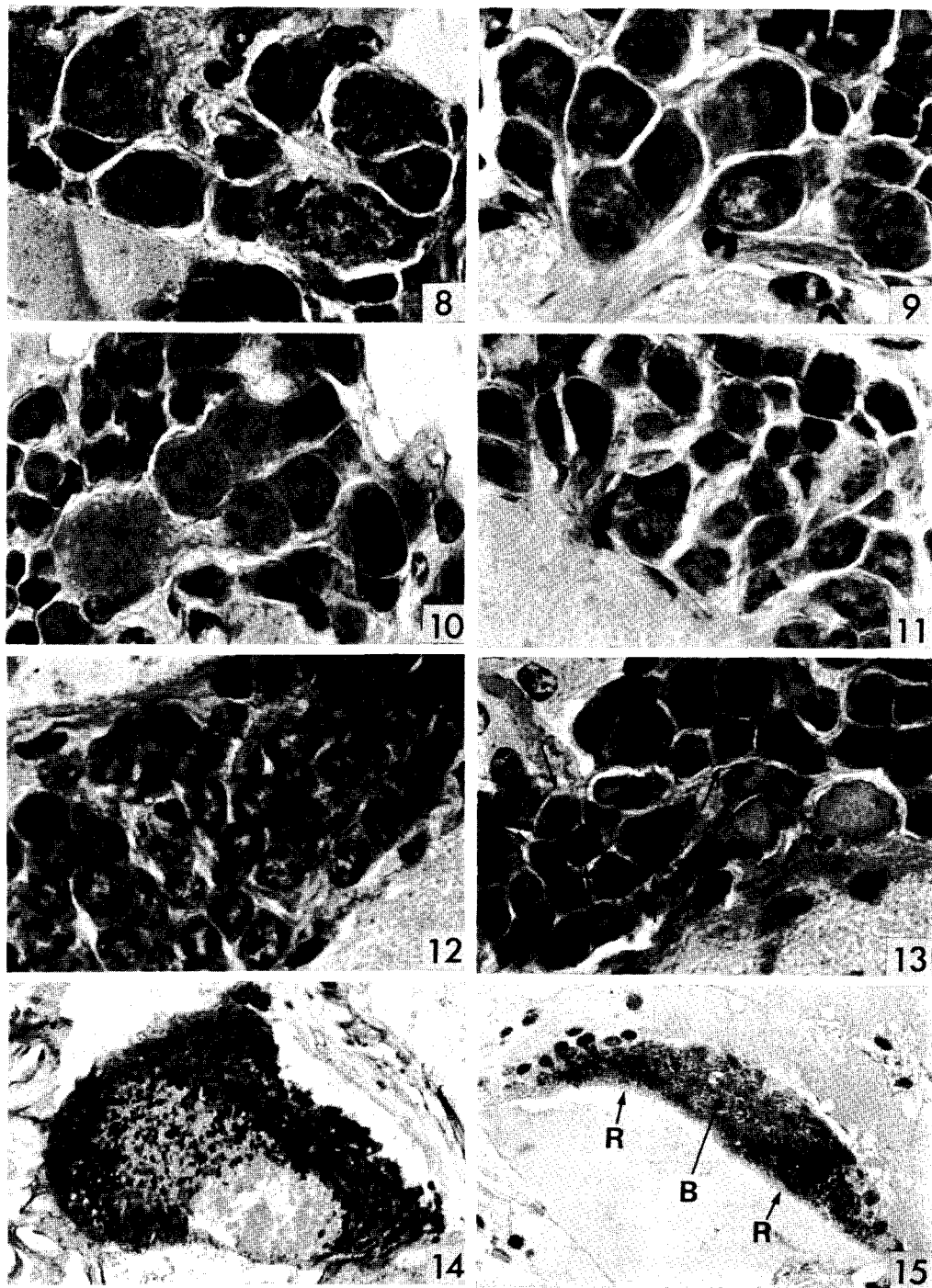
Fig. 14. The sinus gland stained with AF, showing three tinctorially different regions.  $\times 300$ .

Fig. 15. A portion of the sinus gland stained with azan method. Note that two types of axon terminals take place in groups. B, the group of blue terminals; R, the group of red terminals.  $\times 300$ .

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*S. Hisano: Eyestalk Neurosecretory Cells in Palaemon*



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