# THE STRUCTURE OF POSSIBLE PHOTORECEPTIVE ELEMENTS IN THE SIXTH ABDOMINAL GANGLION OF THE CRAYFISH

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It is well known that the sixth abdominal ganglion of the crayfish is photoreceptive. Illumination of this ganglion causes sustained increase in the spontaneous activity of the nerve cord (Prosser, 9). On the basis of physiological investigations, Kennedy (3, 4) postulated that the photoreceptors may be slightly modified neurons equipped with photosensitive pigments. The present investigation employed the electron microscope to search for specialized photoreceptor cells or cell elements in the sixth abdominal ganglion of the crayfish ventral nerve cord. The bodies found and to be described are quite similar to photoreceptive elements described by other investigators in vertebrates and invertebrates.

## MATERIALS AND METHODS

Five sixth abdominal ganglions out of ten animals (*Orconectes virilis*) were examined and compared with other abdominal, thoracic, and brain ganglions. The caudal part of the animal was removed, and the nerve cord was dissected from the ventral side of the abdomen. The translucent exoskeleton enabled the sixth ganglion to be located easily. The ganglion was separated from the rest of the nerve cord and fixed in an ice-chilled osmium tetroxide solution for about 15 minutes at 4°C, and then was dehydrated in alcohol. Luft's precedure (5) was used for embedding in epoxy resin. Sections were cut with a Porter-Blum microtome and mounted on either formvar- or carbon-coated grids. Some were stained with saturated uranyl acetate. A Bendix-Akashi Tronscope 50 electron microscope was used mainly, an RCA-2A occasionally.

## RESULTS

Large oval or spherical bodies 1 to 3 $\mu$ in diameter containing lamellar structures, vesicles, amorphous droplets and rarely a crystal-like structure are scattered throughout neurons (cell bodies and axons) and glial cells of the ganglion. Most frequently, they occur singly, but sometimes they form a group. These bodies are in many cases surrounded by a thin membrane, which at times is poorly defined.

The body contains several groups of lamellated membranes (Figs. 1, 2). The appearance of these piles of membranes suggests a fingerprint. The lines of these fingerprints in any one section are short in length and their course is irregular. At times, the section passes obliquely through several of these lamellae, yielding a honeycomb effect (Figs. 2, 4). In some sections, several honeycomb structures can be seen along a stretch of clustered lamellae, indicating the extreme irregularity of the course of the membranes. The lines of the fingerprints are separated by a space 100 to 250 A wide; each membrane or lamella is 40 A thick. In some sections, the lamellated structure looks like a myelin sheath and, indeed, the size of the membranes and the distances between them are similar to those of a myelin sheath (see Robertson, 10).

In some of these bodies there is also located a droplet containing amorphous material, usually with an irregular border (Figs. 1 to 3). This structure is similar to the so called oil drop identified by Moody and Robertson (7) in the retinal cells of the frog. There is usually only one amorphous droplet found in a body, but occasionally 2 or 3 can be found in a section of one body. In some cases, the lamellae described above appear to be attached to the amorphous droplet (Figs. 2 and 3).

In a few sections, a rectangular crystal-like structure is seen within these bodies (Fig. 1).

As already mentioned, the spherical bodies are scattered throughout the ganglion. Most frequently, they are found in the cytoplasm of glial cells, sometimes near neurons, and sometimes near the nerve fibers. However, it is not rare to see these bodies within a nerve fiber (Figs. 3 and 4) or nerve cell body (Fig. 1). At times, a small nerve fiber less than 1 $\mu$ in diameter swells or bulges to contain a relatively large body 2 $\mu$ or more in diameter.

The evidence suggests that the bodies described here are photosensitive elements. Many investigators have found that photosensitive elements in animals and plants have a layered or lamellated structure essentially similar to that described here in the crayfish (Wolken *et al.*, 12). Similarly, Miller (6) described lamellar or honeycomb structures

in the ommatidium of *Limulus*. The structure of the myeloid body of the pigment epithelial cell of the frog, which may be a photoreactive element, is also lamellar (Porter and Yamada, 8). Lastly, the lamellated structure of the rods and cones of the vertebrate retina may also be cited as evidence of the essential lamellated nature of photoreceptive elements or photoreceptive cells.

The honeycomb structure of the *Limulus* ommatidium apparently is derived from microvilliform processes from the cell membrane (Miller, 6); this is apparently not so for the crayfish. Hama (2) found a compound body in the innermost sheath-cell of a giant fiber and suggested that this structure may be a type of photoreceptor. However, the type of body described by Hame is found in every ganglion of the crayfish nerve cord, whereas physiological evidence indicates that photoreceptive properties are much more restricted exclusively to the sixth abdominal ganglion. Lysosomes (1) in liver cells show some structural resemblance to this photoreceptive element, but their resemblance seems to be coincidental.

It is not yet known whether the connections between the ganglia of the nerve cord of the crayfish contain photoreceptive elements. Histologically (and as suggested by Kennedy, personal communication), photoreceptive elements are found not only in nerve cell bodies but also in axons and usually in very small ones less than 0.5 $\mu$ in diameter. More photoreceptive bodies have been found in axons than in nerve cell bodies.

The way in which these photoreceptive bodies can stimulate axons or nerve cell bodies is unknown. The lamellated structure of the photosensitive elements in the retinal rod and cone is part of the receptor neuron which is in synaptic contact with other neural elements, whereas in the crayfish the photoreceptive elements appear like inclusions within the neural tissues. It is also difficult to account for the presence of many photoreceptive elements in the glial cells, usually considered inexcitable. Perhaps the excitatory substance produced by the glial photoreceptive bodies diffuses into nearby neurons and nerve fibers. Crayfish, when illuminated, aggregate in the dark through a simple photokinetic response manifested by increased locomotor activity (Welsh, 11). It may be that the motor axons in the neuropile of the sixth abdominal ganglion which contain photoreceptive elements are excited by photochemical reaction, thus causing locomotor activity of the animals.

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FIGURE 1

A body in a neuron is surrounded by a poorly defined membrane. The body contains electron-opaque structures with fingerprint-like pattern, a crystal-like structure (*C*), an amorphous drop (*A*), and other vesicular structures. *M*, mitochondria in the neuron; *N*, nucleus of the neuron. × 27,000.

FIGURE 2

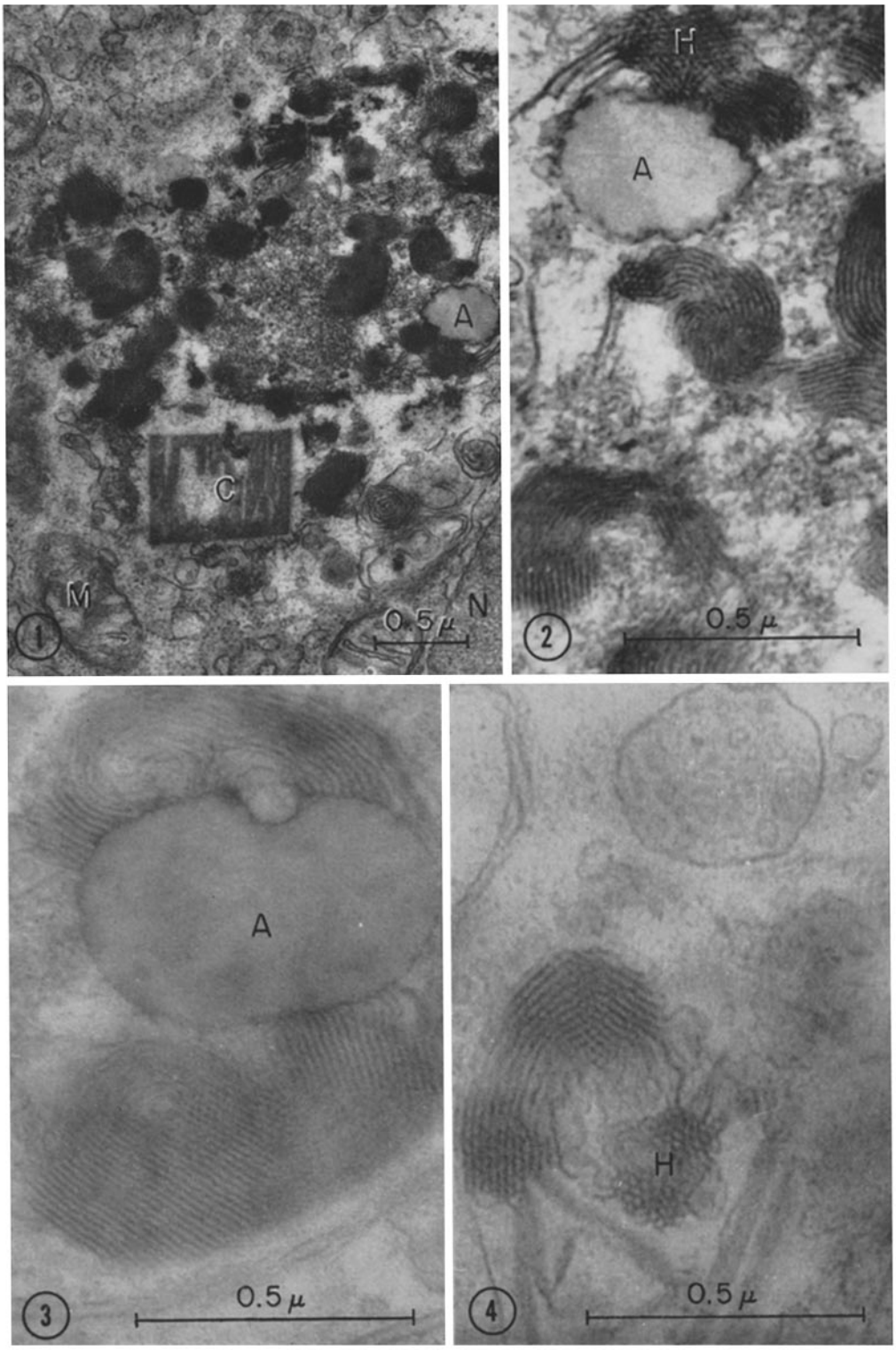
Higher magnification of part of Fig. 1. The lamellated membranes of the fingerprint-like structures are shown. *H* indicates the honeycomb effect which sections through the lamellated membranes sometimes yield. *A* indicates an amorphous drop intimately related to some of the lamellated membranes. The matrix of the body is filled with vesicular particles and homogeneous substances. × 67,000.

FIGURE 3

A body found inside an axon. The double membrane (lower edge of the picture) is the axolemma. The limiting membrane of the body is obscure. The lamellated membranes and amorphous drop (*A*) are intimately related. × 80,000.

FIGURE 4

High magnification of a body which shows clearly the lamellae and their honeycomb appearance *H*. × 80,000.



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