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ORIGINAL ARTICLE

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# Fine structure of the photogenous areas in the bioluminescent ophiuroid *Amphipholis squamata* (Echinodermata, Ophiuridea)

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**Abstract** *Amphipholis squamata* is a small bioluminescent ophiuroid whose arms are the only body part to produce light. The morphology of the arms was described paying particular attention to the spinal ganglia, viz the areas of most intense luminescence. Spinal ganglia consist of five different cell types (A–E) which were studied at different stages of the photogenous reaction. Type D cells have numerous irregularlyshaped vacuoles, widespread Golgi apparatus and well-developed rough endoplasmic reticulum (RER) that show obvious ultrastructural changes after luminescence. Type D cells appear, therefore, to be the best photocyte candidate. Type B and C cells were frequently observed in the nervous system outside spinal ganglia. Type A and E cells have not been described before. Type A cells are ciliated cells and type E cells extend long processes which are intimately associated with type D cells and epidermal ciliated cells. Both type A and type E cells could take part to the stimulation pathway that triggers luminescence.

## A. Introduction

That some echinoderm species are able to produce light has been known for almost two centuries (Viviani 1805; Harvey 1952). Yet, light production by echinoderms has been poorly studied although bioluminescent representatives occur in every living higher taxa except the Echinoida (Herring 1974, 1978, 1995). Investigations were mostly done on ophiuroids, notably on the small intertidal to sublittoral cosmopolitan species, *Amphipholis squamata* Delle Chiaje, 1828. According to Brehm and Morin (1977) luminescence in this species originates from the basal part of the arm spines. Working on another luminescent ophiuroid species (*Ophiopsila californica* Clark, 1921) these authors reported that photogenic cells are close to the nervous tissue.

This and the general assumption that bioluminescence in most metazoans is under nervous control suggest that photogenic cells in *A. squamata* are intimately associated with the nervous tissue of the basal part of the spine. Photocyte identification was tried several times (see Millot 1966, for review) and light emission was often associated with a mucus secreted by glandular cells from either the brachial spines (Reichensperger 1908; Trojan 1909) or the podial tips (Sterzinger 1907). Only Mangold (1907, 1910) reported that the outline of the luminous parts of *A. squamata* remains perfectly constant, which suggests that there is no discharge of a luminous substance. He speculated that the emitted light is intracellular and that photocytes are subepidermal cells. With the exception of Brehm and Morin (1977), no author has worked on the morphology of *A. squamata* luminescence since Mangold's contributions. The present work aims to precisely localize the photogenic areas in the species *A. squamata*, to describe their fine structure and to tentatively identify the photogenic cells.

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## B. Materials and methods

Individuals of *A. squamata* (Fig. 1) were collected intertidally at Langrune-sur-Mer (Normandy, France) from September 1993 to June 1994. They were transported to the marine biology laboratory, Brussels University, and kept alive in a closed-circuit marine aquarium (12°C, 32‰ salinity) until required.

In order to localize the photogenic areas, light emission was triggered by putting entire individuals or dissected body parts (viz disc or arms) in a v/v sea-water-KCl 400 mM solution according to the technique of Mallefet et al. (1989). When necessary, individuals were anaesthetized in a 3.5% $MgCl_2$ solution in artificial sea-water. For transmission electron microscopy (TEM), dissected body parts from individuals which either had or had not emitted

light were fixed for 3 h at 4°C in 3% glutaraldehyde in cacodylate buffer, then rinsed in the buffer and postfixed for 30 min in 1% osmium tetroxide in the same buffer. After a final buffer wash, pieces were decalcified in the dark for 12–15 h at 4°C in 2% ascorbic acid in 0.3 M NaCl (Dietrich and Fontaine 1975). Decalcified pieces were dehydrated in graded ethanol and embedded in Spurr. Semithin sections (0.3 µm) were cut on a Reichert OM2 ultramicrotome and stained with a 1:1 methylene blue-azur II mixture (Richardson et al. 1960). Ultrathin sections (40–50 nm) were cut on an LKB V ultramicrotome, contrasted with uranyl acetate and lead citrate (Reynolds 1963), and examined with a JEOL JEM 2000 FX II transmission electron microscope.

For scanning electron microscopy (SEM) entire individuals were fixed, decalcified and dehydrated as described for TEM preparations. They were then dried by the critical-point method (using $CO_2$ as transition fluid), coated with gold in a sputter coater and observed with a JEOL JSM 6100 scanning electron microscope.

**Figs. 1–5** *Amphipholis squamata*. *ax* axon, *cb* cell bodies, *cu* cuticle, *m* muscle, *os* ossicle, *sc* subcuticular region, *sg* spinal ganglion

**Fig. 1** Aboral view of an individual (SEM)

**Fig. 2** Luminescent areas of the arm as seen using an epifluorescent technique

**Fig. 4** Epidermal indentation (►) contacting a spinal ganglion (*sg*) (parasagittal section)

**Fig. 5** Section through a spinal ganglion

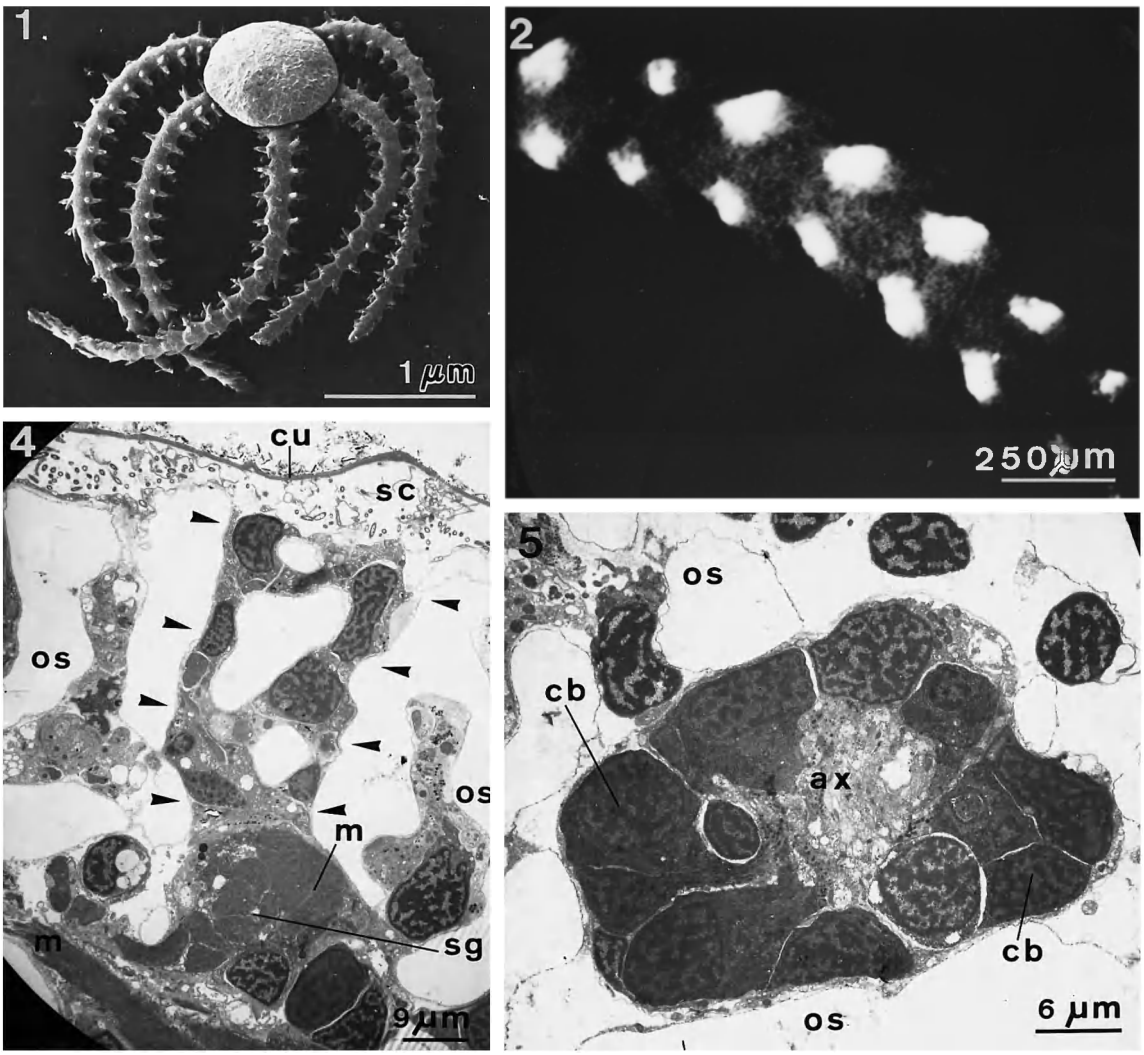
## C. Results

### I. Survey of luminescent areas

Luminescent areas were detected by triggering light production in previously anaesthetized or unanaesthetized individuals using the technique of Mallefet et al. (1989) that was applied to either entire individuals, dissected disc or arms, or arm fragments. The disc never emitted light while the arms always produced it over all their length whether they were attached to the disc, dissected from it or split into fragments. From repeated observations of flashing individuals or arms it could be seen that light originated from areas located under the basal part of the brachial spines, thus confirming the previous observation by Brehm and Morin (1977) (Figs. 2, 3).

### II. Anatomy of the brachial nervous system

The arm of an adult *A. squamata* (disc diameter ca 2.2 mm) measures ca 12 mm long. It consists of about 35 successive segments whose shape and size depend on



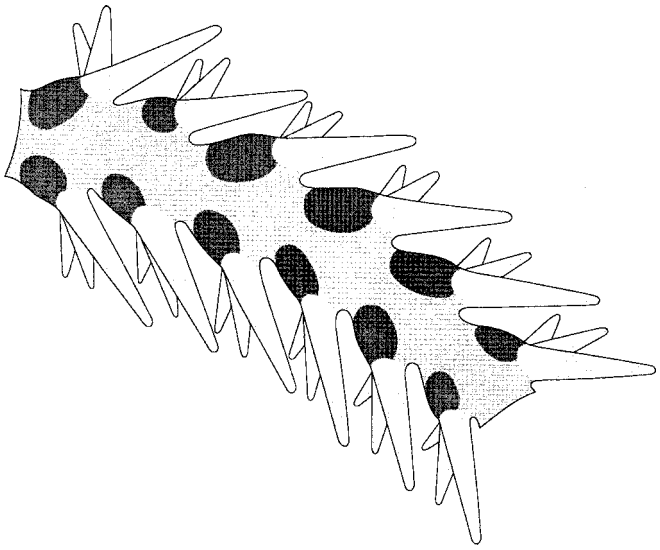


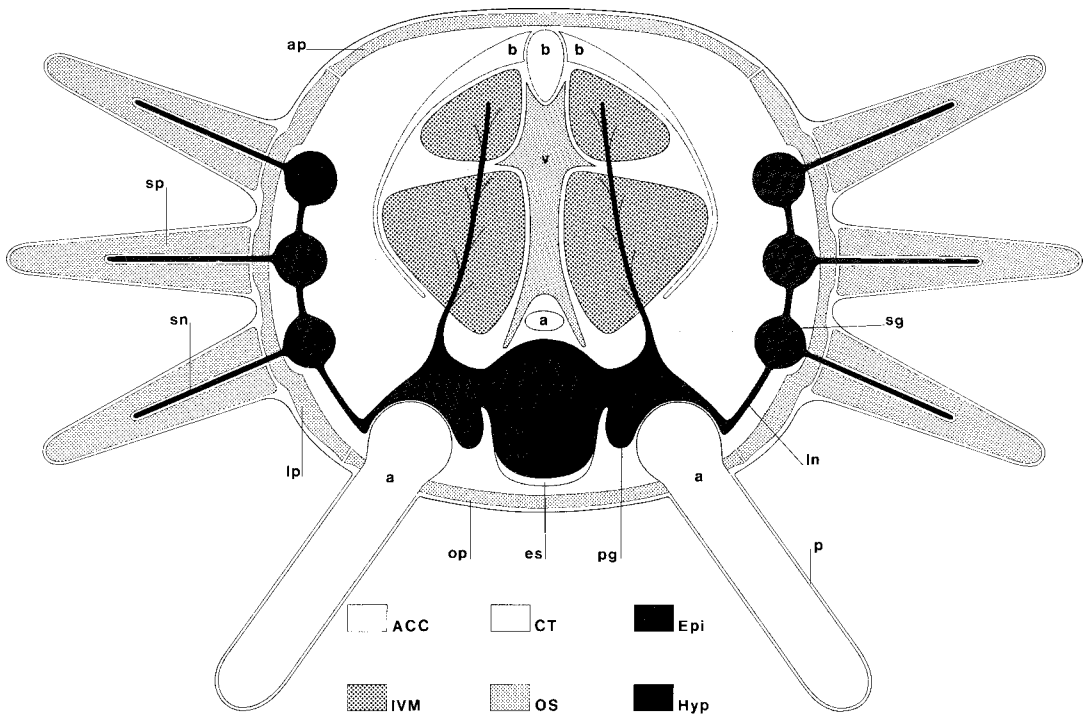
**Fig. 3** Distribution of luminescent areas along the arm (*light grey* brachial spines, *medium grey* arm aboral surface, *dark grey* luminescent areas) (not to scale)

their position along the arm, the distalmost being the smallest (Fig. 1). As in other ophiuroid species (see, for example, Cobb 1987), the brachial nervous system of *A. squamata* is made up of two nerve plexuses, the epineural and the hyponeural, which are superimposed on one another in the oral region of the arm (the epineural plexus is under the hyponeural plexus when going from the aboral to the oral side of the arm). The epineural plexus forms the bulk of the radial nerve cord that travels the length of the arm and of the paired podial ganglia that occur in each segment (Fig. 6). Whilst also contributing to the radial nerve cord and the podial ganglia, the hyponeural plexus forms, mostly on its own, the paired nerves innervating the intervertebral muscles (Fig. 6). As for the left and right lateral nerves, these are epineural and interconnect, respectively, with a left and right group of three successive spinal ganglia from which distinctive spinal nerves originate. (There are three spines and, thus, three spinal ganglia and three spinal nerves on each side of a brachial segment of *A. squamata*.) (Figs. 3–6).

## III. Anatomy of the spinal ganglia

Information gathered on the luminescent areas of *A. squamata* strongly supports the idea that light is produced by cells associated with the spinal ganglia of each arm segment. Spinal ganglia are grossly spherical in shape (ca 30 µm in diameter) (Figs. 4, 5). They are partly located in slight depressions of the internal surface of the lateral skeletal plates and surrounded elsewhere by an uncalcified connective tissue (Fig. 8). Each ganglion is lined by a well-marked basal lamina that is continuous with those surrounding the lateral and the spinal nerves (Fig. 6). That basal lamina is also continuous with the one lining the epidermal indentations (arrowhead) that contact by place the spinal ganglia, and with the lamina surrounding the cells of the spine muscle system (these

**Fig. 6** *A. squamata*. Transverse section at midpoint of arm segment. *ACC* ambulacral and coelomic cavities, *CT* connective tissue, *Epi* epineural nerve plexus, *Hyp* hyponeural nerve plexus, *IVM* intervertebral muscles, *OS* ossicle, *a* ambulacral cavities, *ap* aboral plate, *b* coelomic cavities, *es* epineural sinus, *ln* lateral nerve, *lp* lateral plate, *op* oral plate, *p* podium, *pg* podial ganglion, *sg* spinal ganglia, *sn* spinal nerve, *sp* spine, *v* vertebra (not to scale)



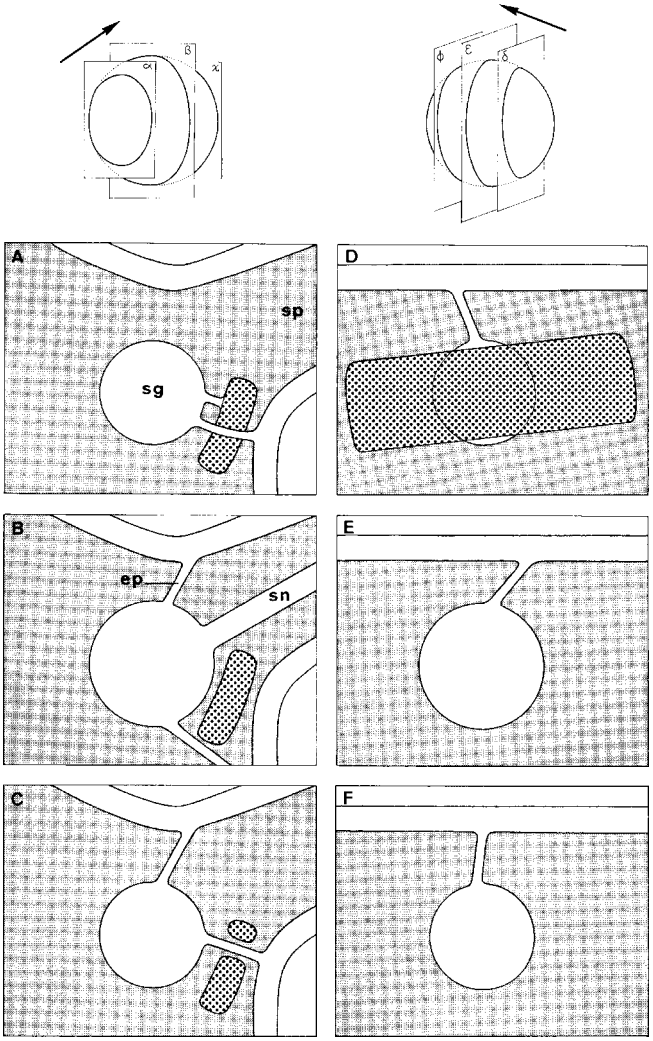



**Fig. 7A–F** *A. squamata.* Diagrammatic representations showing the relationships between a spinal ganglion, its corresponding spinal nerve and muscles, and the epidermal indentations occurring in the area (relationships with lateral nerves are not shown). The drawing illustrates successive sections that are transverse (**A–C** from proximal to distal) and parasagittal (**D–F** from outside to inside). *ep* epidermal indentation, *sg* spinal ganglion, *sn* spinal nerve, *sp* spine, *grey area* connective tissue, *spotted area* spinal musculature

cells are mostly developed at the distal part of ganglia) (Figs. 4, 7, 8).

## IV. Fine structure of spinal ganglia in luminescence-non-stimulated individuals

Spinal ganglia consist of a central bundle of neurites around which cell bodies of different cell types occur (Fig. 5). Table 1 summarizes the major characteristics of each of the ganglionic cell types. Among these cell types, three (i.e. the internal cells) are distributed everywhere in the ganglia and they are, thus, sometimes close to the bundle of neurites, while the two others (i.e. the external cells) always have a strictly peripheral location.

Neurites in spinal ganglia are of three different types according to their cytoplasmic content, the only common feature being the presence of small scattered mitochondria in their peripheral parts. Type 1 neurites (Fig. 9) measure from 0.3 to 0.6 μm in diameter. They are electron-dense, contain dense bundles of microtubules which run parallel to each other and to the neurite longitudinal axis, and have scattered translucent and dense vesicles measuring ca 100 and 130 nm in diameter, respectively. Type 2 neurites (Fig. 9) range from 0.6 to 1.6 μm in diameter. They are rather translucent, contain a few short and isolated microtubules and have dense-core vesicles from 200 to 400 nm in diameter. Type 3 neurites (Fig. 9) measure from 0.6 to 1.4 μm in diameter. They are rather translucent, do not contain microtubules and have translucent vesicles of ca 70 nm in diameter.

Internal cells are grossly ovoid in shape. Whatever their type they measure from 4 to 8 μm in length, have a circular to egg-shaped nucleus with patches of varing density of euchromatin and contain many mitochondria in their cytoplasm. Type A cells (Fig. 10) contain numerous dense vesicles (from 120 to 140 nm in diameter) that are dispersed all over the cytoplasm except in its perinuclear part. These cells also have a widespread and well-developed rough endoplasmic reticulum (RER) and sometimes include a rather inconspicuous Golgi apparatus. Type B cells (Fig. 11) have many vesicles, measuring from 200 to 300 nm in diameter, that either contain a dense central core or a grey finely granular material (one-third of the observed vesicles). These are monociliated cells (their cilium measures up to 4 μm in length) whose cytoplasm contains highly developed RER cisternae as well as a rather conspicuous Golgi apparatus often located close to the cilium basal rootlet (Fig. 11). The cytoplasm of type C cells (Fig. 12) is often reduced to a thin and rather translucent perinuclear layer without any RER cisternae or Golgi apparatus. From serial TEM sections of spinal ganglia it could be established that all neurites observed so far originate from one of the three aforementioned cell types, with type 1 neurites belonging to type A cells, type 2 neurites to type B cells and type 3 neurites to type C cells.

The two types of external cells are branched in shape. They most often show an ovoid nucleus with the euchromatin density depending on the cell type. Type D cells occur at the periphery of spinal ganglia (Figs. 13, 14). They have numerous mitochondria, lipid vesicles (from 400 to 700 nm in diameter) and many irregularlyshaped vacuoles (from 300 to 700 nm in length) that are often translucent though some are grey and full of a fibrillar to finely granular material (Fig. 13). The cytoplasm contains short tubules (length ca 500 μm) in its peripheral part and widespread Golgi apparatus and conspicuous RER in its central part (RER cisternae are often filled with fibrillar material). Type E cells (Figs. 15, 16) have a dense granular cytoplasm in which many translucent or greyish vesicles (from 70 to 100 nm in diameter) and a few mitochondria occur. Type E cells are strongly branched and send out several long processes. Their cell

**Table 1** Main characteristics and location of type A to type E ganglionic cells

| Cell characteristics | | Cell types | | | | |
|---|---|---|---|---|---|---|
| | | Internal cells | | | External cells | |
| | | A | B | C | D | E |
| Nucleus | Euchromatin density | +++ | +++ | + | ++ | ++++ |
| Cytoplasm | Vesicles | Dense | Dense-core or grey | Translucent | Translucent or grey | Translucent or grey |
| | Vesicle size (nm) | 120–140 | 200–300 | 60–70 | 300–700 | 70–100 |
| | RER | Developed | Developed | Undeveloped | Developed | Undeveloped |
| | Golgi | Inconspicuous | Conspicuous | Inconspicuous | Conspicuous | Inconspicuous |
| Location | | All over the nervous system | Restricted to the spinal ganglia and the spinal and lateral nerves | All over the nervous system | Mostly in the outer part of spinal ganglia with some extremities going to the base of epidermal indentations | Mostly in epidermal indentations with some extremities entering the spinal ganglia |

(+ translucent, ++ slightly dense, +++ dense, ++++ very dense)

bodies are located close to but outside the ganglia, often being situated in the most internal part of epidermal indentations and/or close to the muscle cells that surround the most distal part of the spinal ganglia. As for their cell processes, some penetrate the ganglion, contacting intimately the membrane of type D cells (Figs. 13, 14), while others travel through the epidermal indentations contacting the basal part of monociliated (subcuticular cilium) epidermal cells (Fig. 8).

V. Location of ganglionic cell types

Additional TEM investigations were performed to ascertain whether the cells (i.e. cell bodies and/or neurites) found in spinal ganglia occur in other epineural areas, namely in the radial nerve cord, the podial ganglia, the lateral nerves (interganglionic junctions) and the spinal nerves. Type A and type C cells are found equally in these four areas, with the only particularity being that neurites from type A cells (neurites I) appear to be rather scarce in spinal nerves. Apart from the spinal ganglia, type B cells were observed only in lateral and spinal nerves. Cell bodies of type D cells are confined in the spinal ganglia and send out long processes that penetrate lateral and aboral indentations. These processes are surrounded by a basal lamina that is continuous with that of the ganglion (Figs. 13, 14). Type E cell processes mostly occur in epidermal indentations where they are often intimately associated with processes originating from type D cells (Figs. 13, 14). Also, a few type E cell processes were found within the spinal nerves.

VI. Fine structure of spinal ganglia in luminescence-stimulated individuals

Additional observations were performed on arms after the emission of light. They showed that important ultrastructural changes occur in type D cells whose cytoplasm becomes full of large irregularly shaped vacuoles (maximal length from 0.7 to 2.5 µm) which contain fibrillar material in various amounts (Fig. 18). RER cisternae are numerous and of various shapes and sizes (longitudinal axis from 300 to 900 nm). They are filled with homogeneous fibrillar material similar to that filling the vacuoles (Figs. 17, 18). Golgi apparatus are well developed and often surround vacuoles (Fig. 19). Cytoplasmic processes of type D cells contain tubules and vesicles (40–90 nm in diameter) of varing electron density (Fig. 20). Bundles of fibrils (Fig. 19) and lysosomal vesicles (diameter from 0.3 to 1 µm) are other common features found in these cells after the emission of light. Mitochondria and lipid vesicles remain seemingly unaffected by the photogenous reaction.

## D. Discussion

Various earlier investigators tried to identify and describe light-producing cells in different ophiuroid species (see, e.g. Mangold 1907; Reichensperger 1908; Sokolow 1909). The usual way to characterize photocytes was to recognize cells whose distribution matched that of the luminous areas observed in vivo. Although many attempts were made, Byrne (1994) reported that "cells responsible for light production in ophiuroids have not been positively identified".

Among the five different cell types observed in the spinal ganglia of *A. squamata*, two, viz types B and C,

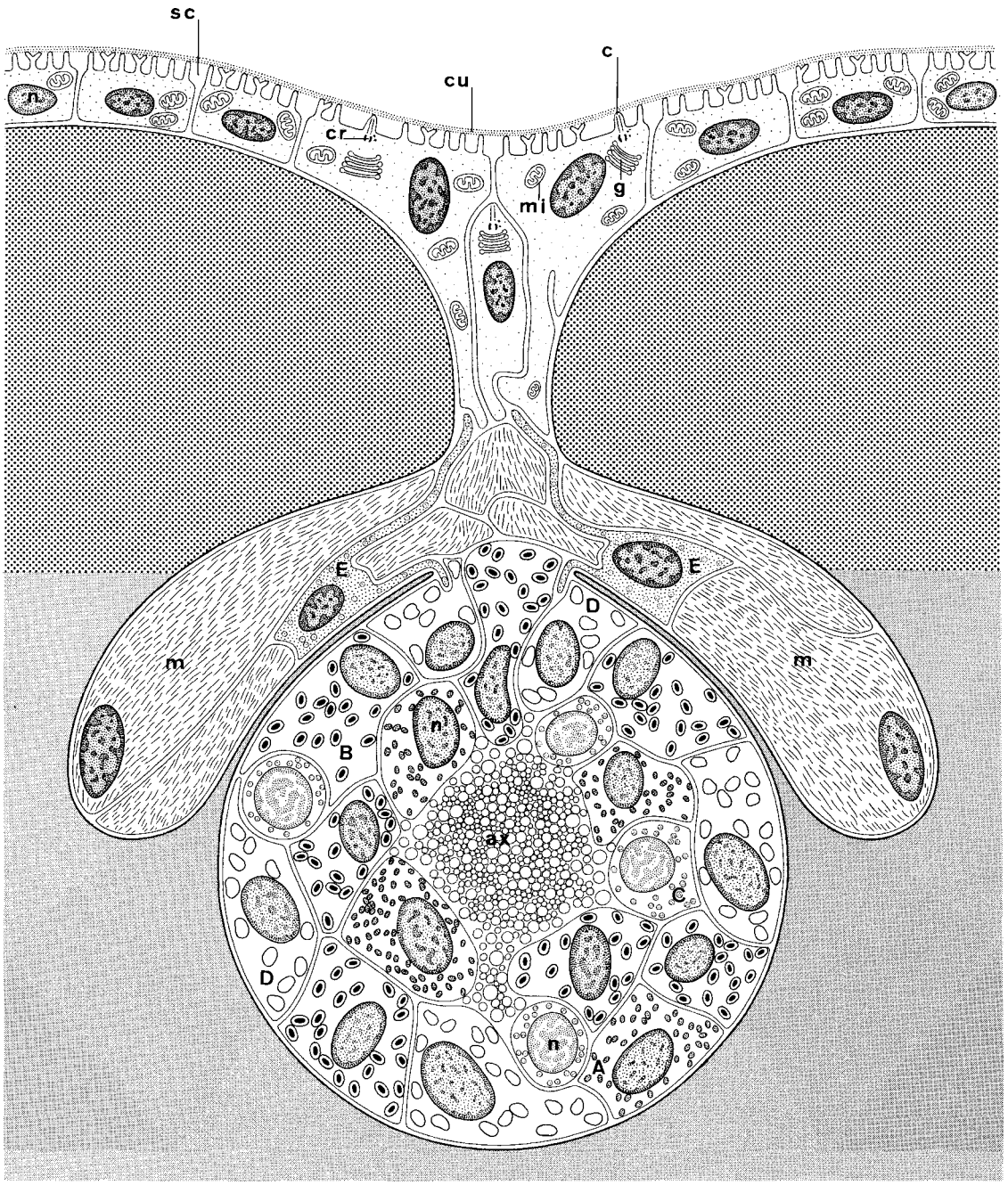



**Fig. 8** *A. squamata.* Fine structure (diagrammatic representation) of a spinal ganglion and its surrounding tissues (muscle and epidermis). *A* type A cell, *ax* axons, *B* type B cells, *C* type C cells, *c* cilium, *cr* cilium rootlet, *cu* cuticle, *D* type D cells, *E* type E cells, *g* Golgi apparatus, *m* muscle, *mi* mitochondria, *n* nucleus, *sc* subcuticular region, *spotted area* ossicle, *grey area* uncalcified connective tissue (not to scale)

are also frequently observed in other parts of the ophiuroid nervous system (Pentreath and Cottrell 1971; Märkel and Röser 1985; Ball and Jangoux 1990, 1996). They were described by Pentreath and Cobb (1972) who suggested that their fine structures are indicative of cholinergic (C cells) and aminergic (B cells) transmissions. As for type A, D and E cells, they have not been described

**Figs. 9–14** Spinal ganglia of *A. squamata* (TEM). *bl* basal lamina, *c* cilium, *cr* cilium rootlet, *dcv* dense-core vesicle, *dv* dense vesicle, *g* Golgi apparatus, *gv* grey vesicle, *n* nucleus, *nt* neurotubule, *m* mitochondria, *pr* processes from type E cell, *rc* RER cisternae, *tv* translucent vesicle, *tiv* translucent irregularly shaped vacuole, *giv* grey irregularly shaped vacuole, *1* type 1 neurite, *2* type 2 neurite, *3* type 3 neurite

**Fig. 9** The different types of neurites (*insert* vesicles of type 2 neurite)

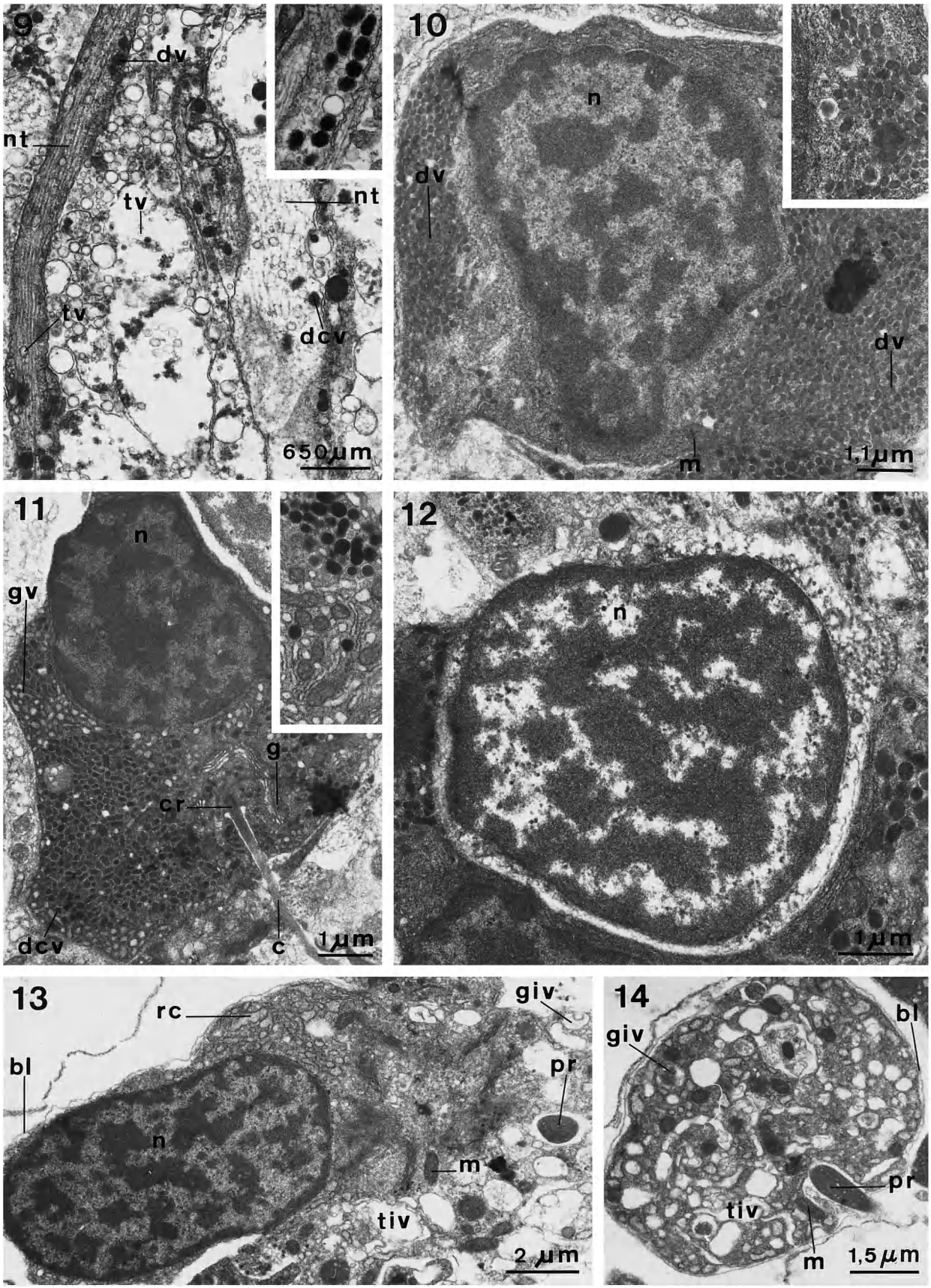
**Fig. 10** Type A cell

**Fig. 11** Type B cell (*insert* enlarged view of vesicles)

**Fig. 12** Type C cell

**Fig. 13** Type D cell

**Fig. 14** Process of type D cell in an epidermal indentation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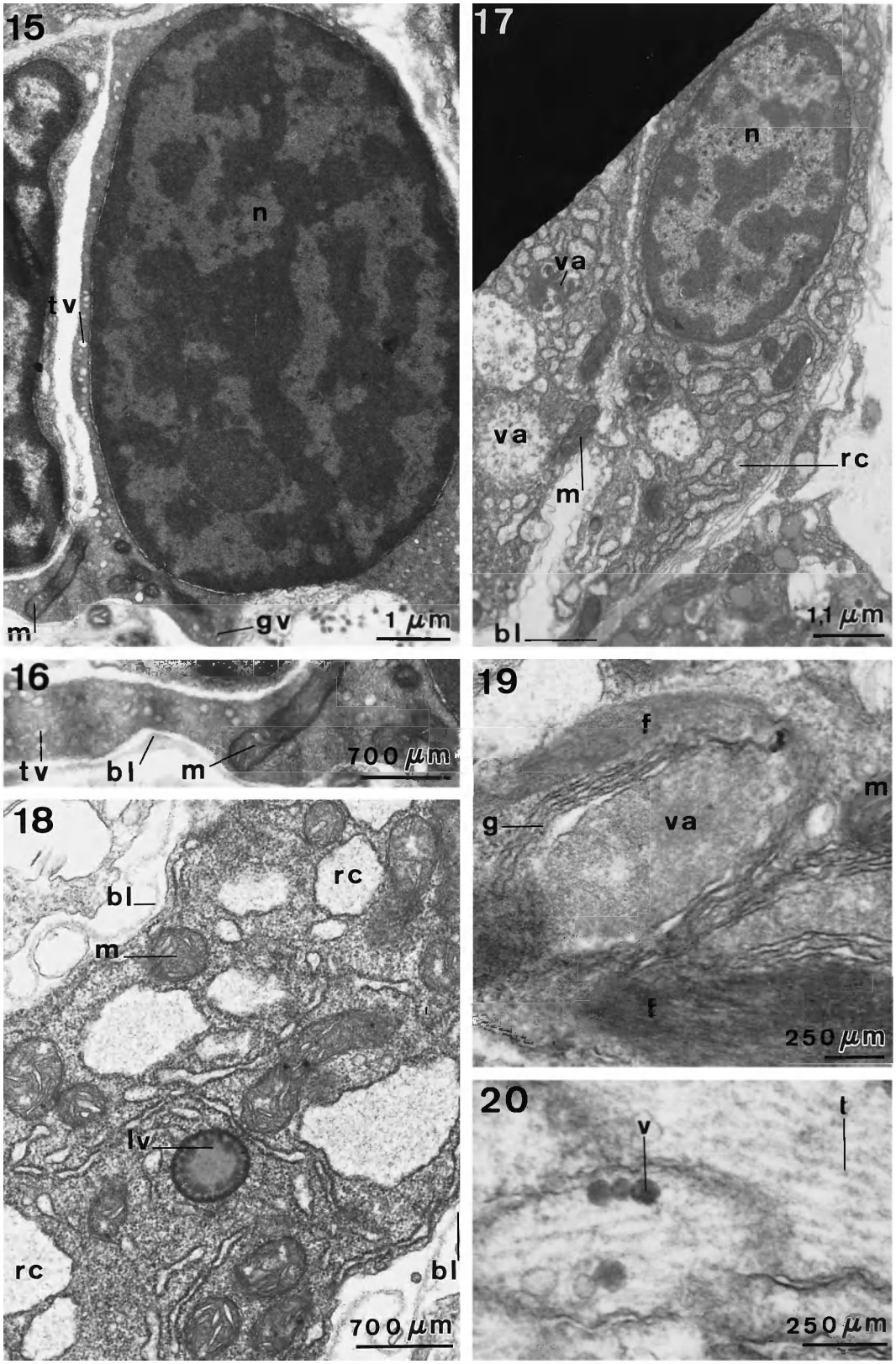


**Figs. 15, 16** Spinal ganglia of *A. squamata* (TEM). *bl* basal lamina, *f* bundle of fibrils, *g* Golgi apparatus, *gv* grey vesicles, *lv* lipid vacuole, *m* mitochondria, *n* nucleus, *rc* RER cisternae, *t* tubule, *tv* translucent vesicle, *v* vesicle, *va* vacuole

**Fig. 15** Type E cell

**Fig. 16** Cell process of type E cell

**Figs. 17–20** View of type D cell after production of luminescence (TEM)

**Fig. 17** General view

**Fig. 18** RER cisternae

**Fig. 19** Fibrils and Golgi apparatus surrounding a vacuole

**Fig. 20** Tubules and vesicles in a cytoplasmic process

before. Type A and E cells may not be associated with luminescent activity in view of the non-agreement between their distribution in the ophiuroid arm and the distribution of areas of luminescence. Type D cells seem to be the best photocyte candidate because: (1) their distribution, established by TEM, matches the distribution of the luminescence on light-producing arms (see also Brehm and Morin 1977) and (2) they are the only cell type showing noticeable ultrastructural changes once light production has occurred. The latter point is indicative of photogenic activity since ultrastructural changes were observed after light production in luminescent organisms from different taxa, changes being important for the photocytes and much more discrete for the surrounding nerve cells (Anctil 1979a,b; Swales et al. 1986).

Light production is usually under nervous control in metazoans (Herring 1990) and this was accepted for ophiuroids regarding the results of various physiological investigations on *Ophiopsila californica* and *A. squamata* (respectively Brehm 1977; Brehm and Morin 1977; Mallefet et al. 1992; De Bremaeker et al. 1994). Luminescence is almost never spontanous in ophiuroids, the light being mostly in response to external stimuli (Herring 1990). Working on luminescent *Ophiopsila* species, Basch (1988) and Grober (1988a,b) described two patterns of luminous reaction in response to mechanical stimuli which depended on the magnitude, duration and frequency of the stimulus. Weak, short and isolated stimuli only trigger light emission of photocytes close to the area of stimulation (this corresponds to the local luminous reflex defined by Reichensperger 1908). Strong, long and repeated stimuli trigger light emission that propagates throughout all the ophiuroid photogenic tissue. This indicates that sensory inputs are integrated by the receptors covering the area of epidermis stimulated before being conducted either to nearby photocytes or to the whole brachial photogenous tissue, presumably by the epineural nervous system, depending on the intensity of the stimulation.

Cobb (1988) drew a general pathway of the ophiuroid neural behaviour. According to him, when stimuli occur on brachial segments, sensory inputs derive from receptors of different modalities that cover the epithelia (sensory perception). The input information is then driven to basic morphological units of integration, ganglia (primary integration), before being spread throughout all the brachial nervous system (secondary integration) to finally reach motor tissues (command behaviour). In the present paper, it has been shown that type E cells from spinal ganglia develop long processes, some of them being located very close to epidermal ciliated cells and some others being closely pressed against type D cells (which are the putative photocytes). This suggests that the type E cell could play a basic role in starting the luminous response by transferring the information from the ciliated epidermal cells (sensory perception) to the putative photocytes (primary integration and command behaviour) and trigger the local luminous reflex. Depending on stimuli, sensory information may also pass from the spinal ganglia (primary integration) to the epineural nervous system (secondary integration) which propagates (command behaviour) stimulation towards the photocytes of successive brachial segments. Yet, this functional scheme remains hypothetical since the photocytic nature of type D cells, while being very likely, has still to be demonstrated. It would, therefore be necessary to adapt the method of Germain and Anctil (1988) to *A. squamata*, a method that would allow the isolation of fluorescent photocytes from a suspension of dissociated cells using density gradients, and the comparison of their ultrastructure with that of the presumed photocyte of the spinal ganglia.

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