

STUDIES ON *CHAETOPTERUS VARIOPEDATUS* (RENIER). I. THE LIGHT-PRODUCING GLANDS

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(Plates I, II and Text-figs. 1-4)

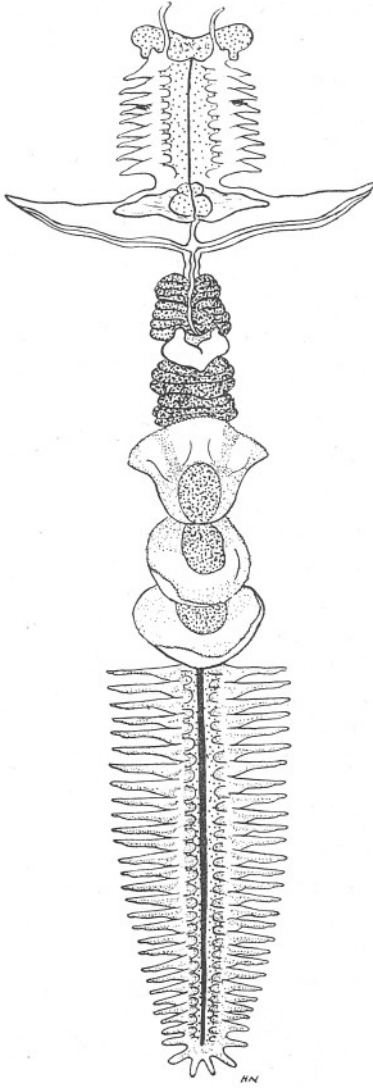
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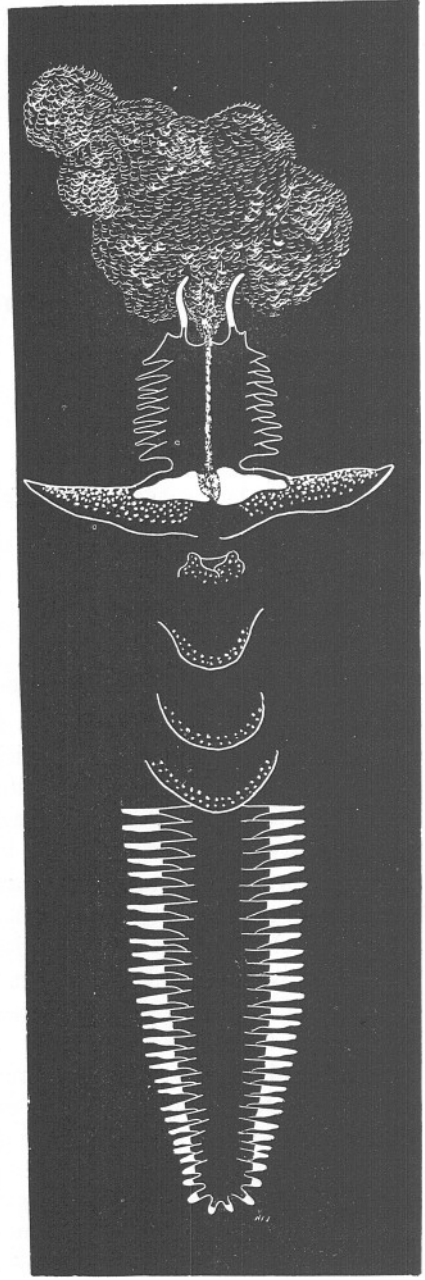
INTRODUCTION

Chaetopterus variopedatus (Renier) is a tube-dwelling worm that has noteworthy luminescent powers. Production of light is by an extracellular process resulting from the discharge of a luminescent slime into the sea water. Because of its luminescent ability, the epidermal glands of *Chaetopterus* have been repeatedly described in detail, but it is still not clear what elements produce the luminescent secretion. I have, therefore, re-examined the histology of the light-producing regions of *Chaetopterus* with a view to determining the character of the photocytes or light-producing glandular cells.

For the convenience of the reader who may be unacquainted with the morphology of *Chaetopterus*, a picture of the animal is given in Text-fig. 1. *Chaetopterus* consists of three greatly dissimilar regions. The anterior region is flattened, and includes eleven segments (nine setigers). There is a pair of peristomial tentacles on the head. The middle region begins with segment XII, which is provided with a large pair of wing-like (aliform) notopodia. There is a lateral ciliated groove on the dorsal surface of each of these notopodia; the two lateral grooves converge medially, and open into a medial dorsal ciliated groove, which extends anteriorly towards the mouth. In the succeeding segments of the middle region there is a conspicuous cup organ (dorsal tubercle) in segment XIII, and a large fan or palette in each of segments XIV-XVI. The posterior region is less differentiated, and contains a large and variable number of segments, each provided with a pair of lateral notopodia.



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Text-fig. 1. Dorsal view of a specimen of *Chaetopterus variopedatus*. About life-size.

Text-fig. 2. Dorsal view of a luminescing specimen of *Chaetopterus*, as seen in the dark. About life-size.

HISTOLOGICAL METHODS

For the examination of glandular cells, material was fixed, double-embedded in Peterfi's celloidin-paraffin, sectioned at 10μ , and stained in various ways. Of several fixatives that were tried, Bouin's solution afforded good fixation and enhanced staining. After a trial of various stains it was concluded that a haematoxylin and eosin coloration afforded the greatest distinction between different gland cells and other epidermal elements, and most sections were stained by this means.

REVIEW OF PREVIOUS WORK

It has been pointed out by several observers that the luminescent regions of *Chaetopterus* are recognizable in the living animal because of their chalky white appearance against the yellowish ground colour of the body. These whitish areas are considered to contain the glandular luminescent cells. These were mentioned by Joyeux-Laffuie (1890), who stated that unicellular gland cells with refringent contents were scattered over the luminescent regions. According to the descriptions of later histologists, the epidermal glandular cells are divisible into categories of granular or homogeneous eosinophile cells, fibrous eosinophile cells, and basophile cells.

Granular and homogeneous eosinophile cells. These are ovoid or flask-shaped cells containing a basal flattened nucleus, and opening directly to the exterior through a secretory pore. The cytoplasm contains numerous closely packed eosinophilic granules, which are sometimes fused to form a homogeneous mass. These cells occur all about the circumference of the peristomial tentacles, but particularly on the dorsal side; in an oval glandular area on either side of the dorsal ciliated groove in segment XII; on the dorsal surface of the aliform notopodia; in a lateral intermediate zone about the dorsal tubercle; in the walls of the fans; and along the notopodia of the posterior region (Krekel, 1920; Trojan, 1913). It is these cells, apparently, that Dahlgren (1916) regarded as luminescent cells or photocytes. He described them as saccular elements, hanging down from the cuticle, and capable of secreting granules of luminescent material. The discharged cells appear empty and shrunken (Harvey, 1920).

Fibrous eosinophile cells. These cells, according to Krekel (1920) and Trojan (1913, 1914), are found in the apical half of notopodia of the posterior region. They are cylindrical or fusiform in shape, with a basal nucleus. The cytoplasm is intensely acidophilic, and contains a peculiar fibrous skein or knot in the shape of a figure-of-eight. These cells had been noticed earlier by Claparède (1870), who designated them 'follicules bacillipares'. A developmental cycle has been traced in the history of these cells in which early stages are represented by ovoid elements possessing a granular cytoplasm. As the cells mature they elongate and extend to the base of the epidermis, and the contained cellular granules aggregate to form a spiral fibrous knot.

Trojan (1914) believes that these fibrous cells secrete the material used in tube-building.

Basophile cells. These cells occur in the following regions: (i) in the tentacles, where they are concentrated as a dorsal band; (ii) in the dorsal triangular glandular areas at the bases of the aliform notopodia; (iii) in the walls of the dorsal tubercle and fans of the middle region; (iv) in a distal band on the anterior side of posterior notopodia; and (v) in special glands at the base of these structures. The cells are pyriform to high cylindrical, and extend through the whole thickness of the epidermis. They become thinner distally, and open to the exterior through a secretory pore. The cellular contents consist of large basophilic granules staining intensely with haematoxylin, thionine and methylene blue; they are also coloured by mucicarmine (Krekel, 1920; Trojan, 1913). It is these cells which have generally been regarded as the photocytes producing the luminescent secretion, although Dahlgren (1916) apparently thought they were merely mucous cells.

Bonhomme (1943) has recently re-examined the histology of *Chaetopterus* gland cells in the aliform notopodia and dorsal tubercle. He found that the luminous organ consists of a high-folded epithelium containing tall prismatic cells. These have a lateral flattened nucleus, and open distally by a secretory pore. The cellular contents consist of a thin basophilic lacework, which Bonhomme regards as the residual framework remaining after secretion induced by the action of fixatives. On the margins of these glandular areas he located premucigenous cells which are large and irregularly prismatic in shape, and are filled with gross basophilic granules.

In another form, *Mesochaetopterus japonicus*, basophilic cells have also been identified with light production. These cells occur on the tentacles, on the dorsal surface of the middle region, and on the posterior notopodia. They are club-shaped, tapering towards a distal opening, and are filled with basophilic secretory granules. Discharged cells appear filled with a spongy coagulum (Fujiwara, 1935).

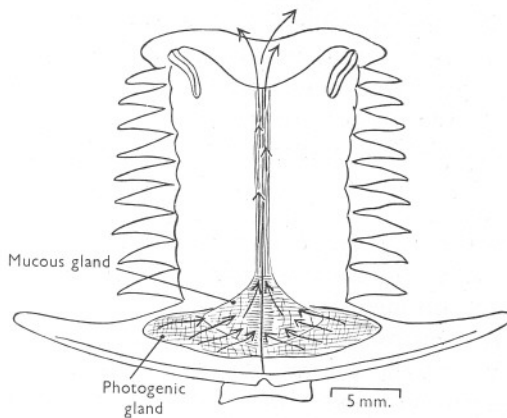
In the following account I present some new observations on the luminescent areas of *Chaetopterus*. My observations link the secretion of photogenic material with eosinophile cells. The other cell types are mucous cells, and basophilic cells which may be concerned with tube-building.

OBSERVATIONS

The luminescent regions have been determined by stimulating the animal to produce light in the dark. Stimuli used have been high-frequency condenser discharges, above six per second, and an isotonic solution of KCl. Both these agencies cause widespread luminescence in the worm. The following regions produce light: the peristomial tentacles; a pair of triangular areas lying on the dorsal surfaces of the aliform notopodia (segment XII), one on either side of the dorsal ciliated groove; the aliform notopodia themselves; the walls of the

dorsal tubercle; the fans in segments XIV–XVI; and all notopodia of the posterior region (Text-fig. 2).

The large glandular areas on the aliform notopodia are the regions most easily brought into luminescence by tactile stimulation. When this region is touched a luminescent secretion is discharged into the sea water; this is carried medially towards the mid-dorsal line by ciliary currents, and is then transported anteriorly towards the mouth through the activity of the dorsal ciliated groove (Text-fig. 3). Arriving in the buccal region, the luminescent secretion streams away from the animal, and illuminates the surrounding sea water. Luminescence from the secretion of this region persists for a considerable time, up to 15 min. or more. Under the binocular microscope the luminous secretion is revealed as a multitude of brightly lighted, discrete particles.



Text-fig. 3. Dorsal view of the anterior region and segment XII of *Chaetopterus*. The arrows indicate the course of luminous particles secreted by the luminescent glands at the bases of the aliform notopodia.

The other regions of the body give off a brief transitory flash, quickly dying away in a minute or two, and they do not discharge a luminescent secretion which is carried away into the surrounding medium. When segments of the posterior region are stimulated to lighten, the notopodia become coated or caked with a thick secretion which adheres for some time to the appendages. This secretion is probably the oxidized photogenic material, which luminesces and becomes exhausted very rapidly after it is released.

Bonhomme (1943) considers that the tentacles do not themselves give off light, but acquire luminescence secondarily when luminous secretion is carried forwards in the dorsal ciliated groove to a ciliated groove lying along each tentacle. This is incorrect, and the peristomial tentacles do lighten, as can be shown by the following experiment. The anterior region of an animal was transected at the level of the third or fourth segment, without inducing luminescence. The anterior fragment was then placed in isotonic KCl, upon

which both tentacles luminesced. There was no question of luminescent secretion being carried to the tentacles from other regions in this fragment, and light originated in the tentacles themselves.

Trojan (1913) and Krekel (1920) regard a whitish glandular area at the base of each posterior notopodium as a luminescent structure, and Panceri (1878) figures this region as luminous. Krekel, unfortunately, did not have living animals for observation. There is a conspicuous whitish fleck at the base of each posterior notopodium, and I find that this region is not luminescent. Distally, beyond this whitish glandular area, the notopodium is brightly luminous.

Epidermal Gland Cells

The story of epidermal secretions in *Chaetopterus* has obviously become rather complicated. In presenting an evaluation of these observations it is necessary to consider the probable functions of epidermal secretions in this species. So far as is known they involve production of mucus, tube-formation, and luminescence. One would, therefore, expect to find at least three kinds of epidermal gland cells corresponding to these functions, and such cells may or may not be visually distinguishable from one another.

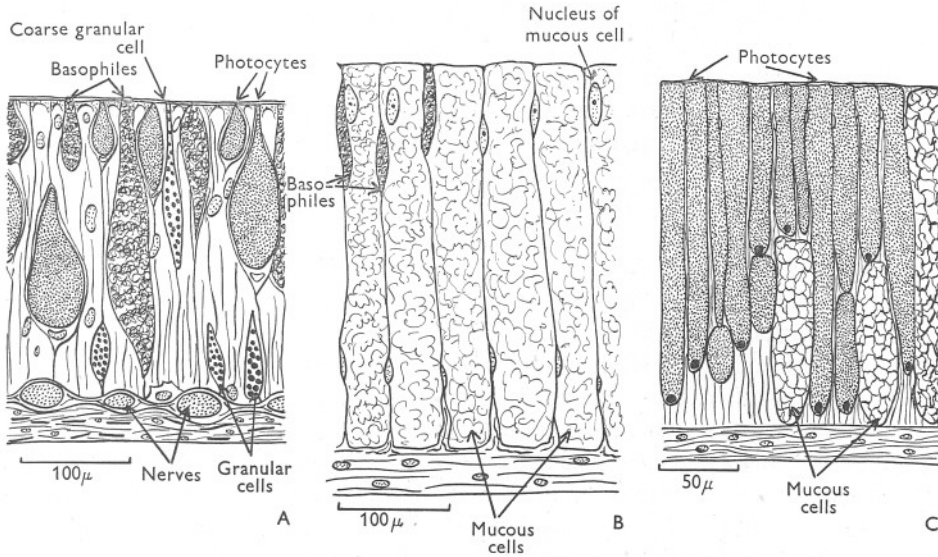
Mucous Cells

As is well known, *Chaetopterus* is a mucous filter-feeder and produces enormous quantities of mucus for trapping and entangling food particles as it pumps water through its tube (MacGinitie, 1939; MacGinitie & MacGinitie, 1949). This mucous material is poured forth from the walls of the dorsal tubercle and the aliform notopodia, and it is carried forward in the dorsal ciliated groove towards the mouth. There is little doubt that it is secreted by the abundant basophilic cells which form conspicuous whitish areas on those organs. Those cells are, accordingly, mucous cells.

The mucous glands occurring as conspicuous masses at the bases of the aliform and posterior notopodia and in the dorsal tubercle are made up of closely packed very large cells (Text-fig. 4; Pl. I, figs. 2-4 and 6). There is also a small number of mucous cells about the longitudinal ciliated groove on each peristomial tentacle. These are greatly elongated prisms about $20 \times 200 \mu$ in the aliform notopodia, up to 350μ long on the dorsal tubercle, and reaching the enormous length of 650μ on the posterior notopodia. Nuclei are present at two levels in the mucous epithelium, and there is reasonable doubt as to which nuclei actually belong to the mucous cells. Towards the base of the epithelium there are small flattened nuclei squeezed between the mucous cells. These apparently belong to connective tissue cells located in a thin strand of connective tissue which extends a short distance between the bases of the mucous cells from the underlying fibrous layer. Distally toward the free surface, there are greatly elongated and faintly staining nuclei lying against the walls of the cells. These correspond to the

nuclei figured by Bonhomme, and seem to be the nuclei of the mucous cells. Cell boundaries are faint but definite. The entire cell is filled with an indistinct alveolar material, the walls of the alveoli seemingly consisting of interlacing fine fibrils. The contents stain faintly with alum haematoxylin and are basophilic. They do not stain with mucicarmine and iron haematoxylin.

The following observations should demonstrate that the mucous cells are not responsible for the luminescent secretion. The secretion of mucus from segments XII and XIII (aliform notopodia and dorsal tubercle) is a continuous



Text-fig. 4. A, section across the epidermis of the aliform notopodium. B, section through the mucous epithelium beside the dorsal ciliated groove. C, section through the light gland on the aliform notopodium.

process, whereas release of luminous material is a discontinuous process, under nervous control. It is difficult to conceive of a cellular organization by which an exocrine glandular cell produces and releases two different substances, one continuously, the other at rare intervals.

The main argument for identifying the basophilic mucous cells with light production has been the exact spatial correspondence between areas containing these cells, and luminescence. As shown above, the three regions containing large accumulations of mucous cells are the dorsal triangular regions on the aliform notopodia, the walls of the dorsal tubercle, and the bases of the posterior notopodia. Only the first of these three areas produces conspicuous light; the tubercle gives off a very weak and transitory flash; and the basal areas of the posterior notopodia do not luminesce. Consequently, there is no correspondence between aggregations of mucous cells and luminescence.

In order to obtain some comparative data on the relative amounts of mucus produced by various regions of the body, fragments of animals were placed in sea water and, after an interval to allow for secretion, the viscosity of the water was estimated in arbitrary units. Pieces of the animal selected were the anterior region (including segment XII); segment XIII and the dorsal tubercle; segments XIV–XVI and fans; and the posterior region. These were placed in separate dishes, an equal amount of water was added to each container and a sample of water drawn after 30 min. Relative viscosity figures were obtained by measuring the time taken for a drop to run through a length of thistle tubing. Mean relative times were: 5.3 sec. for the anterior region; 1.0 sec. for the dorsal tubercle; 0.5 sec. for the fans; and 0.2 sec. for the posterior region. The last figure was equivalent to a determination for sea water. These figures show that most mucus is secreted by the aliform notopodia, a considerable quantity by the dorsal tubercle, and none by the posterior notopodia. In contrast, it may be mentioned again that although a great deal of light is produced by the aliform notopodia, very little originates in the dorsal tubercle; the posterior notopodia, however, are brightly luminescent.

The copious mucus secreted by the aliform notopodia and the dorsal tubercle forms a vehicle for suspending and carrying away the luminous material secreted by the aliform notopodia. The luminescent material released by the dorsal tubercle is negligible. The fact that the posterior notopodia do not produce mucus when the animal is stimulated to luminesce offers an explanation why the photogenic material continues to lie on the surface of the notopodia, and is not dispersed in the surrounding medium. The function of the basal glandular areas on the posterior notopodia remains obscure. These glands are regarded as the modified terminal regions of nephridial organs (Trojan, 1913). Since they are not luminescent they cannot be concerned with luminescence of eggs and larvae, a suggestion that has occasionally been adumbrated. There is a possibility, however, that they secrete only during spawning.

Eosinophilic Light Cells (Photocytes)

These occur in the peristomial tentacles, basal dorsal surface of the aliform notopodia, distally on the aliform notopodia, dorsal tubercle, fans, and on the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 1–6, 7–8, 10–11).

On the tentacles the eosinophilic cells are scattered over the surface, and are more concentrated on one side opposite the longitudinal ciliated groove. The aliform notopodia contain occasional scattered eosinophile cells distributed over both dorsal and ventral surfaces away from the lateral ciliated groove. Towards the base of the aliform notopodium, on the dorsal surface, there is a dense and extensive aggregation of eosinophilic cells. These lie lateral to a more median area which consists of basophilic mucous cells, and

which borders the dorsal ciliated groove. The two kinds of cells are not mutually exclusive for there are a few eosinophilic cells dispersed through the mucous gland, and a few mucous cells scattered through the eosinophile glandular area.

In the dorsal tubercle of the middle region there is a narrow zone containing a few eosinophile cells. This lies at the transition between the dense mucous glandular layer covering the outside of the tubercle, and the ciliated epithelium leading inside the cup. Eosinophile cells are scattered over the dorsal surface of the fans. In the posterior region, the distal surface of each notopodium contains a great number of closely spaced eosinophile cells.

The eosinophile light cells have a similar appearance in all regions of the body in which they occur. On the tentacles, aliform notopodia, dorsal tubercle, fans, and posterior notopodia, they are round or oval to elongate elliptical in shape, depending on the height of the epithelium. Dimensions in these regions lie in the range $12-25 \times 30-50 \mu$. There is a small triangular nucleus at the base of the cell. The dense aggregations of eosinophilic cells lying at the bases of the aliform notopodia are tall cylindrical in shape, and have dimensions of $6 \times 150 \mu$. The nucleus, again basal, is relatively minute compared with the size of the cell. These cells, at the bases of the aliform notopodia, reach the basement membrane. In other regions, however, the oval or elongate cell has the appearance of hanging down from the cuticle, and a long thin tag extends from the base of the cell to the basement membrane. The contents of all these cells are closely similar. The cells are filled with a deeply staining dense mass of eosinophilic material in which there are all gradations from a coarse or fine granular to a homogeneous consistency.

Dahlgren (1916), who has briefly dealt with the photocytes of *Chaetopterus*, describes them as granular cells. His figure seems to be a composite one, based on the structure of the eosinophile light cells described above, and the coarse eosinophile cells described in the next section.

The evidence for regarding these eosinophilic cells as the light-producing cells consists of the following observations. The eosinophilic cells have the same spatial distribution as the photogenic regions. The tentacles glow quite brightly, relative to their area, and contain many eosinophilic cells. Light production is very faint and transitory in the dorsal tubercle and fans, and relatively few eosinophilic cells are present on those structures. The distal regions of all the posterior notopodia luminesce very brightly, and these appendages are abundantly provided with eosinophilic cells. Regions that do not luminesce bear no eosinophile light cells having the characteristics described above.

Three animals were stimulated into luminescence by placing them in isotonic KCl for several minutes. The brightly luminous areas on the basal dorsal surface of the aliform notopodia were dissected out under a binocular microscope. These pieces of tissue were fixed, and were examined

histologically. Two of them contained extensive patches of both basophilic mucous cells, and eosinophilic cells. The third consisted almost entirely of a dense aggregation of eosinophile cells (Pl. I, fig. 3).

An attempt was made to discriminate the photogenic cells by strongly stimulating the animal into luminescence, and then looking for secreting and exhausted cells. The results were ambiguous. Even after prolonged stimulation electrically or by treatment with KCl, it was still possible to elicit further luminescence by mechanical agitation of the glandular regions in segment XII. Histological examinations showed a certain amount of both mucous and eosinophilic material outside the cells, some exhausted eosinophilic cells, and numerous eosinophile cells still replete with secretory material. It appears to be difficult to exhaust all the luminescent cells by prolonged excitation.

It has been a common observation that dropping an animal into a fixative evokes luminescence. A bright flash is produced when an animal is dropped into fixatives like Bouin's, Zenker's, and Helly's fluids. If the animal is previously anaesthetized by immersion in isotonic $MgCl_2$ for 5-15 min., and is then placed in the fixative solution, it does not luminesce. These effects were utilized in searching for the luminescent gland cells. Animals, with and without previous treatment with $MgCl_2$, were dropped into fixative, and histological sections were prepared (Pl. II, figs. 7 and 8). Sections of animals that had been treated with $MgCl_2$ showed no secretion of eosinophile material. Sections of animals that had been dropped directly into fixative solutions showed many eosinophilic cells caught in the act of discharging a secretory mass from a distal cellular orifice, and a dense layer of eosinophilic secretion lying over the surface of the epidermis. Comparative examinations were restricted to the aliform notopodia, as being regions easiest to study.

Finally, dried smears were made of secretions from non-luminous and luminous animals. To do this some of the mucous slime from the dorsal surface of the anterior region was sucked up in a pipette and smeared on a slide. After drying, the smears were fixed in Bouin's fluid, and stained with haematoxylin and eosin. Smears from non-luminous animals showed only a small amount of dispersed basophilic mucous material. Smears from luminous animals showed, in addition, many particles of eosinophilic material scattered in the mucus, or aggregated into lumps. These particles were often in packets closely resembling the contents of eosinophilic cells (Pl. II, fig. 9).

Other Gland Cells

Two additional types of epidermal gland cells must be mentioned. These are densely staining basophilic cells, and coarsely granular eosinophilic cells.

The dense basophilic cells were found scattered singly in the tentacles, on the aliform notopodia, in the walls of the fans, in the dorsal tubercle at the

transition between mucous cells and the internal ciliated layer, and about the circumference of the posterior notopodia (Text-fig. 4; Pls. I and II, figs. 4, 7-8 and 10). They are scattered infrequently between the mucous cells at the bases of the aliform notopodia and on the dorsal tubercle. To a greater or lesser degree they are dispersed over the ventral surface of segment XII, and in the epidermis of the anterior region.

These cells tend to be thin, elongated, and fusiform where the epithelium is high, and irregularly pyriform where the epithelium is low. Dimensions are $3-12\mu$ wide $\times 30-120\mu$ high. The nucleus is small and oval in shape, and lies at the base of the cell. The cell contents are basophilic and stain heavily with alum haematoxylin. They also selectively stain with mucicarmine. After Bouin fixation they have the appearance of a deeply staining alveolar meshwork of fine fibrils, with darkly stained points in the interstices of the meshes. The cells were sometimes seen in the act of secreting, when a slender tongue of secretory material projected through a narrow distal orifice. These darkly staining basophilic cells apparently have a widespread and general distribution over the epidermis. There is no evidence to show that they are in any way concerned with light production.

The coarse granular eosinophilic cells were noted about the circumference of the aliform notopodia, in the posterior notopodia, in the dorsal walls of the fans, and mixed with photocytes in the wall of the dorsal tubercle (Text-fig. 4; Pls. I and II, figs. 4-8, 10 and 11). They are also dispersed over the ventral surface of segment XII and in the epidermis of the anterior region. In shape they are frequently pyriform: the proximal portion is swollen and lies in the basal epidermal region, and a long neck extends up to the free surface. When not compressed by neighbouring glandular cells they are often elongate and cylindrical. Dimensions reach $15 \times 180\mu$. There is a small, elliptical basal nucleus. The cell contains a number of scattered and discrete coarse granules up to 3μ in size which are weakly eosinophilic. There is no evidence that these cells are related to the photocytes or that they are concerned in light production.

Epidermal Gland Cells and Tube-formation

It has not been possible to confirm the existence of fibrous eosinophilic cells, concerned with tube-formation, in the posterior notopodia (Dahlgren, 1916; Trojan, 1914). It is suggested that the fibrous knots and skeins seen in the eosinophilic cells of the posterior notopodia by earlier observers were fixation artifacts resulting from localized condensations and swirls in the secretory contents of the eosinophilic photocytes. In addition, as previously mentioned, coarse eosinophile cells are also scattered over these appendages.

The functions of the dense basophilic and coarse eosinophilic cells lie outside the scope of this investigation since they are not involved in light

production. It is suggested, however, that it would be of interest to investigate whether they are involved in tube-building. For comparison with the various gland cells, the staining reactions of the tube were investigated by peeling off thin strips and fixing in Bouin's fluid, so as to subject them to the same initial treatment as gland cells of the body wall. They were then stained with eosin, haematoxylin or mucicarmine. The preparations so obtained were found to have little affinity for eosin, but to stain deeply with haematoxylin; they were also coloured by mucicarmine. This provides suggestive evidence that the original secretion involved in tube-formation is basophilic, and implicates the dense basophilic cells, although it is not maintained that a correlation in staining affinities of this kind itself affords any conclusive proof. Presumably the material forming the tube is secreted in a fluid, or soft condition, and is moulded and hardened after release. Enders (1907) has studied the tube-building activities of *Chaetopterus*, and he describes how a worm enlarges its tube by splitting it longitudinally, and then produces a new strip of hardened 'mucus' to fill the gap. During this process the ventral lip is used to fashion and shape the new wall of the tube. The possibility should be considered that the coarse eosinophilic cells may also play some role in tube-formation, by hardening the material secreted for the formation of the tube, such as takes place during the secretion of the byssus in *Mytilus* (Brown, 1949).

CONCLUSIONS

It has been shown in this investigation that four recognizably different kinds of gland cells can be seen in the epidermis of *Chaetopterus variopedatus*. These cells are all epicrine in nature in that they discharge their secretion to the external surface. They occur scattered individually over the surface, but are often aggregated into multicellular glands. These consist of groups of a few similar cells, or dense aggregations of cells which form massive glandular surfaces, as in the basal regions of the aliform notopodia. In the latter regions, also, the glandular surfaces are increased by folding of the epithelium.

The four kinds of glandular cells are readily distinguishable by their morphological appearance and staining characteristics. The photocytes, containing a densely staining eosinophilic mass, are confined to the luminescent regions. Mucous cells, containing a loose alveolar mucigen material, are aggregated into multicellular glands at the bases of the aliform notopodia, in the walls of the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell types, coarse granular eosinophilic and densely staining basophilic cells, are scattered singly through the epidermis and have a widespread distribution. Both these latter kinds of cells may be concerned with fabrication of the tube.

Only one kind of cell is implicated in light production in *Chaetopterus*,

and this is of interest when compared with *Cypridina*. In the latter two separate cellular types are involved, one of which contains large yellow granules of luciferin, the other small colourless granules of luciferase. On release the granules dissolve in the water and interact to produce light. Corresponding to the absence of two recognizably different kinds of photogenic particles in *Chaetopterus* is the reported failure to isolate extracts of luciferin and luciferase from this worm (Harvey, 1926, 1940).

In a treatment of luminescence it is usual to make some reference to its function in the economy of the organism. The function of luminescence in *Chaetopterus* is still unknown. Dahlgren (1916) has reproduced a painting by Horsfall in which an eel is depicted as attacking a brightly luminescent worm in its tube. The inference seems to be that the light has biological value in repelling the predator. Harvey (1920), however, has noted that light production by *Chaetopterus* would be of no avail, since an extracted worm cannot build a new tube. In presenting his theory that luminescence may sometimes have survival value to a species in attracting a predator of a predator, Burkenhead (1943) has utilized *Chaetopterus* as a theoretical example, in which luminescence excited as the result of an attack by an eel would attract, secondarily, an attack upon the eel by a dogfish. It may be significant that the anterior region of *Chaetopterus* is easily autotomized under stress and is readily regenerated, and it is this region of the worm which pours forth such an abundant luminous secretion. This suggests the idea of a sacrifice lure. Speculations of this kind obviously need to be checked by experiment and by observation of the living animal.

SUMMARY

The luminescent regions of *Chaetopterus variopedatus* are shown to be: the peristomial tentacles, the aliform notopodia, the dorsal tubercle, fans, and notopodia of the posterior region. The brightest areas are glandular masses on the dorsal basal surfaces of the aliform notopodia and the distal surfaces of the posterior notopodia.

The photogenic glands on the aliform notopodia give off a luminescent secretion that is suspended in mucus and is dispersed into the surrounding sea water. Light from other regions is much more transitory, and the luminescent secretion is not dispersed.

Four kinds of gland cells occur in the epidermis. The photocytes have been identified as eosinophile cells containing a dense secretory mass. These cells are confined to the luminescent regions, and they are most abundant on the two most brightly luminescent areas, namely, distally on the posterior notopodia, and at the base of aliform notopodia. Mucous cells are slightly basophilic cells occurring beside the dorsal ciliated groove in segment XII, on the dorsal tubercle, and at the bases of the posterior notopodia. Two other cell

types are coarse granular eosinophile cells, and darkly staining basophile cells. The latter two kinds of cells may be involved in tube-building.

Earlier work dealing with the epidermal glands of *Chaetopterus* is reviewed, and some comparisons are made with other forms.

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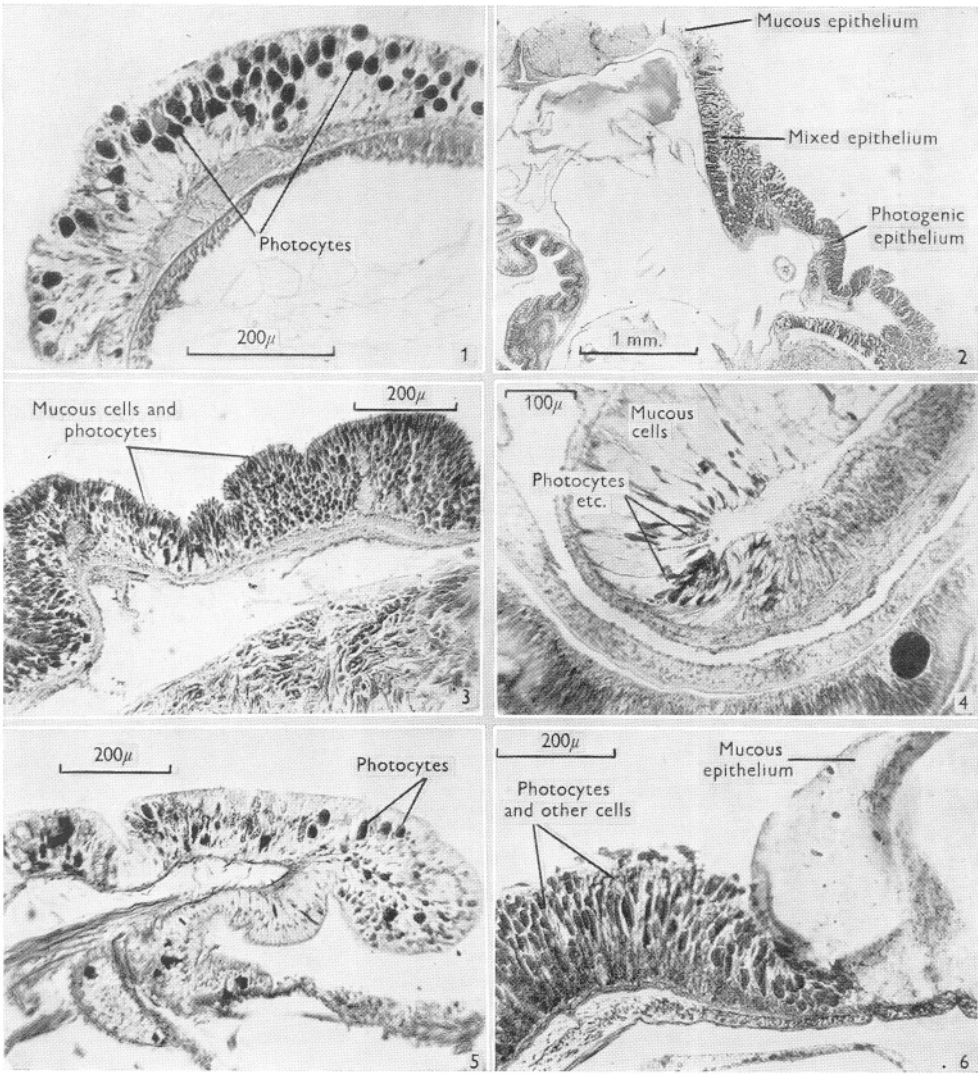
EXPLANATION OF PLATES

PLATE I

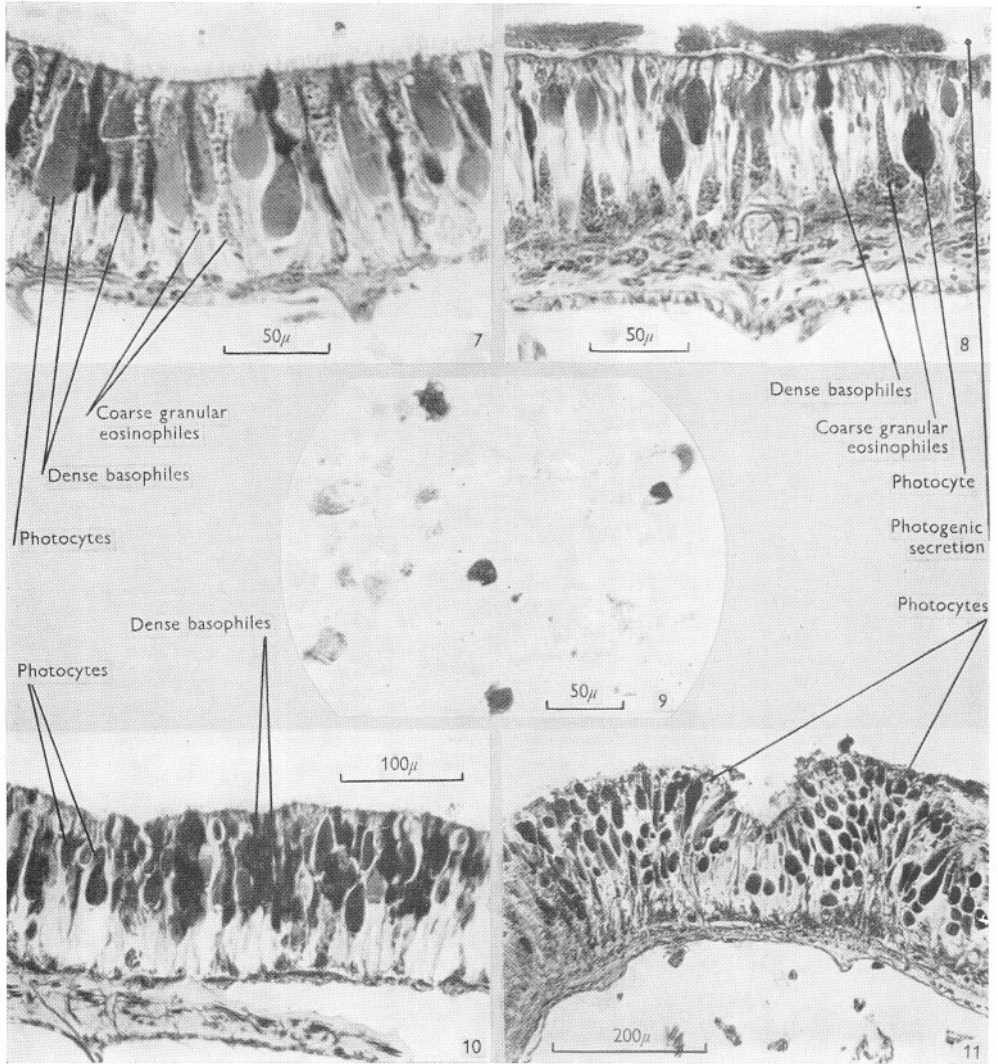
All histological sections shown in these photographs were stained with alum haematoxylin and eosin.

Fig. 1. Part of the wall of the peristomial tentacle in transverse section. Mucous cells and photocytes are interspersed in the epithelium.

Fig. 2. Transverse section through the dorsal body wall in segment XII. Lateral to the dorsal ciliated groove is a thick layer of mucous cells, which is replaced more laterally by a dense aggregation of photocytes.



Figs. 1-6.



Figs. 7-11.

- Fig. 3. Dissected and isolated luminescent glandular epithelium from segment XII. The epidermis consists mostly of photocytes, with a few mucous cells.
- Fig. 4. Transverse section of the dorsal tubercle at the junction of the mucous layer, and the ciliated surface. Mixed together at the junctional zones are photocytes, coarse granular eosinophile cells, and dense basophile cells.
- Fig. 5. Transverse section of a fan. The epidermis contains a few photocytes, coarse granular eosinophile cells, and dense basophile cells.
- Fig. 6. Longitudinal section of a posterior notopodium. Junction between the basal mucous gland (right) and the brightly luminescent epithelium (left). The light-producing epithelium to the left contains predominantly photocytes mixed with some coarse eosinophiles and a few basophiles.

PLATE II

- Fig. 7. Section of the aliform notopodium from a specimen anaesthetized with $MgCl_2$ before fixation. Surface secretion is lacking. Photocytes, coarse eosinophiles, and dense basophiles are interspersed together.
- Fig. 8. Section of the aliform notopodium from a specimen fixed without preliminary anaesthetization. A layer of eosinophilic secretion lies over the surface of the epidermis. Photocytes, coarse eosinophiles, and a few dense basophiles lie interspersed together in the epithelium. A nerve is shown in section at the base of the epithelium.
- Fig. 9. Dry smear of luminescent secretion produced by segment XII. Eosinophile secretory particles are shown.
- Fig. 10. Section across the aliform notopodium to show dense aggregation of photocytes and dense basophilic cells.
- Fig. 11. Section across the distal region of a posterior notopodium. The epidermis contains a dense aggregation of photocytes, together with a few coarse eosinophiles and dense basophiles.