Origin and Development of the Photogenic Organs of Lampyrids, with Special Reference to Those of Luciola cruciata MOTSCHULSKY and Pyrocœlia rufa Ern. OLIVIER

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Origin and Development of the Photogenic Organs of Lampyrids, with Special Reference to Those of *Luciola cruciata* MOTSCHULSKY and *Pyrocœlia rufa* Ern. OLIVIER

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With Plates X & XI and 9 Text-figures.

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Introduction

The photogenic organs of these fire-flies as in their allied forms exist in the shape of thin plates covering the ventral surface of one or two segments of the abdomen near the posterior extremity, viz. the 6th and 7th in the male and the 6th only in the female of *Luciola*. The photogenic organs of the male *Pyrocœlia*, in fact, consist of two plates, but are much reduced to the median-posterior patches. The luminous plates of the female *Pyrocœlia* much resemble those of the male, but the posterior plate is separated into two parts. Anatomically they are, however, uniformly composed of two layers of distinct cells: a proximal (inner) non-photogenic, and a distal (outer) photogenic one in either species and in either sex.

The inner layer which is supposed to function as a reflector, is in life opaque and chalky white containing crystalline granules in a large quantity. The outer layer is in living condition more or less transparent and yellowish, and stains deeply with some dyes in the fixed material owing to the presence of a large quantity of small so-called photogenic granules. This layer contains the actual mechanism of light production. There is neither a membrane which divides the two layers as A. TARGIONI-TOZZETTI (1886) describes in *Luciola italica*, nor an investment which covers the proximal surface

of the organ as H. R. WIELOWIEJSKI (1882) claims to exist in *Lampyris splendidula.* Distal to the photogenic layer comes directly a thin hypodermis and proximal to the non-photogenic layer and in close contact is a mass of fat-bodies.

C. GEGENBAUR (1874) and H. R. WIELOWIEJSKI (1890) advance the theory that two strata of the photogenic organs of lampyrids differ in their origin: the non-photogenic inner layer is related to the fat-cells; whereas the photogenic outer layer to the hypodermic cells (GEGENBAUR) or a derivative from the "small œnocytes," which according to WIELOWIEJSKI, are wanting in the luminous Coleoptera. Such a dual origin of the photogenic organs has found no support and by far the greater number of authors claim either the hypodermic or the fat-cell origin for the organs. The first view is upheld by P. OWSJANNIKOW (1868), C. HEINEMANN (1886), R. DUBOIS (1898, 1913), P. MARCHAL (1911), U. DAHLGREN (1917) and W. N. HESS (1918); and the second view by G. R. TREVIRANUS (1818), W. PETERS (1841), F. LEYDIG (1857), M. SCHULTZE (1865), W. H. SEAMAN (1891), W. M. WHEELER (1892), J. BONGARDT (1903), U. DAHLGREN and W. A. KEPNER (1908), A. BERLESE (1909), R. VOGEL (1913), F. X. WILLIAMS (1916) and W. N. HESS (1922).

While thus a great number of authors have argued on the origin of the photogenic organs of the fire-flies and glow-worms as well as the luminous elaterid, *Pyrophorus noctilucus,* actual embryonic investigation of these organs is rather scanty.

DUBOIS (1898) studied the development of the egg of *Lampyris noctiluca* from the beginning of the segmentation up to the emergence of a larva, and found a close resemblance between the blastoderm cells and the photogenic ones of the larva, pupa and adult. He concluded, therefore, that the photogenic organs of the adult insect were formed in essentially similar manner to those of the larva, the photogenic cells being developed from the outerlying hypodermis. This account was soon hidden behind the shadow of the theory of the fat-cell, viz. mesodermic origin of the organs, and several important works that have more recently appeared apparently settled the problem. But DUBOIS' theory reappeared from time to time and DUBOIS himself (1913), DAHLGREN (1917) and HESS (1918) referred the origin of the photogenic organs to the hypodermic cells.

The mesodermic origin of the organs seems more important. Three important papers supporting it have been published, the first by VOGEL (1913) on *Lampyris noctiluca,* the second by WILLIAMS

(1916) on *Photuris pennsylvanica* and *Photinus consanguineus*, and the third by HESS (1922) on *Photuris pennsylvanica*. These authors agree in stating that the fat-bodies disintegrate at the time of pupation into separate cells, which are arranged on the ventral surface of the abdominal light-bearing segments. The cells grow young again and multiply in number. The karyokinetic figures are said to be found abundantly. Further development of the organs is best studied and quite satisfactorily traced by WILLIAMS in *Photinus consanguineus* and HESS in *Photuris pennsylvanica*, although some small points still remain undetermined.

In the following a few pages are devoted to the description of my own observation on two Japanese lampyrids, *Pyrocœlia rufa* and *Luciola cruciata*, with special reference to the stem cells from which the photogenic organs of the adult insect are produced.

Material

Since the photogenic organs of the adult insect are formed during the pupal period, larvae of *Luciola cruciata* were collected during April and May near Kyoto. From the end of May to the beginning of June most of them built nests and pupated. Several of the active larvae were taken a few days before their normal pupation period and these larvae and pupae were both cut in sections. A number of larvae and pupae of *Pyrocœlia rufa* were collected some time ago in South Corea (at Fusan) in September. They were also cut in sections and the preparations were used as a check of observation.

As there is a considerable variation in the stage of development of the photogenic organs in different larvae and pupae with respect to the time of pupation, it is difficult to correlate exactly the stages in the development of the organs with definite periods preceding and following the pupation. Moreover, specimens collected at different times were often employed in this investigation without determining the age with reference to their pupation periods, I have rather arranged the sections in a series based upon the histogenetic changes of the organs, beginning with the fat-bodies about to disintegrate and ending with the complete differentiation of two layers in the organ.

Observation

Thus we find in the preparations of a fully grown-up larva large spherical or sub-spherical fat-bodies occupying a large part of

the body-cavity. They are not of the same size, but generally very large in *Luciola*, the large ones being about 0.5 mm in diameter. Those of *Pyrocœlia* are much smaller, but present in larger number; they measure about 0.15 mm. In either case the constituent cells have thin and ill-defined walls, so that each fat-body looks much like a syncytium, including a large quantity of dark-staining spherieles, which may be generally described as to be of albuminous or proteid nature.

In *Pyrocœlia* the fat-bodies lying upon the ventral hypodermis of the future luminous segments and destined to give rise to the photogenic organs do not show much difference either in size or in shape from those found more proximally in the general body-cavity; similarly there is no great difference in the fat-bodies lying in the ventral hypodermis of those segments anterior or posterior to the position in question. In *Luciola*, on the contrary, the so-called "photogenic fat-spheres" (after the nomenclature of WILLIAMS, 1916) are exceedingly small, the presence of large fat-bodies in this position being rather exceptional. The small photogenic fat-spheres are not observed to be a derivative of the larger ones through the disintegration of the latter. I have traced them back to their first

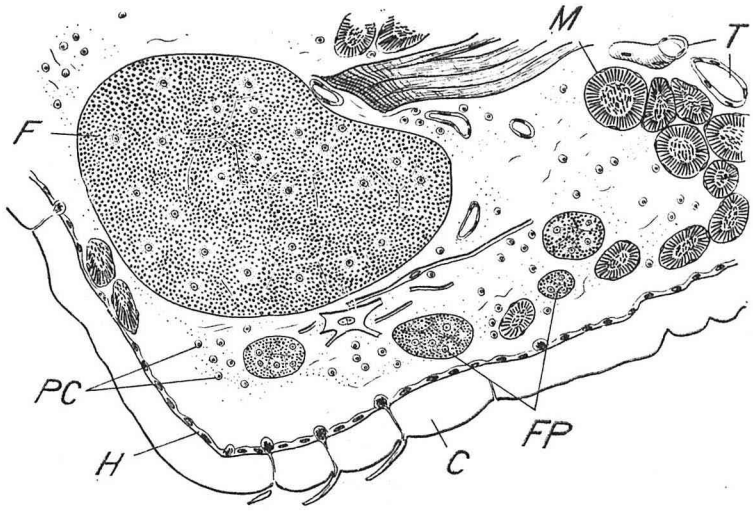

Fig. 1. Portion of a longitudinal section through the 7th abdominal segment of a larva (*Luciola cruciata*), taken some days before pupation, showing small photogenic and large ordinary fat-bodies. *C*, cuticula; *F*, fat-body of the ordinary type; *FP*, fat-bodies of the origin of the photogenic organ; *M*, muscle; *PC*, phagocytes; *T*, trachea. ×ca. 135.

recognizable beginning at a short time before the larva entered the pupal stage. They are found to be placed at the inner surface of the future luminous segments more or less apart from the ventral hypodermis (text-fig. 1, pl.-fig. I).

The fat-bodies in question (*FP*) measure only about 0.05 mm and are composed of five or six cells which contain even a less quantity of the characteristic proteid sphericles than do the ordinary large ones (*F*). WILLIAMS (1916, p. 152) has noticed the smallness of the photogenic fat-bodies, stating that " none of them are among those of large size, such as commonly occur in the mid-abdominal region." No such striking size difference of the fat-bodies between the photogenic and the ordinary ones as existing in the present case has apparently been observed. Moreover, in *Luciola cruciata* the formation of the photogenic organs is simply due to the proliferation of the cells of the small fat-bodies. These augment in number and arrange themselves in a layer on the ventral hypodermis of the future luminous segments (text-fig. 2, pl.-fig. 2). The complex

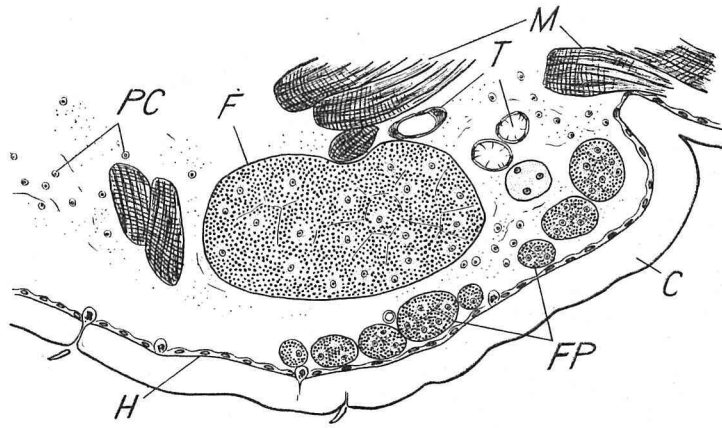

Fig. 2. Same as in fig. 1, the developmental stage being slightly advanced. Earliest stage observed in the formation of the adult photogenic organ of *Luciola cruciata*.

process whereby the fat-bodies are first broken down and the cells set free to renew their external and internal constitutions is in this case undemonstrated.

In *Pyrocœlia rufa* in which no appreciable difference in fat-bodies exists between the photogenic and the ordinary ones, there is a process of disintegration of the photogenic fat-spheres. They are broken down almost at the same time as the ordinary non-

photogenic ones, and the free cells arrange themselves on the ventral hypodermis in regular layers after the same manner as in the development of the photogenic organs of two well-studied American fire-flies, *Photuris pennsylvanica* and *Photinus consanguineus*. As in these the fat-bodies are first broken down. It is done rather mechanically through the contraction of a partially investing cap-like structure of peculiar material (text-fig. 3 *CP*). The cap seems to

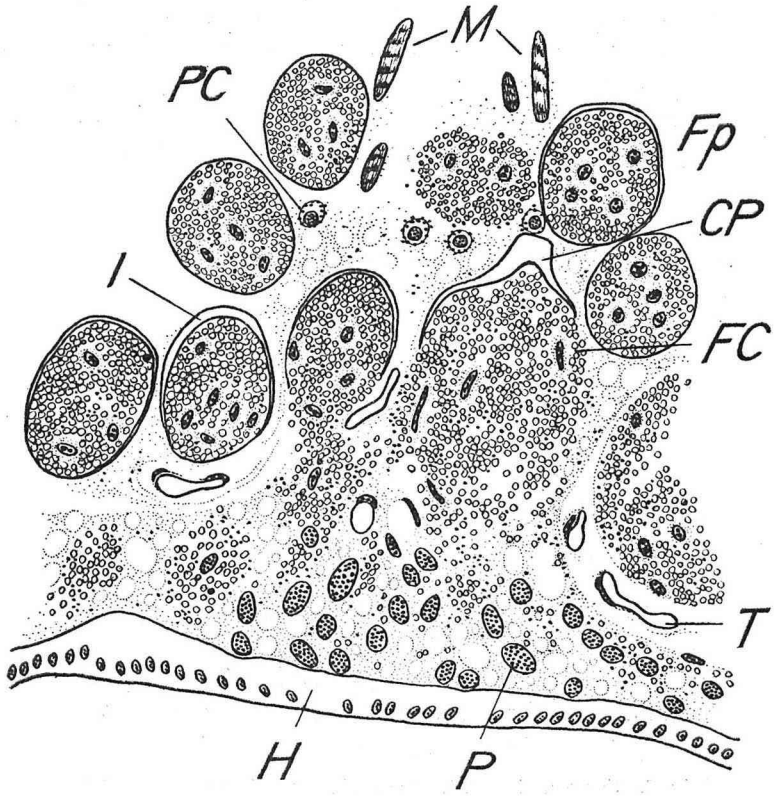

Fig. 3. Earliest phase in development of the adult photogenic organ of *Pyrocœlia rufa*, showing photogenic fat-spheres (*FP*), the cells (*FC*) issuing from the fat-sphere, and the process of cellular rearrangement into the photogenic tissue (*P*).*C P*, partially investing cap; *I*, investment membrane. ×280.

be produced by a one-sided accumulation of the material that has been uniformly distributed over the entire surface of the fat-body, and does not seem to be brought there from without by the blood or hæmocytes, as described by WILLIAMS (*l. c.*, p. 152) in *Photinus consanguineus*.

HESS (1922, p. 255), who denies the presence of such partial investing membrane in *Photuris pennsylvanica*, states that "although considerable attention was given to the nature of the fat-spheres just previous to the formation of the light-organs, no such investment membrane could be made out with any degree of certainty." The same holds true of the large fat-bodies of *Luciola cruciata* at the time of their disintegration. The formation of partial cap-like investment would not be a universal occurrence throughout the entire group of lampyrids in the process of breaking down the fat-bodies. Nevertheless, if the cap-like accumulation of the special material does take place in the outer membrane, it may well be supposed that the cap exerts a contracting force on the fat-body until the thinnest part that opposes the structure can no longer stand the strain and ruptures.

The photogenic fat-cells set free in this way are greatly elongated, the fact being indicated by the shape of their nuclei which, however, soon round up (see text-fig. 3). The cytoplasm still contains the dark-staining proteid sphericles so conspicuous in the ordinary fat-cells. But the liberated fat-cells of photogenic nature soon migrate to the body-wall and apply themselves closely to the ventral hypodermis of the future luminous segments, where they form an even layer. This we hold to be the beginning of the photogenic organs of the adult insect.

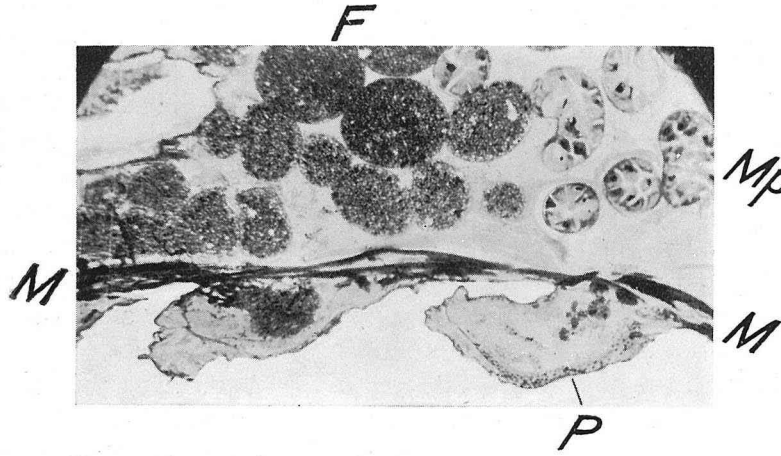

Fig. 4. Photographic reproduction of a longitudinal section of the youngest pupa of female *Luciola*, through its abdominal segments, showing the photogenic organ (*P*) in forming on the ventral hypodermis of the 6th segment. Large fat-bodies of ordinary type (*F*) are observed still intact. *Mp*, Malpighian tubules. ×40.

It should be mentioned that the large fat-bodies of the ordinary type in *Luciola cruciata* remain intact during the stage of development when the primordial photogenic layer becomes quite distinct, though they finally break down (text-fig. 4).

The sections of a fully grown-up larva which is about to shed its larval coat or of a newly formed pupa show a decided advance in the development of photogenic organs. They are now two or three cells deep (pl.-fig. 3). The nuclei are large and contain a dense chromatic substance generally consisting of a number of small spheres. The cytoplasm is highly vacuolated and appears to be of fine network. The dark-staining proteid sphericles once so abundant have greatly diminished, even to the point of disappearance.

Even at this early stage of development some tracheae push through the photogenic layer (pl.-fig. 4, *T*) and may reach the ventral hypodermis (*H*) which at this period also shows evidences of considerable activity, for its cells are much elongated and enlarged. But the nuclei of the latter are always far smaller than those of the developing photogenic tissue, and its cytoplasm is compact and contains absolutely no dark-staining proteid sphericles. Therefore, it is not likely that these would be mistaken for the cells of the developing photogenic organ.

A further development of the photogenic organs consists in (1) the proliferation of the cells in the layers; (2) the differentiation of these into two distinct strata, the distal photogenic and the proximal non-photogenic ones; and (3) the complete establishment of the air supplying system, i. e. trachaetion in the photogenic tissue. As the first two processes have already been described satisfactorily by WILLIAMS in *Photinus consanguineus* and by HESS in *Photuris pennsylvanica*, there is no need to repeat a similar description here. The gradations of serial changes of the imaginal photogenic organ in different developmental stages of *Luciola cruciata* are shown in pl. X, figs. 3-6. The third process requires a few remarks.

In sections of a pupa, the eyes of which are well pigmented, the two strata of the organ are distinctly separated (pl.-fig. 6). The tracheae in the distal layer appear thicker, the constituent cells being actually larger than those in the proximal layer. The tracheal cells in the first part are not very regularly arranged and here and there some of them even depart more or less from the

general arrangement of the epithelium. These adventitious cells have always an excentric nucleus (pl.-fig. 8 *E*). In some preparations the cells, apparently separated from the original epithelial row, are found between the parenchymatous photogenic cells where they evidently constitute the terminal end of the tracheal branchlets. The small round hollow space seen in the cytoplasmic part of the tracheal cells possibly represents the terminal branchlet of a trachea.

On the other side, the photogenic granules being secreted in the cells of the distal layer and the crystalline grains being deposited in the cells of the proximal layer, the development of the photogenic organs of the adult insect is complete, that is to say the organ becomes functional. In *Luciola* the division of two layers is very distinct, the boundary line running almost straight, while in *Pyrocœlia* there is always a group of cells which possess both characters of the non-photogenic upper and the photogenic lower layers (text-fig. 5 *IN*). Since the cells are found between two strata of the organ, they are called the "middle layer" (WIELOWIEJSKI, 1882) or "transitional cells" (BONGARDT, 1903).

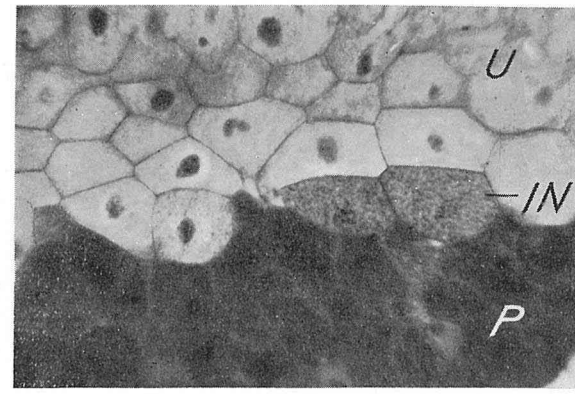

Fig. 5. Portion of fully formed photogenic organ in adult *Pyrocœlia*, showing so-called intermediate cells (*IN*) between photogenic (*P*) and urate ones (*U*). ×260.

The crystalline granules of the proximal layer

A. KÖLLIKER (1857) suggests that the crystals of the proximal non-photogenic layer are urates and would be produced by the oxidation of the photogenic substance. M. SCHULTZE (1865) took up this opinion, and added his theory that the urate cells were transformed from the photogenic cells, the cellular nature of the latter being changed by the process of luminescence. Finding the above mentioned intermediate cells between two layers H. R. WIELOWIEJSKI (1882) believes in the possibility of such transformation. R. DUBOIS (1898) and more recently F. C. GERRESTSEN (1922) advanced the

same transformation theory. But C. EMERY (1884), J. BONGARDT (1903), A. B. TOWNSEND (1904) and most of the more recent authors opposed it.

The above described embryological facts give evidence that the urate cells of the proximal layer and the photogenic cells of the distal layer are both independently differentiated from the so-called photogenic fat-spheres; and that once established, the relative thickness of the two layers remains constant throughout all stages of the life of an insect. The measurement of the thickness of two layers is taken in the following table for different ages of the photogenic organ of *Luciola cruciata*.

Table I

Relative thickness of two strata of the photogenic organ of *Luciola cruciata* in different ages

stage	photogenic layer	urate layer	ratio $\frac{u}{p}$
first indication of two layers	0.06 mm.	0.06 mm.	1
late pupal	0.09–0.1 mm.	0.08–0.09 mm.	0.9
newly hatched	0.07–0.11 mm.	0.06–0.1 mm.	0.9
flying insect	0.06–0.09 mm.	0.09–0.1 mm.	1.26
22 days old	0.04–0.06 mm.	0.06–0.1 mm.	1.6

From this measurement the proximal urate layer apparently thickens with respect to the thickness of the distal photogenic layer according as the age of the insect advances. This is perhaps due to the fact that the photogenic cells gradually wear out by luminescence, while the urate cells bulge or at least remain the same as before by a further addition of the crystals. As to the origin of the crystals E. J. LUND (1911, p. 434) states that "the photogenic cells are at least one if not the main source from which the crystalline deposit is derived." This view is based upon the fact that similar crystalline granules are sometimes found in the peripheral and perinuclear parts of the photogenic cells of *Photuris pennsylvanica* and others. If the possibility of this hypothetical origin of the crystals be granted, while the above mentioned transformation theory is denied, what then follows as the result? The crystals once deposited in the photogenic cells must be dissolved out again to be transformed from cells to cells through permeation, since there is no humoral circulation in this case, up to those of the proximal

non-photogenic layer. The view that the waste products of metabolism of certain cells are dissolved and used once more to fill up the other cells with the same substance for the special purpose seems to be too far fetched. More probably the crystalline deposit in the photogenic cells can be regarded as their senile sign.

To sum up, the urate cells which constitute the proximal stratum of the photogenic organs, as DAHLGREN (1917) has expressed, have the specific property of secreting the crystals and maintaining them in the cytoplasm throughout the entire life of an insect. The cells possess this property from the very first, and no cells from other tissues are ever added to the thickness of the layer.

The so-called photogenic granules of the distal layer

The cells of the ventral stratum are also very heavily granulated and stain especially well with HEIDENHAIN's iron-haematoxylin. In both *Luciola cruciata* and *Pyrocœlia rufa* the granules are uniformly distributed throughout the entire cell, without leaving a clear peripheral zone which is free from them.

Owing to the striking resemblance of the photogenic cells to those of the symbiotic organ of the homopteron *Aphrophora spumaria*, U. PIERANTONI (1914) wants to attribute the luminous property of the lampyrids to the symbiotic photobacteria which are congenitally transmitted from mother to the egg while it is still in the ovary. A similar view is held by P. BUCHNER (1914) who speaks of the light due to the intracellular mycetomes or (1921) to bacteria.

The fat-cells from which the photogenic tissue is derived, as already mentioned, contain, when they are at first set free, dark-staining sphericles in a large quantity. VOGEL (1913) describes in *Lampyris noctiluca* their repeated breaking down into more numerous and finer photogenic granules. This account apparently favours the theory of intracellular symbiotic bacterial nature of the granules. But WILLIAMS (1916) in *Photinus consanguineus* and I myself in both *Luciola cruciata* and *Pyrocœlia rufa* have been unable to follow the origin of the photogenic granules in this manner. As WILLIAMS has correctly interpreted, the proteid sphericles are first dissolved and used up as general food for the developing cells, including the photogenic ones. There is, indeed, a developmental stage in which the cells of the ventral layer are entirely free from both kinds of

granules, the proteid larger and the photogenic finer. The relationship between these two types of granules is but indirect.

In a pupa about 10 days old, the photogenic organ is about 10 cells deep. Although the cellular arrangement is still quite indefinite, it begins to show the differentiation into two strata, the cells of the distal stratum becoming plump (pl.-fig. 7). The photogenic granules begin to be produced from this period onwards. They are very fine at first and distributed diffusely (pl.-fig. 8). As development proceeds the cells become richer in cytoplasm, and the granules increase in number and grow also in size (pl.-fig. 9 *a*, *b*). Although I have been unable to measure the amount of the granules definitely, it is quite certain that during the course of development they increase greatly in number.

Photogenic organs of *Pyrophorus noctilucus*

It is significant to compare what has just been demonstrated with the origin of the photogenic organs of the elaterid *Pyrophorus*. DUBOIS (1898), who investigated the anatomy and embryology of this beetle, holds the view that its light organs are formed from the hypodermic cells. It seems quite unnatural to find here a different origin of the photogenic tissue from that found in the luminous lampyrids just described.

Although I have not actually studied the development of the photogenic organs in this species, there is sufficient evidence of their fat-cell origin. In sections of young specimens of *Pyrophorus noctilucus* brought back by the late Prof. WATASÉ from Jamaica I have found a certain amount of dark-staining proteid sphericles in the proximal urate cells, and the amount becomes proportionally increased towards the periphery where the fat-cells are in closest contact. Moreover, these peripheral cells are more or less vacuolated as the fat-cells are. A glance at fig. 10 on pl. XI will at once show a close resemblance of the urate cells (*UC*) on one side to the fat-cells (*FC*) on the other. There is almost no definite boundary between the urate layer and the mass of fat-cells at the margin of the photogenic organ, while the cells in question differ strikingly from the subjacent hypodermis (*H*). Thus, DUBOIS' account of the ectodermic origin of the photogenic organs is unsubstantiated in the present case of the elaterids, as in the preceding case of lampyrids.

Appendix: Fate of the larval photogenic organs during the metamorphosis

The luminous larva of lampyrids keeps the photogenic organs up to the torpid condition that occurs after it has built the nest in which it pupates. Even in this helpless condition the larva responds to handling or shaking by turning on its light. After the chitinous skin is shed and the larva becomes the pupa, a pair of light spots may still shine until shortly after the time when the adult insect is developed. The light becomes gradually faint and finally disappears in most cases. In some species such as *Lampyris noctiluca* and *Pyrocœlia rufa* (only in the female) the larval photogenic organs remain functional even in the imaginal life.

I have cut larvae of different lampyrids into sections in their pupating periods and have found the breaking down of the photogenic organs to occur in two quite different modes. In one type a one-sided accumulation of a peculiar material takes place in the outer investment of the organ and through this mechanical process the thinnest part of the membrane is burst and the internal structures are squeezed out. In the second type the destructive process is performed by the sole activity of phagocytes, that is to say through the phagocytosis from the very beginning of the process. The first case is found, beside *Pyrocœlia rufa*, in *Photinus consanguineus;* and the second case in *Luciola cruciata*, *L. lateralis*, *Photuris pennsylvanica* and other forms so far studied.

The photogenic organs of a fully grown-up larva of *Pyrocœlia rufa* (text-fig. 6) attain the size of about 0.65 mm length and 0.5 mm breadth. Each organ is surrounded by a thin membranous investment (*I*) of non-cellular nature. The first step observed in the commencement of breaking down the organ during the metamorphosis is that the outer investment gradually thickens on the proximal side through an accumulation of peculiar material on this side. The growth proceeds so far that it finally constitutes a cap-like structure (text-fig. 7 *CP*).

As mentioned in the preceding pages WILLIAMS (1916), who investigated the development of the photogenic organs of American fire-flies, has described a similar partial investing cap in *Photinus consanguineus* at the time of disintegration of fat-bodies during the metamorphosis. According to him the structure is formed from a material in the blood which, together with certain hæmocytes, has been attracted to one side of the fat-body by some chemotactic

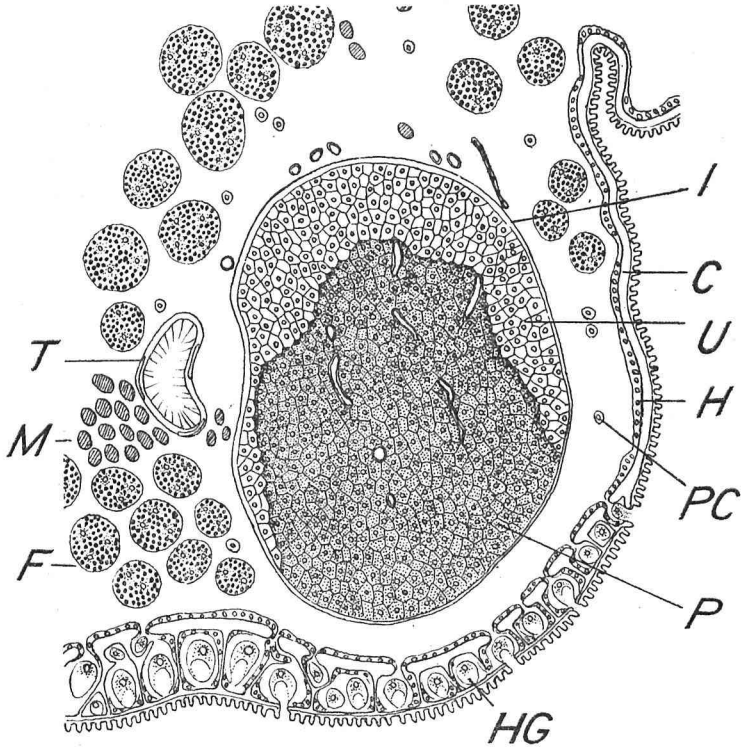

Fig. 6. Photogenic organ of full-grown larva of *Pyrocœlia rufa*. *C*, cuticula; *F*, fat-body; *H*, hypodermis; *HG*, hypodermic gland; *I*, investment membrane; *M*, muscle; *P*, photogenic cells; *PC*, phagocytes; *T*, trachea; *U*, urate cells. ×87.

substance and has thus come partially to invest it. The affinity of phagocytes for various organs is a common feature during the metamorphosis of the insect, and a large number of them are found also around the larval photogenic organs. But in the case of photogenic organs they attack them at various sides and not particularly from the region immediately outside the urate layer. In this case at least, the partial investing cap is formed neither from the blood nor from the accompanying hæmocytes. It is always produced on the proximal side of the organ along the urate layer.

The next change observed is a further condensation of material in the cap. This results sometimes in a meniscus of its shape, exceedingly thick at the middle and gradually thinning out from here to both sides (text-fig. 7). Condensation of material in the cap would naturally generate a compressing force upon the degenerating

organ, and the process would continue until the thinnest part opposite the structure, no longer able to stand the strain, ruptures.

In reality, however, the urate cells have already broken down before the rupture of the outer membrane, with the disappearance of the cellular boundaries. The change begins at the proximal side just beneath the cap-like structure and propagates from here to the distal regions. Nearly simultaneously the cellular boundaries become obscure also in the photogenic tissue, the entire mass apparently composed of a finely granulated cytoplasm with scattered nuclei. This is the condition of the larval photogenic organs at the later stage of pupation.

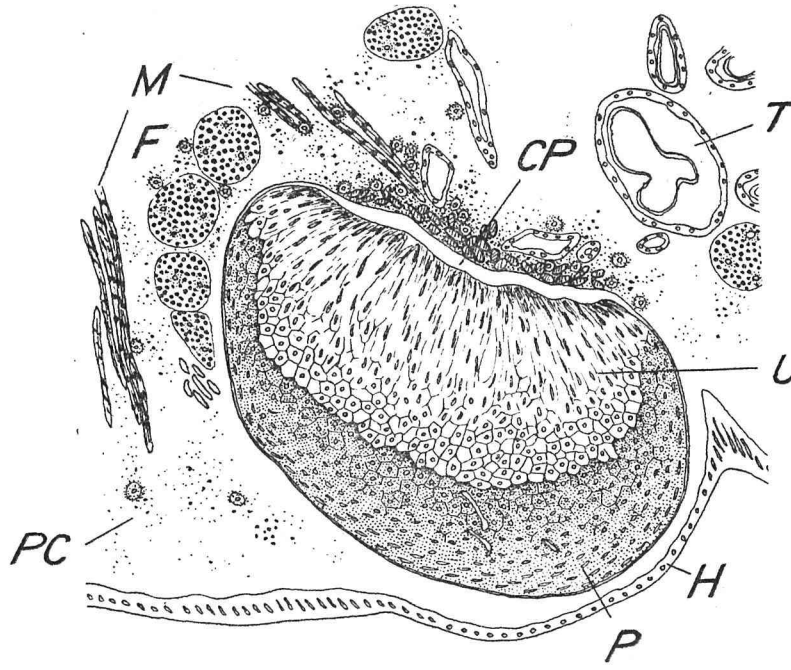

Fig. 7. Section through the larval photogenic organ of *Pyrocœlia rufa* at the stage of its disintegration during metamorphosis of the insect, showing the formation of a partially investing cap-like structure (*CP*). Lettering the same as in the preceding figure. ×120.

The envelope of the organ is finally ruptured mostly at the opposite surface of the cap-like structure as above mentioned and the contents are pressed out. The ultimate fate of the investment and in what way the debris of the organ is cleared I have not definitely studied, yet it may not be improbable to suppose that they would have been gradually taken off in the male insect by the activity of

the phagocytes before the pupa develops into the adult beetle, while the changed organs remain in the female throughout its life.

In *Photinus consanguineus* I could make out the same one-sided accumulation of peculiar material in the outer investment of the larval photogenic organs. The method of destruction of these during the metamorphosis would, therefore, be the same as in the case just considered.

Another method of breaking down of the larval photogenic organs is due to the sole activity of the phagocytes. In *Luciola cruciata*, for example, the larva is possessed of a pair of round organs (text-fig. 8) on the dorsal side of the penultimate segment, which when fully developed measure about 0.4–0.45 mm in diameter. The outer investment is very thin and sometimes difficult to make out definitely. The phenomenon of one-sided accumulation of its material does not take place in this case, while an unusually great number of phagocytes (*PC*) are found attaching to the degenerating photogenic organ

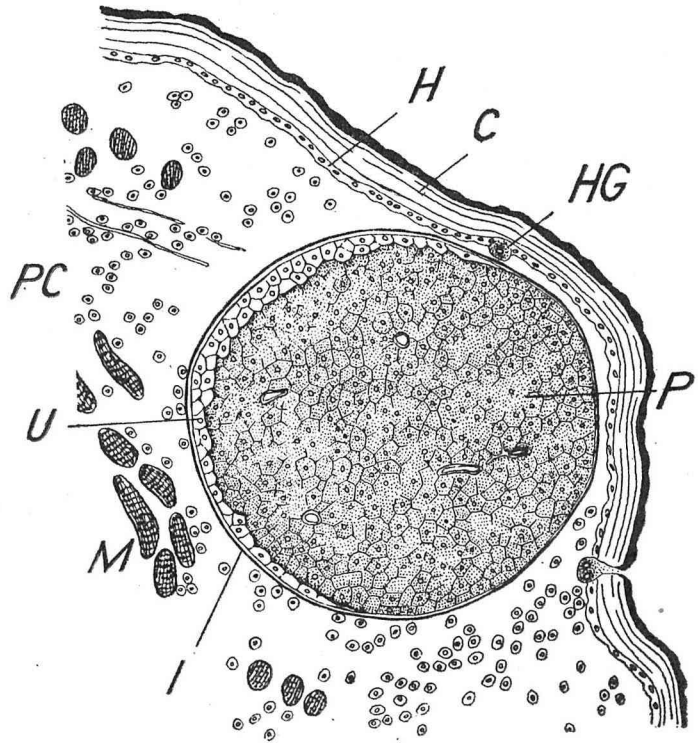

Fig. 8. Photogenic organ of full-grown larva of *Luciola cruciata*. Lettering the same as in fig. 6. ×120.

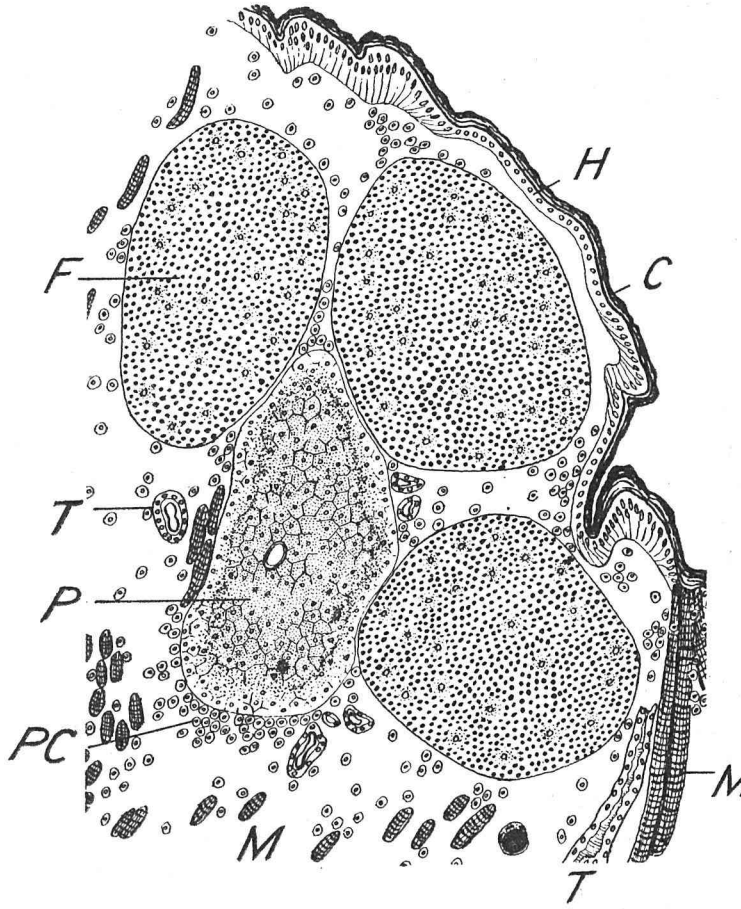

Fig. 9. Showing disintegrating larval photogenic organ of *Luciola cruciata* through phagocytosis. ×120.

on all sides (text-fig. 9). The cellular boundaries becoming obscure from the periphery to the centre, the internal tissue gradually changes into a syncytial mass. The characteristic granules are next dissolved out and cytoplasm becomes cleared probably through the activity of the phagocytes. It may be expected that some of them penetrate into the degenerating organ, but this does not occur in this case.

Summary

1) Two Japanese fire-flies, *Pyrocœlia rufa* and *Luciola cruciata*, greatly differing in their larval habits, are studied with special reference to the origin and development of the adult photogenic organs.

2) In *Pyrocœlia rufa* these organs are derived from the fat-bodies by the expulsion of their cells, which migrate to the ventral hypodermis. The cell-expulsion is effected by the formation of a partially investing cap-like structure of peculiar material which is accumulated on one side of the investment membrane of the fat-bodies. There is almost no difference in shape and in size between the photogenic and the ordinary fat-bodies. The latter are also broken down by the same mechanism as in the photogenic fat-bodies in the beginning of the pupal stage.

3) However, a great difference exists between the photogenic and the ordinary fat-bodies of *Luciola cruciata*. The photogenic fat-bodies are even 10 times as small as the other and they become directly applied to the ventral hypodermis without an intermediate process of cell-expulsion. The investment membrane is very thin also in the ordinary fat-bodies and there occurs no one-sided accumulation of peculiar material at the time of their disintegration. The process of breaking down is then effected by the sole activity of phagocytes.

4) Further development of the photogenic organ proceeds in the same way in either species, and consists of the proliferation of the cells, the differentiation of these into two distinct layers—the distal photogenic cells and the proximal urate cells, and the complete establishment of the air supplying system. Except for these tracheal elements which are ectodermal, the mesodermic origin of photogenic organs is most evident. The ectodermic origin of the same organ in the elaterid, *Pyrophorus noctilucus* is, therefore, also considered to be unsubstantial.

5) The development of the adult photogenic organs has no relation to the larval ones which disintegrate at the time of pupation. The disintegration of the latter occurs in two different modes: in one type a one-sided accumulation of a peculiar material takes place in the outer investment and through the mechanical process of this cap the internal structures are squeezed out. In the second type the destructive process is performed by the sole activity of phagocytes. The first case is found in *Pyrocœlia rufa, Photinus consanguineus;* the second case in *Luciola cruciata, L. lateralis, Photuris pennsylvanica* and other forms so far studied.

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Explanation of plates

Pl. X. Fig. 1. Photographic representation of the same preparation as in the text-fig. 1 on page 212. Magnification about 100 times.

Fig. 2. Same photographic reproduction of the primordial photogenic organ of *Luciola cruciata* as in the text-fig. 2 on page 213. Magnification as in fig. 1.

Figs. 3–6. Four stages in developmental series of the adult photogenic organ of *Luciola cruciata*. Magnification about 200 times.

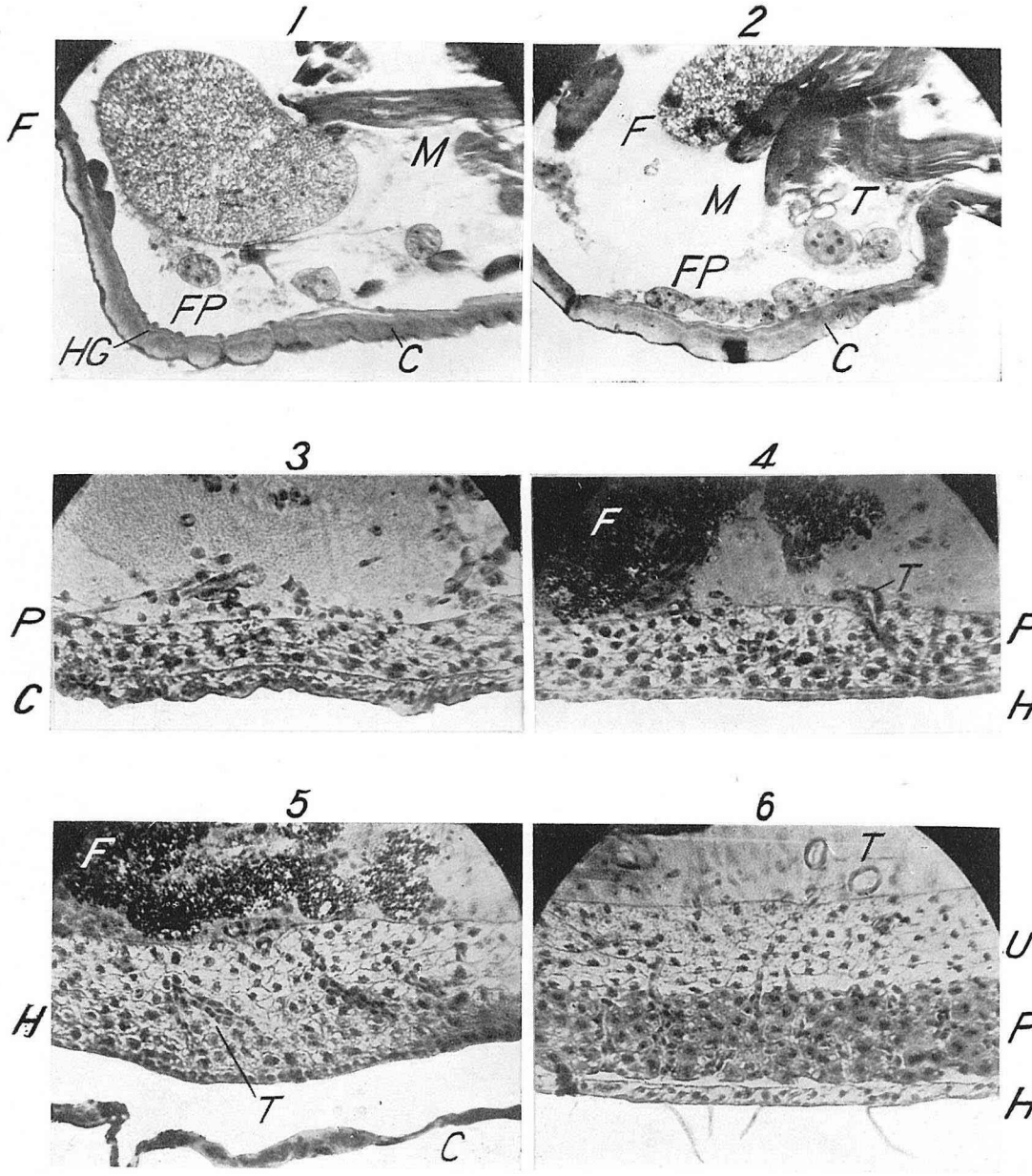
Pl. XI. Fig. 7. Portion of a developing photogenic organ (*L. cruciata*) in which difference of the photogenic and the urate cells is first recognized. Magnification 770 times.

Fig. 8. Same as in the preceding figure, but showing a more advanced stage of differentiation when the photogenic granules begin to be produced.

Fig. 9. Changes of cellular content and nucleus of *L. cruciata* in three different phases of photogenic function; (a) beginning of the function, (b) most active stage of luminescence, (c) cell showing senile sign, taken from a specimen 22 days later. Magnification 1700 times.

Fig. 10. Portion of the ventral photogenic organ of *Pyropholus noctilucus*, showing a transitional structure of the urate cells to the fat-cells at the margin of the organ. Magnification 770 times.

Lettering common to all figures: *C*, cuticula; *F*, fat-sphere of the ordinary type; *FP*, photogenic fat-sphere; *E*, tracheal end-cell; *H*, hypodermis; *HG*, hypodermic gland; *M*, muscle; *P*, developing photogenic organ or photogenic cells when used in contrast with *U* which denotes the urate cells; *T*, trachea.



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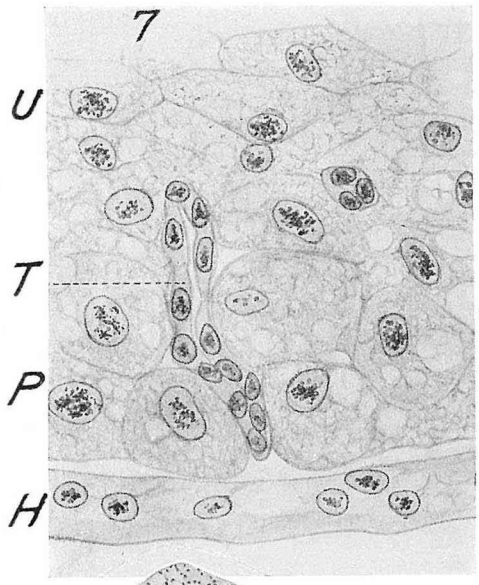

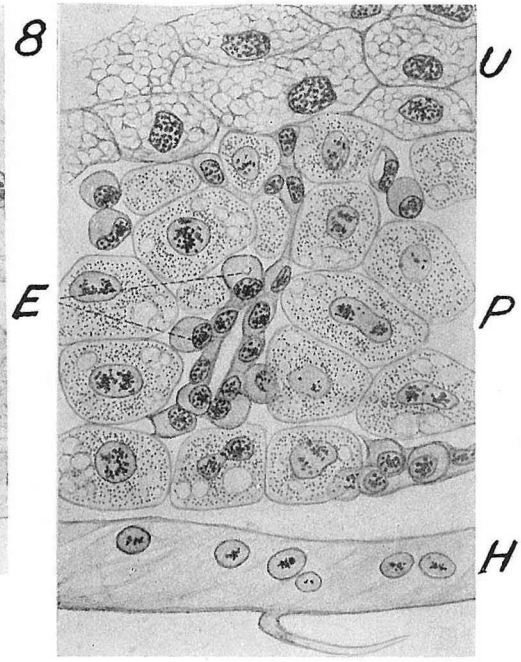

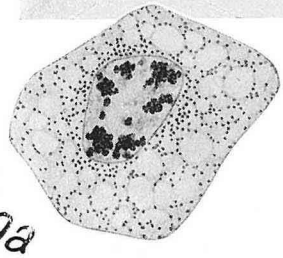

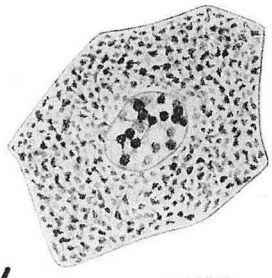

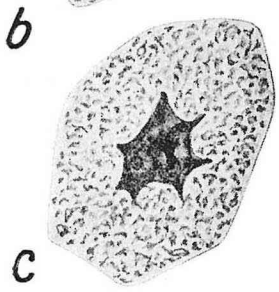

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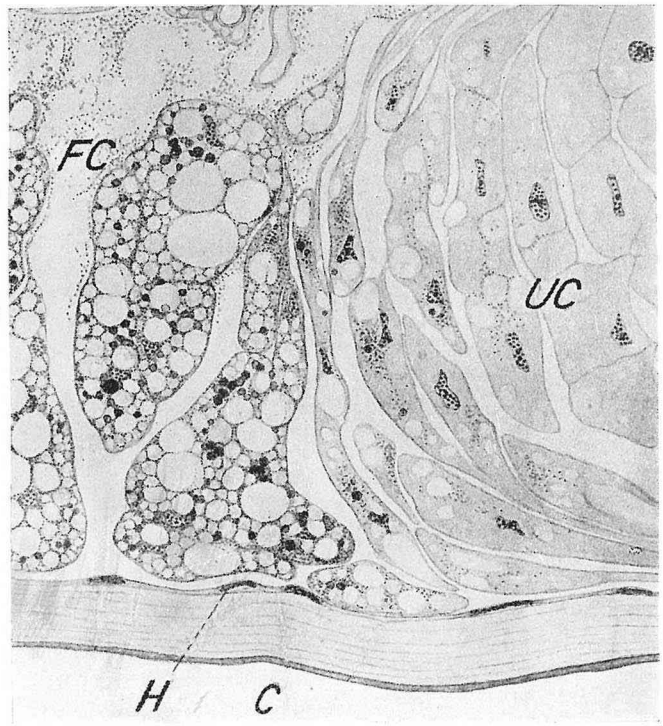

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