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On the Renewal of the Mid-intestinal Epithelium of Collembola.

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With Plates VIII-X

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Introduction

The phenomenon of the periodical degeneration and regeneration of the epithelium of collembolan mid-intestine was first described by SOMMER (1885) in *Tomocerus* (*Macrotoma*) *plumbea*, and next by FERNALD (1900) in *Anurida maritima*. These authors, however, did not go into the physiological process of the interesting renewal of the mid-intestinal epithelium. FOLSOM and WELLES (1906) made a physiological study of the phenomenon in certain Collembola, such as *Tomocerus niger*, *Podula aquatica*, *Isotoma viridis* and *Orchesella cincta*. So far as I know, this is the only previous work relating to this subject.

The object of the present research was to find out the manner of regeneration as well as what physiological significance is involved in the casting off of the entire epithelium of the mid-intestine in Collembola.

Material and Methods

Hypogastrula communis was used in this study. This species is found commonly on the surface of rain puddles in the vicinity of Kyoto. The materials were fixed *in toto* and embedded in paraffin by the ordinary method. Sections were cut 5—7 micra thick.

For fixing, absolute alcohol, 70% alcohol, alcohol-formol, BOUIN's mixture and CARNOY's mixture were tried, and the last one proved to give the best results. Materials must not be left in the fixative more than 5—10 minutes.

For staining sections, HEIDENHAIN's iron-haematoxylin, and DELAFIELD's haematoxylin were employed, with or without counterstaining with eosin.

For the study of the physiological process of the mid-intestinal degeneration and regeneration, the insects were preserved *in toto* with FLEMMING's strong solution without acetic acid, diluted with eqaul parts or with twice the volume of distilled water. Sections were stained with HEIDENHAIN's iron-haematomylin.

Observation

For some time previous to moulting, the insects become inactive. At that time the new chitinous integument has been formed under the old one and the epithelium of the intestine has undergone some degeneration and the formation of the new one has begun to some extent. When the insects are examined within five hours after moulting, it is seen that the old epithelium has become almost entirely deformed except in its anterior half, where the cell-walls are hardly recognizable. In short the renewal of the mid-intestinal epithelium takes place just prior to the external moulting.

The mid-intestine of *Hypogastrula communis* is a simple tube, extending from the beginning of the mesothorax to the end of the fourth abdominal segment, without any appendices such as gastric cæca and Malpighian tubules, as is shown in Pl. I, photo. 1. The epithelial wall consists of a single layer of cylindrical cells, furnished with numerous fine-filaments (Härchensaum) on the periphery and with scattered regeneration cells at the base (Pl. I, photo. 2, Pl. II, photo. 3, and Pl. III, Figs. 1, 3 and 4). No goblet cells, which are found in other insects, can be distinguished among these cells.

At the base of the epithelial wall there is a structureless tunica proprica (basal membrane). Outside this membrane is a single layer of circular muscle bands, which are, in turn, surrounded by a layer of longitudinal muscle bands (Pl. III, Figs., 1, 2 and 3).

As mentioned above, the regeneration cells are found in the basal region of the epithelial wall, scattered here and there. One can find no "nidi" (Krypten) whose function is considered to be exclusively to regenerate the epithelial cells as reported by RENGEL (1898), EVENIUS (1925) and others in Coleoptera and Hymenoptera.

This arrangment of the regeneration cells in Collembola may perhaps be the most primitive form of the "nidi". The regeneration cell is smaller and stains better than the epithelial cell with a round

nucleus, and often shows the mitotic figure of cell division (Pl. III, Fig. 3). The number of them is various according to the age of the insect and the younger it is, the more they are found. FERNALD (1900) and FOLSOM and WELLES (1906) maintain that there are no special regeneration cells in other Collembola. FERNALD believes that in *Anurida maritima*, the nuclear division takes place in the epithelial cell itself and one of the daughter nuclei migrates towards the free end of the cell, while the other passes towards its base; then delamination of cytoplasm occurs between these daughter nuclei and the interior half of each cell is thrown off into the lumen of mid-intestine. FOLSOM and WELLES also observed almost the same phenomenon in *Tomocerus niger*, namely, in somewhat less than half of the epithelial cells the nuclei migrate towards the intestinal lumen to form two layers of cells; then the layer next the lumen is thrown off and the normal number of cells in the epithelium is restored by the mitotic divisions of the remaining nuclei. Contrary to these authors, PROVAZEK (1900) believes that regeneration cells (Mutterzellen) exist in *Isotoma grisea*. He maintains: " Zwischen diesen Zellen (prismatischen epithelartigen Zellen) findet man basalwärts auf Querschnitten undeutliche kleine, dünkler sich tingierende Zellen mit kleinen dünkelen Zellkernen, die als Mutterkeim- oder Urzellen des Mitteldarmepithels aufzufassen sind,....."

I shall now describe the epithelial cell in the normal stage, so far as the renewal of the mid-intestine is concerned. In the young stage of the cell, basophile plasm fills the cell uniformly. As the cell ages, however, an alveolar structure becomes apparent in its middle portion; the alveoli are small and scarce at first, but become larger and more numerous gradually. In material fixed with CARNOY's mixture, cell wall and filaments are distinct, while in material fixed with FLEMMING's strong solution without acetic acid, diluted to 1/2 or 1/3, the individual cells are distinguishable separately only by the state of aggregation of basophile granules in the plasm. The nucleus is situated somewhat below the middle of the cell; it is large and oval and contains many basophile chromatin granules and a few acidophile ones. The nucleus becomes polygonal as the cell grows older; at the same time the basophile granules increase in number. Such granules are not detected in the young cells which are still bearing the old epithelium (Pl. III, Fig. 6), so that it is but natural that they should not be found in the regeneration cells. As the cell ages, they accumulate first in its basal portion, while in a few cases they appear

first in the portion of it next the lumen. They seem to accumulate quicker in the epithelium on the dorsal side than in that on the ventral side. The senescent cells of the epithelium, which have become taller than usual and are ready to be thrown off, are laden with a great number of these granules, while no food is contained in the lumen of the alimentary tract. It is in this stage that the insect becomes inactive for moulting, as described above. In this stage of the cell, heavy vacuolization of the plasm is recognizable in material fixed with CARNOY'S mixture and there are found many acidophile granules in the nucleus. Judging from these facts, it is likely that the process of casting off the old mid-intestinal epithelium has an excretory significance. During the time that the discarded cells are degenerating in the intestinal lumen, these granules dissociate themselves and disappear completely. Thus the main part of the granule seems to consist of the products of insect metabolism, which are soluble in the lumen. In *Tomocerus niger*, FOLSOM and WELLES observed small and round concretions as products of cell-metabolism, but this concretion remains intact in the lumen and is finally ejected from the alimentary tract.

The excretory function of the mid-intestine described above is possibly correlated with the absence of Malpighian tubules in this insect; but it is more probable that it is correlated with the moulting of the integument. During the moulting, in spite of the apparent inactivity of the insect, the internal metabolism is apparently very active, and the metabolic products are probably evacuated by casting off the entire old epithelium. In the metamorphosis of other holometabolic insects and even in the ecdysis of *Anthrenus*- and *Dermestes*-larvae, MÖBUSZ (1897) has observed the total regeneration of the mid-intestinal epithelium. More recently, TCHANG YUNG-TAI (1929) has also reported the same phenomenon in *Galleria mellonella* (Lepidoptera). All these observations seem to favor my opinion that there is a causal relation between moulting and the excretory function of the mid-intestine.

In the resting state of the mid-intestine, a mucous layer weakly acidophile is usually found covering the epithelium. This may be digestive fluid secreted from the epithelium. When the digestive function is at its height, secretion-droplets are sometimes found here and there attached to the free end of the cell. In the posterior portion of the mid-intestine the free ends of the cells are often found to swell out into the lumen; this convexity develops gradually into a spherule

which is constricted off and liberated into the lumen (Pl. III, Fig. 2.). This proliferation of cytoplasm is thought by FOLSOM and WELLES to be a kind of secretory function, and may indeed be so.

Summary

1. The renewal of the mid-intestinal epithelium in Collembola *Hypogastrula* takes place just before moulting.

2. The epithelial regeneration is performed by the regeneration cells situated at the basal portion of the epithelium.

3. The process of the casting off of the old epithelium is possibly correlated with the moulting of the integument and probably has an excretory significance.

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Explanation of Plates. VIII—X.

List of abbreviations

cv = cytoplasmic vesicle
cm = circular muscle
dn = deforming nucleus of the old epithelium
ds = dorsal side of the mid-intestine
ex = excretion granule
f = food material
fi = fore-intestine
ff = fine-filament ("Härchensaum")
hi = *hind-intestine*
in = integument
lm = longitudinal muscle
mi = mid-intestine
mt = mitotic division of the regeneration cell
ne = new epithelium
oe = old epithelium
rg = regeneration cell
v = vacuole
vs = *ventral side of the mid-intestine*

Plate VIII

Photo. 1 Sagittal section of *Hypogastrula communis*, showing the whole alimentary tract. Fixed with CARNOY'S mixture. (ob. 3×oc. 3)

Photo. 2 Anterior portion of the sagittal section of the mid-intestine, showing the old epithelium thrown off in the lumen. Fixed with CARNOY'S mixture. (ob. 7×oc. 1)

Plate IX

Photo. 3 Sagittal section of the mid-intestine. Note the regeneration cells scattered here and there at the base of the epithelium. Middle portion of the dorsal epithelium, fixed with CARNOY'S mixture. (ob. 1/12×oc. 3)

Photo. 4 Longitudinal section, showing the convex periphery of the posterior portion of the mid-intestine. The epithelium is in the senescent state and the new one has been formed. Fixed with CARNOY'S mixture. (ob. 1/12×oc. K 18)

Plate X

Fig. 1 Camera-drawing from the longitudinal section (5 micra) of the mid-intestine, showing the resting stage of the renewal of the epithelium. Cytoplasm of the regeneration cell is dense and stainable. Middle portion of the ventral epithelium, fixed with CARNOY'S mixture for ten minutes. (ob. 1/12×oc. 4)

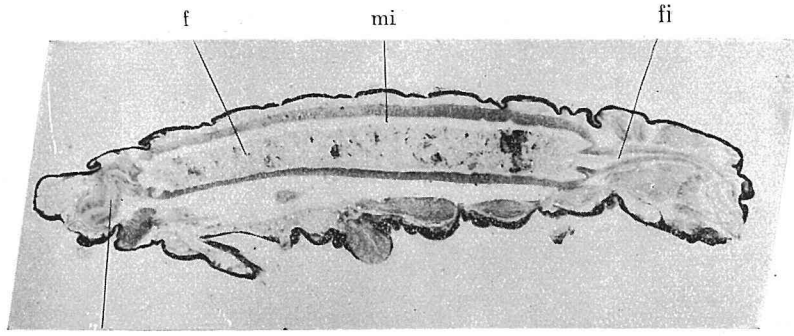
Fig. 2 Camera-drawing from the longitudinal section (5 micra) of the posterior epithelium of the mid-intestine, showing the cytoplasmic proliferation. The senescent cells and the regenerating ones being distinct. Fixed with CARNOY'S mixture. (ob. 1/12× oc. 4)

Fig. 3 Camera-drawing from the longitudinal section (5 micra), showing the degeneration of the old epithelium and the mitotic division of the regeneration cell. On account of the contraction of circular muscles, the shape of the new cells is somewhat irregular. Ventral epithelium, fixed with CARNOY'S mixture. (ob. 1/12×oc. 4)

Fig. 4 Camera-drawing from the cross section (5 micra), showing the degeneration of the old epithelium on the one hand and the regeneration cells scattered here and there on the other hand. Nucleus of the new epithelium is situated in the distal portion of each cell. Fixed with CARNOY'S mixture for 20 minutes. (ob. 7×oc. 4)

Fig. 5 Camera-drawing from the longitudinal section (5 micra), showing that aggregation of excretion granules begins first at the basal portion of the cell. Anterior portion of the ventral epithelium fixed with diluted FLEMMING'S strong solution without acetic acid. (ob. 1/12×oc. 4)

Fig. 6 Camera-drawing from the longitudinal section (5 micra), showing that the excretion granules have filled up the old epithelium, which was ready to be thrown off. Note that there is no excretion granule in the new epithelium. Ventral epithelium fixed with diluted FLEMMING'S strong solution without acetic acid. (ob. 1/12×oc. 4)



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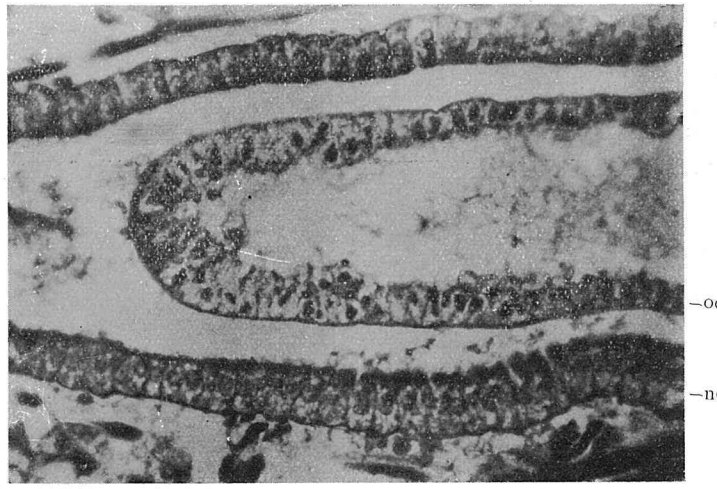

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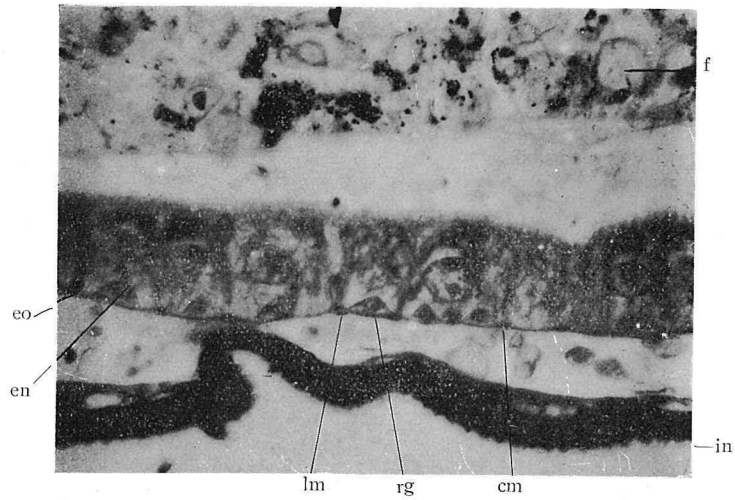

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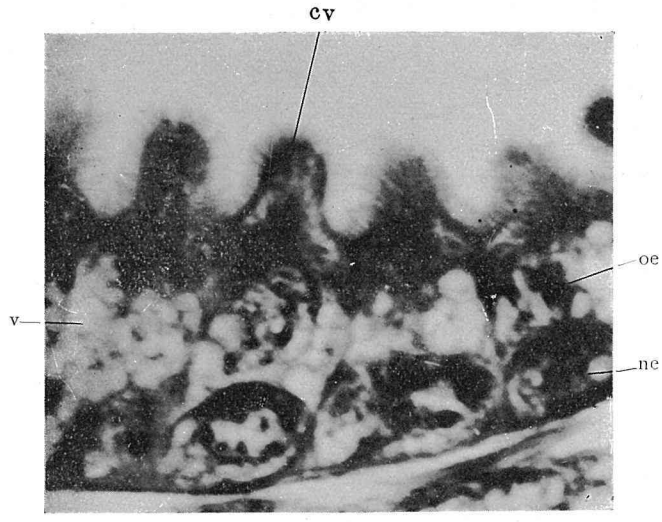

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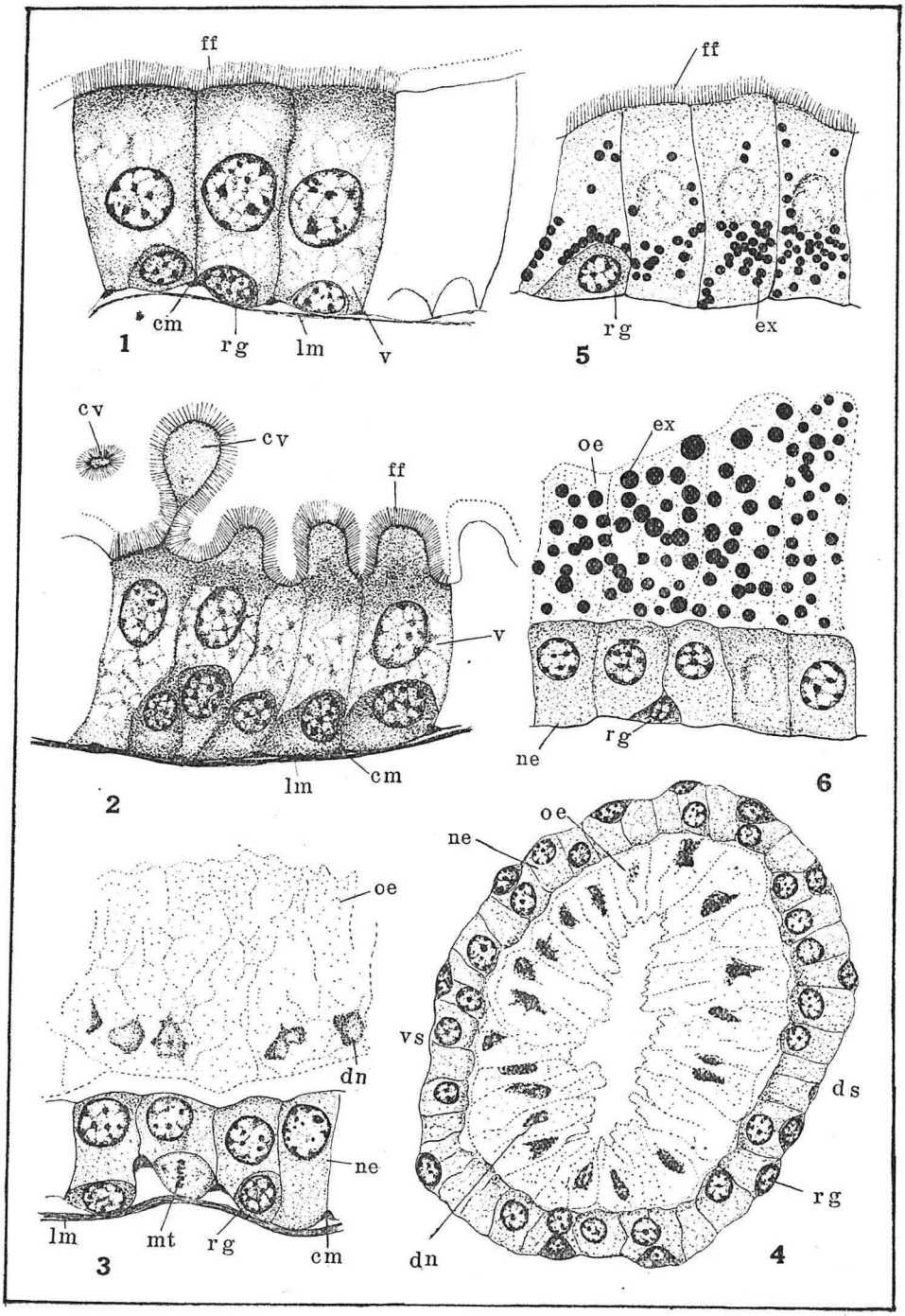
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M. Ichikawa.