CUSHION CELLS OF THE PHARYNX OF PRORHYNCHUS APPLANATUS KENNEL

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ONE TEXT FIGURE AND ONE PLATE

A wide range of variability both in structure and function is presented by the pharynx and proboscis of Rhabdocoela. Of the seven families in this sub-order, the Catenulidae and Microstomidae have but simplex pharynges. In the Prorhynchidae and Dalyelliidae, the pharynx is a well-defined bulbous type. In the Typhloplanidae, there is a rosette-shaped pharynx; in some of these, however, the proboscis lacks a definite sheath. This proboscis is not concerned with ingesting food; but is an organ of both defence and offense. This organ reaches its highest development in the Polycystidae and Gyratricidae.

Prorhynchus applanatus occupies an intermediate place in this series of Rhabdocoeles, ranging from animals having relatively simple pharynges, through those presenting complex pharynges without associated proboscides, to animals in which both pharynges and highly developed proboscides are present. In the simplest pharynx there is but little muscular development and many glands present, so that, in the living specimen, the pharynx appears to be a glandular structure rather than a muscular one (e.g., Stenostoma). In the Dalyelliidae and most Prorhynchidae, the bulbous pharynx is highly muscular. The pharynx of Prorhynchus applanatus is not only highly muscular, but its muscles are so organized that in the living specimen three distinct zones are clearly recognizable, (text-fig. A). The distal zone, (a) of muscles form an 'Endkegel' similar to the terminal cone of such a highly specialized proboscis as that of Gyratrix hermaphroditus Ehrenberg. At the posterior end of the pharynx is a zone of muscles, comparable to the 'Muskel-

zapfen' of Gyratrix (c). A highly refractive third zone of muscles lies between the end cone and the muscle spindle of the base of the pharynx, (b). Thus, in this series of *Prorhynchus* which has no proboscis there is a highly muscular pharynx whose histology is as complex, if not more so, than that of the complex proboscis of a Gyratricid.

Text fig. A Drawing of dorsal aspect of *Prorhynchus applanatus*. *DG*, dorsal ganglion; *E*, eye; *P*, pharynx; *a*, *b*, and *c*, the three regions of the muscular pharynx. $\times 75$.

The functioning of this most complex pharynx of the Rhabdocoela is not supplemented for a long period during the life of each individual by a penis which might act as an organ of defense. Animals are frequently found with the ovaries present. Seldom are the male genitalia encountered. These appear for but a brief period in the history of the individual. Therefore, the

animal does not as a rule carry about with it in its pharyngeal sheath a chitinous penis which could be used defensively as do some Rhabdocoela. *Prorhynchus applanatus*, has of course, no defensive and offensive proboscis.

The structure of this pharynx and the conditions attending it all suggest that it is a bulbous stomodaeum which has assumed the function of a proboscis as well as that of a pharynx.

It is, therefore, interesting to see that Kepner and Taliaferro, ('16), recorded the fact that this animal uses its pharynx as a defensive organ. "Correlated with the absence of a chitinous penis, which in the other forms of *Prorhynchus* is used as an organ of defense, the pharynx of *Prorhynchus applanatus* serves as a defensive structure." Mr. W. H. Taliaferro, while working in this laboratory, was the first to make the observation that such use is made of the pharynx by *Prorhynchus applanatus*. While observing a specimen under a microscope, he saw it plunge its pharynx quite through another animal which passed by, and further, that its pharynx was very quickly withdrawn from the victim to retreat into its pharyngeal sheath.

This method of functioning imposes a peculiar stress upon surrounding organs, both when the pharynx is discharged at an object, and especially when its recoil is to be met. Were it not to have some special method of meeting this recoil, the surrounding parenchyma and other tissues would be greatly taxed to withstand the impact of the rebounding pharynx.

This organ is cushioned laterally by parenchyma. At its base, however, it rests upon the rim of the enteron. Thus, a more delicate situation encounters the recoil of this pharynx than is that which receives the rebound of the highly developed proboscis of the other Rhabdocoelae. The proboscis of the higher Rhabdocoelae is cushioned by an extended lateral mass of parenchyma as well as by a basal pad of mesenchyme, a connection between the enteron and the proboscis not being involved.

In *Prorhynchus applanatus* the pharynx, of course, communicates with the enteron. Its lumen opens into that of the enteron, while its wall is confluent with, or merges into the wall of the latter. There is thus an intimate connection between

the proboscis and the enteron. This connection between the enteron and the vigorously active pharynx must be quite delicate; for there is but a very thin tunic of muscle fibers in the wall of the alimentary canal at this thin and constricted region, and in addition to this, the wall is broken by frequent pores through which the secretion of the glands of the pharynx empty their products (fig. 1, GP).

A demand to protect the delicate connection between the enteron and pharynx, and the enteron itself from the sudden recoil of the peculiar pharynx of *Prorhynchus applanatus* has thus arisen. In other animals, for example, the Crustacea, "Masses of connective tissue uphold and support the various and delicate tissues about them, and protect them from the impact of surrounding organs. The largest and most regular of the cells which compose this tissue are known as Leydig's cells of the first order." page 57, Dahlgren and Kepner ('08).

As in the Crustacea, so here certain mesenchymal cells about the base of this peculiar pharynx have become large and cushion-like to meet the demand made for protecting the delicate enteron from the impact of an adjacent organ. These form a mass of conspicuous tissue which extends laterally along the posterior half of the pharynx and crowds about the base of the pharynx as it unites with the enteron. Anteriorly these cells form but a single layer about the pharynx (figs. 1 and 2cc).

These cushion cells in the fixed condition¹ first appear as irregular polyhedra. The largest ones measuring about $45\mu \times 30\mu \times 30\mu$. The most conspicuous feature of the mature cells is the greatly vacuolated condition of their cytoplasm which is for the most part disposed about the periphery of the cell. At some place this peripheral cytoplasm is piled up as an eccentrically placed mass of protoplasm around the nucleus. Figure 3 shows a section through the nucleus (N). It also shows where the large central cavity encroaches upon the peripheral cyto-

¹ The specimens have been fixed in chrom-aceto-formalin and aceto-sublimate. The former reagent have a better result. The sections were five micra thick and were stained with Mallory's connective tissue stain or iron haematoxylin.

plasm at three regions (a), (b), (c). The nucleus of the mature cell is rarely found well fixed in prepared sections.

Many rhabdocoeles, for example, *Dalyella*, *Stenostoma* and *Microstoma*, have gland-cells projecting into the mesenchyme from the wall of the isthmus which connects the pharynx with the enteron. For a time, we had supposed that the cushion cells of *Prorhynchus applanatus* might be such cells, but in no case have we been able to find that they have ducts. On the other hand, places occur in which the transition from general mesenchymal cells to the typical cushion cells is apparent. In a cell which has departed little from the mesenchymal type, there is a slight vacuolization of the cytoplasm at the pole nearer the mass of more advanced cells. The nucleus of such cells has undergone but little change (fig. 4-A). Later the cell enlarges as shown at figure 4, B. The cytoplasm becomes more vacuolated, and, at this phase in the development of the cushion cell, the nucleus reaches its maximum size (fig. 4, N). When further growth ensues the nucleus decreases in size (fig. 3, N). The cushion cells of *Prorhynchus applanatus* therefore are not homologous with the gland cells of the pharynges of other rhabdocoeles, but are of mesenchymal origin.

In both their function and origin they suggest, therefore, the so-called Leydig's cells, which have been described for Crustacea.

SUMMARY

1. The pharynx of *Prorhynchus* has a double function, (a) food prehension; (b) offense and defense.
2. In correlation with this duplex functional demand there is a structural differentiation analogous to that of the proboscis of the higher rhabdocoeles.
3. There are cushion cells (Leydig-like cells) developed at the base of this highly organized pharynx, which protects the adjacent organs from the recoil of the pharynx.
4. These cells are of mesenchymal origin and are not homologous with the pharyngeal gland-cells of other rhabdocoeles.

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PLATE 1

EXPLANATION OF FIGURES

1 Frontal section involving the entire pharynx. *cc*, cushion cells; *GP*, gland pore opening into the lumen of the enteron; *I*, the approximate plane through which section, shown in figure 2, was taken. $\times 200$.

2 Obliquely transverse section. Approximate plane of this section shown by line *I*, in figure 1. The cushion cells (*cc*) are here shown on the ventral side and extending laterally about the pharynx-base. Had the section been taken through the cells *cc* and strictly at right angles to the axis, the cushion cells would have appeared on all sides of the section of the pharynx. $\times 100$.

3 A section of a mature cushion cell; section taken eccentric to the axis of the cell. *N*, nucleus; *a*, *b*, and *c*, diverticula of large central cavity of the cushion cell. $\times 1500$.

4 Two phases in the growth of cushion cells. *A* younger cell, which resembles the general mesenchyme cell; *B*, older cell. At *B*, the intermediate stage of growth, the nucleus (*N*) reaches its maximum size. $\times 1500$.