THE STOMACH OF PALUDOMUS TANSCHAURICA (GMELIN).

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This paper deals with the structure of the stomach and the style sac in *Paludomus tanschaurica* (Gmelin)¹, and I give below the results of my investigations. I have also added a few comparative notes on the forms in which the structure has been investigated by previous authors. My best thanks are due to Dr. H. S. Rao of the Zoological Survey of India, Calcutta, for the correct identification of the species, and to Lt.-Col. R. B. Seymour Sewell, Dr. Baini Prashad and Dr. F. H. Gravely for suggestions and criticisms. Lt.-Col. Sewell was also kind enough to draw my attention to some of the papers cited in the list of references.

In recent years several papers have appeared on the crystalline style and the associated structures of Gastropods, and lists of the genera, which have a crystalline style, have been published by Robson (11) and Mackintosh (5), but neither of the authors mention *Paludomus* Swainson in their lists. In the family Melaniidae (=Tiaridae), to which *Paludomus* belongs, a crystalline style has been recorded in the genera *Melania*, *Bythoceras* and *Nassopsis*. Mackintosh in the paper cited published a figure of the stomach of *Melania*, and stated that the condition is typical and that the crystalline style is lodged in the anterior chamber of the stomach, but gave no details of the structure. Moore (6) had earlier made passing reference to the stomachs of *Bythoceras* and *Nassopsis*, but he also did not deal with the anatomy in detail.

In describing the structure of the stomach of *Paludomus* it will be useful to indicate the general course of the alimentary canal. The oesophagus is a narrow tube, about 15 mm. in length; it runs in a fairly straight line, and, passing ventral to the stomach, opens into it on the ventral surface slightly to the left of the middle line. The intestine, after leaving the stomach, forms a loop over the anterior part of the stomach, and then passes towards the posterior portion where it turns round to be continued into the mantle cavity. It thus forms a double (\mathcal{O} -shaped) curve, and the anterior portion of the stomach lies under the first part of the curve. The liver or the hepatopancreas does not extend to the dorsal surface of the stomach, but lies below the stomach and along its right, left and posterior margins.

Externally the stomach is marked off by a slight constriction into an anterior and a posterior portion. It is about 10 mm. long, and its posterior portion, which is slightly the longer of the two, is about 5.5 mm. long. The oesophageal opening into the stomach has already been mentioned; the openings of the ducts of the hepatopancreas are two in number and are on the ventral surface in close apposition near the cesophageal opening. The intestine starts from the junction of the anterior and posterior chambers of the stomach, more towards the dorsal surface.

¹ For the synonymy of the species see Preston, H. B.—Faun. Brit. Ind. Freshw. Moll., p. 47 (1915).

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The anterior chamber of the stomach is thimble-shaped, and its walls, owing to a thick investment of connective tissue on the exterior, are fairly thick except in the region of the termination of the style sac. This chamber lodges the crystalline style and may, therefore, be termed The style sac is thus only a diverticulum of the stomach the style sac. proper, and the termination of the style lying inside it can be distinguished externally as a translucent area on the stomach wall. The cavity of the anterior chamber, which is roughly of the shape of the contained style, is club-shaped. The inner surface is brownish, shining, and appears smooth to the naked eye. The style sac opens by a circular opening into the stomach proper, and this opening bears on the pyloric side two projections lying almost opposite one another. Between the projections is a transverse slit, which connects the pyloric portion of the stomach with the opening of the style sac, but there is no well developed pylorus lying alongside the style sac in *Paludomus*. The connection between the pylorus and the style sac is thus confined to the region of the opening of the style sac and does not extend along the whole length of the latter, as has been described by Robson in Hypsobia (10) and Paludestrina (11). On the pyloric side running along the whole length of the style sac is a ciliated groove which is in communication with the cavity of the sac throughout its entire length. It opens posteriorly along with the opening of the style sac and forms the slit-like connection between the opening of the sac and the pyloric region of the posterior chamber of the stomach. Comparing this condition with the forms in which the pylorus and the style sac are in communication for a considerable distance,



TEXT-FIG. 1.—The stomach of *Paludomus tanschaurica* dissected out and viewed from the ventral surface. b. o., openings of the hepatopancreatic ducts; cent., central portion of the dorsal wall; int., intestine; oe., oesophagus; post. st.; posterior chamber of the stomach; st. s., style sac.

the groove is to be considered as a result of the separation of the style sac from the intestine. Anteriorly the groove turns to the anterior wall of the style sac where it is in communication with a transluscent, circular area in which the anterior end of the style appears to be held.

The style is flexible and club-shaped, about 4-5 mm. long. It is thicker at its anterior end, and tapers towards the posterior which is directed into the gastric portion of the stomach. It is usually of a distinct brownish colour, but is often much paler. The structure of the style is the same as in other Gastropods.

The posterior chamber of the stomach forms the gastric portion proper, and is, as noted above, slightly longer than the anterior chamber. It bears on its right margin a lateral protuberance, while its dorsal wall on the inner surface has 40-50 ridges, which for the most part run trans-The central part of the ventral wall has a number of verselv. conspicuous folds which may be designated as the gastric folds. The folds are three in number, an inner, an outer, and a less prominent lateral fold. The central or inner fold is broader and rounded in its posterior portion and tapering in the anterior portion. The outer fold is much narrower than the inner fold, and runs as a ridge round the inner fold along the left, posteriorly and partly on the right side. Between these folds runs a gutter-like structure, while a shallow groove lies along the right margin of the inner fold. As a result of these folds the cavity of the posterior portion of this chamber becomes much less deep than that of the anterior part. The lateral fold runs along the left margin of the ventral wall of the posterior chamber, and near its anterior end The V-shaped bend of the marginal is bent in a V-shaped manner. fold is directed inwards and comes to lie a little below the openings of the oesophagus and the ducts of the hepatopancreas, which on opening the stomach are seen to lie near the commencement of the gutter between the inner and the outer folds. The gutter thus forms a continuation of the oesophageal cavity, but its epithelial lining is of a different type from that of the oesophagus. The function of these folds appears to help in the thorough mixing up of the contents of the gastric chamber. In transverse sections of the posterior chamber the food contents are found lying between the inner and the outer folds, and in the living aninal these appear to be worked into the gutter by the cilia of the epithelium The openings of the oesophagus and the ducts of the lining the folds. hepatopancreas are, as has been noted already, in close proximity, and the food material and the secretions from the hepatopancreas are apparently mixed up and directed into the gutter by the cilia mentioned above. Similarly the marginal fold appears to prevent the food from passing directly into the anterior portion of the stomach. From the gutter the food is later passed into the anterior end of the stomach where it is subjected to the action of the free end of the crystalline style.

In the lower portion of the central gastric fold the epithelium of the stomach develops a cuticular investment which forms the "gastric shield." This shield, on dissection, is found to lie on the ventral wall of the stomach in contact with the lower portion of the inner gastric fold, and appears as a glassy, transparent structure of the consistency of cartilage. It is about 1.5 mm. long and 0.5 mm. broad, and extends to nearly the opening of the style sac. Viewed from above it appears concave and fits in between the right margin of the stomach and the lower

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portion of the inner gastric fold; it does not extend to the dorsal wall. Lying between the inner gastric fold and the margin of the ventral wall of the stomach it forms a trough-like cavity into which the free end of the style can be worked. In favourable sections I have observed the head of the style surrounded by gastric contents lying against the gastric shield.



TEXT-FIG. 2.—A figure of the dissected stomach of Paludomus tanschaurica. The style sac is not shown. b.o., openings of the hepatopancreatic ducts; c., cuticular region of the dorsal wall; c.f., central fold; c. g., ciliated groove; gr 1., gutter between the folds; gr. 2., shallow groove in the central fold; g.s., gastric shield; m.f., marginal fold; oe. o., oesophageal opening; o.f., outer fold; post. st. posterior chamber of the stomach; r., ridges on the inner surface of the dorsal wall; sl., slit of communication between the openings of the style sac and the pylorus; v. f., V-shaped bend of the marginal fold.

Histology.—The wall of the stomach is lined by ciliated epithelium. The ciliated epithelial lining in the region of the folds is placed over specially raised areas, and is well developed with large cilia projecting into the cavity of the stomach. Towards the anterior end the central fold becomes narrower, and acquires a thick, cuticular lining which is continued along the right margin and forms the gastric shield. The cells underlying the cuticular investment are devoid of cilia. The region opposite that of the gastric shield is also covered with a cuticular lining, but this is not so thick as that of the gastric shield ; it extends over the major portion of the lower part of the posterior chamber. Except in the cuticular region the dorsal inner surface of the stomach shows ridges, running transversely for the most part. In longitudinal sections these ridges are seen as folds, each of which is roughly conical with a rounded apex. The epithelial cells covering the folds are ciliated, but the cilia are not so numerous as those on the gastric folds described already. Similar folds are present in the regions of the openings of the oesophagus and the ducts of the hepatopancreas.

The entire stomach is lined by ciliated epithelial cells except in the region of the gastric shield and the cuticular investment described above. The cells of the gastric folds are narrow, columnar cells with well developed cilia, and are densely crowded. The cilia are less than a quarter of the length of the cells, and do not form an even coating as in the case of the style sac epithelium.

The region of the openings of the oesophageal and hepatopancreatic ducts is, as noted already, characterised by the presence of conical folds. The cells forming these folds are large and possess prominent, oval nuclei. The cells are broader than those of the general epithelial covering and have fewer cilia. The function of these folds appears to be glandular as some of the cells are filled with a clear secretion.

The cells underlying the gastric shield are devoid of cilia, and apparently secrete the gastric shield. The shield, when viewed in sections, shows faint striations corresponding to the outlines of the cells underlying it. The cells on the right side of the gastric shield are narrow, columnar and devoid of cilia, and have a cuticular covering. The cells further have a characteristic black pigment similar to the one noticed by Robson (11) in the case of *Paludestrina*.

Ciliated cells are also present on the projections bounding the region of communication between the pylorus and the style sac. The epithelium of the style sac consists of columnar cells of strikingly uniform size and shape. The cells are longer than broad, and each cell has a single nucleus. Mackintosh (5) mentions two in the case of *Crepidula*. The cytoplasm in the upper portion of the cells is densely granulated. The cilia on the surface form a uniform coating along the entire inner surface of the style sac, and all the cilia are of the same length, being about one-third the length of the cells themselves.

General.—The chief feature of the stomach of Paludomus is the nature of the connection between the pyloric region of the stomach and the style sac. A slit-like connection between the pylorus and the style sac has been described by Robson in Hypsobia (10) and Paludestrina (11). In Paludestrina there is a well developed pylorus from the anterior extremity of which the intestine is given off, while the opening of the style sac lies parallel to it and in the same plane. Further the style sac and the pylorus are in communication by a "narrow slit extending down the whole of their length." In Paludomus on the other hand a well developed pylorus is absent, and the slit-like communication is confined only to the region of the opening of the style sac, which in this case is reduced to a transverse slit. The separation between the pyloric and caecal elements of the stomach in Paludomus is much greater than in Paludestrina. In genera like *Turritella* and *Pterocera* the style sac is separated from the intestine, while in *Fissurella* and *Cyclostoma* a style is found in the intestine itself. Forms like *Hypsobia* and *Paludestrina* are intermediate between these two types as there is a separate communication between the style sac and the pylorus. The condition in *Paludomus* appears to be more specialised than in *Paludestrina* as there is almost a complete separation between the style sac and the intestine. The course of evolution appears to be one of progressive separation between the style sac and the pylorus from one of primitive union, and *Paludomus* appears to supply the last link in the series. The transverse slit-like communication between the style sac and the pylorus in *Paludomus* is merely the termination of the ciliated groove, and this may be taken as an additional argument for the hypothesis that the ciliated groove is the result of the separation between the intestine and the style sac.

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