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THE GUT OF THE RED CURRANT BLISTER APHID *CRYPTOMYZUS RIBIS* (HOMOPTERA: APHIDIDAE)

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INTRODUCTION

The red currant blister aphid, *Cryptomyzus ribis* L., belongs to the Aphididae sensu BÖRNER (1938) of which only three genera are known to have a filter-chamber. LINDEMANN (1948) mentions the presence of a filterchamber in this aphid but gives no description of it. The morphology and biology of *C. ribis* has been described by HILLE RIS LAMBERS (1953) and more recently by BESHIER (1966).

The aphids cause striking red blisters on the upper leaf surfaces. The pale yellowish-green aphids live beneath the blistered areas. It is a vector of the virus of vein banding disease which is presumably circulative (VAN DER MEER, 1970).

In the present study the anatomy of the gut, especially the filterchamber of *C. ribis* is investigated.

MATERIALS AND METHODS

Red currant blister aphids, *Cryptomyzus ribis*, were collected from *Ribes rubrum* in the demonstration garden of the Laboratory of Virology. They were fixed in Dubosq Brasil's fluid, embedded in paraplast (Sherwood Medical Industries, U.S.A.), and sectioned at 5 μ . Sections were stained in Ehrlich's haematoxylin-eosin.

RESULTS

The most anterior part of the alimentary tract is the food canal of the maxillary stylets. From the stylets it passes into the pharyngeal duct which in turn leads into the pharynx. This structure passes upwards through the head, and

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leads over the tentorium into the foregut to open into the coiled filtergut by way of a valve (Figs. 1–2). The filtergut enters into the filterchamber, forming the anterior part of the hindgut, and after the fourth loop it leaves the filterchamber to pass into the stomach, a sac-like dilation of the midgut. The stomach narrows towards its posterior end, and leads into the coiled intestine, from which the hindgut passes to the rectum terminating into the anal opening.

The entire gut, including the filtergut, is enclosed by a nucleated sheath (tunica propria) consisting of conspicuous flattened cells. The muscularis of the sheath is mainly built up of circular muscle fibres; the hindgut (including the filterchamber) and the rectum muscularis contains also longitudinal muscle fibres (Figs. 3–4).

During larval life the entire gut retains the same position in the aphid's body cavity. The total length of the gut is three times that of the aphid's body.

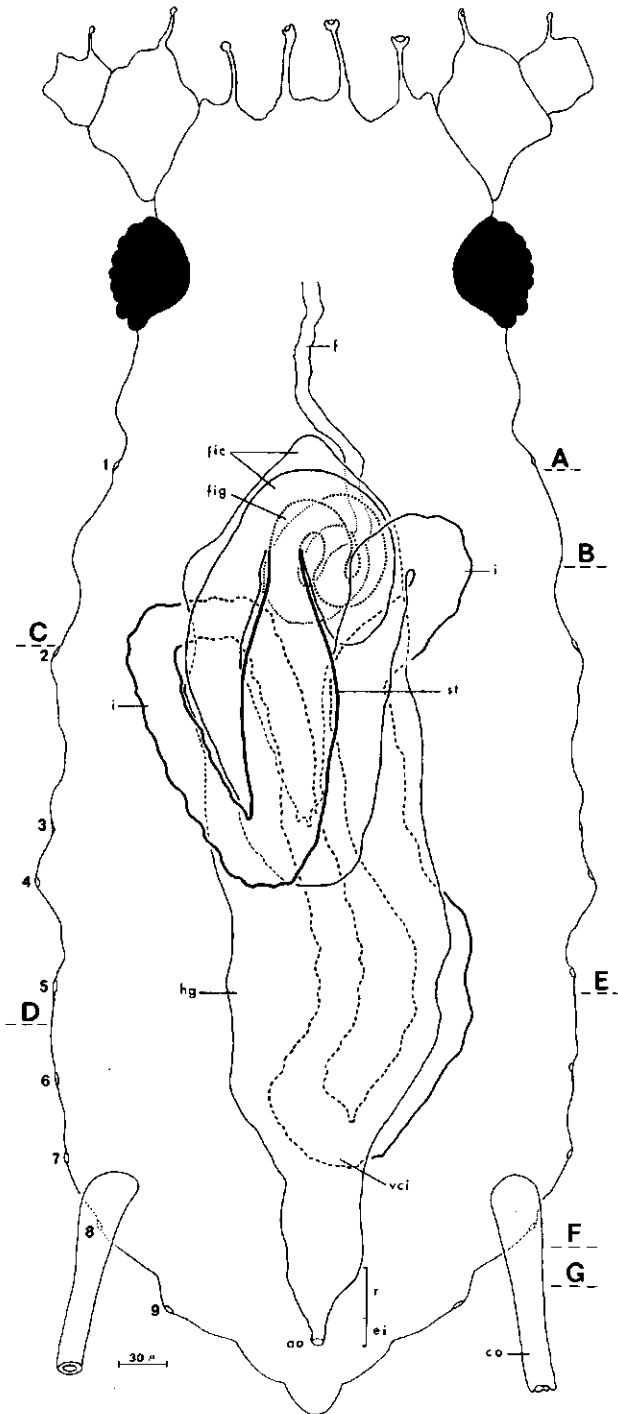
The foregut (oesophagus) runs posteriad between the two salivary glands and dorsally of the suboesophageal ganglion to terminate into the oesophageal valve half-way the thoracic ganglion and ventrally of the filterchamber. It is a uniform thin tube with a lining of squamous epithelial cells resting upon a basement membrane and secreting a delicate chitinous intima (Fig. 4 A).

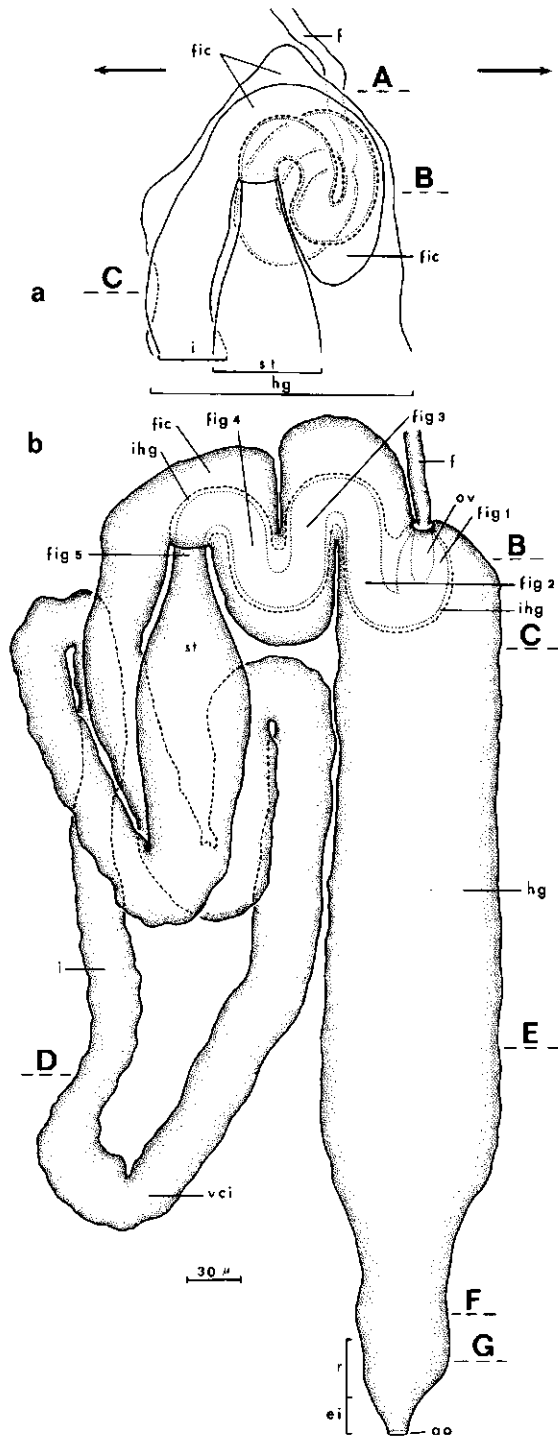
The oesophageal valve is a short invagination of the foregut projecting into the filtergut lumen. The inner surface consists of squamous epithelial cells and the outer surface of cuboidal epithelium. The valve is covered with an intima which adheres to the cell layers (Fig. 3).

The midgut is composed of the filtergut, the stomach, and the intestine (Figs. 1–2). The filtergut is located in the anterior part of the hindgut forming the filterchamber and enters it at the junction of the foregut and the oesophageal valve. Its trajectory has five loops, the first one of which is somewhat bulbous, while the other ones are tubular. After the fourth loop it leaves the filterchamber to pass into the stomach. The first two loops lie ventrally of the last two (Fig. 3). The length of the filtergut is about twice that of the foregut and that of the stomach (Fig. 5).

The epithelium of the entire filtergut consists of a single layer of cells resting upon a basement membrane joining the epithelial cells of the valve. The bulbous part of the filtergut is composed of cuboidal cells with ellipsoid – shaped to spherical nuclei, while in the tubular part the epithelial cells are pyramid-shaped with big, somewhat spherical nuclei. The cells contain nonhomogeneous basophilic cytoplasm filled with very small vacuoles; each cell has a nucleus with regularly scattered basophilic chromatin and an eosinophilic nucleolus.

FIG. 1. Dorsal aspect of a graphic reconstruction of a two days old *Cryptomyzus ribis* larva showing foregut (f), filtergut (fig), stomach (st), intestine (i), filterchamber (fic), hindgut (hg), rectum (r), epidermal invagination (ei), and anal opening (ao). The cornicles (co) are outgrowths of the fifth abdominal segment. 1–2, meso and metathoracic spiracles; 3–9, abdominal spiracles. vci, voluminous coil of intestine. The letters A–G correspond with transverse sections given in Figs. 3–4.





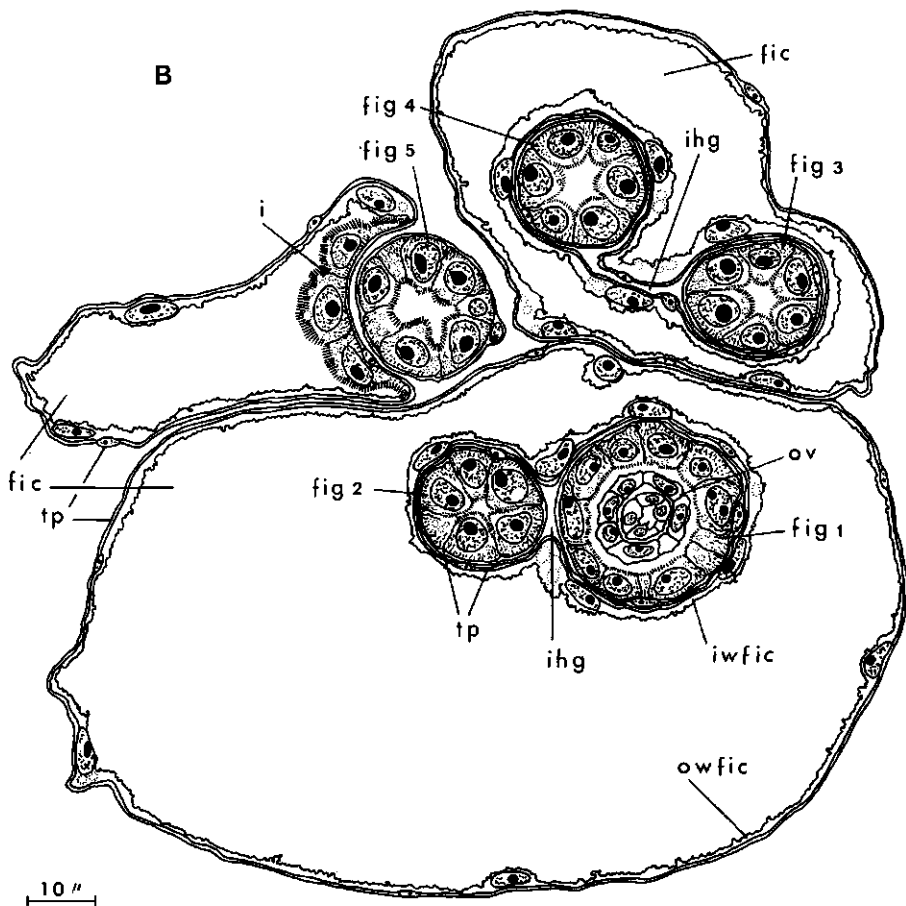


FIG. 3. Transverse section of filter system showing position of the two big loops of the filterchamber in which are situated the bulbous part of the filtergut (fig 1) with the oesophageal valve (ov) and three tubular parts of the filtergut (fig 2-4). The fifth loop (fig 5) leaves the filterchamber and lies beside them, partly enclosed by the intestine (i) which gradually passes into the filterchamber (fic), the anterior part of the hindgut. iwfic, inner wall of filterchamber; owfic, outer wall of filterchamber; tp, tunica propria (nucleated sheath), others as Fig. 1. The position of this section (B) is given in Figs. 1-2.

FIG. 2 a. Dorsal aspect of a graphic reconstruction of the filterchamber (fic). b. Schematic representation of the filterchamber of which the two big loops are pulled from each other in the direction of the arrows. Note the invagination of the anterior part of the hindgut (ihg) communicating with the haemoceum and in which the filtergut runs (fig 1-5). ov, oesophageal valve, others as Fig. 1.

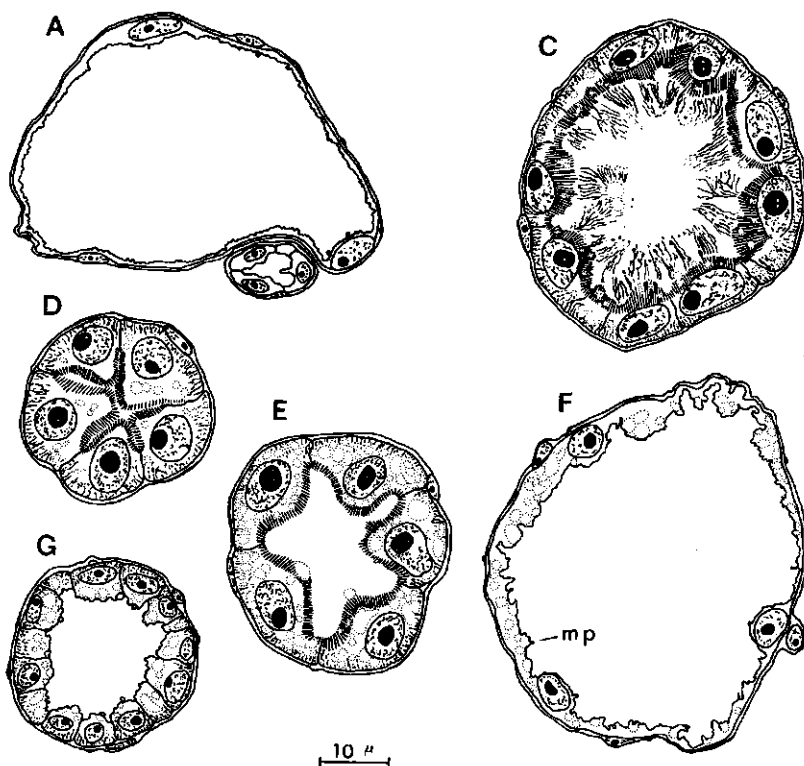


FIG. 4. Transverse sections of upper part of filterchamber and foregut (A), stomach (C), first (D) and second (E) part of intestine, hindgut (F), and rectum (G). mp, minute projections. The position of these sections are given in Figs. 1-2.

The second part of the midgut is the stomach the anterior part of which is situated closely to the filterchamber. In the abdomen it extends as far as the second abdominal spiracle. The stomach is occupied by cuboidal digestive cells containing nonhomogeneous basophilic vacuolated cytoplasm. The cells secrete material by forming buds which swell and extend between the rods of the well developed striated border. These small swellings become constricted at their base and dissolve into the lumen. Buds form continuously during larval life which proceeds into the adult stage without degeneration of cells (Fig. 4 C). Histologically the cells have similar structures and secretions as those in the posterior region of the stomach of *Myzus persicae* Sulz. (PONSEN, 1972).

The intestine is the tubular continuation of the stomach and can be divided histologically into two distinct parts. The first part is a small tube which runs from the stomach to the voluminous coil extending far into the abdomen; from there it passes gradually into a broader one forming the second part of the intestine which terminates in the filterchamber which is the anterior part

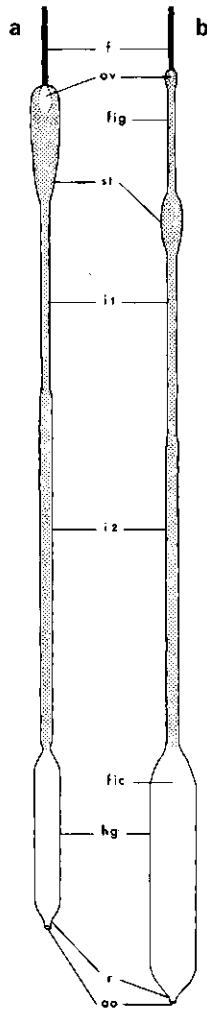


FIG. 5. Diagram of actual sizes of the gut of a one day old *Myzus persicae* larva (a) and those of a three days old *Cryptomyzus ribis* larva (b). Both larvae have approximately the same size. The stippling represent the midgut. i 1, first part of intestine; i 2, second part of intestine, others as Figs. 1-2.

of the hindgut. The second part is about twice as long as the first part, and the entire intestine is eight times as long as the stomach (Fig. 5). The large squamous cells of the first part protrude far into the lumen forming a stellate closed or partly closed lumen (Fig. 4D). They contain nonhomogeneous basophilic cytoplasm with some vacuoles and a spherical to ovoid-shaped nucleus. In the second part of the intestine (Fig. 4E) the cells are situated around a wide lumen; they are strongly vacuolated and the cytoplasm is homogeneously

basophilic with ovoid-shaped nuclei. The organization of the intestine of *C. ribis* agrees with that of *M. persicae*.

The basal plasma membrane of the cells lining the entire midgut is finely infolded; their free surface is lined by a well developed striated border, although in the filtergut it is smaller than in the stomach or in the intestine.

The anterior part of the hindgut is the filterchamber in which the filtergut is situated. The filterchamber is composed of two big loops, the first one of which receiving the second part of the intestine, lies dorsally of the second loop (Fig. 2 a). The last one runs as a big sac caudad ventrally of the stomach and dorsally of the voluminous coil of the intestine towards the rectum. The two big loops of the filterchamber lie close to each other between the two salivary glands and dorsally of the thoracic and abdominal ganglion. In paraplasm sections (Fig. 3) it seems that they are connected with each other although in dissections the two loops can be separated from one another without damage. A schematic representation of the filter complex is given in Fig. 2 b.

The hindgut, including the filterchamber, is highly transparent and consists of a single layer of long, flattened, epithelial cells with long ellipsoid-shaped nuclei. The cells rest upon a basement membrane; their apical membrane is somewhat folded and coated by a delicate intima showing a mass of minute projections into the lumen. After the fourth abdominal spiracle the hindgut cells become gradually thicker (Fig. 4 F); they contain vacuoles and large ovoid nuclei which protrude into the lumen. The inner wall is strongly folded consisting of minute projections.

The coiled filtergut is surrounded by an epithelial sheath the cells of which have the same structure as those of the filterchamber and the hindgut. Transverse sections of the filterchamber (Fig. 3) show the filtergut epithelium with its nucleated sheath (*tunica propria*) surrounded by the epithelial cells of the filterchamber and its nucleated sheath, the lumen of the filterchamber, which in its turn is enclosed by an epithelial sheath of the filterchamber. Consequently the filtergut runs through an invagination of the anterior part of the hindgut. The space between the two nucleated sheaths of both the filtergut and the filterchamber, especially that at the inner side of each filtergut loop (Figs. 2 b and 3), suggests that this invagination is in open connection with the haemocoel allowing the haemolymph to circulate freely through the invagination. The invagination guarantees the peristaltic movements of the filtergut.

The rectum is built up of a single layer of columnar cells having small vesicles or exudations liberating secretion into the lumen (Fig. 4 G). The basal part of these cells shows laminated structures and the inner wall is coated by a delicate intima.

The posterior part of the rectum is an invagination of the epidermis. Near the anal opening muscle fibres are attached to the intima, originating laterally and dorsally from the wall of the ninth abdominal segment or cauda.

DISCUSSION

The first description of a 'filterchamber' has been given by DUFOR (1825) in his study on the digestive system of the cicadoids, *Cicada orni* and *Cicada plebeia*, and by MARK (1877) in his study of the coccoid, *Lecanium hesperidum*. According to BERLESE (1893), working with the same coccoid, this organ serves to filtrate the excess of liquid food directly from the anterior region of the midgut to the hindgut. The term filterchamber was introduced by WEBER (1930. Filterkammer). Later on many investigators studied the filter complex of representatives of *Cicadoidea*, *Coccoidea*, *Psyllidae*, and *Aleyrodidae* which has been reviewed by PESSON (1944) and GOODCHILD (1966). The presence of a filterchamber in the *Aphididae* has been described for *Trama troglodytes* v. Heyd., *Lachnus pineus* (= *Cinara pinea* Mordv.), *Lachnus viminalis* (= *Tuberolachnus salignus* Gmelin), *Lachnus bogdanowi* (= *Cinara pruinosa* Hartig), *Lachnus nudus* (= *Cinara escherichi* Börner), *Lachnus quercus* (= *Stomaphis quercus* L.) (MORDWILKO, 1895), *Lachnus pineti* (= *Schizolachnus pineti* F.) (MORDWILKO, 1895; LEONHARDT, 1940), *Longistigma caryae* Harris (KNOWLTON, 1925), *Lachnus piceae* (= *Cinara piceae* Pz.) (LEONHARDT, 1940), *Lachnus roboris* L. (MICHEL, 1942), and *Schizolachnus* sp. (BRAMSTEDT, 1948). Moreover, BÖRNER (1938) reported a filterchamber in the lachnid genera, *Stomaphis* and *Eulachnus*, and in the aphidid genera *Capitophorus*, *Cryptomyzus*, and *Acaudinum*. Later, BÖRNER (1952) stated that all his *Lachnidae* have a filterchamber. According to these authors the parts involved in the filterchamber are the anterior tubular midgut and the anterior part of the hindgut (MORDWILKO, 1895; BRAMSTEDT, 1948), the anterior tubular midgut and the junction of the midgut and the hindgut (LEONHARDT, 1940), the anterior dilated midgut (stomach) and the posterior part of the midgut (KNOWLTON, 1925; MICHEL, 1942). In *C. ribis* the anterior tubular part of the midgut (filtergut) is composed of five coils situated in the anterior part of the hindgut (Fig. 2), while in the aphids mentioned above the anterior part of the midgut within the filterchamber is a rather straight tube.

In the green peach aphid, *M. persicae*, which does not possess a filterchamber, the anterior and posterior region of the stomach consists of cuboidal epithelial cells, while the middle region is occupied by tall, fingerlike columnar digestive cells. The latter secrete material by constricting of apical cell parts. The cells of the posterior region secrete material by forming buds. Both processes continue during larval life without any degeneration or multiplication of cells (PONSEN, 1972). It is interesting to note that histologically the epithelial cells of the filtergut of *C. ribis* (Fig. 3), especially those in the bulbous part, show a similar structure as the epithelial cells in the anterior region of the stomach of *M. persicae*. Presumably these latter cells have a similar function as those of the filtergut in *C. ribis*, namely to filtrate an excess of liquid food from the stomach of *M. persicae* to the haemoceul. On the other hand the stomach of *C. ribis* consists of one type of digestive cells (Fig. 4C) which are in a histological sense similar to those lying in the posterior region of the

stomach of *M. persicae*. The tall, fingerlike columnar digestive cells in the middle region of the stomach of *M. persicae* are completely lacking in the gut of *C. ribis*. However, in the aphids investigated by MORDWILKO (1895), LEONHARDT (1940), and MICHEL (1942), the stomach is completely occupied by tall columnar digestive cells, although a striated border has not been observed.

As shown in Fig. 5 the stomach of *M. persicae* is approximately three times as large as that of *C. ribis*, while in both aphids the intestine has a similar structure and the length of the entire midgut is practically equal. On the other hand the hindgut of *C. ribis* is approximately three and a half times as large as that of *M. persicae*. This may be necessary to digest the excess of liquid food which is transported through the filtergut to the filterchamber. The suggestion is made that the filter complex in *C. ribis* is a primitive relic and that in case of *M. persicae* the function of the filtergut has been taken over by the epithelial cells in the anterior region of the stomach.

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