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THE DIGESTIVE SYSTEM OF *EULACHNUS BREVIPILOSUS* BÖRNER (HOMOPTERA: APHIDIDAE)

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INTRODUCTION

The aphid *Eulachnus brevipilosus* BÖRNER belongs to the Lachnidae sensu BÖRNER (1952), of which all species have a filterchamber (BÖRNER, 1938; BÖRNER and HEINZE, 1957; Table 1). This narrow and elongate aphid was found on the needles of *Pinus montana* MILL. PINTERA (1968) described the morphology and biology of this and the following aphids: *Eulachnus agilis* (KLTB.), *E. rileyi* (WILLIAMS), *E. alticola* BÖRNER, *E. nigricola* (PAŠEK), and *E. cembrae* BÖRNER. The filtersystem of a number of aphids within the family Lachnidae has been studied by MORDWILKO (1895), KNOWLTON (1925), LEONHARDT (1940), MICHEL (1942), and BRAMSTEDT (1948).

Investigations into the anatomy of the digestive system of *Eulachnus brevipilosus* BÖRNER were carried out because BÖRNER (1938) and KUNKEL and KLOFT (1977) mention a filtersystem in *Eulachnus* sp.

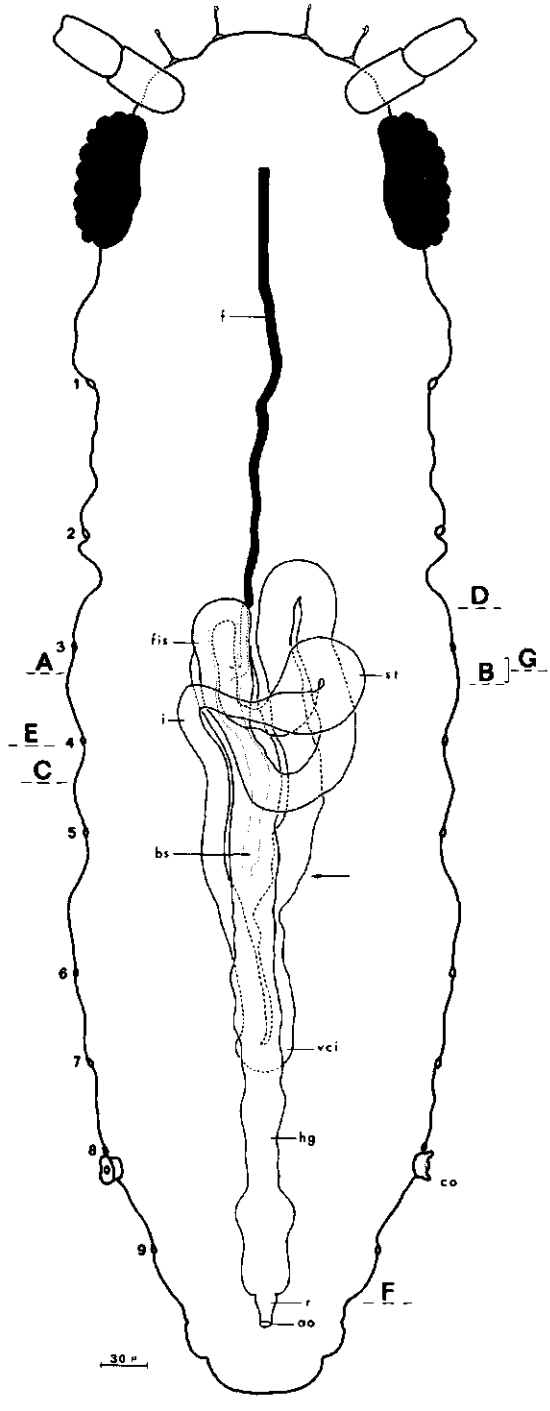
MATERIALS AND METHODS

The lachnids *Eulachnus brevipilosus*, *E. agilis*, and *E. rileyi* were collected from *Pinus montana* MILL. at Wageningen, and *E. nigricola* and *E. rileyi* from *Pinus nigra* ARNOLD at Bennekom. The latter aphid is called in America the powdery pine needle aphid (MEDLER and GHOSH, 1969).

The aphids were fixed in DUBOSQ BRASIL'S fluid, embedded in paraplast, 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 leads over the tentorium into the foregut to open laterally into the filtergut by way of a valve (Figs. 1 and 2). The ∧-shaped filtergut is completely surrounded by the filterchamber forming a concentric filtersystem. Subsequently the filtergut leads into the stomach, a coiled tubular part of the midgut. The stomach continues into the coiled intestine, from which the hindgut passes into the rectum terminating in the anal opening. During larval life the entire gut retains the same position in the aphid's body cavity. The total length of the gut is two and a half times that of the aphid's body.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The foregut (oesophagus) extends from the tentorium to the metathorax. It starts as a uniform thin tube which runs posteriad between the two salivary glands and dorsally to the nervous system. At the end of the abdominal ganglion the foregut opens laterally into the filtergut. The length of the foregut is about one and a half times that of *Myzus persicae* and about two times that of *Cryptomyzus ribis* (PONSEN, 1972, 1977; Fig. 6). This long tube consists of a single layer of squamous epithelial cells secreting a chitinous intima (Fig. 3A).

The oesophageal valve is a short invagination of the foregut projecting laterally into the filtergut lumen (Fig. 4d). Its situation is asymmetric; 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. 3A).

The midgut is the longest part of the alimentary canal and is composed of the filtergut, stomach, intestine, and blindsack.

The filtergut can be divided into an ascending part and a descending one forming a $\wedge$-shaped structure (Figs. 2 and 4d). The ascending filtergut is somewhat bulbous and its epithelium consists of thick squamous cells with ellipsoid-shaped nuclei. The descending filtergut is tubular and lined with triangular epithelial cells forming a closed stellate lumen; their nuclei are somewhat spherical (Fig. 3A). On the level of the second abdominal spiracles the filtergut opens into the stomach.

The second part of the midgut is the stomach; it has a tubular structure consisting of one loop and is situated in the first abdominal segment (Figs. 1 and 2). The diameter of the tubular stomach is approximately the same as that of the second part of the intestine (Fig. 6d). Both in dissections and paraplast sections the tubular stomach is readily distinguished from the rest of the gut by the secretory activity of the stomach epithelium. The histology and secretion of this epithelium resemble those of the posterior region of the stomach of *M. persicae* and the entire stomach of *C. ribis* (Fig. 3B).

The intestine can be divided histologically into two distinct parts. The first part is a small tube which runs from the tubular stomach to a point (see arrow in Fig. 1) beyond the voluminous coil extending far into the abdomen; from there it passes into a broader one forming the second part of the intestine which terminates into the filterchamber. In dissections it was seen that the union of the small intestine with the broader one is supplied by a nerve originating from the main abdominal nerve cord. The second part of the intestine is about one and a half times as long as the first part. Transverse sections of the first part of the intestine show 3–4 triangular cells containing some vacuoles and a spherical to ovoid-shaped nucleus (Fig. 3C). The wide region of the intestine shows, in

◀ Fig. 1. Dorsal aspect of a graphic reconstruction of a two day old *Eulachnus brevipilosus* larva showing foregut (f), stomach (st), intestine (i), filtersystem (fis), blindsack (bs), hindgut (hg), rectum (r), and anal opening (ao). The poriform, small cornicles (co) are outgrowths of the sixth adbominal 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 and 5.

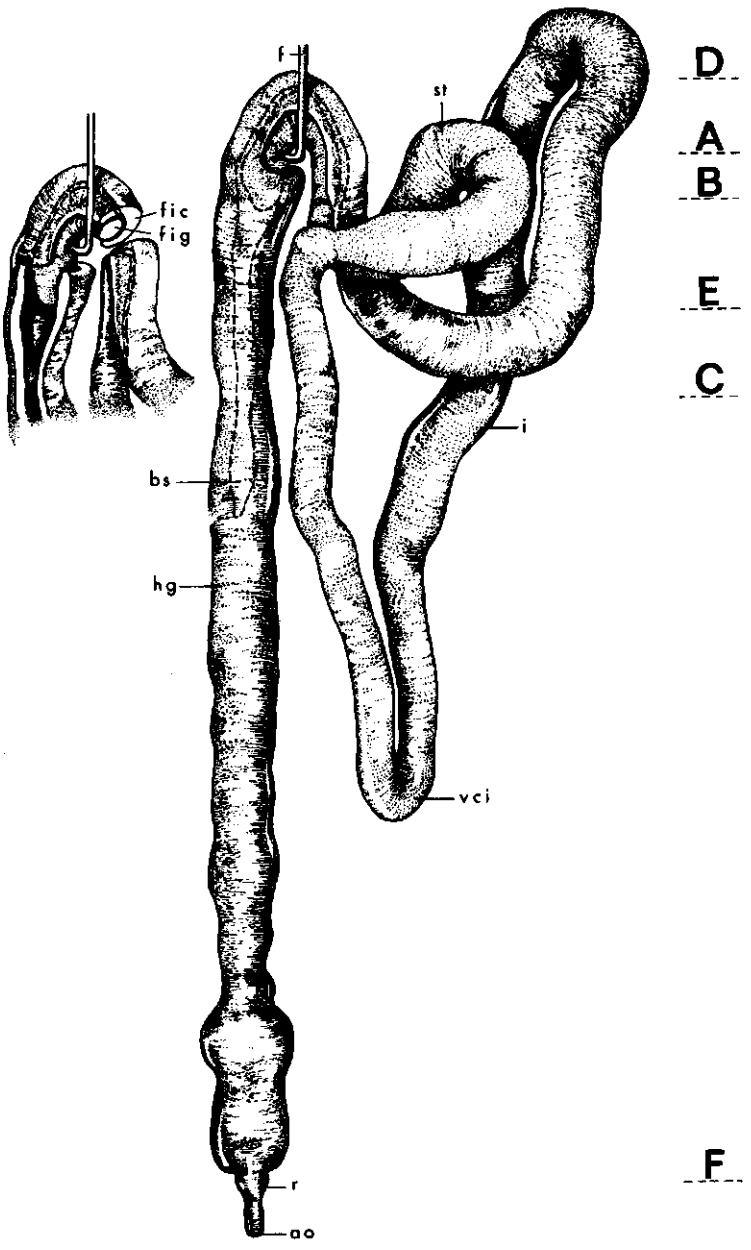

Fig. 2. Semi-schematic representation of the digestive system of *Eulachnus brevipilosus*. fic, filter-chamber; fig, filtergut, other abbreviations as in Fig. 1. The letters A-F correspond with transverse sections given in Fig. 3.

transverse sections, an arrangement of 5–6 triangular cells which are strongly vacuolated and have an somewhat spherical nucleus (Fig. 3D). The basal plasma membrane of both cell types is finely infolded; their free surface is lined by a well developed striated border forming a stellate closed or partly closed lumen.

The filterchamber resembles in transverse sections a horseshoe-shaped tube situated around the filtergut and forming a concentric filtersystem (Figs. 2 and

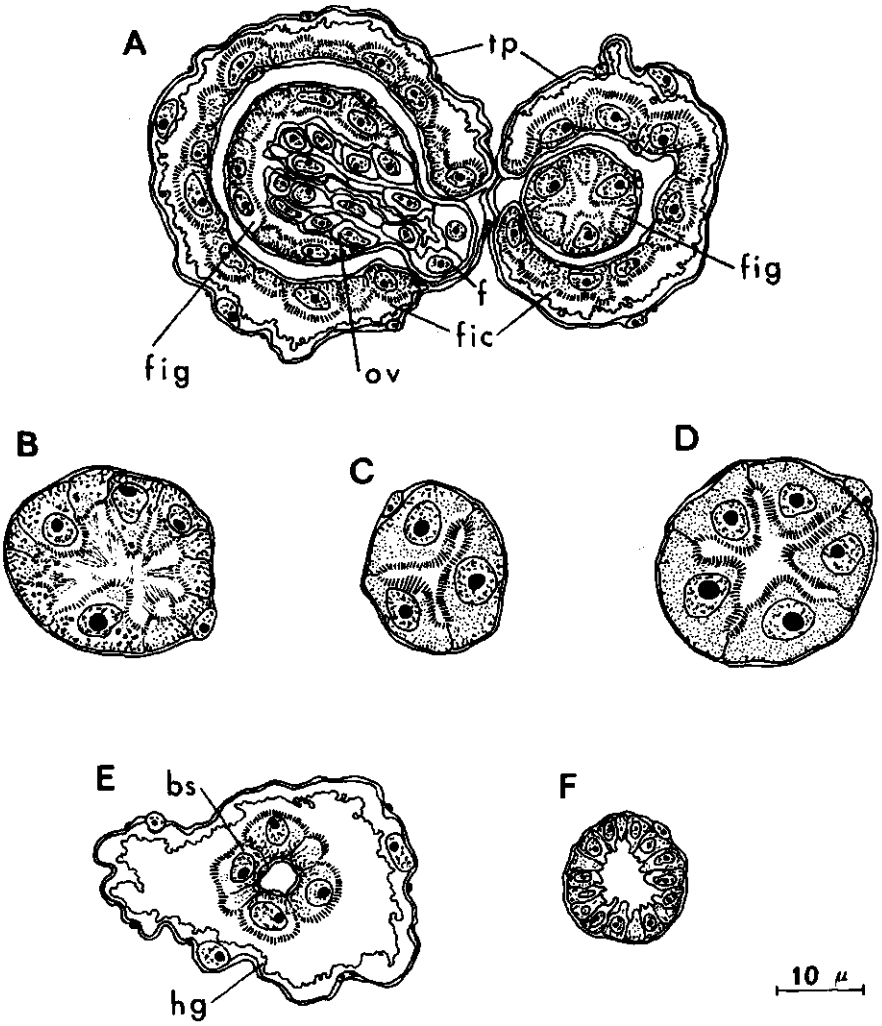

Fig. 3. Transverse section of the middle part of the filtersystem (A) showing encapsulation of the filtergut by the filterchamber, and the entrance of the foregut into the filtergut. Its position in the aphid is given in Fig. 5. Transverse sections of the tubular stomach (B), the first (C) and second part of the intestine (D), the hindgut and invagination of the filterchamber or blindsack (E), and the rectum (F). ov, oesophageal valve; tp, tunica propria, other abbreviations as in Figs. 1 and 2. The position of the sections (A-F) are given in Figs. 1 and 2.

4c). It is lined with both endodermal and ectodermal epithelium but so arranged that the endodermal cells are situated on the side facing the filtergut and the very thin ectodermal cells on the outer wall of the filterchamber (Fig. 3A). The entire gut, including the filtergut and inner wall of the filterchamber, is enclosed by a nucleated sheath (tunica propria) consisting of elongate cells housing the circular muscle fibres. The ectodermal part of the filterchamber as well as the hindgut are still provided with longitudinal muscles. Moreover, the two extremities of the filterchamber are connected together by a nucleated sheath which in turn is fused with the nucleated sheath of the opposite filtersystem (Fig. 4e).

The endodermal part of the filterchamber possesses an invagination which runs caudad inside the hindgut to terminate blindly on the level where the first part of the intestine passes into the second one (Fig. 1, see arrow). On the other hand this invagination or blindsack may be also considered as a bulge of the second part of the intestine (Figs. 4b and 6d). The blindsack is connected on each side of its termination with the hindgut by a 'membrane' presumably to keep the blindsack in position. The membranes are attached to the nucleated sheath of the blindsack and to that of the hindgut, running between the epithelial cells of both organs. Between the two nucleated sheaths of both the inner wall of the filterchamber and the filtergut is a space by which the haemolymph can circulate freely and into the blindsack.

In contrast to the triangular epithelial cells of the intestine the endodermal part of the filterchamber including the blindsack consists of thick squamous cells. They have a distinct striated border and numerous basal infoldings; their homogeneous cytoplasm contains some vacuoles and an ellipsoidal nucleus. The ectodermal part of the filterchamber is lined with very thin cells which are identical to those of the hindgut (Figs. 3A and 3E).

The sac-like hindgut is highly transparent and consist of a single layer of long flattened cells of which the ovoid nuclei bulge out into the lumen. Their apical membrane shows a mass of irregular projections and is coated by a delicate intima. The hindgut is surrounded by a nucleated sheath containing circular and longitudinal muscle fibres. However no peristaltic movements have been observed during dissections.

The rectum is built up of a single layer of small columnar cells quite different from the epithelial cells of the hindgut (Fig. 3F). It is a very short tube and continues in an epidermal invagination of which the cuticular lining is thicker than that of the rectal epithelium. 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. The rectum is innervated by a nerve originating from the medial dorsal nerve which runs alongside the dorsal vessel.

In *E. brevipilosus* as well as in *M. persicae*, *C. ribis*, and *Subsaltusaphis ornata* (PONSEN, 1972, 1979) the haemolymph is characterized by the absence of circulating haemocytes. On the other hand, numerous waxy droplets originating from fat cells are visible throughout the body cavity of the aphid during its life. The tapering cell processes of the spindle-shaped or stellate connective tissue

cells extend throughout the haemocoel and are connected with the various internal organs including the digestive system.

The digestive system especially the filtersystem of the lachnids, *Eulachnus agilis*, *E. nigricola*, and *E. rileyi* is anatomically and histologically identical to that of *E. brevipilosus*. All four species have a somewhat long foregut which laterally opens by way of a oesophageal valve into a ∧-shaped filtergut, a tubular coiled stomach, a coiled intestine, a filterchamber which completely surronds the filtergut, a long blindsack, a sac-like hindgut, and a rectum terminating in the anal opening.

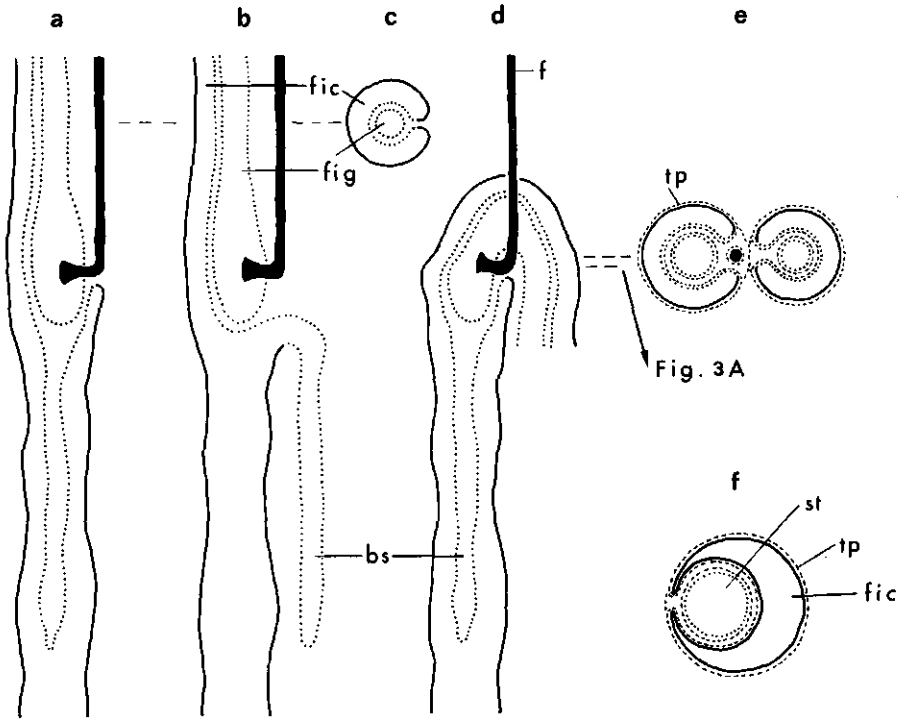

Fig. 4. Diagrams illustrating the concentric filtersystem of *Eulachnus brevipilosus* (a-e). Axial longitudinal section of the filtersystem in a straightened position (a), and of which the blindsack is turned outside (b) as depicted in Fig. 6d. Transverse section of the filtersystem to show encapsulation of the filtergut by the filterchamber (c). Axial longitudinal section of the filtersystem in its original position (d) as depicted in Fig. 2. Transverse section of the filtersystem showing the tunica propria surrounding the foregut, filtergut, and filterchamber, and connecting together the two extremities of the filterchamber (e). Transverse section of the concentric filtersystem of *Subsaltusaphis ornata* to show encapsulating fo the stomach by the filterchamber with the tunica propria (f). The dotted line represents the endodermal epithelium and the continuous line the ectodermal epithelium. For explanation of abbreviations see Fig. 3.

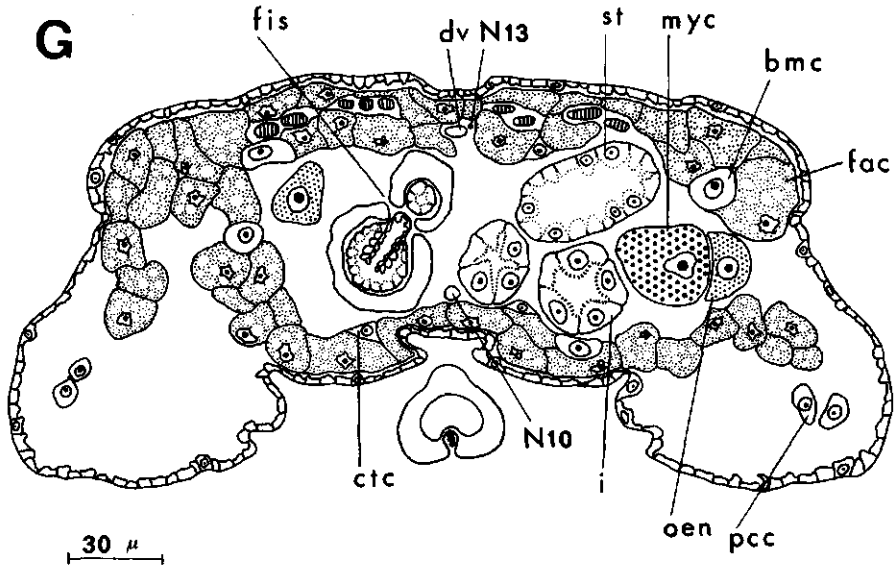

Fig. 5. Composition made from four successive transverse serial sections through the metathorax of a two day old *Eulachnus brevipilosus* larva. Note the filtersystem (fis) in its original position. The stylet bundle lies in a dorsal groove of the proboscis (= labium) and shows in its course a torsion of 180°. The muscles of the legs are omitted. bmc, basophilic mesodermal cell; ctc, connective tissue cell; dv, dorsal vessel; fac, fat cell; myc, mycetocyte; N10, main abdominal nerve; N13, medial dorsal nerve; oen, oenocyte; pcc, pericardial cells lying in the coxae of the third pairs of legs, other abbreviations as in Fig. 1. The position of this section (G) is given in Fig. 1.

Discussion

In many aphid species (table 1 in Ponsen, 1979) the digestive system comprises three regions, foregut, midgut, and hindgut, whereas the midgut is subdivided into the stomach, a dilated part of the midgut and a coiled intestine. However, in *Trama troglodytes* v. Heyd., *Lachnus piceae* (= *Cinara piceae* (Pz.)), *Lachnus roboris* L. (= *L. roboris* (L.)), and *Longistigma caryae* (Harris) the first part of the midgut has a tubular structure which is enveloped by the filterchamber forming a filtersystem. This tubular structure has been called 'Vordermagen' (forestomach) by Mordwilko (1895), Leonhardt (1940), and Michel (1942), and mid-intestine or stomach by Knowlton (1925). From the descriptions and photographs presented by these authors, it may be concluded that this tubular structure can be considered as a filtergut which in turn passes into what is a true stomach as judged by the presence of digestive and secretory epithelial cells. A similar division of the midgut is observed in *C. ribis* (Ponsen, 1977) and *E. brevipilosus* (Fig. 2) namely filtergut, stomach, and intestine. The tubular filtergut may occur in various forms, curved in *T. troglodytes* (Mordwilko, 1895), *C. piceae* (Leonhardt, 1940), and *L. roboris* (Michel, 1942), straight and som-

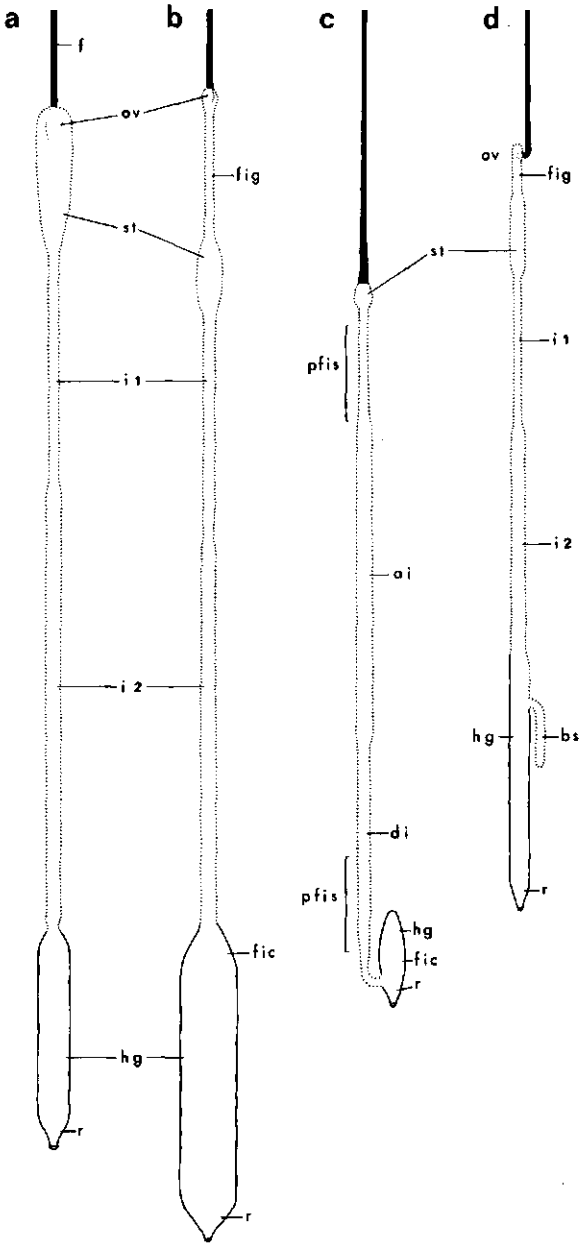

Fig. 6. Diagram of actual sizes of the digestive system of a one day old *Myzus persicae* larva (a), those of a three day old *Cryptomyzus ribis* larva (b), those of a two day old *Subsaltusaphis ornata* larva (c), and those of a two day old *Eulachnus brevipilosus* larva (d). The dotted line represents the endodermal epithelium and the continuous line the ectodermal epithelium. ai, ascending intestine; di, descending intestine; i1, first part of intestine; i2, second part of intestine; pfis, parallel filtersystem, other abbreviations as in Fig. 3.

Table 1. A list of investigated aphids within the family Lachnidae.

Name used by author	Present name	Filter system	Author
Cinara brauni BÖRNER	*Cinara brauni* BÖRNER	+	KUNKEL and KLOFT, 1977
Cinara cembrae (SEITNER)	*Cinara cembrae* (SEITNER)	+	KUNKEL and KLOFT, 1977
Cinara confinis (KOCH)	*Cinara confinis* (KOCH)	+	KUNKEL and KLOFT, 1977
Lachnus farinosus CHOLODK.	*Cinara costata* (ZETT.)	+	LEONHARDT, 1940; KUNKEL and KLOFT, 1977
Cinara cuneomaculata (DEL GUERCIO)	*Cinara cuneomaculata* (GUERCIO)	+	KUNKEL and KLOFT, 1977
Cinara cupressi (BUCKTON)	*Cinara cupressi* (BUCKTON)	+	KUNKEL and KLOFT, 1977
Lachnus nudus DE GEER	*Cinara escherichi* (BÖRNER)	+	MORDWILKO, 1895; KUNKEL and KLOFT, 1977
Cinara juniperi (DE GEER)	*Cinara juniperi* (DE GEER)	+	KUNKEL and KLOFT, 1977
Cinara laricis (HTG.)	*Cinara laricis* (HTG).	+	KUNKEL and KLOFT, 1977
Cinara neubergi (ARNHART)	*Cinara neubergi* (ARNHART)	+	KUNKEL and KLOFT, 1977
Lachnus pichtae MORDV.	*Cinara pectinatae* (NÖRDLINGER)	+	LEONHARDT, 1940; KUNKEL and KLOFT, 1977
Lachnus piceae	*Cinara piceae* (PZ.)	+	LEONHARDT, 1940; KUNKEL and KLOFT, 1977
Lachnus hyalinus KOCH	*Cinara pilicornis* (HTG.)	+	LEONHARDT, 1940; KUNKEL and KLOFT, 1977
Lachnus pineus	*Cinara pinea* (MORDV.)	+	MORDWILKO, 1895; KUNKEL and KLOFT, 1977
Cinara pini (L.)	*Cinara pini* (L.)	+	KUNKEL and KLOFT, 1977
Lachnus bogdanowi	*Cinara pruinosa* (HTG.)	+	MORDWILKO, 1895
Cinara stroyani (PAŠEK)	*Cinara stroyani* (PAŠEK)	+	KUNKEL and KLOFT, 1977
Eulachnus sp.	*Eulachnus* sp.	+	BÖRNER, 1938; KUNKEL and KLOFT, 1977
Lachnus iliciphilus (GUERCIO)	*Lachnus iliciphilus* (GUERCIO)	+	PONSEN
Lachnus pallipes (HTG.)	*Lachnus pallipes* (HTG.)	+	KUNKEL and KLOFT, 1977
Dryobius roboris L.	*Lachnus roboris* (L.)	+	WITLACZIL, 1884, 1885
Lachnus roboris L.	*Lachnus roboris* (L.)	+	MICHEL, 1942; KUNKEL and KLOFT, 1977
Longistigma caryae (HARRIS)	*Longistigma caryae* (HARRIS)	+	KNOWLTON, 1925
Maculolachnus submacula (WLK.)	*Maculolachnus submacula* (WLK.)	+	PONSEN
Lachnus pineti KOCH	*Schizolachnus pineti* (F.)	+	LEONHARDT, 1940; KUNKEL and KLOFT, 1977
Lachnus quercus L.	*Stomaphis quercus* (L.)	+	MORDWILKO, 1895
Stomaphis sp.	*Stomaphis* sp.	+	BÖRNER, 1938
Trama troglodytes v. HEYD.	*Trama troglodytes* v. HEYD.	+	MORDWILKO, 1895
Lachnus viminalis BOYER DE FONSC.	*Tuberolachnus salignus* (GMELIN)	+	MORDWILKO, 1895; KUNKEL and KLOFT, 1977

ewhat dilated in *L. caryae* (KNOWLTON, 1925) and *Schizolachnus* sp. (BRAMSTEDT, 1948), coiled in *C. ribis* (PONSEN, 1977), or ∧-shaped in *E. brevipilosus* (Figs. 2 and 4d).

In general the foregut passes frontally into the stomach (Table 1 in PONSEN, 1979) or frontally into the filtergut (LEONHARDT, 1940; MICHEL, 1942; PONSEN, 1977), in which the foregut terminates into an oesophageal valve. Such a symmetric position of the oesophageal valve is not found in *E. brevipilosus* (Figs. 2 and 4d), *T. troglodytes* (MORDWILKO, 1895), *L. caryae* (KNOWLTON, 1925), and *Schizolachnus* sp. (BRAMSTEDT, 1948). In these species the foregut opens laterally into the filtergut. In *S. ornata* it terminates laterally in the stomach, although an oesophageal invagination is lacking in this aphid (PONSEN, 1979).

After MORDWILKO (1895) PONSEN (1979) stated that the filterchamber first enfolds the filtergut so the latter is completely surrounded after which the two extremities of the filterchamber fuse together. After this process the filterchamber is closed and the filtergut lies inside the filterchamber forming a concentric filtersystem. On the other hand, in the lachnids studied by KNOWLTON (1925), LEONHARDT (1940), and MICHEL (1942) (Table 1) the two extremities of the filterchamber are separated as depicted in Fig. 4. A similar structure is observed for the filtersystem of *E. brevipilosus*. On reflection it appears that both the filtergut of *C. ribis* (Fig. 4c) and the stomach of *S. ornata* (Fig. 4f) are encapsulated by the filterchamber in the same way as described for the above mentioned lachnids.

Paraplast sections have shown that the filtergut of *C. ribis* (PONSEN, 1977) and *E. brevipilosus* (Fig. 3A), and the stomach of *S. ornata* (PONSEN, 1979) are not fused with the inner wall of the filterchamber. The presence of a space between the filtergut and the inner wall of the filterchamber is also observed in the aphids studied by MORDWILKO (1895), KNOWLTON (1925), LEONHARDT (1940), and MICHEL (1942). Moreover, LEONHARDT (1940) mentions that the filterchamber can move away from the filtergut during dissections. Further it appears that in *L. caryae* (KNOWLTON, 1925; Plate II, Fig. 2) and *E. brevipilosus* (Figs. 3A and 4e) the two extremities of the filterchamber which surround the filtergut completely, are connected together by a nucleated sheath (tunica propria) housing the muscle fibres. A similar connection is also found between the two extremities of the filterchamber of *C. ribis* and *S. ornata*. Although the two extremities of the filterchamber are not fused together, the filtersystem seems to be effectively a concentric one. This in contrast to the parallel filtersystem in which two regions are fused together as in *S. ornata* (PONSEN, 1979).

Summarizing it appears that (1) the concentric filtersystem of the lachnids and *C. ribis* consists of the filtergut and filterchamber, (2) the filterchamber completely encapsulates the filtergut (Fig. 4), (3) the two extremities of the filterchamber are not fused together, but are connected together by a nucleated sheath (tunica propria), (4) there exists a space between the filtergut and the inner wall of the filterchamber. These features apply also to the concentric filtersystem of *S. ornata* although in this aphid the filtergut represents the stomach (Fig. 4f).

In *L. roboris* (MICHEL, 1942), *C. ribis*, and *S. ornata* (PONSEN, 1977, 1979) the

filterchamber of the concentric filtersystem is lined with very thin ectodermal epithelium. On the other hand, in the aphids studied by MORDWILKO (1895) and LEONHARDT (1940) (Table 1) the inner wall of the filterchamber is lined with ectodermal cells which are rather tall compared with those of the outer wall. From the drawings (MORDWILKO, 1895) and photographs (LEONHARDT, 1940) given by these authors, it may be concluded that these rather tall cells are in fact endodermal epithelial cells. A similar structure is observed in *E. brevipilosus* (Fig. 3A) where the inner wall of the filterchamber facing the filtergut is lined with thick squamous cells in contrast to the triangular endodermal cells of the intestine. The thick squamous cells are endodermal in origin as judged by the presence of a distinct striated border. As in *L. caryae* (KNOWLTON, 1925), the inner wall of the filterchamber is lined with endodermal cells, whereas the epithelium of the outer wall is ectodermal in origin and contains flat cells. To summarize: in all aphids at present known to posses a concentric filtersystem the inner wall of the filterchamber is lined either with endodermal cells or with ectodermal cells, whereas the outer wall of the filterchamber consists only of ectodermal epithelium. Both the filtergut and the stomach are endodermal.

The term blindsack was introduced by LEONHARDT (1940; Blindsack) to describe an invagination of the filterchamber inside the hindgut. In the aphids studied by LEONHARDT (1940) and MICHEL (1942) the blindsack is very short and lined with very thin ectodermal epithelium. On the other hand, *E. brevipilosus* possesses a very long blindsack (Figs. 1, 2, 4, and 6) consisting of endodermal cells with a distinct striated border (FIG. 3E).

In contrast to the majority of investigated aphid species, *E. brevipilosus* possesses a tubular stomach with one coil and a diameter similar to that of the second part of the intestine (Figs. 1 and 2). In a schematic drawing of the digestive system of *Eulachnus* sp. given by BÖRNER (1938) the stomach is lacking, presumably because it is not easily distinguishable from the intestine. A tubular stomach is also observed in *L. caryae* (KNOWLTON, 1925), *Lachnus pineti* KOCH (= *Schizolachnus pineti* (F.)) (LEÓNHARDT, 1940), and *L. roboris* (MICHEL, 1942), as well as in *Symydobius* sp. and *Drepanosiphon* sp. (BÖRNER, 1938).

SUMMARY

The digestive system of the aphid, *Eulachnus brevipilosus* BÖRNER, has a somewhat elongated foregut which opens laterally into the ∧-shaped filtergut by way of a valve. The filtergut is completely encapsulated by the filterchamber forming what is effectively a concentric filtersystem. It passes into a tubular stomach with one coil which leads into the coiled intestine; this is followed in succession by the filterchamber, the hindgut, and the rectum which terminates in the anal opening. The filterchamber possesses an invagination or blindsack which runs caudad inside the hindgut.

Samenvatting

Het spijsverteringskanaal van de bladluis, *Eulachnus brevipilosus* Börner, heeft een tamelijk lange slokdarm die lateraal in de ∧-vormige filterdarm uitmondt via een oesophageale klep (Fig. 1–3). De filterdarm is door de filterkamer geheel ingekapseld en vormt daarmee een concentrisch filter-systeem. Vervolgens gaat de filterdarm over in een buisvormige maag bestaande uit één winding en vandaar naar een lange kronkelende darm die in de filterkamer uitmondt. De filterkamer gaat over in de einddarm die via het rectum in de anale opening eindigt. De filterkamer bezit een lange invaginatie of blindzak die zich in de einddarm bevindt en halverwege deze darm blind eindigt.

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