Structure of the digestive system of aphids, in particular *Hyalopterus* and *Coloradoa*, and its bearing on the evolution of filterchambers in the Aphidoidea

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Introduction

The genera *Hyalopterus* and *Coloradoa* belong to the family Aphididae sensu Börner (1952). Within the genus *Hyalopterus* there are two species, viz. the mealy peach aphid, *Hyalopterus amygdali* (Blanchard), and the mealy plum aphid, *H. pruni* (Geoffroy).

Detailed studies carried out by Basky (1978) and Basky and Szalay-Marszó (1987) revealed no morphological features for separating these species, nevertheless, they are distinct species as they can not live on each other's primary hosts, and the males do not copulate with females of the other species. According to Spampinato et al. (1988) there are electrophoretically three different species within the genus *Hyalopterus*, which are correlated with their primary host-plants: *H. pruni* on plum and apricot trees, *H. amygdali* A on almond and more rarely peach trees, while the opposite is true for *H. amygdali* B; in summer the three species migrate to the secondary host, *Phragmites australis*. The primary and secondary hostplants of *Hyalopterus* are listed in Table 9. Descriptions of all morphs of *H. pruni* are given by Smith (1936) and Stroyan (1984).

The digestive system of *H. pruni* feeding on *Prunus domestica* and *Phragmites communis (= Phragmites australis)* consists of a foregut, a dilated stomach, a tubular intestine, and a hindgut (Janiszewska, 1932), but lacks a filterchamber (Kunkel and Kloft, 1977).

An investigation of the anatomy of the digestive system of *Hyalopterus* and *Coloradoa* was carried out as dissections of aphids of these genera revealed the presence of a filtersystem in some specimens. Within the family Aphididae only three genera are known to have a filtersystem, viz. *Acaudinum, Capitophorus,* and *Cryptomyzus* (Börner, 1938; Ponsen, 1977).

Materials and methods

Specimens of the species listed in Table 1, 10, and 13, were collected from the hostplants and put in Duboscq- Brasil's fluid. After fixation the aphids were dehydrated in a graded series of ethanol and in methyl benzoate, stored in methyl benzoate celluidin (2%) for three days or longer, and then in toluene and finally embedded in paraplast. Serial sections, 8 μm thick, were stained in 1% methyl-green aqueous solution, rinsed in tap-water, dehydrated in methanol and in methyl benzoate, cleared in xylene, and finally mounted in xylene-dammar. The sections were examined under a Wild phase microscope. The drawings were made with help of a Wild drawing tube.

The morphology of a digestive system was reconstructed from the drawings of serial sections of a whole larva viewed at a magnification of 600 times. The

Table 1. A list of *Hyalopterus* specimens studied, their hostplant, and relevant locality data.

Hostplant	Locality
Prunus amygdalus	Koutouloufari, Crete (Greece), 29.IV.1989
Prunus amygdalus var. *dulcis*	Passo Martino, Sicilia (Italy), 19.VI.1989
Prunus armeniaca	Festos, Crete (Greece), 10.V.1989
Prunus domestica	Wageningen, 29.V.1983
	Wageningen, 30.V.1988
	Hódmezővasárhely (Hungary), V.1988
	Cannizzaro, Sicilia (Italy), 19.VI.1989
	Wageningen, X.1989
Prunus insititia	Ede, 10.VI.1989
Prunus persica	Bennekom, 6.VII.1983
	Carcavelos, Cascais (Portugal), 18.V.1988
	Ami, Ibaraki (Japan), 20.V.1988
	Canchipur (India), IV.1989
	Trecastagni, Sicilia (Italy), 19.VI.1989
	Wageningen, 5.X.1989
Prunus spinosa	Mehren, Eifel (Germany), 22.VII.1986
	Heudicourt, Champagne (France), 21.VII.1987
	Wageningen, 5.VIII.1987
Arundo donax	Mália, Crete (Greece), 8.V.1989
Molinia coerulea	Culture Department of Entomology, Wageningen, 1989-1990
Phragmites australis	Wageningen, 12.VII.1982
	Wageningen, X.1987
	Wageningen, X.1988
	Lyme Regis, Dorset (England), 18.VII.1983
	Hastière (Belgium), 11.VII.1987
	Saint-Mihiel, Champagne (France), 20.VII.1987
	Billy- s/s-les Côtes, Champagne (France), 24.VII.1987
	Tihany, Balaton (Hungary), 9.VIII.1987
	Tidbinbilla, ACT (Australia), 10.IV.1988
	Passo Martino, Sicilia (Italy), 19.VI.1989
Phragmites karka	Canchipur (India), IV.1989
Phragmites mauritianus	Gisenye, Lake Kivu (Rwanda, Central Africa), V.1988
	Kisosi (Burundi, Central Africa), V.1988
Phragmites sp.	Long Beach, Calvert County, Maryland (U.S.A.), 16.IX.1989
Typha latifolia	Ede, 24.VII.1989

number of nuclei with their conspicuous big nucleoli, which correspond to the number of cells, were counted at a magnification of 1500 times. The length of the aphid and that of the digestive system was calculated by multiplying the number of serial sections by the thickness of each section, 8 μm (Table 8).

The investigation was mainly done on young larvae the morph of which could only be determined after microscopical examination of the sections.

In order to dissect the digestive system, aphids were placed on double sided self-adhesive tape attached to a black plastic plate. Under a dissecting microscope each aphid was covered with a drop of Levy solution and dissected using

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Table 2. Source and number of sectioned specimens of *Hyalopterus* and *Coloradoa* with (+) and without (−) a filtersystem, and with one or two additional loops in the second region of the intestine.

Aphid	Hostplant	Total number of sectioned aphids	Morph	Filtersystem +	Filtersystem −	One additional loop	Two additional loops
Hyalopterus	*Prunus amygdalus*	4	apterous viviparous	3	1	1	3
		16	alate viviparous	3	13	3	13
	Prunus armeniaca	18	alate viviparous	9	9	13	5
	Prunus domestica	6	apterous viviparous	6	0	4	2
		32	alate viviparous	13	19	12	20
		20	apterous oviparous	10	10	15	5
	Prunus institia	10	alate viviparous	5	5	2	8
	Prunus persica	11	apterous viviparous	6	5	7	4
		46	alate viviparous	11	35	32	14
		20	apterous oviparous	16	4	8	12
	Prunus spinosa	4	apterous viviparous	0	4	1	3
		22	alate viviparous	4	18	4	18
	Arundo donax	11	green apterous viviparous	8	3	1	10
		9	green alate viviparous	4	5	1	8
	Molinia coerulea	16	green apterous viviparous	7	9	2	14
		3	green alate viviparous	1	2	1	2
	Phragmites australis	39	green apterous viviparous	28	11	4	35
		29	pink apterous viviparous	24	5	0	29
		14	green alate viviparous	5	9	3	11
		4	pink alate viviparous	4	0	0	4
		26	yellow alate males	14	12	18	8
	Phragmites karka	20	pink apterous viviparous	19	1	5	15
	Phragmites mauritianus	14	green apterous viviparous	12	2	0	14
		6	green alate viviparous	5	1	0	6
	Phragmites sp.	6	green apterous viviparous	2	4	0	6
		11	pink apterous viviparous	9	2	1	10
	Typha latifolia	10	green apterous viviparous	5	5	4	6
		9	pink apterous viviparous	5	4	0	9
Coloradoa tanacetina	*Tanacetum vulgare*	11	apterous viviparous	4	7	7	4
		1	apterous oviparous	1	0	1	0
		7	apterous males	0	7	3	4

Table 3. Source and number of dissected specimens of *Hyalopterus* with (+) and without (−) a filtersystem, and relevant locality data.

Hostplant	Locality	Total number of dissected aphids	Morph	Filtersystem +	Filtersystem −
Prunus domestica	Wageningen, V-VIII.1988	170	green apterous viviparous	16	154
		200	green alate viviparous	14	186
	Wageningen, VIII.1989	70	green apterous viviparous	16	54
		70	green alate viviparous	9	61
	Wageningen, X.1989	200	green apterous oviparous	15	185
	Utrecht, 19.VI.1988	100	green apterous viviparous	15	85
		100	green alate viviparous	1	99
Prunus insititia	Ede, 10.VI.1989	140	green apterous viviparous	37	103
		150	green alate viviparous	33	117
Prunus spinosa	Wageningen, V-VI.1988	116	green apterous viviparous	35	81
		121	green alate viviparous	17	104
	Hellevoetsluis, 13.VI.1988	80	green apterous viviparous	35	45
		100	green alate viviparous	24	76
Prunus spinosa x St. Julien	Wageningen, 28.VI.1989	120	green apterous viviparous	33	87
		140	green alate viviparous	30	110
Molinia coerulea	Culture Department of Entomology, VIII-X.1989	300	green apterous viviparous	84	216
		7	green alate viviparous	1	6
Phragmites australis	Wageningen, X.1987	31	pink apterous viviparous	25	6
		43	pink alate viviparous	28	15
		62	yellow alate males	15	47
	Wageningen, IX-X.1988	33	green apterous viviparous	29	4
		39	green alate viviparous	17	22
		160	pink apterous viviparous	118	42
		44	pink alate viviparous	23	21
		152	yellow alate males	29	123
	Wageningen, VI-VII.1989	100	green apterous viviparous	67	33
		16	green alate viviparous	5	11
		50	pink apterous viviparous	29	21
Typha latifolia	Winterswijk, 20.VII.1989	25	green apterous viviparous	5	20
		10	pink apterous viviparous	2	8
	Ede, 24.VII.1989	90	green apterous viviparous	24	66
		10	green alate viviparous	1	9
		90	pink apterous viviparous	25	65
		7	pink alate viviparous	3	4

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Table 4. Source and number of specimens of *Hyalopterus* with (+) and without (−) a filtersystem summarized from Table 2 and 3.

Hostplant	Total number of aphids		Apterous viviparous Filtersystem		Alate viviparous Filtersystem		Apterous oviparous Filtersystem		Alate males Filtersystem		Morph
	Dissected	Sectioned	+	−	+	−	+	−	+	−	
Prunus amygdalus		20	3	1	3	13					
Prunus armeniaca		18			9	9					
Prunus domestica	910	58	53	293	37	365	25	195			
Prunus insititia	290	10	37	103	38	122					
Prunus persica		77	6	5	11	35	16	4			
Prunus spinosa	417	26	70	130	45	198					
Prunus spinosa x St. Julien	260		33	87	30	110					
Arundo donax		20	8	3	4	5					
Molinia coerulea	307	19	91	225	2	8					
Phragmitis australis	730	112	320	122	82	78			58	182	
Phragmitis karka		20	19	1							
Phragmitis mauritianus		20	12	2	5	1					
Phragmitis sp.		17	11	6							
Typha latifolia	232	19	66	168	4	13					
Prunus	1877	209	25%		17%		17%				20%
Molinia coerulea	307	19	29%		20%						29%
Phragmites	730	169	73%		52%				24%		56%
Typha latifolia	232	19	28%		24%						28%

Table 5. Number of dissected specimens of *Hyalopterus* with (+) and without (−) a filtersystem. The green apterous viviparous offspring is produced by green apterous viviparous females (fundatrix) on *Prunus domestica* (1-10) and on *Prunus spinosa* (11-20) (Wageningen, V.1990). Each female lays from two to four eggs (Willcocks, 1916).

No. of fundatrix	Filtersystem	Total number of offspring	Apterous viviparae	
			Filtersystem	
			+	−
1	−	15	3	12
2	−	10	0	10
3	−	9	1	8
4	−	15	5	10
5	−	24	9	15
6	+	17	1	16
7	−	11	2	9
8	−	13	1	12
9	−	20	5	15
10	−	25	1	24
11	−	12	3	9
12	−	13	2	11
13	−	10	3	7
14	−	15	7	8
15	−	13	3	10
16	−	10	4	6
17	−	14	1	13
18	+	14	2	12
19	+	14	4	10
20	−	15	6	9

watchmakers forceps (Table 3-7).

Hyalopterus were collected (29.VI.1989) from *Prunus domestica* growing in the Demonstration Garden for Plant Diseases at Wageningen. The aphids were reared continuously on field collected *Molinia coerulea* in a greenhouse at 20 $\pm$ 3 °C with a photoperiod of 16 hours and a relative humidity of 70-80% (Table 1-3).

Specimens of the species listed in Table 12 were collected from their host plants. Under a stereomicroscope they were put one by one in 96% ethanol for 10 seconds to extract the air-bubbles from the surface of the cuticle and out of the tracheal system. Thereafter they were transferred to 0.1 M cacodylate buffered (pH 7.4) glutaraldehyde (3%) for 2 to 4 hours and then prepared for electron microscopical study following Ponsen (1972).

Table 6. Number of dissected specimens of *Hyalopterus* with (+) and without (−) a filtersystem. The apterous viviparous offspring is produced by green alate viviparous females (spring migrants) on *Phragmites australis*. These females originated from *Prunus domestica* in the direct neighbourhood of *Phragmites australis* in the Demonstration Garden for Plant Diseases (Wageningen, VI.1988).

No. of spring migrant	Filtersystem	Total number of offspring	Colour of apterous viviparae			
			green		pink	
			Filtersystem		Filtersystem	
			+	−	+	−
1	−	16	7	3	3	3
2	−	18	7	9	0	2
3	−	24	4	6	5	9
4	+	8	3	0	2	3
5	−	8	3	0	0	5
6	+	24	9	0	5	10
7	+	21	10	5	0	6
8	−	21	0	2	6	13
9	−	20	12	5	1	2
10	−	14	4	3	1	6
11	−	13	5	8		
12	−	14	2	7	1	4
13	+	19	2	1	5	11
			58%		28%	

Table 7. Number of dissected specimens of *Hyalopterus* with (+) and without (−) a filtersystem. The green apterous oviparous offspring is produced by green and pink alate viviparous females (gynoparae) on *Prunus domestica* in the orchard of the Plant Protection Centre (Wageningen, X.1989). Each gynopara produces an average of 9.8 oviparous females (Smith, 1936).

No. of gynopara	Colour	Filtersystem	Total number of offspring	Apterous oviparae	
				Filtersystem	
				+	−
1	green	+	6	0	6
2		+	8	0	8
3		+	6	0	6
4		+	7	0	7
5		−	8	0	8
6		+	6	1	5
7	pink	−	5	0	5
8		+	9	1	8
9		+	9	0	9
10		+	9	0	9
11		+	9	1	8
12		+	9	0	9

Pharynx

The alimentary tract starts with the food canal that is formed by the interlocked maxillary stylets. This food canal leads into the pharyngeal duct, formed by the epipharynx and the hypopharynx lip. The pharyngeal duct is separated from the pharyngeal pump by a valve, of which both the dorsal and ventral walls are marked by two cuticular dome-shaped prominences. The epipharyngeal gustatory organ has 14 se illary pores, of which eight are arranged in a row in the epipharynx of the pharyngeal duct. Six sensillary pores are located in the dorsal wall of the pharyngeal valve, three on each side of the two insertions of the cuticular tendons to which the divaricator muscles of the pharyngeal valve are attached. The hypopharyngeal gustatory organ has four sensillary pores: two in the hypopharynx of the pharyngeal duct just anterior to the valve and the other two at the foot of the salivary pumpstem. Both the structure of the pharynx, including the muscles of the valve and the pump, and the structure of the gustatory organ are identical to those of *Aphis* species (Ponsen, 1990 b).

Foregut

The foregut (oesophagus) runs posteriad from the tentorium, between the salivary glands, along the median dorsal furrow of the suboesophageal ganglion and terminates in the oesophageal valve (Figure 1). In transverse sections the uniform thin tube consists of 2-4 squamous cells of which the irregular-shaped nuclei protrude into the lumen (Figure 2F). Just before the stomach the foregut is supplied by a branch of the medial dorsal nerve, which runs alongside the dorsal vessel.

The oesophageal valve is an invagination of the foregut into the lumen of the stomach. It consists of two layers of non muscular epithelium, which form an intravalvular space (Figure 2F). The inner layer is a continuation of the foregut, whereas the outer layer is built up of cuboidal cells, each containing a spherical, relatively large nucleus. The epithelial cells of both the foregut and the outer layer of the valve secrete a chitinous intima.

Cuticular lining

The cuticular lining of the epidermis consists of an inner achromatic structureless layer, then a layer of a darkly coloured substance, and a delicate very dark layer, respectively the endo-, exo-, and epicuticle. During moulting the old cuticle consists of only the last two layers and it is quite separate from the new cuticle of which the two layers are already distinctly present. Inside the achromatic structureless endocuticle there are many waxy droplets (Figure 11B, 12, 13D and 18I), which presumably are responsible for the rather heavy coating of mealy wax on *Hyalopterus* aphids. The waxy droplets originate from fat cells and are

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scattered in the haemolymph throughout the body cavity. In phase microscopy the waxy droplets are recognizable by their white refractive appearance. They are soluble in acetone, chloroform, and ether, but not in alcohol (Ponsen, 1972).

The cuticular lining or intima of the foregut and the oesophageal valve is an achromatic structureless mass with on the luminal surface a delicate dark line (Figure 2F, 14B, 17B, and 18B). Although the intima of the foregut is very narrow and that of the valve relatively voluminous extending far into the stomach lumen, waxy droplets are never observed inside the endocuticle.

Ultrathin sections of some aphid species (Table 12) show that the intima of the foregut consists of an endocuticle and an exocuticle, but lacks an epicuticle (Figure 5A and 19A-B). The endocuticle completely dissolves, and the exocuticle remains in the lumen of the foregut. The exocuticle of the outer layer of the valve disintegrates into fragments.

The integument of 'mature' embryo's in a nine days old viviparous *Myzus persicae* larva secrete a cuticle. This embryonic cuticle soon separates from the epidermis and the first instar cuticle is laid down in its place. The embryonic cuticle is not shed and remains round the embryo until its birth (as well as in the egg of *Adelges (Dreyfusia) nordmannianae*). After birth the embryo is enclosed in a delicate membranous structure, the embryonic exocuticle, from which the first stage larva emerges within five minutes. This is a critical phase in the life cycle of the aphid because under field conditions a large proportion of the aphids fail to emerge from the embryonic exocuticle, especially in dry, hot summers.

Hyalopterus pruni (Smith, 1973), *M. persicae* (Ponsen, 1969), and many other aphid species complete four instars within about 10 days at a mean temperature of 20 °C, so that in an imaginal aphid five exocuticles remain inside the foregut, namely one embryonic and four larval. These five exocuticles inside the foregut are presumably not a barrier for the sap flow from the pharyngeal pump to the stomach or to prevent regurgitation.

Stomach

The stomach begins in the mesothorax or metathorax, and joins the intestine in the first, second, or third abdominal segment (Figure 1). It has a dilated structure and lies centrally in the dorsal region of the aphid and dorsal to the caecal intestine. The maximum diameter of the stomach is situated beyond the end of the oesophageal valve; in *Hyalopterus* on its primary hostplants it consists of 17-23 cells and on the secondary ones 13-18 cells. In *C. tanacetina* the maximum diameter of the stomach consists of 11-13 cells.

The epithelium of the stomach of *Hyalopterus* consists of two forms of cells: in the anterior region triangular cells with more or less spherical nuclei (Figure 2A), and in the posterior region of the stomach cuboidal cells with oval nuclei (Figure 2B). Both cell forms contain small vacuoles and granules, and the basal cell membranes are strongly invaginated. The apical cell membrane presents
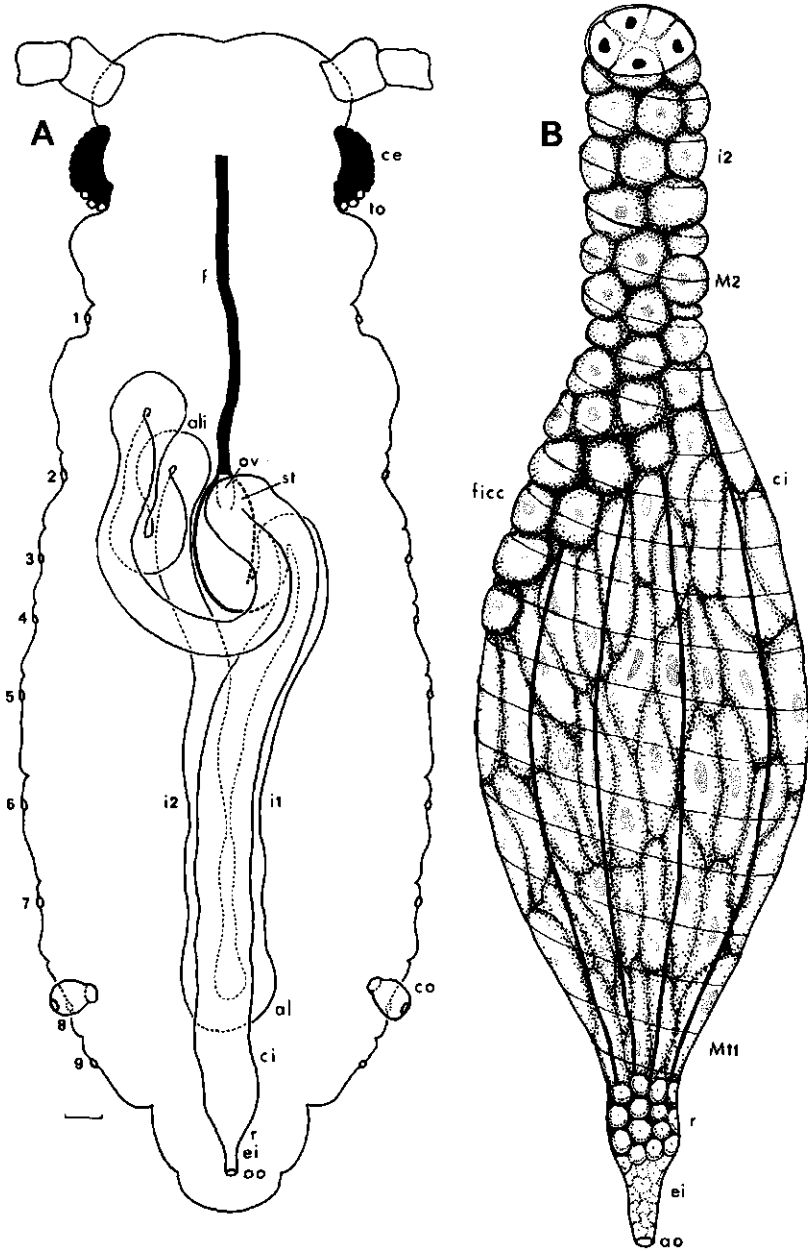
Figure 1.A. Dorsal view of the digestive system of an apterous viviparous female of *Hyalopterus* from *Phragmites australis*, reconstructed from serial transverse sections.

1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. The siphunculi (co) are situated on the sixth abdominal tergite. Bar represents 30 μm. B. Schematic impression of the transition from the crenated opaque intestine to the smooth transparent caecal intestine. Note the position of the filterchamber cells. For list of abbreviations see page 61.
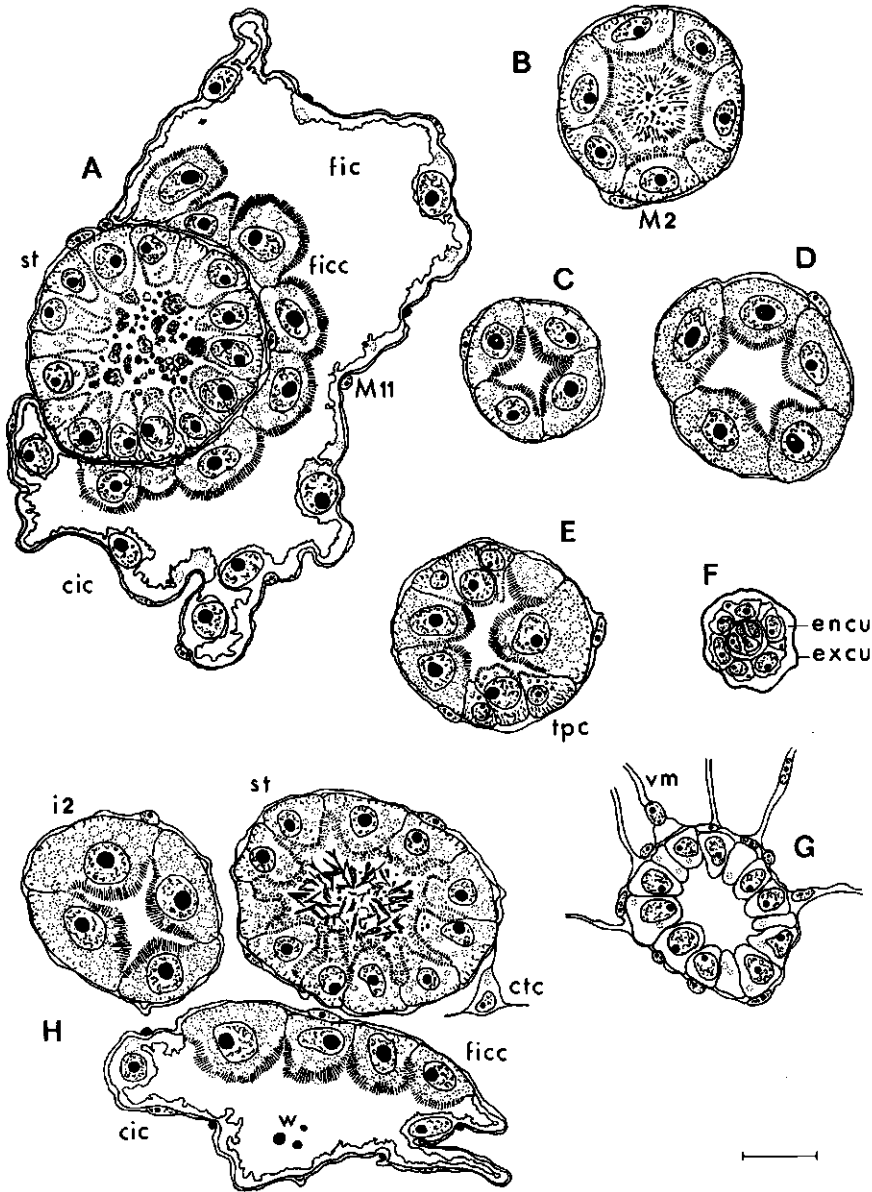
Figure 2. Transverse section of the filtersystem showing encapsulation of the anterior region of the stomach by the anterior region of the caecal intestine (A), the posterior region of the stomach (B), the first (C) and second region of the crenated intestine (D), the second region of the crenated intestine with triplet cells (E), the oesophageal valve (F), and the rectum (G) of *Hyalopterus*. (H). Transverse section of the stomach, the second region of the crenated intestine, and the anterior region of the caecal intestine of *Coloradoa tanacetina*. For list of abbreviations see page 61. Bar represents $10 \, \mu m$.
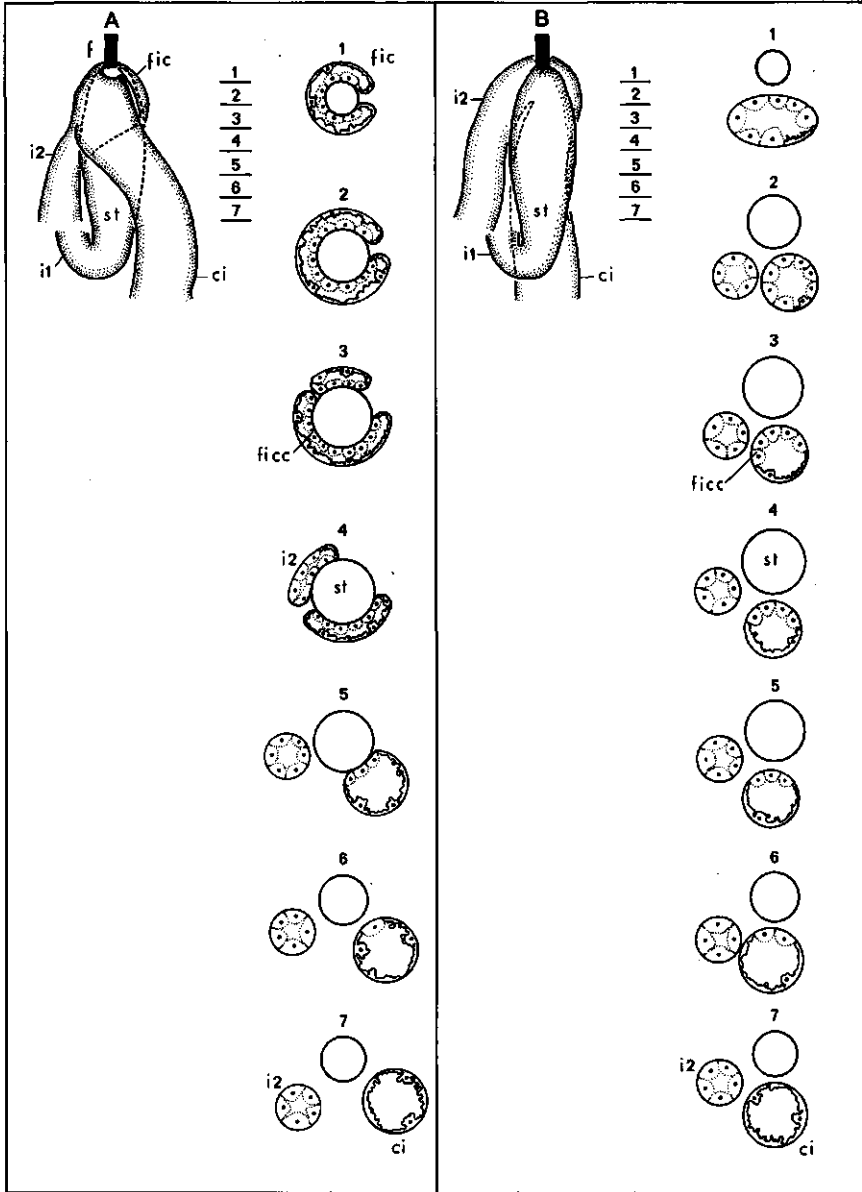
Figure 3. Semi-schematic representation of the gut of specimens of *Hyalopterus* with (A) and without a filtersystem (B). The transverse serial sections 1-7 are from the region of the stomach and illustrate the relationship between the stomach and caecal intestine in those specimens that have (A) and lack a filtersystem (B). For list of abbreviations see page 61.

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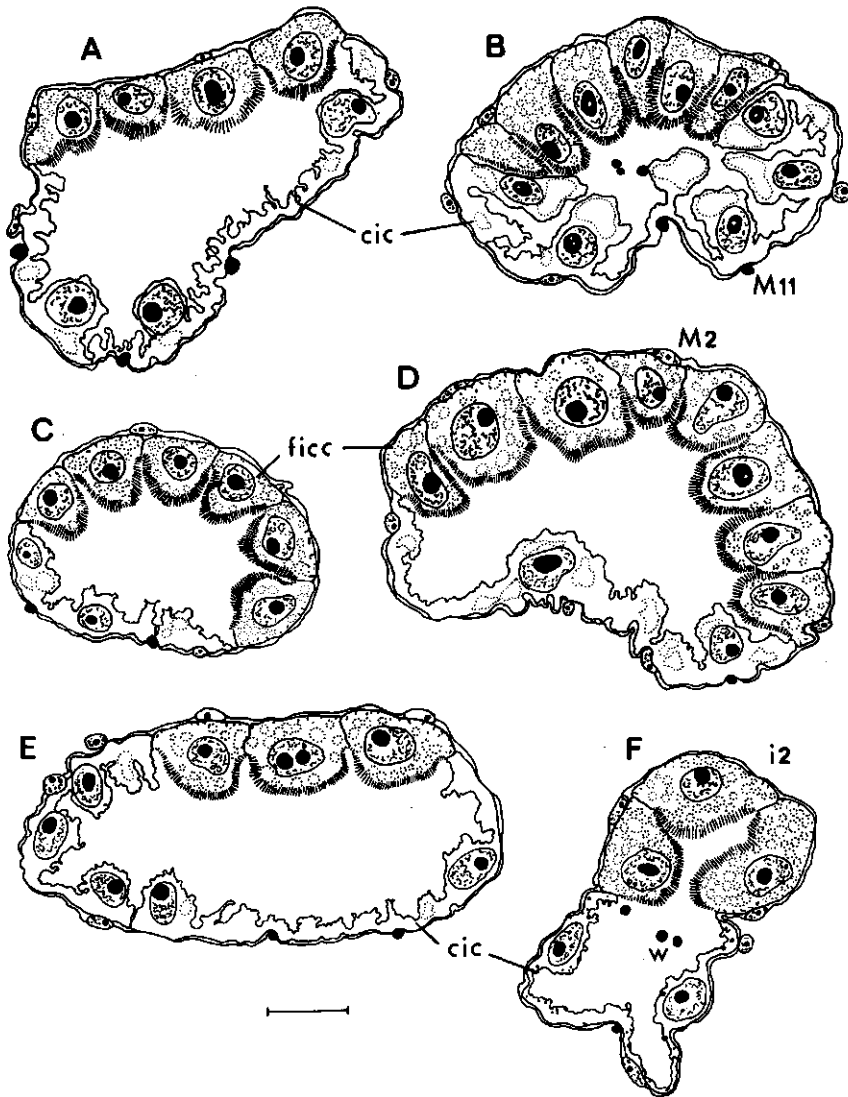
Figure 4. Transverse sections of the anterior region of the caecal intestine of which the filterchamber cells are situated on the side of the stomach and the caecal intestine cells on the opposite wall. A. *Hyalopterus* sp.; B. *Metopolophium dirhodum*; C. *Uroleucon sonchi*; D. *Acyrthosiphon caraganae*; E. *Macrosiphum albifrons* (Table 10). F. In *Phloeomyzus passerinii* (Signoret) the intestinal cells end abruptly, and the caecal intestine cells begin. For list of abbreviations see page 61. Bar represents 10 μm.

a labyrinthine system of closely packed irregular invaginations of different dimensions (Figure 5B and 19C-D) and its luminal surface is lined with extracellular microtubules (see page 22).

The triangular cells produce an apocrine secretion, which is discharged together with parts of the apical cytoplasm which gradually dissolve in the stomach lumen. The cuboidal cells produce a merocrine secretion; in ultrathin sections of *Myzus persicae* involve breaking off of parts of the labyrinthine system, which dissolve in the stomach lumen forming an amorphous threadlike mass (Figure 5B and 19C-D). The stomach cells secrete continuously throughout larval and adult life.

The anterior region of the stomach lumen is nearly completely filled with solid material and the posterior region with fine-grained material (Figure 2A and B). In dissections, this is clearly seen in a number of specimens, where the posterior region of the opaque stomach is less dense than the anterior region. Probably there is no mixing occurring between both luminal secretory products as a result of the very slow peristaltic movements. These products are strictly limited to the lumen of the stomach and do not occur in the intestinal lumen which shows a clear appearance.

The stomach of *C. tanacetina* consists of only triangular cells with a merocrine secretion (Figure 2H). In very young specimens the lumen is filled with fine-grained material and small thread-like structures, but in older specimens the stomach cells are more flattened and the lumen is completely filled with very big thread-like structures.

The presence of two types of gland cells in the stomach of *Hyalopterus* (Figure 2A and B) indicates that this species belongs to the polyphagous aphids which ar able to feed on plants in many different families (Table 1 and 9). This phenomenon has already been discussed (Ponsen, 1990 b). The stomach of the monophagous aphid *C. tanacetina* consists of only one type of gland cells, viz. merocrine cells.

Tubular intestine

In dissections of living aphids the foregut, stomach, and tubular intestine are opaque structures which show slow peristaltic movements generated by circular muscles. The tubular intestine has over its entire length a crenated structure (Figure 1B) and its posterior region shows some distinct white dots which are the triplets.

Histologically the tubular intestine consists of two distinct regions (Figure 1). The first region of the intestine (small crenated intestine) runs from the stomach to the abdominal loop situated in the fifth, sixth, or seventh abdominal segment. From there it passes gradually into a broader one, forming the second region of the intestine (large crenated intestine), which terminates at the caecal intestine. Both in *Hyalopterus* on *Prunus*, and in *Coloradoa* the second region of the intestine forms one or two additional loops situated between the mesoth-

orax and the fourth abdominal segment; in *Hyalopterus* feeding on *Arundo, Molinia, Phragmites,* and *Typha* there occur mainly two additional loops (Table 2). The number of additional loops is independent of the morph, and the presence of a filtersystem. Within the specimens the first region of the intestine bends either to the right or to the left of the caecal intestine and the transition from the stomach to the intestine is marked by a sharp loop. The intestinal loops are closely applied to the side of the stomach. The voluminous abdominal loop is connected with a branch of the main abdominal nerve.

In the second region of the intestine the cells and nuclei are bigger, and the cytoplasm more vacuolated than in the first region of the intestine. The apical cell membranes of the triangular intestinal cells are distinctly striated. In ultrathin sections (Table 12) they present a labyrinthine system of closely packed irregular invaginations of different dimensions (Figure 6C and 20F). Transverse sections of the entire tubular intestine of both *Hyalopterus* and *Coloradoa* consists of 3-5 triangular cells forming a more or less stellate lumen (Figure 2C and D).

The second region of the intestine is characterized by the presence of 6-8 groups of three conical-shaped cells (triplet). They occur mainly in the second half of the second region of the intestine including the additional loops at irregular intervals among the triangular intestinal cells. The majority of the triplets occur singly. Occasionaly, however, two triplets or rarely three triplets occur together. The middle cell of each triplet is very large with a large nucleus, and the other two are very small each with a relatively small nucleus. The cytoplasm contains numerous minute vacuoles; the apical cell membrane has a small striated zone (Figure 19E) and the basal cell membrane is strongly invaginated. The radial cell membranes of the triplet cells are about twice as long as those of the intestinal cells (Figure 2E).

Rectification

Histologically there are two types of hindgut in the digestive system of *Subsaltusaphis ornata* (Theobald) (Figure 9). The first type of hindgut is an extension of the ascending intestine and consists of triangular cells which present a striated border on their luminal surface closely resembling the striated border of the ascending intestine (Figure 20). This is the endodermal hindgut or descending intestine. The second type is a blindly ending evagination of the rectum and for this structure the term ectodermal hindgut was introduced by the presence of a delicate intima lining the apical cell membrane of the squamous cells. In dissections both types of hindgut have a smooth transparent structure showing vigorous peristaltic movements generated by circular and longitudinal muscles, although the cellular structure of both types is quite different (Ponsen, 1979).

In ultrathin sections of the digestive system of *Rhopalosiphum maidis*, *S. ornata*, and *Uroleucon sonchi* (Table 12), it appears that a distinct cuticular lining or intima, such as that present in the foregut and the rectum (Figure 5A, 8I,
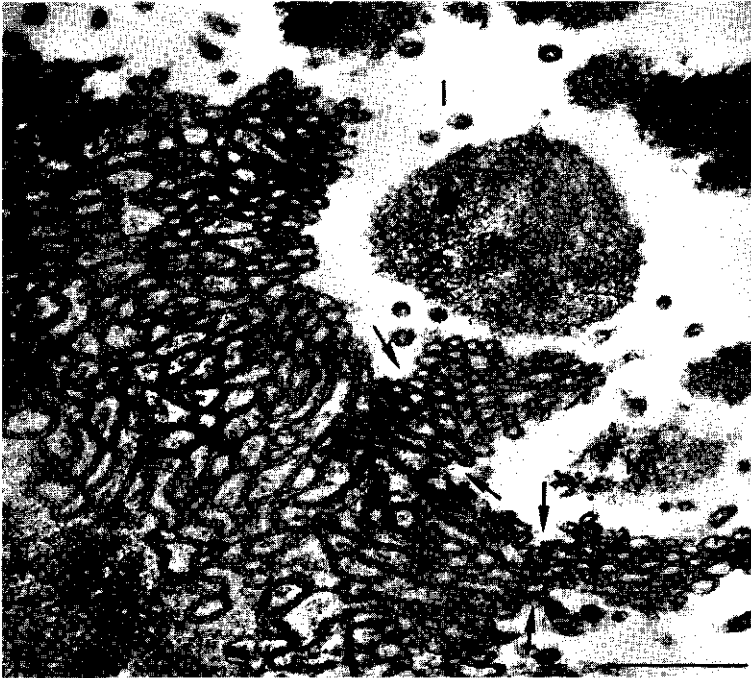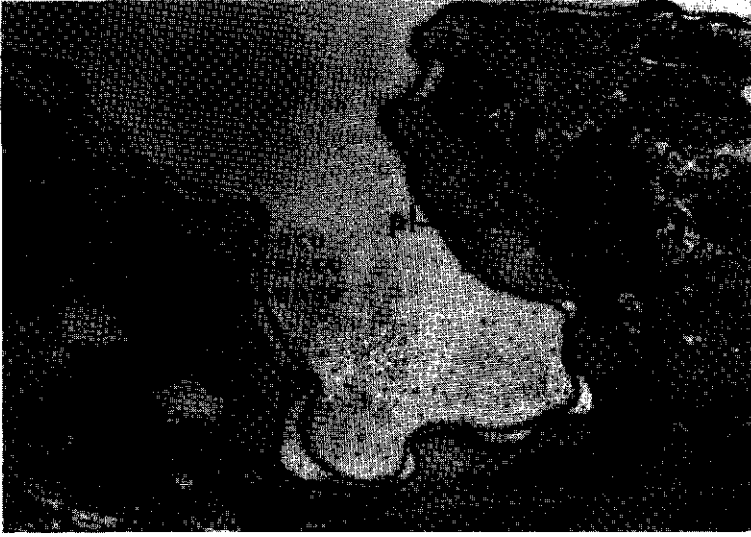
Figure 5.A. Apical cell membrane of the foregut of *Myzus persicae*. Note the plaques at the tips of the irregular fingerlike evaginations of the apical cell membrane and the non-lamellate structure of the endocuticle .B. Apical cell membrane of the stomach of *Myzus persicae*. Arrows breaking off of parts of the labyrinthine system (merocrine secretion). For list of abbreviations see page 61. Bar represents 0.5 μm.
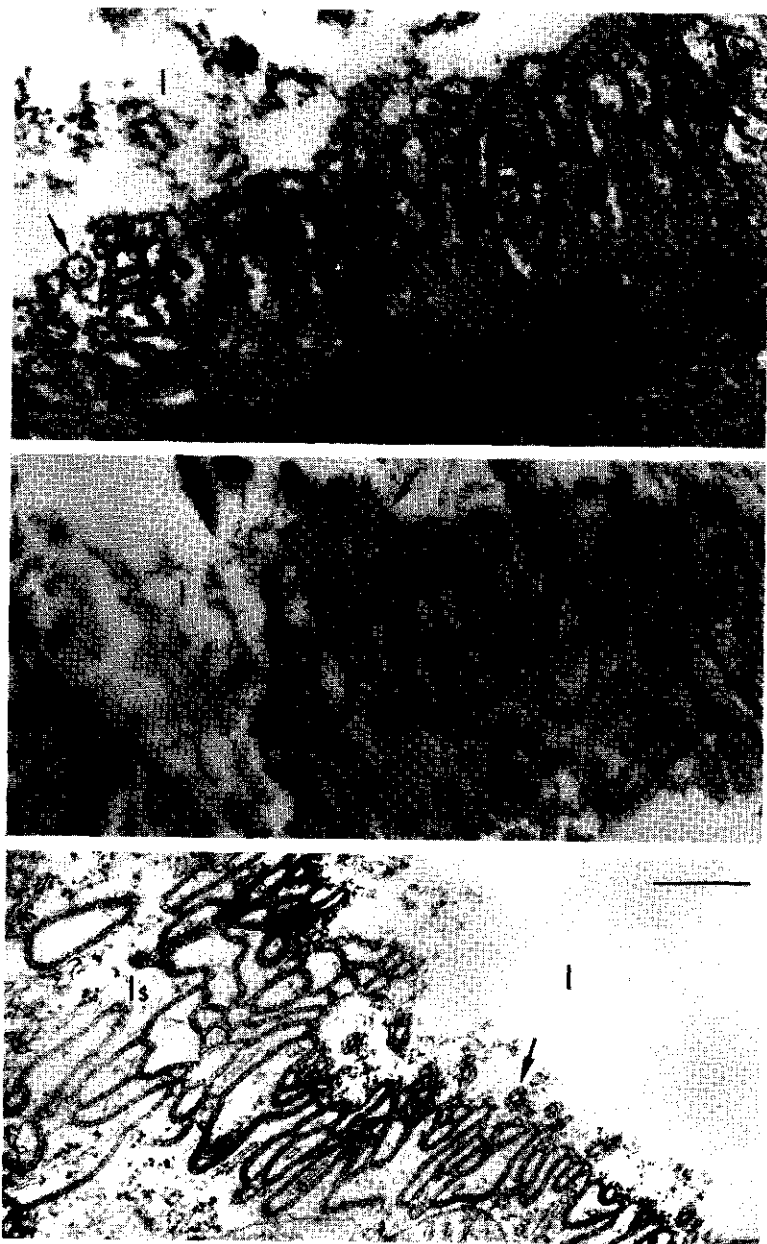
Figure 6. Apical cell membrane of the small crenated intestine of *Rhopalosiphum maidis* (C), and the descending intestine of *Drepanosiphum platanoidis* (D) and *Subsaltusaphis ornata* (E). Note the extracellular microtubules (see arrow). For list of abbreviations see page 61. Bar represents 0.5 μm.

Figure 7. Apical cell membrane of the descending intestine of *Adelges* (*Dreyfusia*) nordmannianae (F) and of the caecal intestine of *Rhopalosiphum maidis* (G). Note the extracellular microtubules (see arrow). For list of abbreviations see page 61. Bar represents 1 μm.
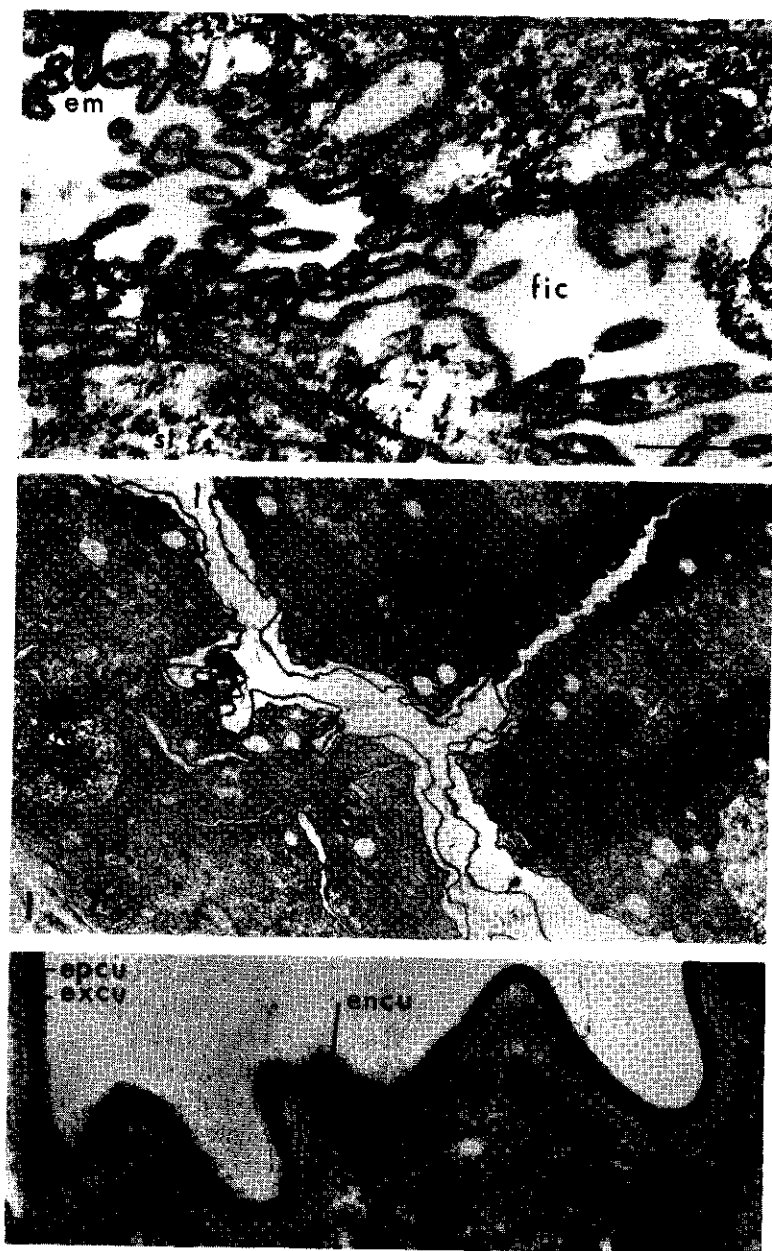
Figure 8. Apical cell membrane of the caecal intestine of *Subsaltusaphis ornata* (H), the rectum of *Uroleucon sonchi* with an old and new exocuticle (I), and the epidermal invagination of *Drepanosiphum platanoidis* (J) showing the lamellate structure of the endocuticle (see arrow). For list of abbreviations see page 61. Bar represents 0.5 μm.

19 and 20), is absent in their respective 'ectodermal hindgut'. On the other hand, the apical cell membrane of the 'ectodermal hindgut', presenting irregular finger-like evaginations in which occur small oblong mitochondria, is lined with a single row of extracellular microtubulelike structures (Figure 7G and 8H). The term extracellular microtubules was introduced by O'Loughlin and Chambers (1972) lying along the luminal surface of the intestinal and hindgut cells of *Acyrthosiphon solani* (Kaltenbach) (= *Aulacorthum solani* (Kaltenbach), *Aphis craccivora* (Koch), *Hyperomyzus lactucae* (Linnaeus), *Macrosiphum euphorbiae* (Thomas), and *Myzus persicae* (Sulzer). Later on these structures were also observed facing the hindgut cells of *Rhopalosiphum padi* (Linnaeus) (Gildow, 1985). In the coccid, *Planococcus citri* Risso, identical extracellular microtubules occur along the luminal surface of the intestinal cells (Foldi, 1973).

The apical cell membrane of the endodermal hindgut or descending intestine of *S. ornata* (Figure 6E) as well as of *Drepanosiphum platanoidis* and *Adelges (Dreyfusia) nordmannianae* (Figure 6D and 7F; Table 12) presents a labyrinthine system of closely packed irregular invaginations of different dimensions (Figure 20). Such a labyrinthine system of the apical cell membrane occurs also in the cells of the stomach and the crenated intestine of the above mentioned species, including *M. persicae* (Forbes, 1964).

Since electron microscopic examination revealed the absence of a cuticular intima in the blindly ending evagination of the rectum or 'ectodermal hindgut' of *S. ornata*, it follows that the term 'ectodermal hindgut' is wrong and has to be replaced by the term caecal intestine being a part of the midgut. Moreover, as the hindgut in insects is lined by a cuticular layer the term 'endodermal hindgut' is no longer applicable.

Within the families Adelgidae (Figure 17), Mindaridae (Figure 18), Thelaxidae, Chaitophoridae, Greenideidae, Drepanosiphidae without a filtersystem, Anoeciidae, and the genera *Anuraphis, Aphis, Brachycaudus, Plocamaphis*, and *Pterocomma*, the midgut consists of a stomach, a tubular crenated intestine, and a smooth transparent descending intestine (Figure 10A). Species of Drepanosiphidae with a filtersystem (Table 4 in Ponsen, 1990 a) have two smooth transparent intestines (Figure 9): the descending intestine which is a continuation of the ascending intestine, and the caecal intestine which is a blindly ending evagination of the rectum (Figure 10B). Both transparent intestines form a filtersystem: a concentric filtersystem in which the stomach is encapsulated by the caecal intestine (previously named the 'ectodermal hindgut') (Figure 9B) and a parallel filtersystem in which the anterior region of the ascending intestine is fused with the posterior region of the descending intestine (previously named the 'endodermal hindgut') (Figure 9C). However, within the families Phylloxeridae (Figure 14), Phloeomyzidae, Lachnidae, and Aphididae (Table 10), the transparent descending intestine is completely lost and replaced by the caecal intestine (Figure 10C). In this group of aphid species the midgut consists of a stomach, a tubular crenated intestine, and a smooth transparent caecal intestine.

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Caecal intestine and filtersystem

The caecal intestine of *Hyalopterus* and *C. tanacetina* starts in the meso – or metathorax and runs directly caudad ventrally of the stomach and dorsally of the voluminous abdominal loop of intestine to open into the rectum (Figure 1). Its simple epithelium consists of long squamous cells with elliptic nuclei. The long axis of the nucleus is parallel to the main axis of the cell and the short axis protrudes into the lumen (Figure 2 and 4). The long cells contain granules and irregular membraneless 'vesicles' (Figure 7G) in which occur waxy droplets. The waxy droplets originate from fat cells and are scattered throughout the body cavity from which they are released by the caecal intestinal cells into the lumen. The irregular apical cell membrane presents minute projections (Figure 20I). Halfway, on its ventral side, the caecal intestine is connected with a branch of the main abdominal nerve.

In dissections of living aphids the caecal intestine is a smooth transparent structure that shows vigorous peristaltic movements generated by circular muscles and about eleven longitudinal muscles; the latter are external to the circular muscles. As a result of the vigorous peristalsis the caecal intestine can take several forms, from the most contractile condition to the most dilated condition forming a more or less spherical structure to the most bizarre irregular ones (Figure 21). In the most dilated condition the caecal intestine can attain a volume of about 6 times its original one; the cells are very flat and the elliptic nuclei are situated against the basal cell membrane.

In a number of specimens the anterior region of the stomach is completely encapsulated by the anterior region of the caecal intestine forming a concentric filtersystem (Figure 2A and 3A). On the other hand, there are specimens of which the stomach is not encapsulated by the caecal intestine; the caecal intestine is completely separate from the stomach showing a kidney-shaped to a more or less spherical structure (Figure 2H). Moreover, there occur intermediate forms of which the caecal intestine is partly fused with the stomach. In dissections the two parts of the filtersystem are so intimately fused that they cannot be separated easely from each other. In ultrathin sections of *Subsaltusaphis ornata* the opposite basal cell membranes of both filtersystems are anchored to each other by the basal lamina which extends into irregular invaginations of the opposite epithelial cells (Figure 8H).

The segment of the caecal intestine which envelopes the stomach is the filterchamber (Figure 2A). The length of the filterchamber is about two fifths of that of the stomach (Figure 3A). The filterchamber is lined with both filterchamber cells and caecal intestine cells but so arranged that the filterchamber cells are situated on the side adjacent to the stomach and the squamous caecal intestine cells on the opposite wall of the filterchamber. The filterchamber cells in the filterchamber are a continuation of those of the second region of the intestine.

By the bending of the filterchamber around the stomach the filterchamber cells loose their triangular structure and transform to a more or less cuboidal
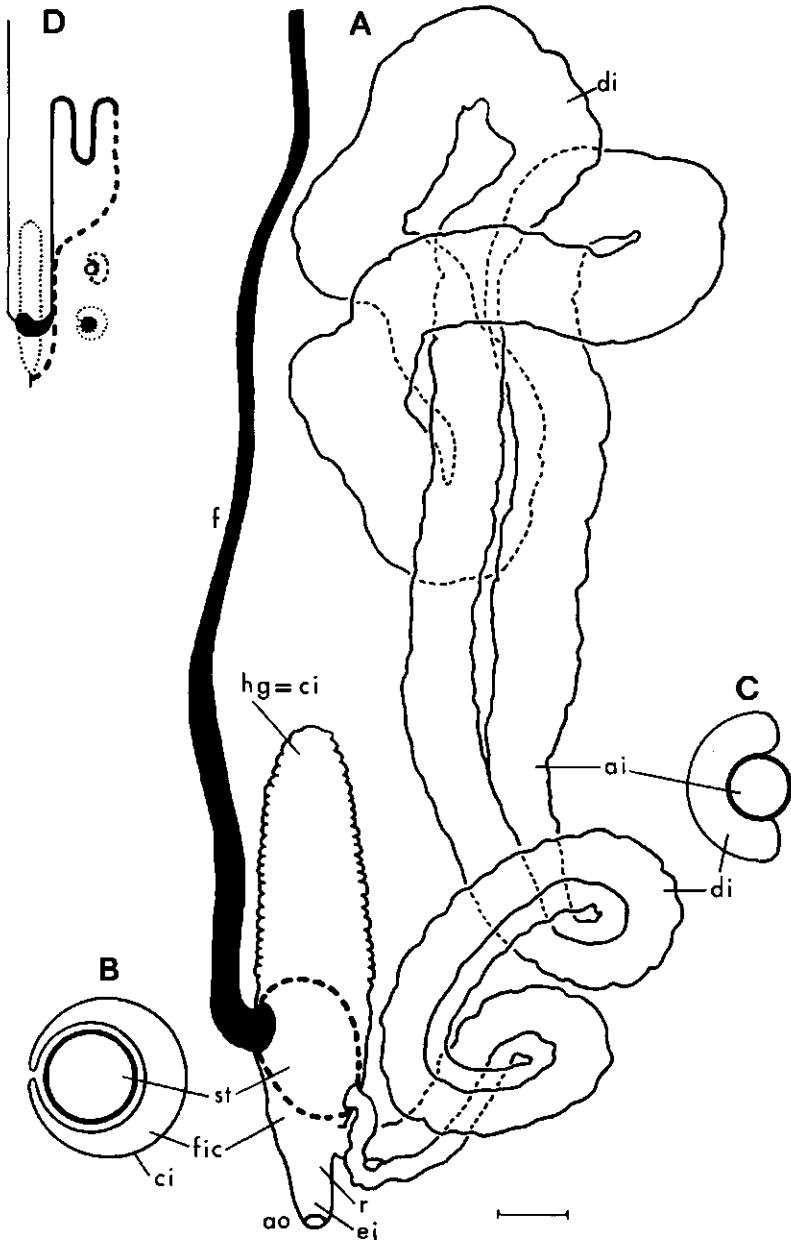
Figure 9. Semi-schematic representation of the digestive system of *Subsaltusaphis ornata* reconstructed from serial transverse sections. Bar represents 30 μm. Schematic transverse sections of the concentric filtersystem (B) of which the stomach is encapsulated by the caecal intestine and the parallel filtersystem (C) of which the ascending intestine and the descending intestine are fused together. For list of abbreviations see page 61.
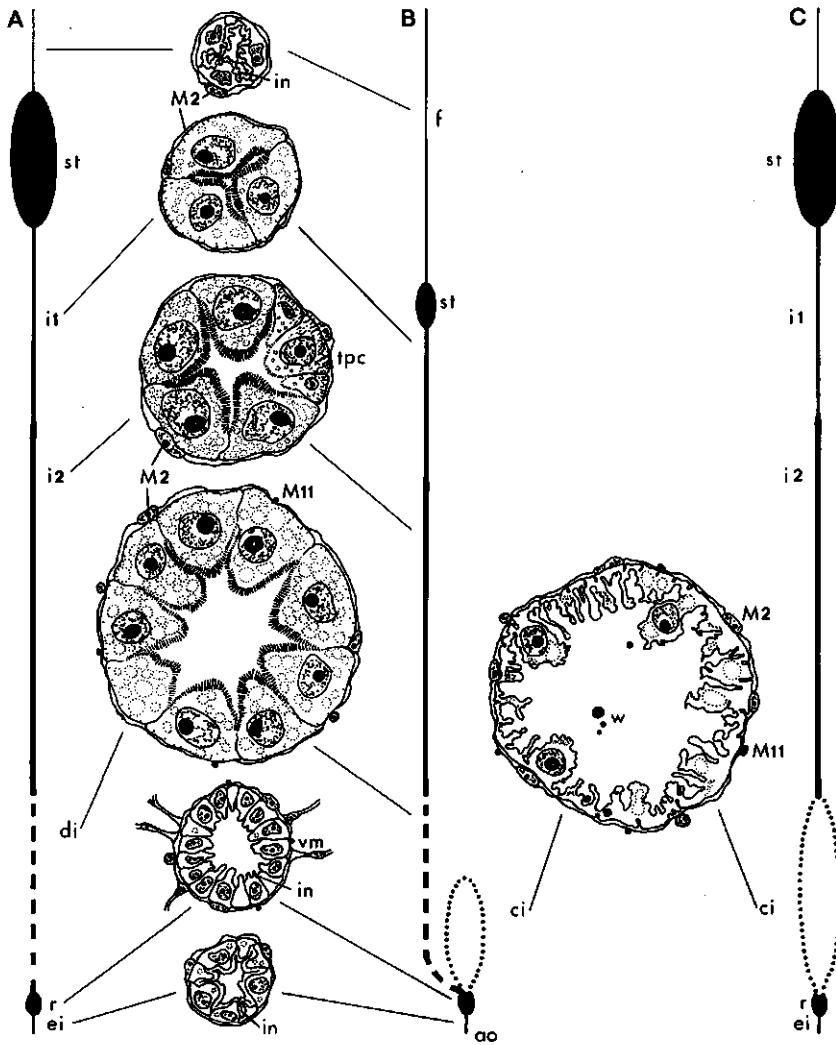
Figure 10. General impression of the digestive system of an aphid with a descending intestine (A), an aphid with both a descending intestine and a caecal intestine (blindly ending intestine) (B, see Figure 9), and an aphid in which during evolution the descending intestine disappeared and was replaced by the caecal intestine (C). The transverse sections correspond with the several subdivisions of the digestive system. For list of abbreviations see page 61.

form (Figure 2A). In some specimens they have less vacuoles in their cytoplasm than those in the second region of the intestine. In transverse serial sections they start as a ring of cells adjacent to the stomach, after which the number of filterchamber cells gradually decreases until the caecal intestine consists of only squamous cells (Figure 3A, 1-7). The part of the filterchamber with the filterchamber cells is opaque and only enveloped by circular muscles. The opposite part of the filterchamber is transparent and has both circular and longitudinal muscles as well as the entire caecal intestine. As a result of the transparent structure of the caecal intestine, the filterchamber cells are clearly seen especially when after dissection a drop of saturated picric acid or Duboscq-Brasil's fluid is added to the Levy solution (Figure 1B).

In the specimens where the stomach is not encapsulated by the caecal intestine, the epithelial lining of the anterior region of the caecal intestine is identical to that of the specimens with a filtersystem (Figure 3). Although the caecal intestine is completely separate from the stomach and has a more or less spherical structure, the filterchamber cells are situated on the side of the stomach with the squamous caecal intestine cells on the opposite wall (Figure 2H and 4A-E). In dissections, the region of the caecal intestine with the filterchamber cells shows an opaque crenated structure similar to the entire crenated intestine; the opposite wall of the caecal intestine with the squamous cells shows a smooth transparent structure like the rest of the caecal intestine (Figure 1B).

The percentage of specimens of *Hyalopterus* with a filtersystem is significantly higher on *Phragmites* than on *Prunus, Molinia*, and *Typha* (Table 4; G-test,P < 0.0001). However, there is no difference between the percentages of apterous viviparous females with a filtersystem feeding on *Prunus, Molinia*, and *Typha*, although the latter two are secondary hostplants (Table 4). On *Prunus* the percentage of apterous viviparous females with a filtersystem is higher than for alate viviparous females, but there is no difference in percentage between alate viviparous females and apterous oviparous females (Table 4). In the first generation on *Phragmites* the percentage of the green apterous viviparous females with a filtersystem is higher than for the pink apterous viviparous females (Table 6), although in the subsequent generations there is no difference (Table 2 and 3). On *Phragmites* the percentage of apterous viviparae with a filtersystem is higher than for alate viviparae (Table 3) as on *Prunus*, while it is higher for alate viviparae than for alate males (Table 4). Adults with or without a filtersystem can produce both progeny with a filtersystem and progeny without a filtersystem (Table 5-7).

In *Coloradoa* 26% of the specimens have a filtersystem (Table 2) wich is similar to the percentage of *Hyalopterus* feeding on *Prunus, Molinia*, and *Typha* (Table 4).

The caecal intestine is about half as long as the aphid (Table 8) and the total number of cells varies from 96 to 113 for *Hyalopterus*, and 58 to 67 for *Coloradoa*. There is no difference in length and total number of cells in the caecal intestine in specimens with or without a filtersystem, or from different hostplants. After birth cell division in the digestive system ceases and during larval growth the

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Table 8. Body length, and length and total number of cells of the caecal intestine in specimens of *Hyalopterus* and *Coloradoa*. 1 = Body length μ (A); 2 = Length caecal intestine μ (B); 3 = B/A; 4 = Total number of filterchamber cells in the anterior region of the caecal intestine; 5 = Total number of caecal intestine cells.

Aphid	Hostplant	Locality	Morph	Filtersystem	1	2	3	4	5
Hyalopterus	*Prunus domestica*	Hungary	apterous viviparous	+	730	460	0.64	19	110
		Wageningen	alate viviparous	−	900	500	0.56	18	106
	Prunus persica	Wageningen	alate viviparous	+	840	350	0.42	20	96
			alate viviparous	+	720	350	0.50	17	104
		Japan	alate viviparous	−	820	470	0.58	17	98
			alate viviparous	−	1240	660	0.54	20	109
	Phragmites australis	Wageningen	green apterous viviparous	−	600	240	0.40	19	99
			green apterous viviparous	+	610	300	0.50	17	98
			yellow alate male	−	990	500	0.50	18	111
			yellow alate male	+	930	540	0.58	17	111
		England	green apterous viviparous	+	720	410	0.57	27	96
			pink alate viviparous	−	530	270	0.52	22	97
		France	pink apterous viviparous	+	950	550	0.58	30	100
		Hungary	green alate viviparous	+	780	420	0.54	20	109
			pink alate viviparous	+	820	420	0.52	19	113
		Australia	apterous viviparous	+	1100	740	0.66	14	113
			alate viviparous	−	850	370	0.43	18	112
		C. Africa	apterous viviparous	+	1340	820	0.61	24	100
			apterous viviparous	+	860	510	0.59	16	99
	Phragmites mauritianus		alate viviparous	+	1860	1100	0.59	22	103
			alate viviparous	+	910	440	0.41	19	97
Coloradoa tanacetina	*Tanacetum vulgare*	Wageningen	apterous viviparous	+	930	580	0.63	9	63
			apterous viviparous	−	840	570	0.68	9	67
			apterous viviparous	+	580	380	0.67	5	60
			apterous male	−	660	340	0.52	6	58
			apterous male	−	750	390	0.52	9	60

Table 9. A list of the hostplants of *Hyalopterus* according to different authors.

Family	Hostplant	Author
Betulaceae	*Alnus glutinosa*	Hille Ris Lambers, 1944
Chenopodiaceae	*Chenopodium bonus-henricus*	Taylor and Gair, 1954
	Salsola kali	Theobald, 1927
Gramineae	*Arundo donax*	Theobald, 1927; Ilharco, 1966; El-Kady et al., 1970; Noordam (personel communication, Indonesia)
	Bamboo	Leonard, 1968; Basky, 1978; Stroyan, 1984
	Calamagrostis arenarius	Theobald, 1927
	Calamagrostis epigeios	Theobald, 1927
	Deschampsia sp.	Stroyan, 1984
	Molinia coerulea	Börner, 1952; Noordam (personel communication)
	Phragmites australis	Theobald, 1927; Smith, 1936; Börner, 1952
	Phragmites karka	Noordam (personel communication)
	Phragmites kiski (= P. karka)	Theobald, 1927
	Poa annua	Theobald, 1927
	Thysanolaena maxima	Robinson, 1972
Iridaceae	*Iris germamica*	Basky, 1978; Ponsen (Arcen, 16.VI.1990)
Juglandaceae	*Juglans regia*	Hille Ris Lambers, 1944
Liliaceae	*Allium cepa*	Basky, 1978
Loganiaceae	*Buddleia madagascariensis*	Bodenheimer and Swirski, 1957
Rosaceae	*Chaenomeles japonica*	Börner and Heinze, 1957
	Prunus americana	Smith, 1936; Shen and Chia, 1936
	Prunus amygdalus	Börner and Heinze, 1957; Ilharco, 1966
	Prunus armeniaca	Willcocks, 1916; Börner, 1952, Ilharco, 1966
	Prunus cerasifera	Ilharco, 1966; Basky, 1978
	Prunus domestica	Theobald, 1927; Hille Ris Lambers, 1944; Börner, 1952
	Prunus insititia	Theobald, 1927; Börner and Heinze, 1957
	Prunus mahaleb	Ilharco, 1966
	Prunus mume	Shen and Chia, 1936
	Prunus nigra	Robinson and Bradley, 1968
	Prunus padus	Ilharco, 1966
	Prunus persica	Theobald, 1927; Shen and Chia, 1936; Ilharco, 1966
	Prunus pissardii	Janiszewska, 1932

Family	Species	Reference
	Prunus prunophora	Schouteden, 1903
	Prunus salicina	Shen and Chia, 1936
	Prunus spinosa	Theobald, 1927; Börner, 1952
	Pyrus communis (young shoots)	Basky, 1974
	Rubus idaeus	Hille Ris Lambers, 1944
Salicaceae	*Salix* sp.	Theobald, 1927; Hille Ris Lambers, 1944
Typhaceae	*Typha angustifolia*	Smith, 1936; Börner, 1952
	Typha latifolia	Smith, 1936; Börner and Heinze, 1957; Noordam (personel communication)
Umbelliferae	*Foeniculum vulgare*	Bodenheimer and Swirski, 1957
Vitaceae	*Vitis vinifera*	Theobald, 1927

Table 10. Aphid species of the family Aphididae of which (1) the transition from the dilated stomach to the crenated intestine is marked by a sharp loop, (2) the second region of the crenated intestine has one or two additional loops (Figure 16), and (3) the anterior region of the smooth transparent caecal intestine is lined with filterchamber cells situated to the side of the stomach (Figure 3 and 4). Order of species as in Table 11.

Aphid	Hostplant	Locality
Macrosiphum albifrons Essig	Lupinus arboreus	Culture University East Anglia (England), 14.XII.1983
Macrosiphum euphorbiae (Thomas)	Lactuca sativa	Culture Department of Entomology, 1983
Macrosiphum euphorbiae (Thomas)	Tulipa sp.	Culture Institute for Plant Protection, 1982
Macrosiphum euphorbiae (Thomas)	Solanum tuberosum	Culture Institute for Plant Protection, 1983
Macrosiphum rosae (Linnaeus)	Rosa sp.	Wageningen, 27.V.1982
Megoura viciae (Buckton)	Vicia fabae	Culture University East Anglia (England), 11.XI.1983
Uroleucon cirsii (Linnaeus)	Cirsium arvense	Wageningen, 21.VI.1982
Uroleucon cichorii ssp. grossus (Hille Ris Lambers)	Crepis capillaris	Culture Institute for Plant Protection, 1983
Uroleucon sonchi (Linnaeus)	Lactuca sativa	Culture Department of Entomology, 1983
Uroleucon muralis (Buckton)	Mycelis muralis	Bennekom, 3.VI.1982
Uroleucon (Uromelan) jaceae (Linnaeus)	Centaurea jacea	Wageningen, 7.VII.1982
Uroleucon (Uromelan) jaceae ssp.aeneum (Hille Ris Lambers)	Carduis sp.	Renkum, 12.VI.1977
Metopolophium dirhodum (Walker)	Triticum vulgare	Culture Department of Entomology, 1982
Metopolophium festucae ssp.cerealium Stroyan	Triticum vulgare cv Capelle	Culture Rothamsted Experimental Station (England), 1983
Acyrthosiphon pisum (Harris)	Vicia fabae	Culture Department of Virology, 1977
Acyrthosiphon loti (Theobald)	Lotus corniculatus	Wageningen, 26.VI.1984
Acyrthosiphon caraganae (Cholodkovsky)	Caragana frutex latifolia	Wageningen, 17.VI.1984
Microlophium carnosum (Buckton)	Urtica dioica	Wageningen, 23.V.1983
Rhopalosiphum insertum (Walker)	Malus sp.	East Malling (England), 21.VI.1983
Rhopalosiphum padi (Linnaeus)	Prunus padus	Wageningen, 13.V.1977
Rhopalosiphum padi (Linnaeus)	Hordeum vulgare	Culture Department of Entomology, 1982
Rhopalosiphum maidis (Fitch)	Hordeum vulgare	Culture Department of Entomology, 1982
Dysaphis radicola (Mordvilko)	Rumex sp.	Wageningen, 20.VI.1982
Dysaphis angelicae (Koch)	Angelica archangelica	Wageningen, 5.VII.1984
Dysaphis (Pomaphis) plantaginea (Passerini)	Malus sp.	Wageningen, 22.VI.1977
Sitobion avenae (Fabricius)	Hordeum vulgare	Culture Department of Entomology,1983
Macrosiphoniella tanacetaria (Kaltenbach)	Tanacetum vulgare	Wageningen, 7.VII.1982
Macrosiphoniella ptarmicae Hille Ris Lambers	Achillea ptarmica	Wageningen, 7.VII.1982

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Macrosiphoniella artemisiae (Boyer de Fonscolombe)	*Artemisia vulgaris*	Wageningen, 30.VI.1984
Macrosiphoniella sanborni (Gillette)	*Chrysanthemum* sp.	Culture Glasshouse Crops Research Institute (England), 1983
Metopeurum fuscoviride Stroyan	*Tanacetum vulgare*	Wageningen, 12.VI.1982
Brachysiphum thalictri (Koch)	*Thalictrum aquilegifolium*	Bennekom, 3.VI.1982
Schizaphis longicaudata Hille Ris Lambers	*Phalaris arundinacea*	Wageningen, 11.VII.1982
Pleotrichophorus glandulosus (Kaltenbach)	*Artemisia vulgaris*	Wageningen, 21.VI.1977
Amphorophora rubi (Kaltenbach)	*Rubus caesius*	Wageningen, 10.VI.1982
Impatientinum asiaticum Nevsky	*Impatiens parviflorum*	Wageningen, 30.VII.1984
Rhopalomyzus (Judenkoa) lonicera (Siebold)	*Phalaris arundinacea*	Wageningen, 9.VIII.1984
Aulacorthum solani (Kaltenbach)	*Tulipa* sp.	Culture Institute for Plant Protection, 1982
Aulacorthum (Neomyzus) circumflexum Buckton	*Crocus* sp.	Wageningen, 9.I.1978
Brevicoryne brassicae (Linnaeus)	*Brassica oleracea*	Wageningen, 5.XI.1976
Nasonovia ribisnigri (Mosley)	*Crepis capillaris*	Wageningen, 8.VI.1977
Nasonovia ribisnigri (Mosley)	*Lactuca sativa*	Culture Department of Entomology, 1983
Myzus cerasi (Fabricius)	*Prunus cerasus*	Wageningen, 2.VI.1982
Myzus persicae (Sulzer)	*Vicia fabae*	Culture Department of Entomology, 1983
Myzus persicae (Sulzer)	*Brassica pekinensis* cv Granaat	Culture Department of Virology, 1965
Myzus persicae (Sulzer)	*Beta vulgaris*	Culture Department of Virology, 1983
Myzus ascalonicus Doncaster	*Brassica pekinensis* cv Granaat	Culture Department of Entomology, 1982
Cavariella theobaldi (Gillette & Bragg)	*Heracleum sphondylium*	Wageningen, 13.X.1983
Cavariella theobaldi (Gillette & Bragg)	*Salix* sp.	Wageningen, 9.VII.1982
Cavariella aegopodii (Scopoli)	*Daucus carota*	Culture Institute for Plant Protection, 1982
Lipaphis erysimi (Kaltenbach)	*Capsella bursa – pastoris*	Lent, 10.VI.1982
Hyadaphis foeniculi Passerini	*Lonicera periclymenum*	Wageningen, 22.VI.1977
Hyadaphis foeniculi Passerini	*Angelica archangelica*	*Wageningen, 14.VII.1982*
Hyperomyzus lactucae (Linnaeus)	*Sonchus oleraceus*	Culture Department of Virology, 1976
Longicaudus trirhodus (Walker)	*Aquilegia vulgaris*	Wageningen, 22.VI.1977
Illinoia (Masonaphis) lambersi (MacGillivray)	*Rhododendron ponticum*	Wageningen, 16.V.1977
Hayhurstia atriplicis Linnaeus	*Chenopodium album*	Wageningen, 14.VII.1982
Liosomaphis berberidis (Kaltenbach)	*Mahonia aquifolium*	Wageningen, 2.VII.1982
Phorodon humuli (Schrank)	*Humulus lupulus*	Culture East Malling Research Station (England), 1983
Pentatrichopus tetrarhodus (Walker)	*Rosa* sp.	Wageningen, 13.V.1982
Diuraphis (Holcaphis) holci (Hille Ris Lambers)	grass	Zimmerbach, Alsace (France), 26.VII.1981
Ovatus sp.	*Crataegus monogyna*	Wageningen, 18.VI.1982
Tubaphis ranunculina (Walker)	*Ranunculus repens*	Opheusden, 22.IX.1982
Xerophilaphis suaedae (Mimeur)	*Suaeda maritima*	Cadzand – Bad (Zwin), 29.VII.1982
Idiopterus nephrolepidis Davis	*Nephrolepis exaltata*	Wageningen, 15.VII.1981

Table 11. Mean number of caecal intestine cells and filterchamber cells in aphid species of the family Aphididae (Table 10). In brackets total number of aphids of which both cell types were counted. The genera are arranged in order of the average number of caecal intestine cells.

Aphid	Hostplant	Total number of aphids sectioned	Morph	Mean number of caecal intestine cells	Mean number of filter-chamber cells
Macrosiphum albifrons	*Lupinus arboreus*	4	alate viviparous	322(2)	6
Macrosiphum euphorbiae	*Lactuca sativa*	4	alate viviparous	169(2)	11
Macrosiphum euphorbiae	*Tulipa* sp.	7	alate viviparous	167(2)	11
Macrosiphum euphorbiae	*Solanum tuberosum*	4	apterous viviparous	159(1)	7
			alate viviparous	154(1)	10
Macrosiphum rosae	*Rosa* sp.	4	green alate viviparous	109(2)	10
			pink alate viviparous	104(2)	12
Megoura viciae	*Vicia fabae*	4	alate viviparous	196(2)	11
Uroleucon cirsii	*Cirsium arvense*	8	alate viviparous	189(2)	18
Uroleucon cichorii ssp. *grossus*	*Crepis capillaris*	3	apterous oviparous	161(2)	19
Uroleucon sonchi	*Lactuca sativa*	5	alate viviparous	154(2)	21
Uroleucon muralis	*Mycelis muralis*	8	alate viviparous	143(2)	16
Uroleucon (Uromelan) jaceae	*Centaurea jacea*	4	alate viviparous	181(2)	17
Uroleucon (Uromelan) jaceae ssp. *aeneum*	*Garduus* sp.	8	alate viviparous	209(2)	20
Metopolophium dirhodum	*Triticum vulgare*	6	apterous viviparous	147(1)	16
			alate viviparous	164(1)	20
Metopolophium festucae ssp. *cerealium*	*Triticum vulgare* cv Capelle	4	alate viviparous	121(2)	8
Acyrthosiphon pisum	*Vicia fabae*	5	alate viviparous	163(2)	19
Acyrthosiphon loti	*Lotus corniculatus*	4	alate viviparous	142(1)	22
Acyrthosiphon caraganae	*Caragana frutex latifolia*	4	apterous viviparous	123(1)	36
Microlophium carnosum	*Urtica dioica*	10	alate viviparous	161(2)	10
Rhopalosiphum insertum	*Malus* sp.	4	alate viviparous	146(2)	20
Rhopalosiphum padi	*Prunus padus*	3	alate viviparous	127(2)	6
Rhopalosiphum padi	*Hordeum vulgare*	6	apterous viviparous	76(2)	6
Rhopalosiphum maidis	*Hordeum vulgare*	6	alate viviparous	74(3)	3
Dysaphis radicola	*Rumex* sp.	8	alate viviparous	142(2)	12
Dysaphis angelicae	*Angelica archangelica*	4	alate viviparous	99(2)	6

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Species	Host plant	n	Morph	Value (n)	n
Dysaphis (Pomaphis) plantaginea	Malus sp.	10	alate viviparous	101(3)	10
Sitobion avenae	Hordeum vulgare	5	apterous viviparous	127(1)	16
			alate viviparous	132(2)	14
Macrosiphoniella tanacetaria	Tanacetum vulgare	5	apterous viviparous	125(1)	11
Macrosiphoniella ptarmicae	Achillea ptarmicae	4	apterous viviparous	120(1)	14
			alate viviparous	123(1)	14
Macrosiphoniella artemisiae	Artemisia vulgaris	4	alate viviparous	116(1)	19
Macrosiphoniella saniborni	Chrysanthenum sp.	4	apterous viviparous	71(2)	8
			alate viviparous	72(2)	9
Metopeurum fuscoviride	Tanacetum vulgare	12	alate viviparous	122(3)	37
Brachysiphum thalictri	Thalictrum aquilegifolium	8	apterous viviparous	109(2)	6
			alate viviparous	109(1)	5
Schizaphis longicaudata	Phalaris arundinacea	8	apterous viviparous	107(1)	15
			alate viviparous	104(2)	14
Pleotrichophorus glandulosus	Artemisia vulgaris	8	apterous viviparous	104(3)	8
Amphorophora rubi	Rubus caesius	7	alate viviparous	103(3)	9
Impatientinum asiaticum	Impatiens parviflorum	4	alate viviparous	97(2)	4
Rhopalomyzus (Judenkoa) lonicera	Phalaris arundinacea	4	apterous viviparous	96(3)	5
Aulacorthum solani	Tulipa sp.	3	apterous viviparous	92(2)	9
			alate viviparous	88(1)	7
Aulacorthum (Neomyzus) circumflexum	Crocus sp.	3	apterous viviparous	79(3)	8
Brevicoryne brassicae	Brassica oleracea	3	apterous viviparous	89(3)	3
Nasonovia ribisnigri	Crepis capillaris	6	alate viviparous	89(2)	5
Nasonovia ribisnigri	Lactuca sativa	5	alate viviparous	82(2)	8
Myzus cerasi	Prunus cerasus	8	alate viviparous	89(3)	5
Myzus persicae	Vicia fabae	4	apterous viviparous	86(1)	5
			alate viviparous	80(1)	2
Myzus persicae	Brassica pekinensis cv Granaat		apterous viviparous	84(11)	5
			alate viviparous	79(1)	3
Myzus persicae	Beta vulgaris	4	apterous viviparous	60(1)	6
			alate viviparous	61(1)	8
Myzus ascalonicus	Brassica pekinensis	8	apterous viviparous	50(3)	2

Species	Host plant		Morph	%	
Cavariella theobaldi	*Heracleum sphondylium*	4	apterous oviparous	87(2)	4
Cavariella theobaldi	*Salix sp.*	4	alate viviparous	79(2)	5
Cavariella aegopodii	*Daucus carota*	7	apterous viviparous	76(1)	4
			alate viviparous	75(2)	3
Lipaphis erysimi	*Capsella bursa-pastoris*	4	alate viviparous	86(3)	5
Hyadaphis foeniculi	*Lonicera periclymenum*	7	apterous viviparous	82(1)	11
			alate viviparous	86(1)	12
Hyadaphis foeniculi	*Angelica archangelica*	4	alate viviparous	76(2)	8
Hyperomyzus lactucae	*Sonchus oleraceus*	7	alate viviparous	84(3)	4
Longicaudus trirhodus	*Aquilegia vulgaris*	7	alate viviparous	76(3)	8
Illinoia (Masonaphis) lambersi	*Rhododendron ponticum*	13	apterous viviparous	76(3)	3
Hayhurstia atriplicis	*Chenopodium album*	4	alate viviparous	75(3)	4
Liosomaphis berberidis	*Mahonia aquifolium*	4	apterous viviparous	74(3)	6
Phorodon humuli	*Humulus lupulus*	3	apterous viviparous	73(3)	4
Pentatrichopus tetrarhodus	*Rosa sp.*	3	alate viviparous	72(3)	8
Diuraphis (Holcaphis) holci	grass	6	apterous viviparous	72(3)	2
Ovatus sp.	*Crataegus monogyna*	4	apterous viviparous	58(1)	8
			alate viviparous	62(2)	9
Tubaphis ranunculina	*Ranunculus repens*	5	alate viviparous	61(1)	3
			apterous oviparous	56(2)	4
Xerophilaphis suaedae	*Suaeda maritima*	14	apterous viviparous	53(3)	2
Idiopterus nephrolepidis	*Nephrolepis exaltata*	6	apterous viviparous	40(3)	2
Cryptomyzus galeopsidis	*Galeopsis tetrahit*		alate viviparous	74(1)	25 (filtersystem)
Cryptomyzus ribis	*Ribes rubrum*		apterous viviparous	69(2)	23 (filtersystem)

caecal intestine and its cells increase in size proportionally with the aphid. Because of the vigorous peristaltic movements the caecal intestine may become so dilated (Figure 21), that it is difficult to count the nuclei in transverse serial sections. Therefore only a few caecal intestines have been examined in detail.

In *Hyalopterus* the total number of filterchamber cells in the anterior region of the caecal intestine varies from 14 to 30, and in *Coloradoa* from 5 to 9 (Table 8). The total number of filterchamber cells in *Coloradoa* is distinctly less than in *Hyalopterus*, which agrees with the total number of caecal intestine cells, which is also distinctly less in *Coloradoa* (from 58 to 67) than in *Hyalopterus* (from 96 to 113). This feature is not observed in the other species of the family Aphididae (Table 11).

Rectum

The rectum is situated in the seventh abdominal segment and passes into the epidermal invagination (Figure 1). It consists of small columnar cells with elliptic nuclei; the apical cell membrane is lined with an intima (Figure 2G). Both dorsally and laterally the muscular coat of the posterior end of the caecal intestine and that of the rectum is connected to the abdominal body wall by visceral muscles.

The cellular structure of the epidermal invagination is identical to that of the foregut. The invagination opens to the exterior via the anal opening which is situated ventral to the cauda (Figure 11A). The anus is opened by six dorsal muscles. They arise on the dorsal abdominal wall, at the junction of the eighth and ninth tergites, and pass downward to their point of insertion on the middle of the dorsal wall of the epidermal invagination. Two pairs of lateral muscles serve to close the anus. Each pair of muscles originates at the junction of the seventh and eighth sternites just lateral to the gonopore, and are inserted on the dorsolateral and ventrolateral walls of the anus, respectively (Figure 12A and 18I).

The presence of a cuticular lining facing the luminal surface of the rectal cells includes the rectum with the foregut as an ectodermal part of the digestive system (Figure 19 and 20). The cuticle of the epidermal invagination (Figure 8J) is identical to that of the body wall. The endocuticle has a lamellate structure whereas that of the foregut (Figure 5A) and rectum (Figure 8I) is an amorphous mass. The exocuticle of the last two organs is very thin compared with that of the epidermal invagination (Figure 20L). The exocuticle of the rectum and that of the epidermal invagination is shed at each moult with the rest of the exuviae. In the coccid, *Planococcus citri* Risso, the luminal surface of the rectal cells is lined only with an epicuticle consisting of three well defined electron dense layers (Foldi, 1973).

The excrement of the aphid is passed out here as honeydew. Smith (1937) observed that *Hyalopterus pruni* first raises the tip of its abdomen and then excretes a liquid drop of honeydew which is thrown with considerable force by the distal part of the tibia of one of both hindlegs.
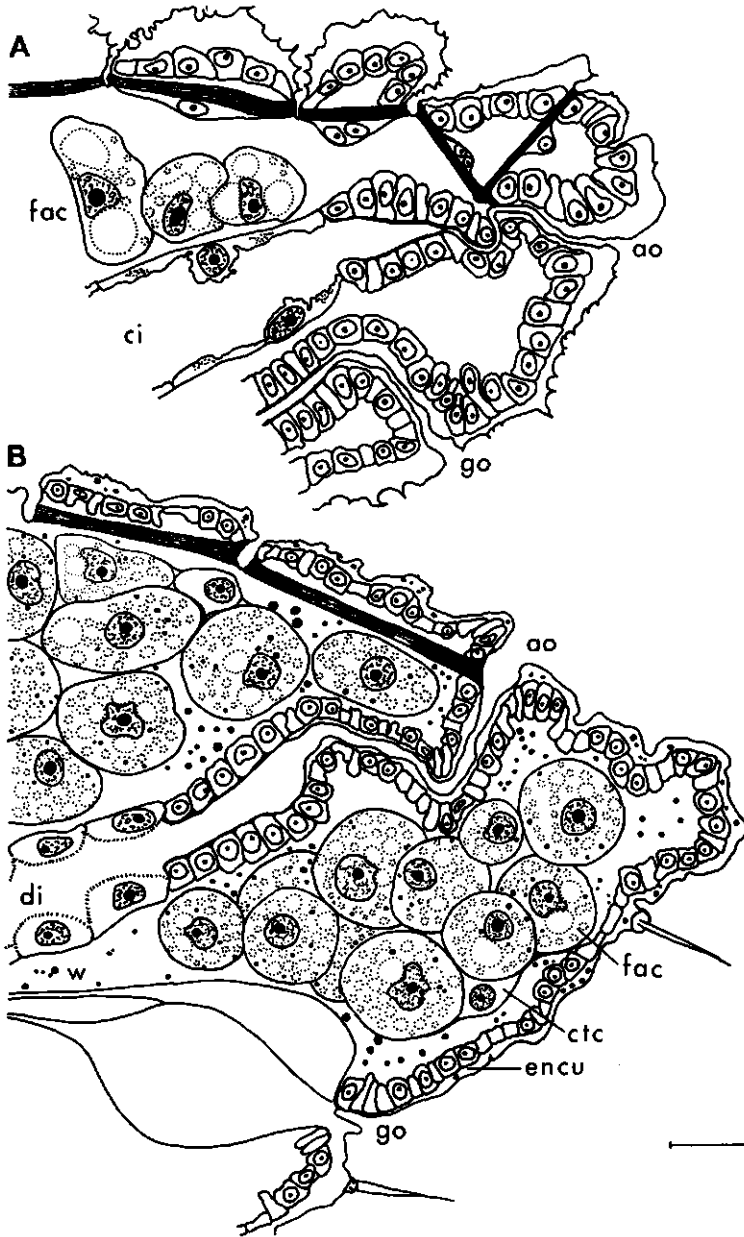
Figure 11.A. Median longitudinal section of an apterous oviparous fourth stage larva of *Phylloxera coccinea* von Heyden. Note the S-shaped flexure of the epidermal invagination. Anal opening in ventral position. B. Median longitudinal section of an alate oviparous larva of *Adelges (Sacchiphantes) abietis*. Anal opening in dorsal position. The anal musculature is given in Figures 14H and 12B respectively. For list of abbreviations see page 61. Bar represents 10 μm.
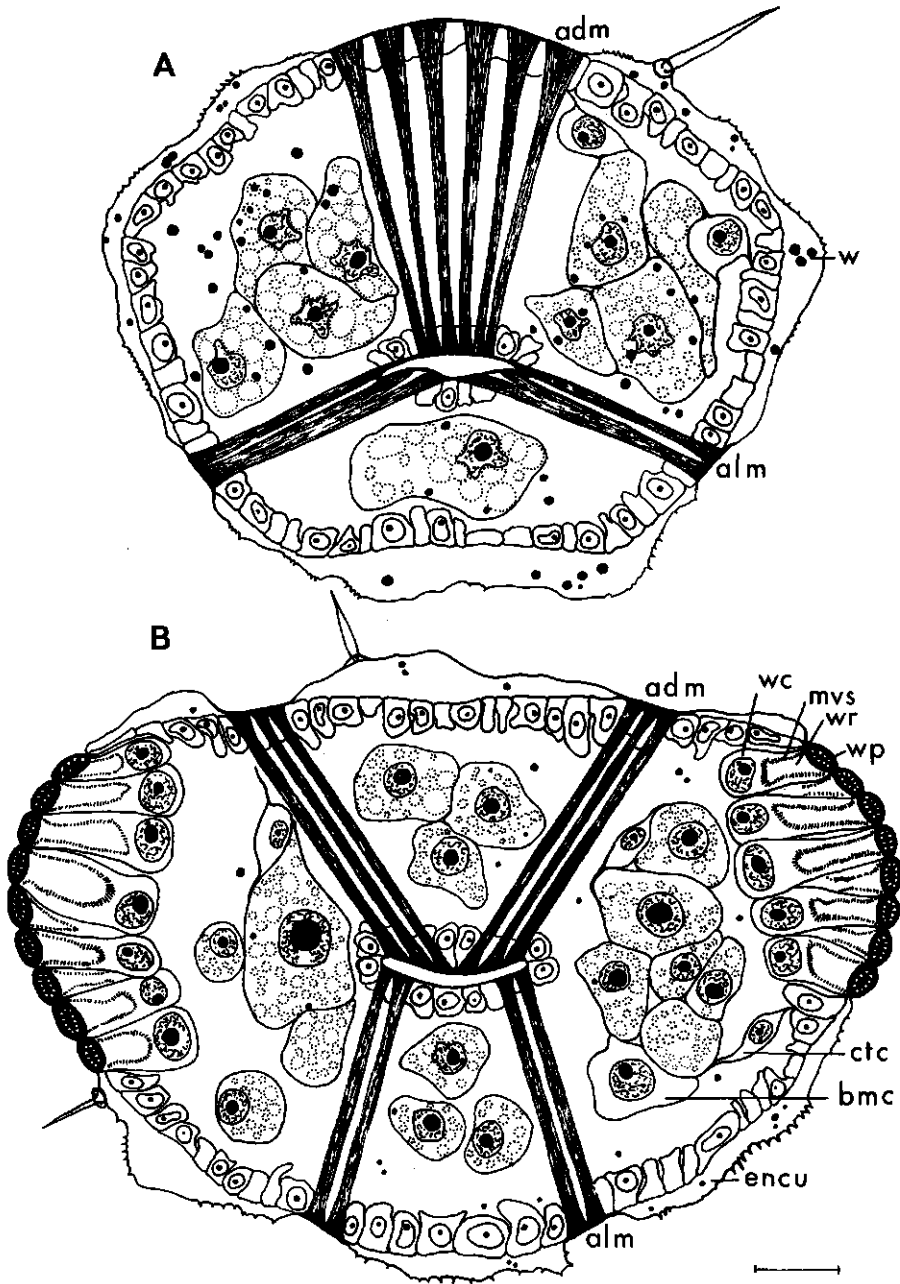
Figure 12. Transverse sections of the anal musculature of (A) *Smynthurodes betae* (anal opening in ventral position) and (B) *Adelges (Cholodkovskya) viridana* (anal opening in dorsal position). Note the waxy droplets in the fat cells, haemolymph, and endocuticle. For list of abbreviations see page 61. Bar represents 10 μm.
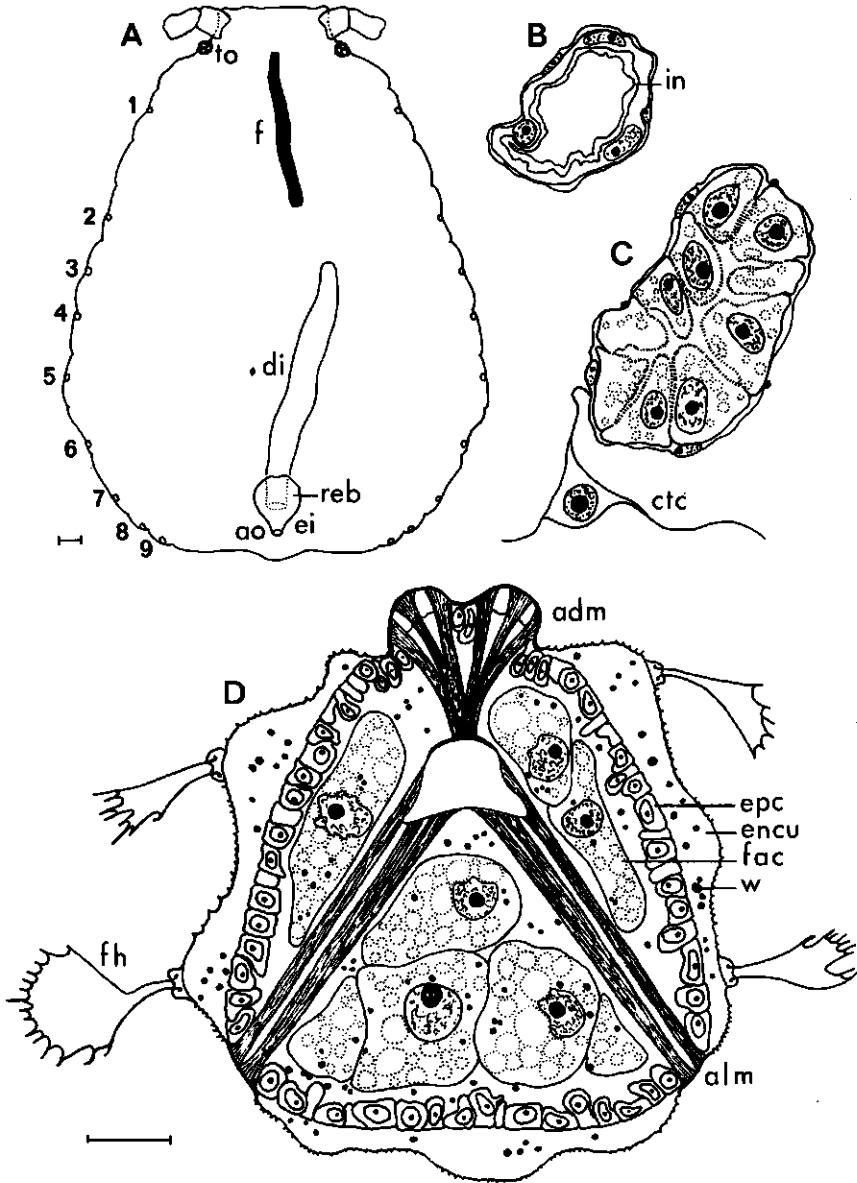
Figure 13.A. Dorsal view of the digestive system of an apterous viviparous larva of *Geoica setulosa* reconstructed from serial transverse sections. 1-2, pro- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 μm. Transverse sections of (B) the foregut and (C) descending intestine of *G. setulosa*; and (D) the anal musculature of *G. utricularia*. Note the presence of waxy droplets in the fat cells, haemolymph, and endocuticle. For list of abbreviations see page 61. Bar represents 10 μm.
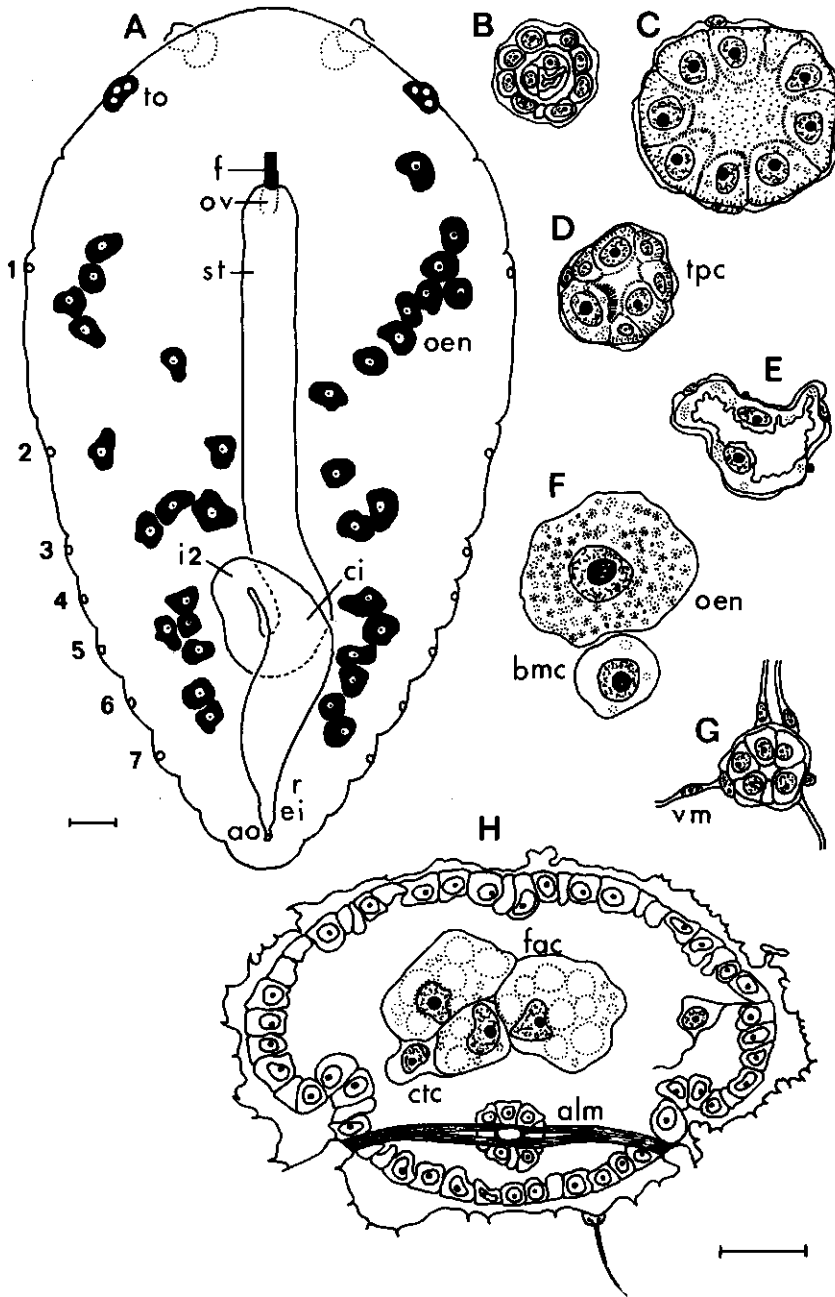
Figure 14.A. Dorsal view of the digestive system and topographical position of the oenocytes of an apterous oviparous third stage larva of *Phylloxera coccinea* reconstructed from serial transverse sections. 1-2, meso- and metathoracic spiracles; 3-7, abdominal spiracles. Note the absence of a mycetome. Bar represents 30 μm. Transverse sections of the oesophageal valve (B), stomach with merocrine gland cells (C), second region of the intestine (D), caecal intestine (E), oenocyte and a basophilic mesodermal cell (F), rectum (G), and anal musculature (H) of a second stage larva of *P. coccinea*. Anal opening in ventral position (Figure 11A). For list of abbreviations see page 61. Bar represents 10 μm.

Discussion

Morphologically and histologically the digestive system of *Hyalopterus pruni* is identical to that of *H. amygdali*. Moreover, there is no difference between the several morphs of *Hyalopterus*, viz. apterous and alate viviparous females, apterous oviparous females, and alate males. Similar results have been obtained for *Aphis (Doralis) frangulae* Koch (= *Aphis frangulae* Kaltenbach complex) (Roberti, 1946), *Aphis tripolii* Laing, and *Aphis farinosa* Gmelin, although in the latter an additional loop was lacking in eight out of sixteen apterous males (Ponsen, 1990 b).

Foregut

The digestive system of *Geoica setulosa* (Table 13) consists only of a foregut which is closed at its posterior end without an oesophageal valve, and a blindly ending descending intestine (Figure 13A). The stomach and the first and second region of the intestine is completely lacking. In all other aphids the foregut is a thin tube, but in *G. setulosa* it is a dilated structure and the squamous cells are lined with an intima (Figure 13B).

In general it is assumed that the function of the foregut is transporting liquid food quickly from the pharynx to the stomach. However, in *G. setulosa* the ingested water and nutrients must be able to pass through the cuticular lining of the foregut. From this it can be concluded that the luminal surface of the intima of the foregut is not lined with an epicuticle (Figure 5A and 19A), since an epicuticle provides the waterproof layer of the epidermal cuticle (Wigglesworth, 1990).

Triplet cells

In all aphid species investigated the second region of the crenated intestine is characterized by the presence of 6-8 groups of three conical-shaped cells (triplet) at irregular intervals among the intestinal cells (Figure 2E, 14D, 17D, and 18E). However, in *Phylloxera coccinea* von Heyden, feeding on *Quercus robur*, the first and second region of the crenated intestine is reduced to a very short tube which consists of 2-3 intestinal cells and 7-10 triplets (Figure 14). The triplet cells are presumably peptidergic endocrine cells which occur as single cells among the midgut cells of a number of insects (Billingsley, 1990). In *G. setulosa* the stomach and the first and second region of the crenated intestine are completely lacking and so also are the triplet cells (Figure 13). This implies that in aphids the release of the substance from the 'endocrine' triplet cells is strictly confined to the intestine.

Filtersystem

In the genera *Cryptomyzus* (Aphididae; Table 10) and *Eulachnus* (Lachnidae),

Table 12. Aphid species used for electron microscopical studies, their hostplant, and relevant locality data.

Aphid	Hostplant	Locality
Adelges (Dreyfusia) nordmannianae (Eckstein)	Picea orientalis	Wageningen, 15.VII.1982
Aphis fabae Scopoli	Vicia fabae	Culture Plant Protection Service, Wageningen, 22.III.1983
Drepanosiphum platanoidis (Schrank)	Acer pseudoplatanus	Wageningen, 10.VII.1981
Myzus persicae (Sulzer)	Brassica pekinensis cv Granaat	Culture Department of Virology, Wageningen, 26.XI.1979
Rhopalosiphum maidis (Fitch)	Hordeum vulgare	Culture Department of Entomology, Wageningen, 20.I.1983
Subsaltusaphis ornata (Theobald)	Carex riparia	Ex culture Institute for Plant Protection, Wageningen, II.1977
Uroleucon sonchi (Linnaeus)	Lactuca sativa	Culture Department of Entomology, Wageningen, 3.V.1983

Table 13. Aphid species of the family Eriosomatidae, their hostplant, and relevant locality data.

Aphid	Hostplant	Locality
Aploneura lentisci (Passerini)	Festuca ovina	Glasshouse Department of Entomology, Wageningen, IX.1982
Cerataphis palmae (Ghesquière)	palms	Madeira (Portugal), 13.X.1981
Eriosoma (Schizoneura) lanuginosum (Hartig)	Ulmus sp.	Herveld, 29.VI.1984
Eriosoma (Schizoneura) ulmi (Linnaeus)	Ulmus campestris	Wageningen, 18.VI.1977
Forda formicaria von Heyden	Deschampsia flexuosa	Ede, 21.IX.1982
Forda marginata Koch	Deschampsia flexuosa	Ede, 21.IX.1982
Geoica setulosa (Passerini)	Agrostis canina	Ede, 26.VIII.1982
Geoica utricularia (Passerini)	Agrostis canina	Ede, 26.VIII.1982
Pemphigus bursarius (Linnaeus)	Populus nigra	Wageningen, 19.VI.1984
Pemphigus spyrothecae Passerini	Populus nigra	Wageningen, 17.VIII.1984
Smynthurodes betae Westwood	Cardamine flexuosa	Bennekom, 21.IX.1982
Tetraneura ulmi (Linnaeus)	Lolium multiflorum	Wageningen, 12.VII.1982

Table 14. Aphid species of the family Adelgidae, their hostplant, and relevant locality data.

Aphid	Hostplant	Locality
Adelges lapponicus Cholodkovsky	*Picea abies*	Weissensee (Austria), 20.VII.1984
Adelges (Cholodkovskya) viridana (Cholodkovsky)	*Larix kaempferi*	Wageningen, 23.VI.1984
Adelges (Dreyfusia) nordmannianae (Eckstein)	*Picea orientalis*	Wageningen, 15.VII.1982
Adelges (Gilletteella) cooleyi (Gillette)	*Picea sitchensis*	Hardenberg, 23.VII.1982
Adelges (Sacchiphantes) abietis (Linnaeus)	*Picea abies*	Wageningen, 3.VII.1982
Adelges (Sacchiphantes) viridis (Ratzeburg)	*Picea abies*	Weissensee (Austria), 20.VII.1984
Adelges (Sacchiphantes) viridis (Ratzeburg)	*Picea abies*	Hastière (Belgium), 25.VII.1985
Pineus orientalis (Dreyfus)	*Picea orientalis*	Wageningen, 24.VII.1984

where the entire filtergut (= the anterior region of the midgut) is encapsulated by the anterior region of the caecal intestine, the wall of the filterchamber adjacent to the stomach is lined with filterchamber cells, whereas the opposite wall is lined with caecal intestine cells (Figure 22). An identical cellular arrangement occurs in the filterchamber of *Longistigma caryae* (Harris) (Lachnidae) where the entire stomach is encapsulated by the anterior region of the 'hindgut' (Knowlton, 1925), and in the filterchamber of *Hyalopterus* an *Coloradoa* where only the anterior region of the stomach is encapsulated by the anterior region of the caecal intestine (Figure 3A). In the Drepanosiphidae where the entire stomach is encapsulated by the blindly ending intestine, filterchamber cells do not occur in the filterchamber (Ponsen, 1979). *Phloeomyzus passerinii* (Signoret) does not have filterchamber cells in the anterior region of the caecal intestine (Figure 4F); the intestinal cells end abruptly, and the squamous cells of the caecal intestine begin.

In the superfamily Cicadoidea the filtersystem comprises the anterior region of the stomach, around which are looped the posterior extremity of the midgut and the anterior portion of the Malpighian tubules each being enveloped by the walls of the stomach between two adjacent folds (Figure 10 and Table 5 in Ponsen, 1979). In this system the anterior region of the stomach is formed on one side by cuboidal cells, whereas the surface in contact with the internal Malpighian tubules and internal midgut consists of very flattened epithelial cells (Licent, 1912; Marshall and Cheung, 1974). In *Cicadula sexnotata* (= *Macrosteles sexnotatus* (Fallen)) the character of the stomach cells adjacent to the fused midgut changes abruptly after staining with Wright's solution (Dobroscky, 1931). On the other hand, in *Hyalopterus* and *Coloradoa* there is no difference in structure of the cells adjacent to the filterchamber and those on the opposite wall of the stomach (Figure 2A), as is also the case in specimens without a filtersystem. The several forms of the filtersystem and their cellular arrangement within the order Hemiptera has already been discussed (Ponsen, 1979).

It is interesting that on *Phragmites* three times more *Hyalopterus* specimens with a filtersystem occur than on *Prunus* (Table 4). This feature indicates that

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the filtersystem must have a function. The function of the filtersystem is the removal of the excess of water in the ingested liquid food from the filtergut or stomach via the filterchamber cells to the lumen of the caecal intestine. In aphid species without a filtersystem (Table 11) the excess water is removed from the foregut or stomach to the haemolymph and from there via the filterchamber cells to the lumen of the caecal intestine (Figure 4). However, aphid species of the families Adelgidae, Mindaridae, Thelaxidae, Chaitophoridae, Drepanosiphidae, Anoeciidae and Greenideidae, and the *Aphis*group, wich have no filterchambers cells, the excess water is removed from the haemolymph via the descending intestine cells to the exterior as honeydew. In conclusion the filterchamber cells are probably a remnant of the descending intestine and have the function of water regulation in aphid species with a caecal intestine.

Rectum

Generally in insects the transition from the endodermal midgut to the ectodermal hindgut is inserted with Malpighian tubules. In the superfamily Aphidoidea Malpighian tubules are absent (Ramdohr, 1811; Morren, 1836; Witlaczil, 1882), as well as in all morphs of *Hyalopterus* (Figure 1) and *C. tanacetina.*

In *Geoica setulosa, G. utricularia, Smynthurodes betae,* and *Tetraneura ulmi* (Eriosomatidae; Table 13) the descending intestine passes ventrally into a rectal bladder, a relatively voluminous structure somewhat extended anteriorly (Figure 15). The rectal bladder consists of squamous cells and their luminal surface is lined with an intima similar to that of the foregut. The bladder is kept in position by visceral muscles which are connected to the abdominal integument. Inside the rectal bladder is a glandlike organ consisting of about 22 long conical cells. The cytoplasmic filaments of the conical cells are joined to a stalk inserted on the transition from the descending intestine to the rectum. This organ is probably homologous with the original Malpighian tubules which have disappeared during the evolution of the Aphidoidea.

A similar glandlike organ is lacking in the remaining species listed in Table 13, and in all other aphid species investigated. However, in *Forda formicaria* and *F. marginata* the posterior end of the descending intestine, the rectum, and the anterior region of the epidermal invagination are encapsulated by a ring of polygonal cells (Figure 23). These cells are identical to the individual basophilic mesodermal cells, which are evenly dispersed among the fat cells (Figure 23 in Ponsen, 1972). The dorsal region of the rectum of *Schoutedenia lutea* (van der Goot) (Family Greenideidae) is built up of columnar 'gland' cells but without a cuticular lining (Figure 15B).

Anal opening

In the majority of aphid species including *Hyalopterus* and *Coloradoa* the anal opening is situated ventral to the cauda (Figure 11A). In the Adelgidae (Balch, 1952), *Geoica setulosa, G. utricularia,* and *Smynthurodes betae* the anus is dorsal
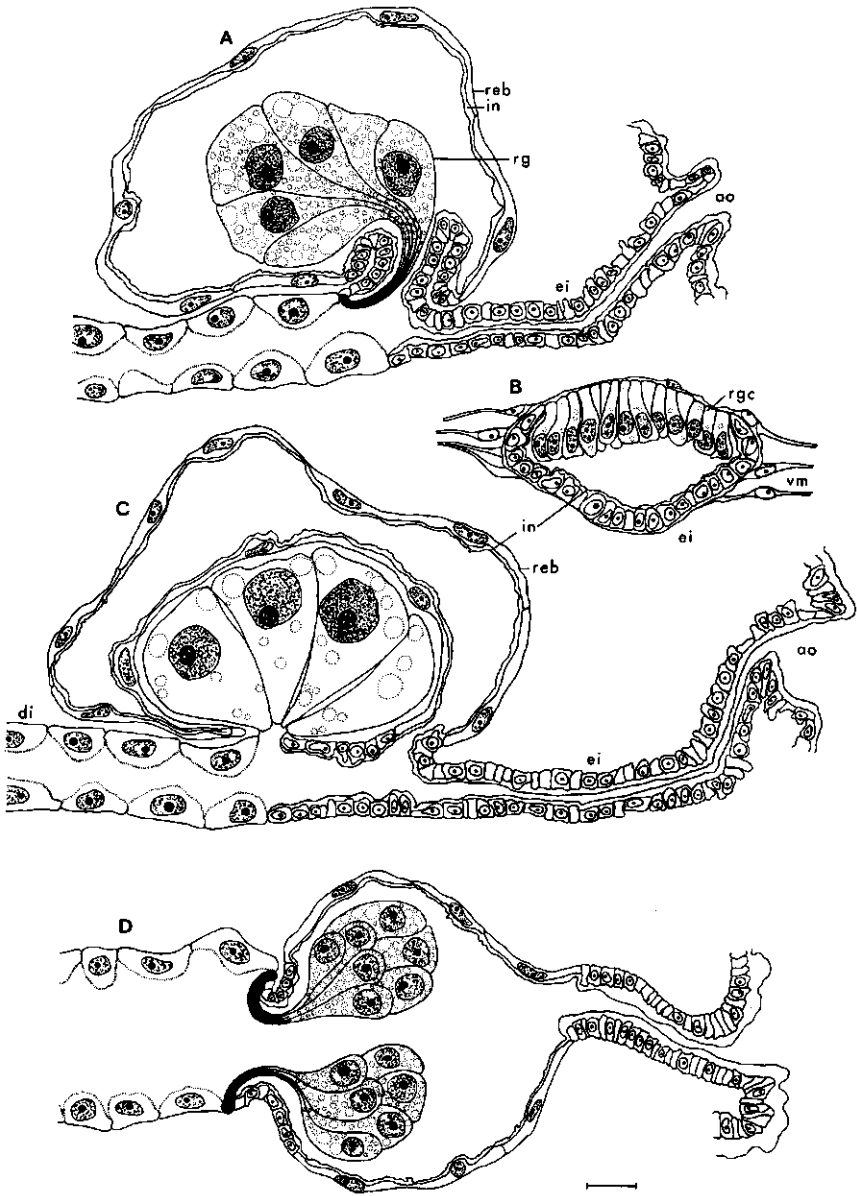
Figure 15. Median longitudinal section of the rectal bladder and rectal gland of *Geoica utricularia* (A), *Smynthurodes betae (C)*, and *Tetraneura ulmi* (D) (Table 12). B. Transverse section of the rectal gland cells on the transition of the descending intestine and the epidermal invagination in *Schoutedenia lutea* (van der Goot). For list of abbreviations see page 61. Bar represents 10 μm.
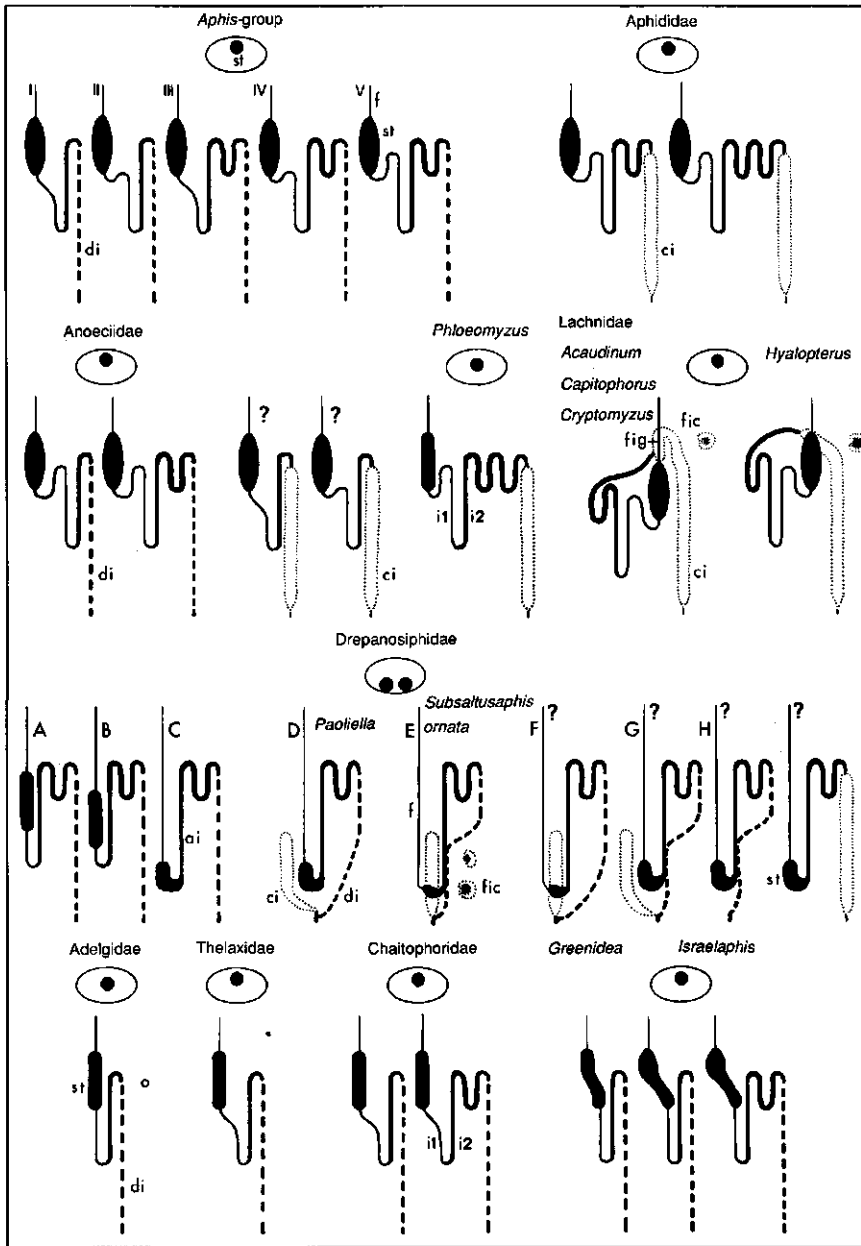
Figure 16. Diagrams illustrating the existing and hypothetical (?) forms of the digestive system within the Aphidoidea. The dashed line represents the descending intestine, and the dotted line the caecal intestine. For list of abbreviations see page 61.

to the cauda (Figure 11B), and in *Forda formicaria* and *F. marginata the* anus is in a terminal position (Heie, 1980). In the Phylloxeridae an anal opening is lacking since they do not emit honeydew (Dreyfus, 1894; Kunkel, 1966).

However, in *Phylloxera coccinea* the epidermal invagination is a very thin tube showing a S-shaped flexure which terminates at the anal opening ventral to the cauda (Figure 11A). The anus is controlled by two pairs of lateral muscles (Figure 14H), but lacks the anal dorsal muscles (Figure 12A). An identical S-shaped flexure occurs in the common afferent salivary duct of which the opening to the pumpchamber is controlled by one pair of muscles (Figure 5 in Ponsen, 1972).

Phylogeny

In general the digestive system of aphids consists of a foregut which opens into an oesophageal valve, a tubular or dilated stomach, the first and second region of the crenated intestine, a smooth transparent intestine, a rectum, and an epidermal invagination terminating at the anal opening (Figure 10).

According to Hille Ris Lambers (1964) and Heie (1967) the Adelgidae and Phylloxeridae may be considered as the phylogenetically oldest family of the Aphidoidea. The digestive system of the Adelgidae consists of a short foregut, a tubular stomach situated in the middle of the aphid, and a descending intestine. The first region of the crenated intestine lies in a direct line with the stomach (Figure 16 and 17). In the Thelaxidae the tubular stomach is situated centrally, close to the dorsum of the aphid, whereas the crenated intestine runs from the stomach directly ventrally and then passes posteriorly to the abdominal loop. The digestive system of the Chaitophoridae is similar to that of the Thelaxidae, however, in the Chaitophoridae there are genera and even individuals of some species that have or lack an additional loop in the second region of the crenated intestine (Ponsen, 1990 C). In the genera *Greenidea* and *Israelaphis* of the family Greenideidae, the stomach bends ventrally to join the crenated intestine (Figure 16). The most characteristic structure of the *Aphis*-group is the transition from the dilated stomach to the crenated intestine, which could have evolved from the type (Figure 16, I and III) seen in the Thelaxidae and Chaitophoridae, via a weak loop being an intermediate form (II and IV) to the evolutionary final form, marked by a sharp loop (V). This final form of transition (V) in *Aphis* is representative for the Anoeciidae, with or without an additional loop.

Within the family Drepanosiphidae there are certainly three, and possibly six anatomically distinct groups of aphids. In the first group the tubular stomach lies ventrally, and starts in one of the first five abdominal segments (Figure 16A-B). In *Drepanosiphum acerinum* and *D. aceris* the stomach starts in the sixth abdominal segment and is curved (Figure 16C). The second group (Figure 16E) has two smooth transparent intestines: the descending intestine which is a continuation of the ascending intestine, and the caecal intestine which is a blindly ending evagination of the rectum (Figure 10B). Both transparent intestines form

a filtersystem: a concentric filtersystem in which the stomach is encapsulated by the caecal intestine (Figure 9B) and a parallel filtersystem in which the anterior region of the ascending intestine is fused with the posterior region of the descending intestine (Figure 9C). *Paoliella terminaliae* (Hall), a representative of the third group, lacks a filtersystem (Figure 16D). The other three groups are hypothetical (Figure 16F-H). They are likely to have either a concentric filtersystem or a parallel filtersystem, with or without a caecal intestine.

The two types of smooth transparent intestines can be histologically distinguished from each other. The caecal intestine has a simple squamous epithelial lining the cells of which have elongated or elliptical nuclei. The cells contain granules and irregular membraneless 'vesicles' (Figure 7G) in which occur waxy droplets. The apical cell membrane presents irregular fingerlike evaginations in which occur small oblong mitochondria. The descending intestine consists of either cuboidal or triangular cells with more or less spherical nuclei and cytoplasmic vacuoles. The apical cell membrane presents a labyrinthine system of closely packed irregular invaginations of different dimensions (Figure 6D, 7F and 20). In dissections both smooth transparent intestines exhibits vigorous peristaltic movements generated by circular and longitudinal muscles. The transition from the second region of the crenated intestine to the descending intestine is marked by a gradual increase of 2-4 intestinal cells followed by an abrupt change to the typical cellular structure of the descending intestine. Species belonging to the families Adelgidae (Figure 17), Mindaridae (Figure 18), Thelaxidae, Chaitophoridae, Greenideidae, Drepanosiphidae, Anoeciidae, and the genus *Aphis* all have a descending intestine (Figure 16).

During evolution the descending intestine was presumably replaced by the caecal intestine (Figure 10), but with the retention of the concentric filtersystem. Species with such a structure occur in the family Lachnidae, and the genera *Acaudinum, Capitophorus*, and *Cryptomyzus* (Figure 16) (Ponsen, 1977, 1981). In these species the anterior region of the midgut (= filtergut) is encapsulated by the anterior region of the caecal intestine (Figure 22). A similar structure occurs in *Hyalopterus* and *Coloradoa*, where the anterior region of the stomach is encapsulated by the anterior region of the caecal intestine. This concentric filtersystem is very primitive in comparison with that of the above mentioned family and genera. This primitive filtersystem occurs in 20% of the specimens of *Hyalopterus* on *Prunus* and 56% of those on *Phragmites* (Table 4). The presence of a filtersystem in *Coloradoa* is 26% (Table 2). In the remaining specimens the stomach is not encapsulated by the caecal intestine which is completely separated from the stomach and forms a more or less spherical structure (Figure 2H, 3 and 4A).

The anterior region of the caecal intestine that envelopes the filtergut or the anterior region of the stomach is the filterchamber (Figure 2A). It is lined with both filterchamber and caecal intestine cells, but arranged so that the filterchamber cells are situated on the side adjacent to the stomach while the squamous caecal intestine cells are on the opposite wall of the filterchamber. The number of filterchamber cellls gradually decreases until the caecal intestine con-
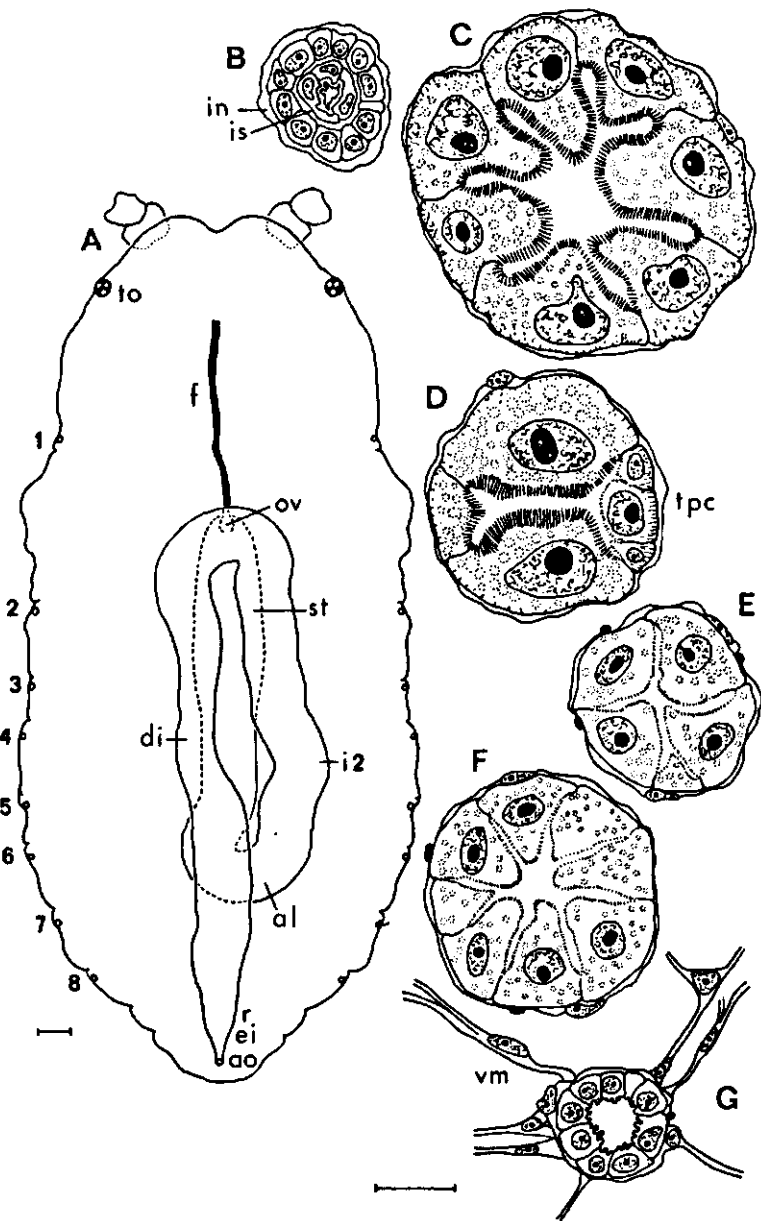
Figure 17.A. Dorsal view of the digestive system of an alate oviparous larva of *Adelges (Sacchiphantes) abietis* reconstructed from serial transverse sections. 1-2, pro- and metathoracic spiracles; 3-8, abdominal spiracles. Bar represents 30 μm. Transverse sections of the (B) oesophageal valve and (C) stomach of *Adelges (Dreyfusia) nordmannianae*; (D) second region of the intestine of *Pineus orientalis*; (E) the beginning and (F) halfway the descending intestine of *Adelges (Sacchiphantes) viridis*; and (G) the rectum of *Adelges (Gilletteella) cooleyi* (Table 14). For list of abbreviations see page 61. Bar represents 10 μm.
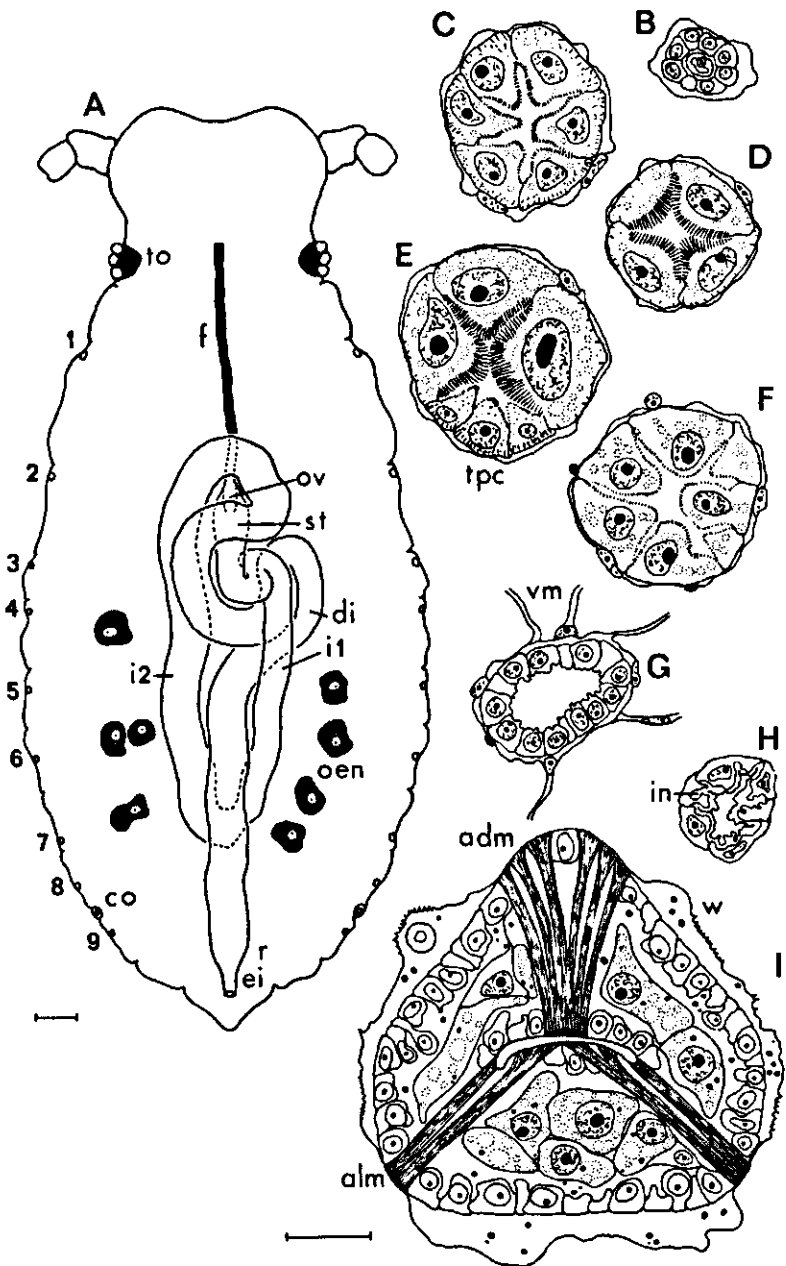
Figure 18.A. Dorsal view of the digestive system and topographical position of the oenocytes of an apterous oviparous larva of *Mindarus abietinus* Koch reconstructed from serial transverse sections. The siphuncular pores (CO) are situated on the sixth abdominal tergite. Bar represents 30 μm. Transverse sections of the oesophageal valve (B), stomach (C), first (D) and second region of the intestine (E), descending intestine (F), rectum (G), epidermal invagination (H), and anal musculature (I) of *M. abietinus*. Anal opening in ventral position. Note the waxy droplets (W) in the fat cells, haemolymph, and endocuticle. For list of abbreviations see page 61. Bar represents 10 μm.
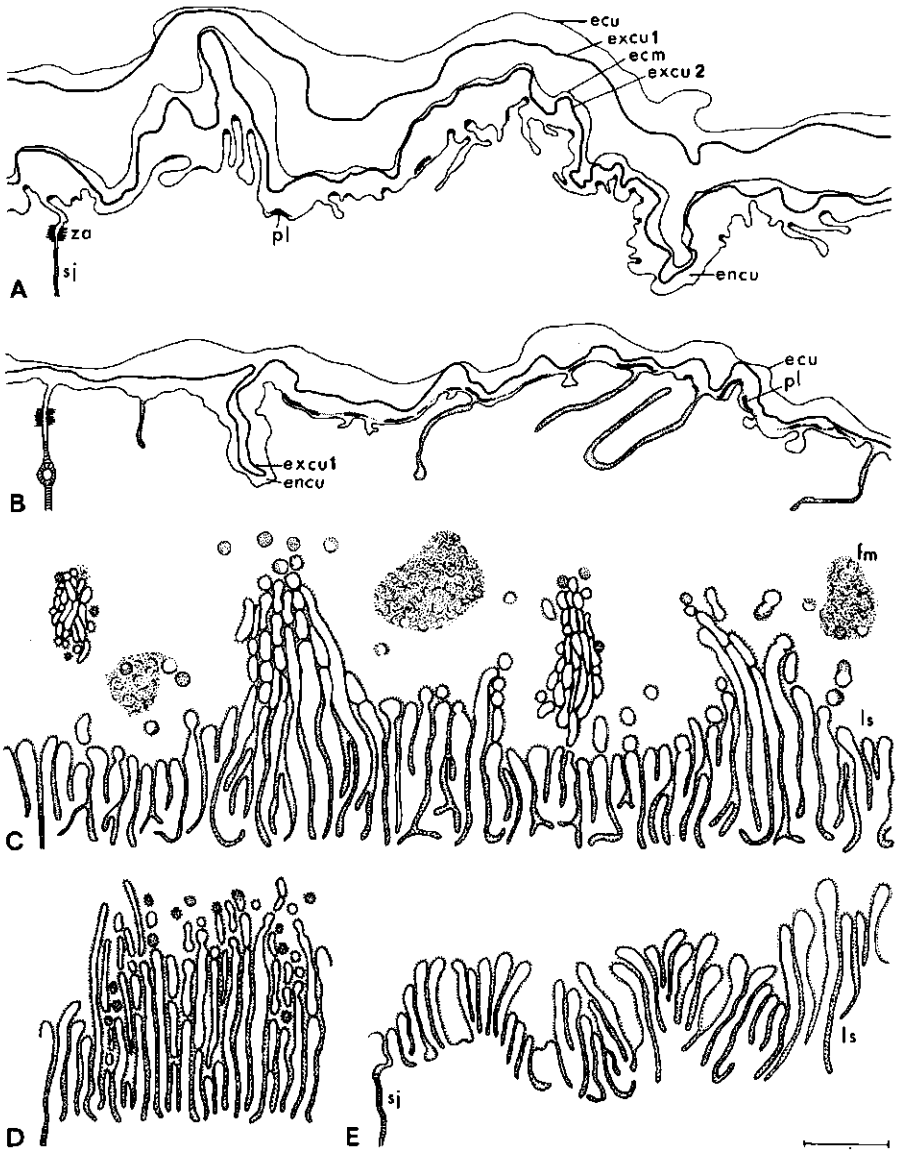
Figure 19. Schematic representation of the apical cell membrane of the foregut (A, second stage), outer layer of the oesophageal valve (B, first stage), stomach (merocrine secretion; C, *Myzus persicae*; D, *Subsaltusaphis ornata*), and triplet cell (E) (Table 12). For list of abbreviations see page 61. Bar represents 0.5 µm.
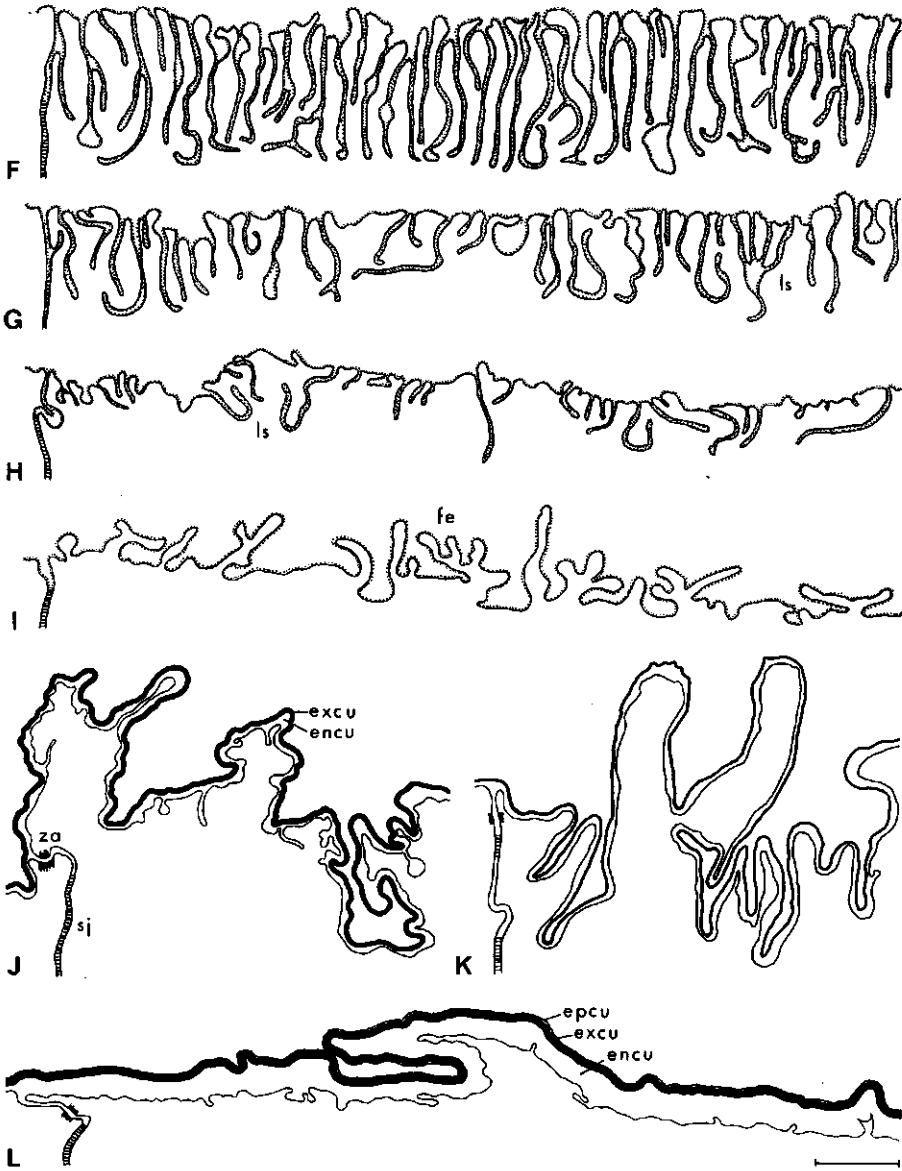
Figure 20. Schematic representation of the apical cell membrane of the crenated intestine (F), descending intestine (G, *Subsaltusaphis ornata*; H, *Aphis fabae*), caecal intestine (I), rectum (J, *Drepanosiphum platanoidis*; K, *Subsaltusaphis ornata*), and epidermal invagination (L) (Table 12). For list of abbreviations see page 61. Bar represents 0.5 μm.
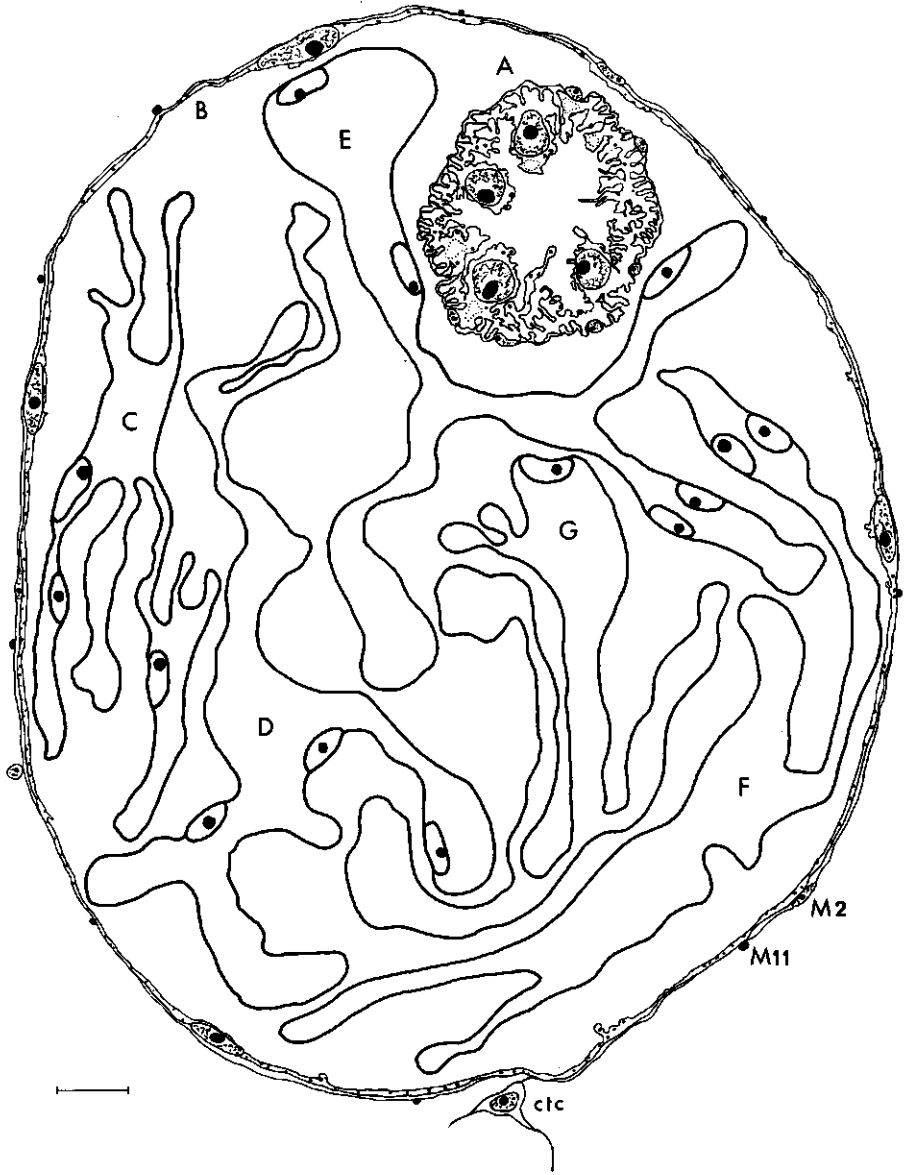
Figure 21. Transverse sections of the most contracted (A) to the most dilated position of the caecal intestine forming a more or less spherical shape (B) to the most bizarre shapes (C-G). For list of abbreviations see page 61. Bar represents 10 μm.
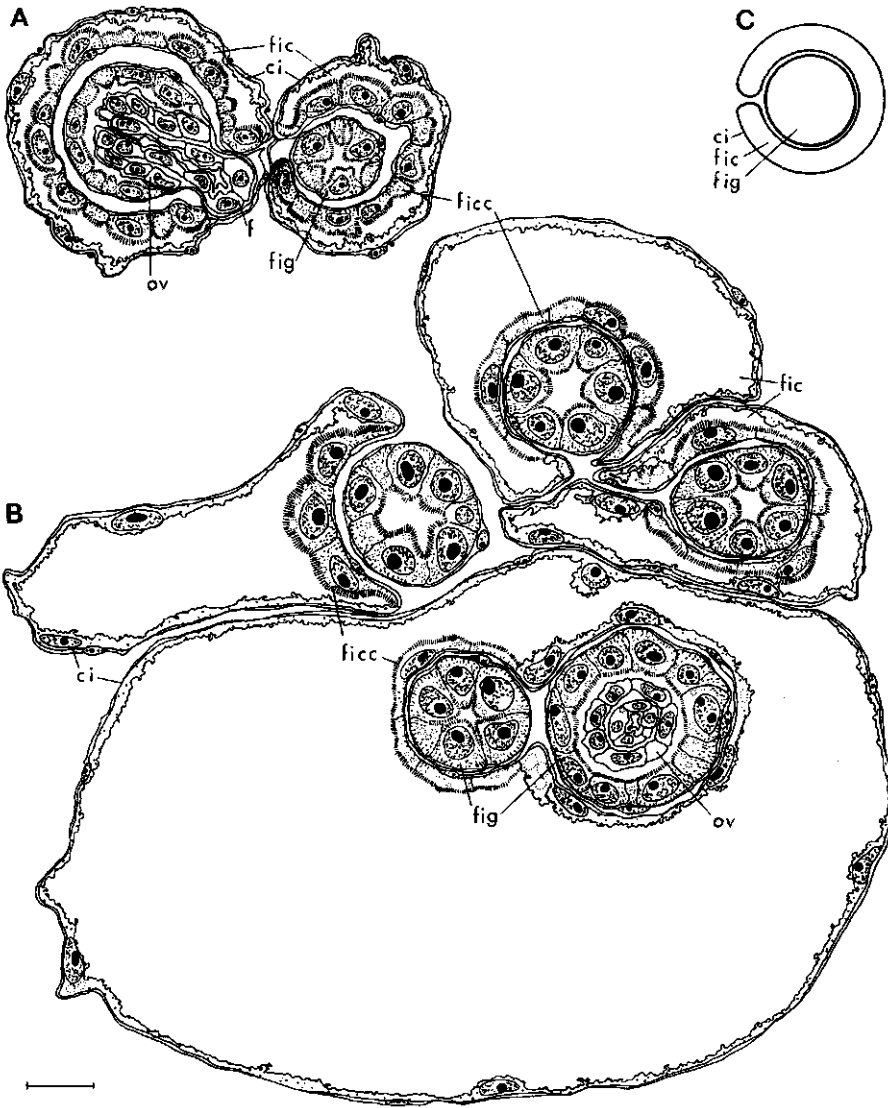
Figure 22. Transverse section of the filtersystem of *Eulachnus brevipilosus* Börner (A) and that of *Cryptomyzus ribis* Linnaeus (B, modified after Ponsen, 1977) showing encapsulation of the filtergut by the anterior region of the caecal intestine. Bar represents 10 µm. C. The basic principle of the filtersystem. For list of abbreviations see page 61.
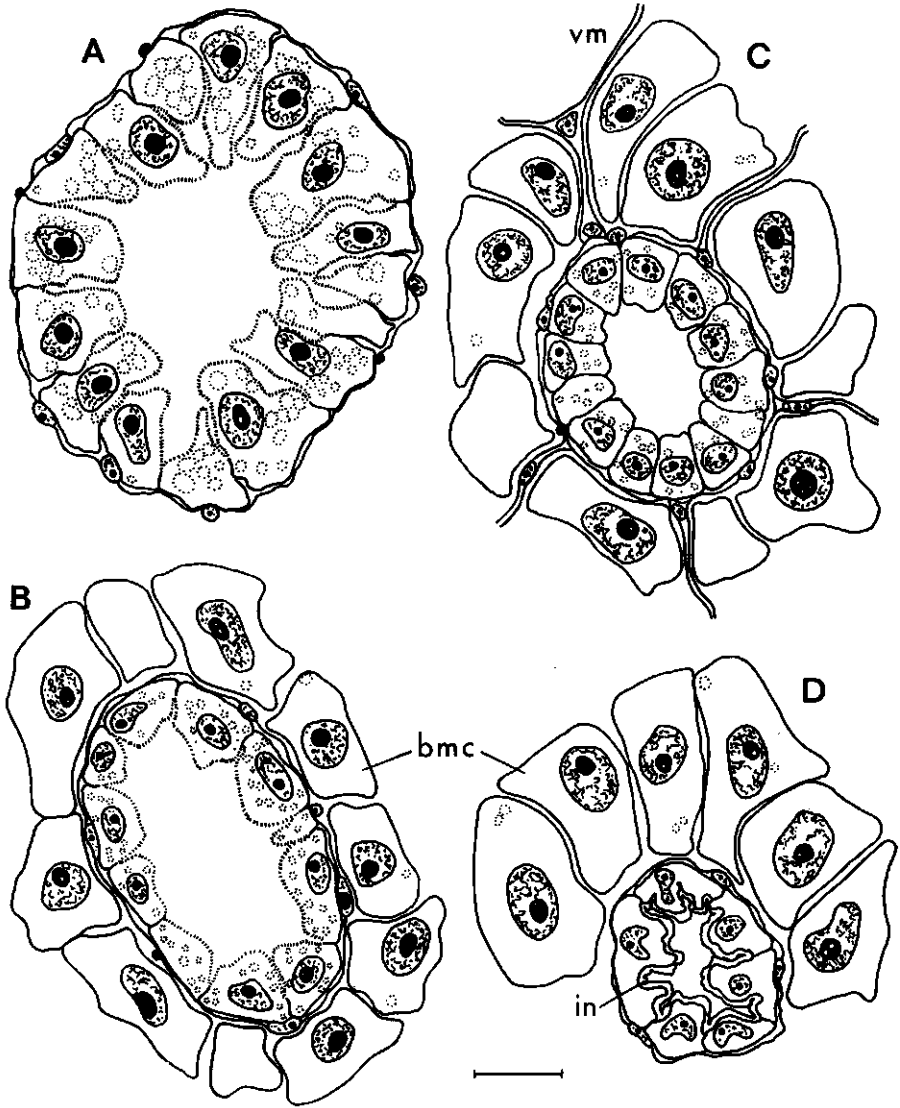
Figure 23. Transverse sections of the middle region (A) and the posterior end of the descending intestine (B), rectum (C), and epidermal invagination (D) of *Forda marginata* showing position of the 'basophilic mesodermal cells'. Bar represents 10 μm. For list of abbreviations see page 61.
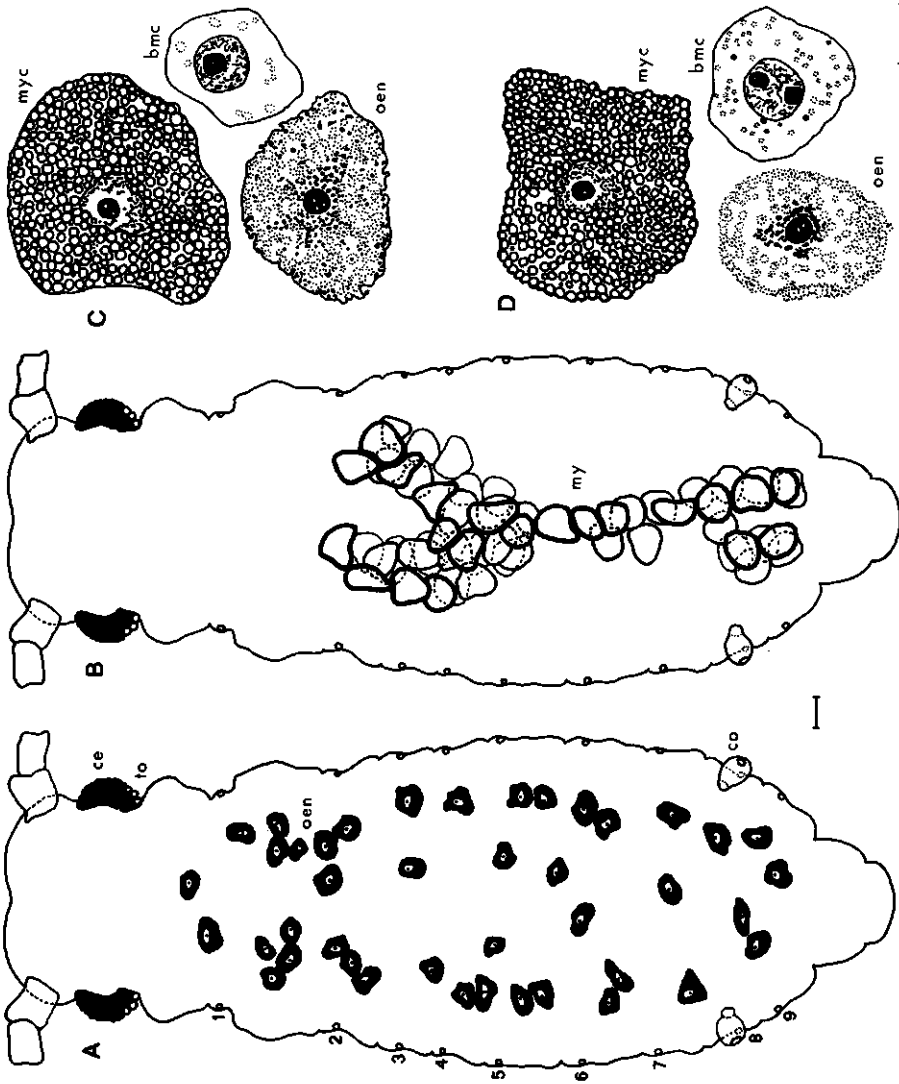
Figure 24. Topographical position of oenocytes (A) and mycetome (B) of an apterous viviparous larva of *Hyalopterus*, reconstructed from serial sections. 1-2, meso – and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 μm. A mycetocyte, oenocyte, and a basophilic mesodermal cell of an alate male of *Hyalopterus* (C), and those of an apterous oviparous larva of *Coloradoa tanacetina* (D). Bar represents 10 μm. For list of abbreviations see page 61.

sists of only squamous cells (Figure 1B and 3A). This cellular arrangement also occurs in the filterchamber of aphid species belonging to the family Lachnidae (including *Eulachnus*, Figure 22A), and the genera *Acaudinum, Capitophorus, Cryptomyzus* (Figure 22B), *Hyalopterus*(Figure 2A), and *Coloradoa*. An identical cellular arrangement is present in the anterior region of the caecal intestine of those specimens of *Hyalopterus* and *Coloradoa* that lack a filtersystem (Figure 2H and 3B).

It appears that all aphid genera with a filtersystem have a caecal intestine. On the other hand, there are genera, listed in Table 11, that have a caecal intestine but lack a filtersystem. In these genera the cellular arrangement in the anterior region of the caecal intestine is identical to that in specimens of *Hyalopterus* and *Coloradoa* with and without a filtersystem (Figure 3 and 4A-E). Probably all the species in Table 11 that have a caecal intestine may have had a filtersystem, which has been lost during evolution. All genera in Table 11 belong to the family Aphididae, excluding the genera *Anuraphis, Aphis, Brachycaudus, Plocamaphis,* and *Pterocomma*, which have a descending intestine.

During evolution the caecal intestine has increased in length with an exponential increase in the number of cells. In the species of the family Drepanosiphidae with a filtersystem the total number of cells of the caecal intestine varies from 13 to 19, in *Phylloxera coccinea* from 14 to 16, in *Phloeomyzus passerinii* from 52 to 54, and in the family Aphididae from 40 in *Idiopterus nephrolepidis* to 322 in *Macrosiphum albifrons* (Table 11).

It is interesting that within the family Aphididae (Table 11) the majority of the genera have had a filtersystem, whereas in three genera all specimens possess a filtersystem (*Acaudinum, Capitophorus*, and *Cryptomyzus*), and in two genera specimens occur with or without a filtersystem (*Hyalopterus* and *Coloradoa*). Probably there occur among the not yet investigated genera within the family Aphididae, other genera of the *Acaudinum* (Figure 22) as *Hyalopterus*-type (Figure 3).

Mycetome and oenocytes

In both alate and apterous viviparous females, oviparous females and males of *Hyalopterus* and *C. tanacetina* the mycetome consists of two longitudinal masses of mycetocytes which run from the metathorax to the seventh abdominal segment; in the fourth abdominal segment they join together to separate subsequently in the sixth abdominal segment (Figure 24B).

The total number of mycetocytes in *Hyalopterus* is about 52 and that in *Coloradoa* about 34. The scanty cytoplasm of the mycetocytes is completely filled with globular cell organelles. These organelles multiply by binary fission and have a diameter of 2.7 μm. Each mycetocyte has an irregularly-shaped nucleus due to the pressure of the multiplying globular organelles (Figure 24C-D).

The mycetome is surrounded by a nucleated sheath. During larval life the mycetome disintegrates into clusters of mycetocytes or individual ones. The nuc-

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leated sheath breaks open and a part of it remains connected with the separated mycetocytes. The degeneration process of the mycetocytes by which the globules are liberated into the haemolymph, has already been described (Ponsen, 1972).

Against the lateral mycetome the oenocytes are situated. During larval life the oenocytes partly become separated from the mycetome. They are situated in the body cavity between the mesodermal tissue and the internal organs of the thorax and the first seven abdominal segments (Figure 24A). The majority of them occur as single cells, but sometimes in groups of 2-3 cells in intimate contact with each other. The oenocytes contain many vacuoles and granules; their development during embryonic and larval life has already been described (Ponsen, 1972). In *Hyalopterus* there are about 40 oenocytes and in *Coloradoa* about 20.

In all aphid species investigated there occur in the body cavity oenocytes and a mycetome. The total number of oenocytes varies from 4 for *Phloeomyzus passerinii* to 56 for *Macrosiphum albifrons*. However, both *Phylloxera coccinea* and *Cerataphis palmae* lack a mycetome (Profft, 1937; Buchner, 1958), but the oenocytes are present (Figure 14). On the other hand, in *Geoica utricularia* there occurs a mycetome, but no oenocytes. In another species of this genus, *Geoica setulosa*, both the mycetome and the mycetocytes are lacking, but the viviparous embryos in various stages of development growing parthenogenetically in their mother's ovarioles, all have a mycetome. The mycetocytes are completely filled with globular cell organelles, identical to those of *Geoica utricularia, Hyalopterus,* and *Coloradoa* (Figure 24C-D). The mycetocytes in *Subsaltusophis ornata* are completely filled with irregular-shaped organelles which multiply by a budding process.

The oenocytes are situated in the body cavity and the basophilic mesodermal cells are even dispersed individually among the fat cells (Figure 12B, 14, and 24C-D).

Summary

The digestive system of *Hyalopterus* and *Coloradoa* consists of a foregut, oesophageal valve, a dilated stomach, a crenated intestine, caecal intestine, rectum, and an epidermal invagination, which terminates at the anal opening. The anterior region of the stomach of *Hyalopterus* consists of apocrine cells and the posterior region of merocrine cells. In *Coloradoa* the stomach is lined with merocrine cells. The transition from the stomach to the crenated intestine is marked by a sharp loop. The second region of the crenated intestine contains one or two additional loops and is characterized by the presence of 6-8 groups of three cells (triplets) at irregular intervals among the intestinal cells. The caecal intestine is a smooth transparent structure made up of squamous cells with elliptic nuclei. In about 20% of the specimens of *Hyalopterus* on *Prunus* and in about 56% of those on *Phragmites* the anterior region of the stomach is encapsulated by the anterior region of the caecal intestine, forming a concentric filter-system. In *Coloradoa* about 26% of the specimens have a filtersystem. In the remaining specimens of both genera the stomach is not encapsulated by the caecal intestine. This phenomenon is described in detail and is discussed in the context of the family Aphididae.

Acknowledgements

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Abbreviations used in figures

adm	anal dorsal muscles	hg	hindgut
ai	ascending intestine	i1	first region of intestine
al	abdominal loop	i2	second region of intestine
ali	additional loop of intestine	in	intima
alm	anal lateral muscles	is	intravalvular space
ao	anal opening	l	lumen
bl	basal lamina	ls	labyrinthine system
bmc	basophilic mesodermal cell	m	mitochondrion
ce	compound eye	mbv	membraneless vesicle
ci	caecal intestine	mvs	microvillar system
cic	caecal intestine cell	M2	circular muscle fibres
co	siphunculus (cornicle)	M11	longitudinal muscle fibres
ctc	connective tissue cell	n	nucleus
di	descending intestine	oen	oenocyte
ecm	ecdysial membrane	ov	oesophageal valve
ecu	embryonic cuticle	pl	plaques
ei	epidermal invagination	r	rectum
em	extracellular microtubules	reb	rectal bladder
encu	endocuticle	rg	rectal gland
epcu	epicuticle	rgc	rectal gland cell
excu	exocuticle	sj	septate junction
f	foregut	st	stomach
fac	fat cell	to	triommatidion
fe	fingerlike evaginations	tpc	triplet cells
fh	flabellate hair	vm	visceral muscles
fic	filterchamber	w	waxy droplet
ficc	filterchamber cell	wc	wax cell
fig	filtergut	wp	wax plate with pores
fm	fibrous mass	wr	wax reservoir
go	gonopore	za	zonula adherens