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THE DIGESTIVE SYSTEM OF SOME
SPECIES OF CHAITOPHORIDAE
(HOMOPTERA: APHIDOIDEA)

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THE DIGESTIVE SYSTEM OF SOME SPECIES OF CHAITOPHORIDAE (HOMOPTERA: APHIDOIDEA)

INTRODUCTION

The digestive system of the Chaitophoridae, sensu BÖRNER, consists of a short foregut, a tubular or egg-shaped stomach, and a normal intestine but lacks a filterchamber (BÖRNER, 1952; BÖRNER and HEINZE, 1957; KUNKEL and KLOFT, 1977). These morphological features were illustrated by WITLACZIL (1882) in a drawing of the digestive system of *Chaitophorus populi* L. and by BÖRNER (1938) in that of *Periphyllus* sp., *Sipha* sp., and *Tranaphis* sp. (= *Chaitophorus* sp.).

In the present study the anatomy of the digestive system of a number of species of Chaitophoridae is investigated in more detail.

MATERIALS AND METHODS

Specimens of the species listed in Table 1, were fixed in DUBOSQ BRASIL's fluid, embedded in paraplast, and sectioned at 8 μ . Sections were stained in EHRlich's haematoxylin-eosin or in 1% methylgreen aqueous solution (CALBERLA, 1887).

RESULTS

The most anterior part of the alimentary tract, the food canal in the maxillary stylets leads into the pharyngeal duct which in turn leads into the pharynx. This structure passes upwards through the head, over the tentorium and into the foregut which opens into the stomach via a valve. The stomach opens into the intestine which extends forwards and which after one additional loop or coil or neither (Fig. 2), runs posteriad to open into the rectum which ends at the anal opening (Fig. 1). The total length of the gut of *Chaitophorus populeti*, *C. populiabae*, *C. vitellinae*, *Periphyllus obscurus*, and *P. testudinaceus* is about twice that of the body (Fig. 2).

The foregut (oesophagus) runs posteriad between the two salivary glands, and dorsal to the nervous system, to end in the oesophageal valve. It consists of a thin tube made up of a single layer of squamous epithelial cells which secrete the chitinous intima.

The oesophageal valve is a short invagination of the foregut into the stomach. The inner surface is lined with squamous epithelium and the outer surface with cuboidal cells. The valve is covered with an intima.

TABLE 1. List of the species of Chaitophoridae studied, their hostplant, and relevant locality data.

Aphid	Hostplant	Locality
<i>Atheroides serrulatus</i> HALIDAY	grass	Wageningen, 12.VII.1982
<i>Caricosipha paniculatae</i> BÖRNER	<i>Carex otrubae</i>	Opheusden, 22.IX.1982
<i>Chaitophorus capreae</i> (MOSLEY)	<i>Salix</i> sp.	Wageningen, 23.VI.1981
<i>Chaitophorus horii</i> subsp. <i>beuthani</i> (BÖRNER)	<i>Salix</i> sp.	Wageningen, 19.V.1979
<i>Chaitophorus leucomelas</i> KOCH	<i>Populus</i> sp.	Wageningen, 9.VI.1981
<i>Chaitophorus salijaponicus</i> subsp. <i>niger</i> MORDV.	<i>Salix</i> sp.	Wageningen, 2.VII.1981
<i>Chaitophorus populeti</i> (PZ.)	<i>Populus alba</i>	Heemskerck, 18.VI.1981
<i>Chaitophorus populialbae</i> (BOYER de FONSC.)	<i>Populus alba</i>	Wageningen, 16.VI.1981
<i>Chaitophorus saliciti</i> (SCHRANK)	<i>Salix cinerea</i>	Winterswijk, 29.VIII.1981
<i>Chaitophorus truncatus</i> (HSMNN.)	<i>Salix</i> sp.	Wageningen, 29.VI.1981
<i>Chaitophorus vitellinae</i> (SCHRANK)	<i>Salix</i> sp.	Lienden, 14.VI.1981
<i>Laingia psammae</i> THEOBALD	<i>Ammophila arenaria</i>	Cadzand-Bad, 25.VII.1982
<i>Periphyllus acericola</i> (WLK.)	<i>Acer pseudoplatanus</i>	Bennekom, 1.VIII.1980
<i>Periphyllus obscurus</i> MAMONTOVA	<i>Acer campestre</i>	Wageningen, 6.IX.1981
<i>Periphyllus testudinaceus</i> (FERNIE)	<i>Acer campestre</i>	Slijk-Ewijk, 22.V.1977
<i>Sipha elegans</i> del GUERCIO	grass	Wageningen, 10.VII.1981
<i>Sipha glyceriae</i> (KLTB.)	<i>Agrostis tenuis</i>	Bennekom, 24.VI.1981

The midgut is the longest part of the alimentary tract and consists of a stomach, first and second part of intestine, and descending intestine.

The stomach either starts in the mesothorax, metathorax, or first abdominal segment and joins the intestine in the first or second abdominal segment (Table 2). The stomach lies in the dorsal region of the aphid and has a tubular structure of which the anterior or middle region is somewhat dilated (Fig. 2; Table 3), depending on the species. The triangular cells of the stomach contain heterogeneous basophilic cytoplasm, small vacuoles, granules, and a spherical to oval nucleus. Their basal cell membranes have numerous invaginations and their free surfaces a striated border. These cells do not show any cytological manifestations of secretion (Fig. 3A), but in *Laingia psammae*, *Sipha elegans*, and *S. glyceriae* the lumen of the stomach is filled with flocculent material (Fig. 3B). However, KUNKEL (1966) reports merocrine secretion by the stomach cells in *Chaitophorus* (*Eichochaitophorus*) *versicolor* (KOCH) (= *Chaitophorus leucomelas* KOCH).

The first part of the intestine consists of a small tube which runs from the stomach directly ventrad, then posteriad before reversing its direction (the abdominal loop) which may occur in the third, fourth, fifth, sixth, or seventh abdominal segment (Table 3). A similar structure is found in *Glyphina* and *Thelaxes* (PONSEN, 1982). In each aphid mentioned in Table 2 the first part of the intestine bends either to the right or to the left of the descending intestine. The abdominal loop is connected to the cauda by 'membranes'. The broader second part of the intestine starts at the abdominal loop and runs either directly anteriorad to the thoracic loop, or before reaching the thoracic loop forms one loop or one

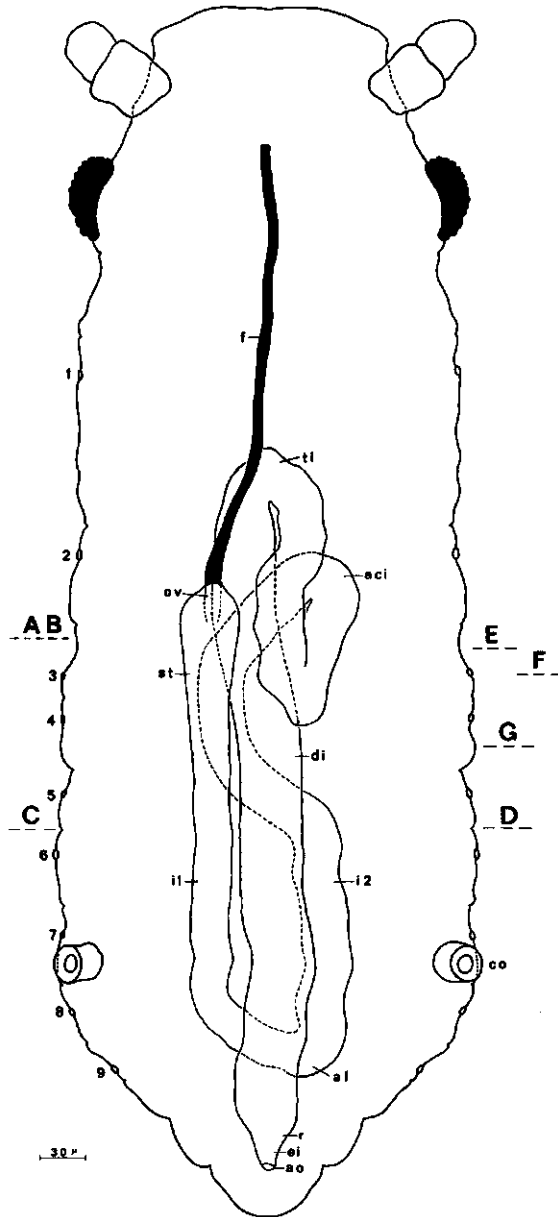


FIG. 1. Dorsal view of the digestive system of a larva of *Chaitophorus populeti* reconstructed from serial sections. The siphunculi (co) are situated on the fifth abdominal tergite. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. aci, additional coil of intestine; al, abdominal loop; ali, additional loop of intestine; ao, anal opening; di, descending intestine; ci, epidermal invagination; f, foregut; i1, first part of intestine; i2, second part of intestine; ov, oesophageal valve; r, rectum; st, stomach; tl, thoracic loop. The letters A-G correspond with transverse sections given in Fig. 3.

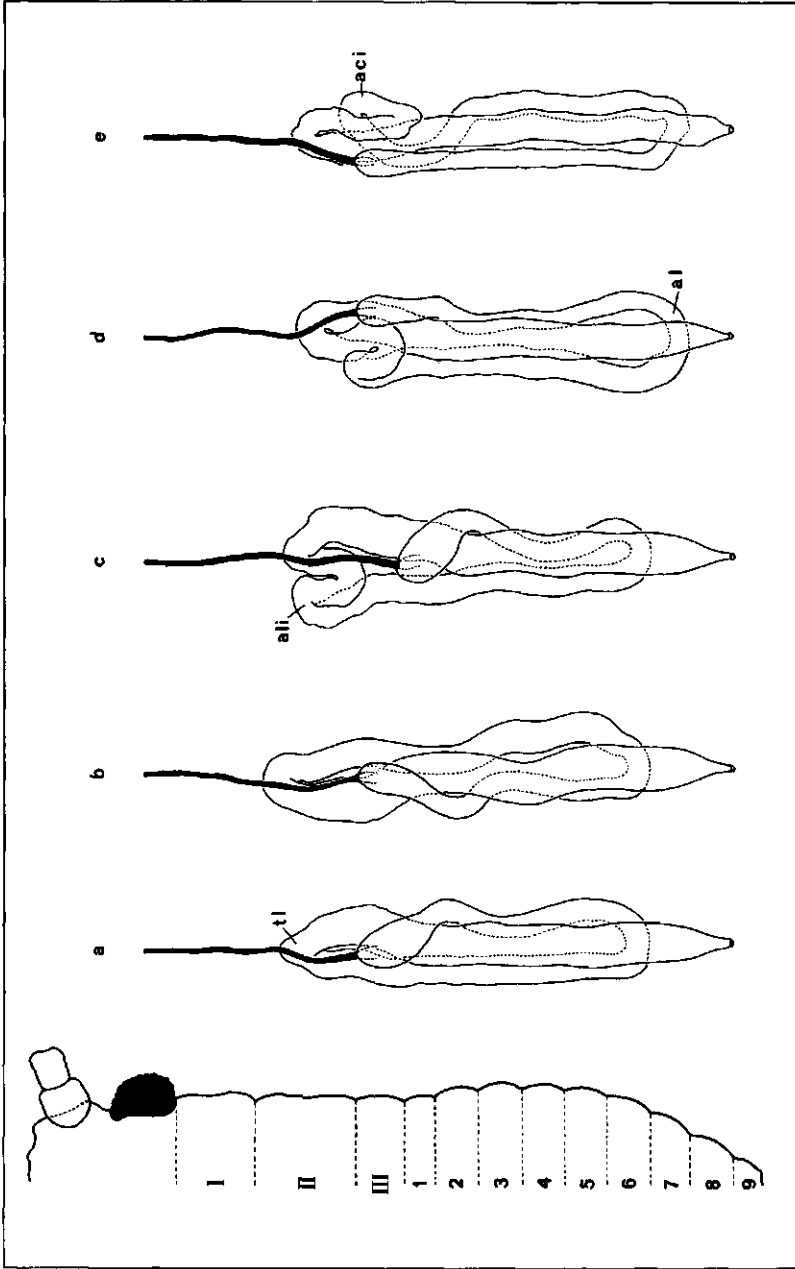


FIG. 2. Semi-schematic representation of the digestive system of *Periphyllus testudinaceus* (a), *Chaitophorus viellinae* (b), *Periphyllus obscurus* (c), *Chaitophorus populiabae* (d), and *C. populeti* (e). I-III, thoracic segments; 1-9, abdominal segments. The letters a-e correspond with those in Table 3. For explanation of abbreviations see Fig. 1.

TABLE 2. The structure of the midgut and position of the stomach in the species of Chaitophoridae studied.

Aphid	Total number of aphids	Morph	Stomach starts in	Stomach ends in	Stomach ¹	Number of cells in transverse sections of		Siphunculi on abdominal tergite
						First part of intestine	Second part of intestine	
<i>Atheroides serrulatus</i>	1	wingless	II	2	9	4-5	3-5	5
<i>Caricosipha paniculatae</i>	4	oviparous	II (1) III (3)	1 (2) 2 (2)	10	4-6	4-6	6
<i>Chaitophorus capreae</i>	10	wingless	II (8) III (2)	1 (8) 2 (2)	8	4-5	3-5	6
<i>Chaitophorus horii</i> subsp. <i>beuthani</i>	9	wingless	II (4) III (5)	1	11	3-5	3-5	6
<i>Chaitophorus leucomelas</i>	9	wingless	III	2	10	4-6	4-5	6
<i>Chaitophorus salijaponicus</i> subsp. <i>niger</i>	7	wingless	II (1) III (6)	2	10	4-5	4-5	6
<i>Chaitophorus populeti</i>	8	wingless (5) winged (3)	III	1 (2) 2 (6)	10	5-6	4-6	5
<i>Chaitophorus populialbae</i>	9	wingless (4) winged (5)	III	1 (6) 2 (3)	10	4-5	3-5	6
<i>Chaitophorus salicti</i>	8	wingless (4) oviparous (4)	III	1 (6) 2 (2)	12	4-6	4-6	6
<i>Chaitophorus truncatus</i>	9	wingless	III	2	10	4-6	4-6	6
<i>Chaitophorus vitellinae</i>	9	wingless (3) winged (6)	II (1) III (8)	1 (6) 2 (3)	10	4-6	4-6	6
<i>Laingia psammae</i>	5	wingless	III	2	14	4-6	4-6	6
<i>Periphyllus acericola</i>	9	wingless	III	1 (7) 2 (2)	10	3-5	3-5	5
<i>Periphyllus obscurus</i>	8	wingless	I	2	12	4-6	4-6	5
<i>Periphyllus testudinaceus</i>	8	wingless	III	1	12	5-6	5-6	6
<i>Sipha elegans</i>	8	wingless	III	1 (5) 2 (3)	12	4-5	4-5	5
<i>Sipha glyceriae</i>	9	wingless	II (1) III (8)	1 (4) 2 (5)	12	3-5	3-5	5

¹Maximum number of cells in cross sections of the stomach
I-III refer to thoracic segments
1-9 refer to abdominal segments
In brackets number of aphids sectioned

TABLE 3. The position of the intestine in the body cavity of the species of Chaitophoridae studied. The letters a–e correspond to those in Fig. 2.

Aphid	Abdominal loop of intestine in	Thoracic loop of intestine in	Additional loop of intestine in	Additional coil of intestine in
a <i>Caricosipha paniculatae</i>	5 (4)	II (4)	– (3)	
<i>Laingia psammae</i>	5 (2)	II (3)	– (5)	
	6 (3)	III (2)		
<i>Periphyllus acericola</i>	5 (3)	II (7)	– (9)	
	6 (6)	III (2)		
<i>Periphyllus obscurus</i>	6 (6)	II (8)	– (2)	
	7 (2)			
<i>Periphyllus testudinaceus</i>	5 (1)	II (8)	– (8)	
	6 (7)			
<i>Sipha elegans</i>	4 (8)	II (6)	– (8)	
		III (2)		
<i>Sipha glyceriae</i>	5 (5)	II (5)	– (9)	
b <i>Atheroides serrulatus</i>	3 (1)	II (1)	– (1)	
<i>Chaitophorus capreae</i>	6 (10)	II (8)	– (9)	
		III (2)		
<i>Chaitophorus horii</i> subsp. <i>beuthani</i>	5 (3)	II (8)	– (9)	
	6 (6)	III (1)		
<i>Chaitophorus leucomelas</i>	6 (5)	II (7)	– (4)	
	7 (4)	III (2)		
<i>Chaitophorus salijaponicus</i> subsp. <i>niger</i>	7 (7)	II (3)	– (5)	
		III (4)		
<i>Chaitophorus populialbae</i>	6 (2)	II (9)	– (5)	
	7 (7)			
<i>Chaitophorus salicti</i>	4 (1)	I (1)	– (4)	
	5 (2)	II (7)		
	6 (5)			
<i>Chaitophorus truncatus</i>	7 (9)	II (5)	– (5)	
		III (4)		
<i>Chaitophorus vitellinae</i>	5 (1)	II (9)	– (9)	
	6 (8)			
c <i>Caricosipha paniculatae</i>			III – 1 (1)	
<i>Periphyllus obscurus</i>			II – III (2)	
			III (2)	
			III – 1 (2)	
d <i>Chaitophorus capreae</i>			2 – 3 (1)	
<i>Chaitophorus leucomelas</i>			III (5)	
<i>Chaitophorus populialbae</i>			III – 1 (3)	
			1 – 2 (1)	
<i>Chaitophorus salijaponicus</i> subsp. <i>niger</i>			III – 1 (1)	
			1 – 2 (1)	
<i>Chaitophorus truncatus</i>			III – 2 (4)	
e <i>Chaitophorus populeti</i>	6 (1)	II (8)		III (4)
	7 (7)			III – 1 (3)
				III – 2 (1)
<i>Chaitophorus salicti</i>				III – 1 (3)
				III – 2 (1)

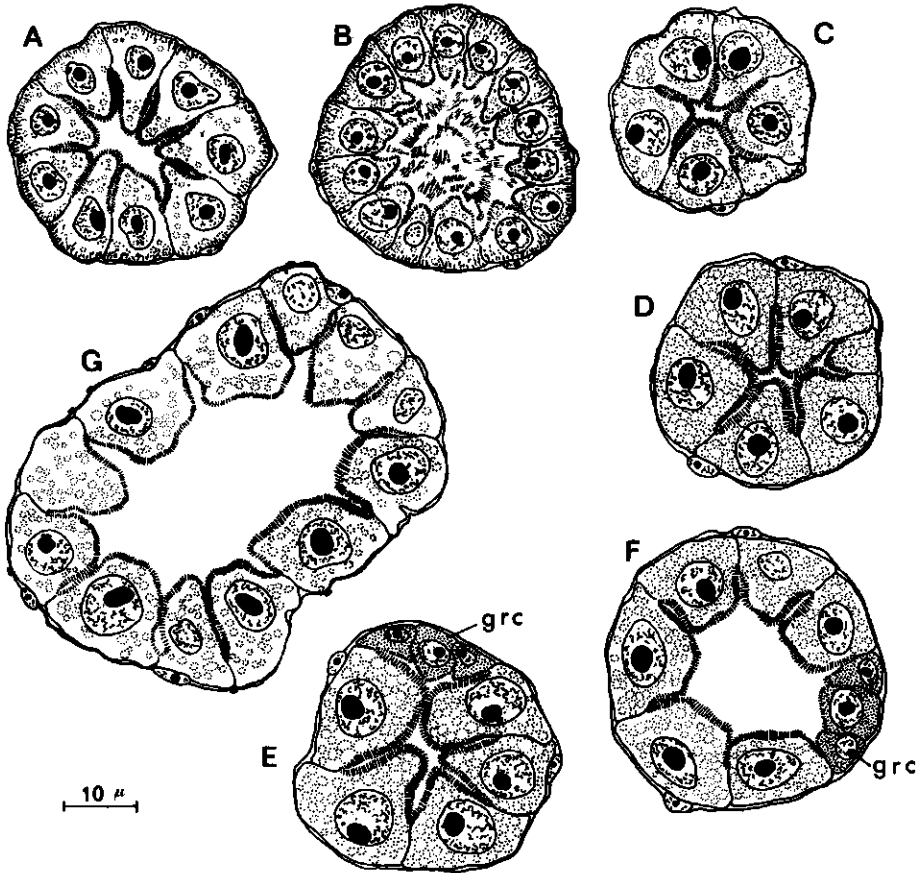


FIG. 3. Transverse sections of the stomach of *Chaitophorus leucomelas* (A) and *Laingia psammae* (B), the first part of the intestine (C) and second part of the intestine of *Chaitophorus populeti* (D), the second part of the intestine showing granulated cells (grc) of *C. populeti* (E) and *Periphyllus testudinaceus* (F), and the descending intestine of *P. testudinaceus* (G). The position of the sections A–G are given in Fig. 1.

coil (Fig. 2; Table 3). The epithelial cells of the first part of the intestine contain few vacuoles and a somewhat spherical nucleus, whereas the cells of the second part of the intestine are strongly vacuolated and have ovoid nuclei (Fig. 3C and D). The free surfaces of these cells are striated and line a more or less stellate lumen.

In the second part of the intestine, particularly in the thoracic region and also in the additional loop or coil, there are groups of three small cells (Fig. 3E and F). The middle cell in each group has a large spherical nucleus, whereas the other two cells have relatively small nuclei. The cells contain granules, some vacuoles, and their free surfaces are presumably striated. In dissections of the aphids these groups of cells are seen as round white structures on an opaque intestine.

After the thoracic loop the second part of the intestine leads gradually into the descending intestine, which runs directly caudad and leads into the rectum. In dissections it is a transparent, sac-like structure with vigorous peristaltic movements. Histologically the descending intestine of all Chaitophoridae investigated (Table 2; Fig. 3G) is similar in structure to that of the species of Callaphididae that lack a filtersystem, *Glyphina*, *Thelexes* (PONSEN, 1982), and the aphids listed in Table 4.

The rectum is made up of a single layer of small cuboidal cells and is connected to an epidermal invagination, the anal opening, which is both laterally and dorsally connected by muscles to the ninth abdominal segment.

DISCUSSION

Morphologically the digestive system of the chaitophorids investigated (Fig. 1 and 2) is similar to the description given by WITLACZIL (1882) for *Chaitophorus populi* L. and BÖRNER (1938) for *Sipha* sp. and *Tranaphis* sp. (= *Chaitophorus* sp.). But according to BÖRNER (1938) the intestine of *Periphyllus* sp. has a number of coils in the anterior region of the aphid. They both reported that these aphids have a hindgut, but did not describe it. However, in all the chaitophorids investigated the hindgut is of endodermal origin and an extension of the midgut, and therefore more correctly called a descending intestine.

Scattered groups of three small granulated cells occur in the wall of the second part of the intestine that otherwise consists of strongly vacuolated cells (Fig. 3E and F). These groups of cells occur mainly in the walls of the posterior portion (thoracic loop and additional loop or coil) of the second part of the intestine and are absent in the first part of the intestine. Granulated cells are found throughout the midgut of many insects and have been called gut endocrine cells (ENDO and NISHITSUTSUI-UWO, 1981). They are singly intercalated among the epithelial cells or the regenerative cells of the midgut. The regenerative cells may be scattered singly beneath the epithelial cells or grouped into clusters (nidi) there, or variously arranged in crypt-like outpocketings of the midgut (RICHARDS and DAVIES, 1957). These granulated cells also occur in the posterior portion of the ascending intestine of the Callaphididae with and without a filtersystem, in the posterior portion of the intestine of *Phloeomyzus passerinii* (SIGNORET), and in the posterior portion of the second part of the intestine of *Myzus persicae* (SULZ.), *Cryptomyzus ribis* (L.), *Eulachnus*, *Glyphina*, *Thelexes*, as well as in the aphids listed in Table 4.

SUMMARY

The digestive system of the Chaitophoridae has a short foregut which opens into the stomach via a valve (Fig. 1). The stomach has a tubular structure and leads into the first part of the intestine which runs from the stomach directly ventrad and then posteriad to end in the abdominal loop. From there a broader

TABLE 4. List of aphids studied which have a hindgut of endodermal origin (= descending intestine), their hostplant, and relevant locality data.

Aphid	Family	Hostplant	Locality
<i>Adelges (Dreyfusia) nordmannianae</i> ECKST.	Adelgidae	<i>Picea orientalis</i>	Wageningen, 15.VII.1982
<i>Adelges (Gillesteella) cooleyi</i> GILL.		<i>Picea sitchensis</i>	Hardenberg, 23.VII.1982
<i>Adelges (Sacchiphantes) abietis</i> (L.)		<i>Picea abies</i>	Wageningen, 3.VII.1982
<i>Anoecia corni</i> (F.)	Aphididae	<i>Agrostis stolonifera</i>	Bennekom, 5.VIII.1982
<i>Anoecia</i> sp.		<i>Cornus</i>	Wageningen, 7.IX.1977
<i>Anoecia</i> sp.		<i>Poa annua</i>	Wageningen, 14.VII.1982
<i>Anuraphis farfarae</i> (Koch)		<i>Tussilago farfara</i>	Wageningen, 15.VI.1982
<i>Anuraphis subterranea</i> (WILK.)		<i>Heracleum sphondylium</i>	Wageningen, 9.VI.1982
<i>Aphis armata</i> HSMNN.		<i>Digitalis purpurea</i>	Wageningen, 15.VI.1982
<i>Aphis brokmeri</i> BÖRNER		<i>Anthriscus sylvestris</i>	Wageningen, 14.VII.1982
<i>Aphis fabae</i> SCOP.		<i>Vicia fabae</i>	Wageningen, Plant Protection Service
<i>Aphis farinosa</i> GMELIN		<i>Salix</i> sp.	Wageningen, 21.V.1980
<i>Aphis pomi</i> de GEER		<i>Malus</i> sp.	Wageningen, 13.VI.1982
<i>Aphis sambuci</i> L.		<i>Melandrium rubrum</i>	Wageningen, 18.VI.1979
<i>Aphis sarothamni</i> FRANSSEN		<i>Sarothamnus scoparius</i>	Wageningen, 2.VI.1982
<i>Aphis schneideri</i> (BÖRNER)		<i>Ribes sanguineum</i>	Wageningen, 23.V.1982
<i>Aphis taraxacicola</i> (BÖRNER)		<i>Taraxacum officinale</i>	Wageningen, 15.VI.1982
<i>Aphis violae</i> SCHOUTEDEN		<i>Viola tricolor</i>	Wageningen, 8.VII.1982
<i>Aphis (Toxoptera) vandersooti</i> (BÖRNER)		<i>Matricaria matricarioides</i>	Wageningen, 15.VI.1982
<i>Brachycaudus (Acaudus) cardui</i> (L.)		<i>Matricaria matricarioides</i>	Wageningen, 13.VI.1982
<i>Brachycaudus (Acaudus) linariae</i> STROYAN		<i>Linaria vulgaris</i>	Bennekom, 7.VI.1982
<i>Brachycaudus (Appelia) irigopogonis</i> KLTB.		<i>Tragopogon</i> sp.	Wageningen, 16.V.1982
<i>Greenidea eugeniae</i> TAKAHASHI		<i>Eugenia jambalana</i>	Gujranwala (Pakistan), 8.III.1980
<i>Greenidea formosana</i> (MAKI)		<i>Psidium guajava</i>	Dacca (Bangladesh), 17.II.1981
<i>Greenidea</i> sp.		<i>Eugenia jambalana</i>	Dacca (Bangladesh), 2.III.1981
<i>Israelaphis tavaresi</i> ILHARCO*		<i>Anisantha rigida</i>	Cascais (Portugal), 9.III.1981
<i>Israelaphis</i> sp. (40 tubercles)		<i>Podocarpus</i> sp.	Sintra (Portugal), 4.I.1983
<i>Neophyllaphis grobleri</i> EASTOP		<i>Salix</i> sp.	Pretoria (South Africa), XII.1982
<i>Plocamaphis bituberculata</i> (THEOBALD)		<i>Salix</i> sp.	Wageningen, 23.VIII.1982
<i>Pterocomma jacksoni</i> THEOBALD		<i>Salix</i> sp.	Wageningen, 7.VII.1981
<i>Pterocomma pilosum</i> BUCKT.		<i>Salix</i> sp.	Wageningen, 3.VII.1982
<i>Pterocomma populeum</i> (KLTB.)		<i>Populus nigra</i>	Bennekom, 8.VI.1982
<i>Pterocomma salicis</i> (L.)		<i>Salix</i> sp.	Wageningen, 7.X.1977

*According to information received from Dr. ILHARCO *Israelaphis tavaresi* ILHARCO is a synonymy of *I. carmini* ESSIG

intestine, the second part, runs either directly anteriorly to the thoracic loop, or before the thoracic loop forms one additional loop or coil (Fig. 2). The descending intestine runs from the thoracic loop directly caudad to open into the rectum which ends at the anal opening.

SAMENVATTING

Het spijsverteringskanaal van de Chaitophoridae heeft een korte slokdarm die in de maag uitmondt via een oesophageale klep (Fig. 1). De maag heeft een buisvormige structuur en gaat over in het eerste gedeelte van de darm dat van de maag direct ventraalwaarts loopt en vervolgens caudaalwaarts om in de abdominale lis te eindigen. Vandaar loopt een wijder darmdeel of direct voorwaarts tot de thoracale lis, of het vormt voor de thoracale lis nog een lis (Fig. 2). De neerdalende darm zet zich vanaf de thoracale lis caudaalwaarts voort in het rectum dat via de epidermale invaginatie in de anale opening uitmondt.

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