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THE DIGESTIVE SYSTEM OF *GLYPHINA* AND *THELAXES* (HOMOPTERA: APHIDOIDEA)

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INTRODUCTION

THE APHIDS *Glyphina betulae* (L.), *G. schrankiana* BÖRNER, *Thelaxes dryophila* (SCHRANK), and *T. suberi* (del GUERCIO) belong to BÖRNER's family Thelaxidae (BÖRNER, 1952). The digestive system of this tribe Thelaxini is structurally primitive with a tubular stomach (BÖRNER and HEINZE, 1957) as illustrated in BÖRNER's (1938) drawing of the digestive system of *Hamamelistes* sp.

In the present study the anatomy of the digestive system of these four species of 'Thelaxidae' is investigated in more detail.

MATERIALS AND METHODS

Inviduals 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.

TABLE 1. List of thelaxids studied, their hostplant, and relevant locality data.

	Hostplant	Locality
Glyphina betulae (L.)	*Betula pubescens*	Wageningen, 27. VI. 1980
Glyphina schrankiana BÖRNER	*Alnus glutinosa*	Ede, 25. VIII. 1981
Thelaxes dryophila (SCHRANK)	*Quercus* sp.	Wageningen, 30. V. 1979
Thelaxes suberi (del GUERCIO)	*Quercus suber*	Alcochete (Portugal), 27. VII. 1980

RESULTS

The alimentary tract starts with the food canal which is formed by the interlocked maxillary stylets. From the stylets the food canal passes into the pharyngeal duct which subsequently leads into the pharyngeal valve, pharyngeal pump, foregut, oesophageal valve, stomach, intestine, and rectum terminating at the anal opening (Fig. 1). The total length of the gut is about twice that of the aphid's body.

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

The oesophageal valve marks the junction of the foregut and the stomach. It consists of two layers of cells of which the inner layer is the continuation

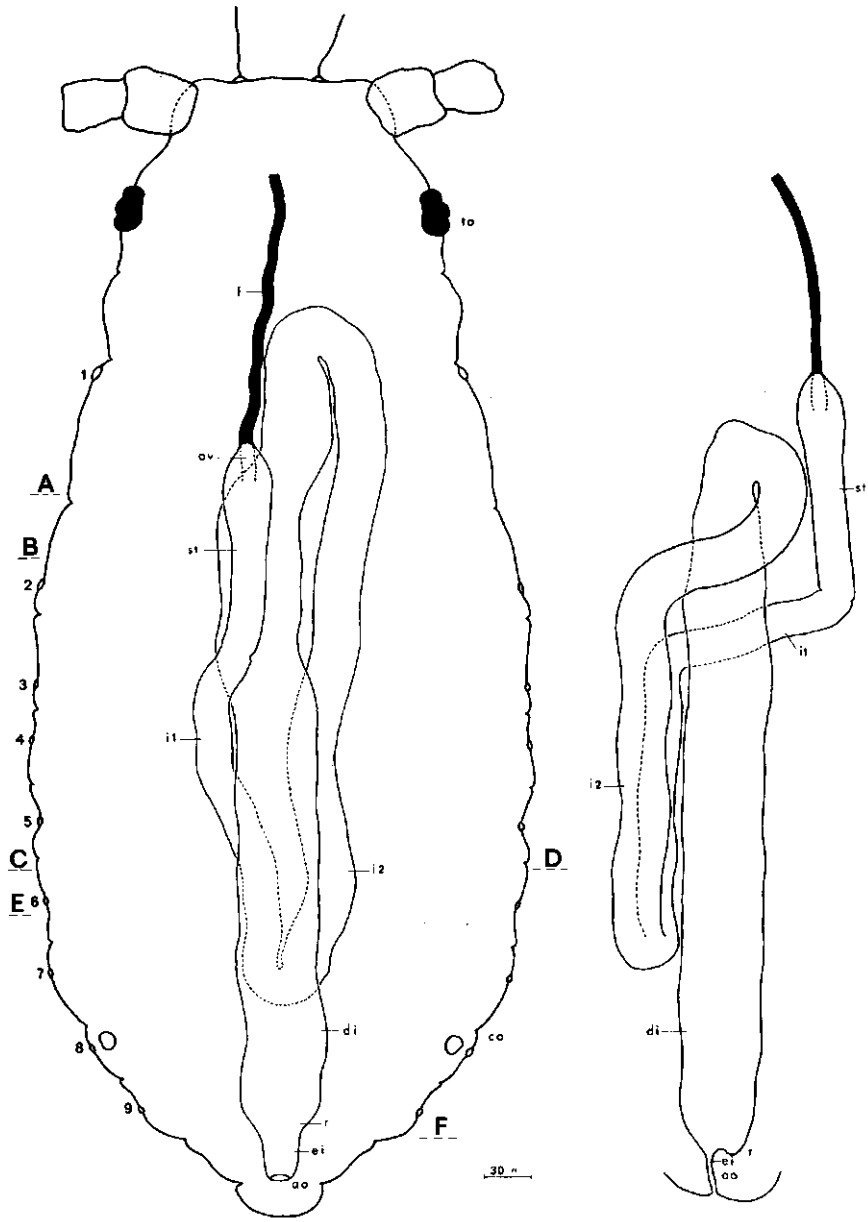

Fig. 1. Dorsal aspect of the digestive system of a *Thelaxes dryophila* larva and sagittal aspect of that of a *Glyphina schrankiana* larva reconstructed from serial sections showing foregut (f), oesophageal valve (ov), tubular stomach (st), first part of intestine (i1), second part of intestine (i2), descending intestine (di), rectum (r), epidermal invagination (ei), and anal opening (ao). The cornicles (pores, co) are situated on the sixth abdominal tergite. 1–2, meso and metathoracic spiracles; 3–9, abdominal spiracles. to, triommatidion. The letters A–F correspond with transverse sections illustrated in Fig. 2.

TABLE 2. The structure and position of the digestive system and its subdivisions in *Glyphina* and *Thelaxes*.

Aphid	Total number of aphids		Stomach starts in	Stomach ends in	Abdominal loop of intestine in	Thoracic loop of intestine in	Number of cells in transverse section of		
							Stomach[1]	First part of intestine	Second part of intestine
Glyphina betulae	8	wingless	II (5)	III (5)	4 (4)	I (5)	8–9	3–4	3–5
		wingless			5 (1)				
		winged	II (3)	III (3)	4 (3)	I (3)			
Glyphina schrankiana	8	wingless	II (7)	III (4)	4 (2)	II (7)	8–10	3–5	4–5
		wingless		1 (3)	5 (4)				
		wingless			6 (1)				
		winged	II (1)	III (1)	5 (1)	III (1)			
Thelaxes dryophila	7	wingless	II (6)	1 (6)	5 (5)	I (1)	7–9	3–4	4–5
		wingless			6 (1)	II (5)			
		winged	II (1)	1 (1)	6 (1)	II (1)			
Thelaxes suberi	7	wingless	1 (3)	3 (3)	5 (2)	II (3)	7–9	3–4	3–4
		wingless			6 (1)				
		winged	1 (3)	3 (3)	6 (4)	II (2)			
		winged	2 (1)	4 (1)		III (2)			

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

TABLE 3. A list of aphid species of which the transition from the stomach to intestine is marked by a sharp loop (c), or the intestine runs posteriad from the stomach (d). The letters c and d correspond with those in Fig. 3. The names are corrected according to EASTOP and HILLE RIS LAMBERS (1976).

		Present name	Name used by author	Author
c	1	*Acyrthosiphon pisum* (HARRIS)		
	2	*Adelges laricis* VALL.	*Adelges laricis* VALL.	KUNKEL, 1966
	3	*Anoecia* sp.	*Anoecia* sp.	BÖRNER, 1938
	4	*Aphis fabae* SCOP.	*Aphis fabae* SCOP.	WEBER, 1928
	5	*Aphis frangulae* KLTB. complex	*Aphis (Dorsalis) frangulae* KOCH	ROBERTI, 1946
	6	*Aphis sambuci* L.		
	7	*Aulacorthum solani* (KLTB.)		
	8	*Aulacorthum (Neomyzus) circumflexum* (BUCKT.)		
	9	*Brevicoryne brassicae* (L.)		
	10	*Cavariella aegopodii* (SCOP.)		
	11	*Chaetosiphon (Pentatrichopus) tetrarhodus* (WLK.)	*Siphonophora rosarum* WALK.	GROVE, 1909
	12	*Diuraphis (Holcaphis) holci* (H.R.L.)		
	13	*Dysaphis (Pomaphis) plantaginea* (PASSERINI)		
	14	*Hyperomyzus lactucae* (L.)		
	15	*Hysteroneura setariae* (THOS.)	*Hysteroneura setariae* (THOMAS)	TATE, 1936
	16	*Idiopterus nephrelepidis* DAVIS		
	17	*Illinoia (Masonaphis) lambersi* (MACGILLIVRAY)		
	18	*Longicaudus trirhodus* (WLK.)		
	19	*Macrosiphum euphorbiae* (THOS.)	*Macrosiphum solanifolii* (ASH.)	SMITH, 1939
	20	*Megoura viciae* BUCKT.	*Megoura viciae* BUCKT.	EHRHARDT, 1963
	21	*Metopolophium dirhodum* (WLK.)		
	22	Myzus ascalonicus DONC.	*Myzus ascalonicus* DONC.	KUNKEL, 1966
	23	*Myzus persicae* (SULZ.)	*Myzus persicae* (SULZER)	SCHMIDT, 1959
	24	*Nasonovia ribisnigri* (MOSLEY)		
	25	*Pachypappa* sp.	*Pachypappa* sp.	BÖRNER, 1938
	26	*Paraprociphilus tessellatus* (FITCH)	*Prociphilus tessellata* FITCH	PELTON, 1938
	27	*Pemphigus spyrothecae* PASSERINI		
	28	*Phloeomyzus passerinii* (SIGNORET)	*Phloeomyzus* sp.	BÖRNER, 1938
	29	*Phylloxera coccinea* v. HEYD.	*Phylloxera coccinea* (v. HEYD.)	KUNKEL, 1966
	30	*Phylloxera* sp.	*Phylloxera* sp.	BÖRNER, 1938

	31	*Pleotrichophorus glandulosus* (KLTB.)		
	32	*Pterocomma jacksoni* THEOBALD		
	33	*Pterocomma salicis* (L.)		
	34	*Pterocomma* sp.	*Pterocomma* sp.	BÖRNER, 1938
	35	*Rhopalosiphum maidis* (FITCH)		
	36	*Rhopalosiphum padi* (L.)		
	37	*Sitobion avenae* (F.)		
	38	*Uroleucon tanaceti* (L.)		
	39	*Uroleucon (Uromelan) jaceae* (L.)		
d	1	? *Acyrthosiphon malvae* (MOSLEY)	*Aphis pelargonii* KALT.	WITLACZIL, 1882
	2	*Eriosoma lanigerum* (HSMNN.)	*Schizoneura lanigera* HAUSMANN	DAVIDSON, 1913
	3	*Eriosoma (Schizoneura) ulmi* (L.)		
	4	*Eriosoma* sp.	*Eriosoma* sp.	BÖRNER, 1938
	5	*Schizaphis graminum* (ROND.)	*Schizaphis graminum* (RONDANI)	SAXENA and CHADA, 1971

of the foregut. The outer layer consists of small cuboidal epithelial cells covered with a chitinous intima.

The midgut is the longest part of the alimentary tract and is composed of stomach, first and second part of intestine, and descending intestine. In *G. schrankiana* and *T. dryophila* the first and second part of the intestine together are about five times as long and the descending intestine about four times as long as the stomach (Fig. 1).

The stomach either starts at the anterior part of the mesothorax, half-way the mesothorax, or in the first abdominal segment and passes into the intestine in the first, second, or third abdominal segment, respectively (Table 2). In the region of the oesophageal valve the stomach is somewhat dilated and then continues as a tubular structure of which the diameter is the same as that of the first part of the intestine. In transverse sections of the fore part of the stomach there are twice as many cells (Table 2) as in sections of the following first and second parts of the intestine. The number of cells in each section of the stomach gradually decreases and is equal to the number of cells in sections of the first and second parts of the intestine at the point where the hind stomach passes into the first part of intestine. Both in longitudinal and in transverse sections the epithelial cells of the stomach are smaller than those of the first and second part of the intestine. The stomach wall is made up of triangular cells, with heterogenous basophilic cytoplasm, small vacuoles and a spherical to oval nucleus. The basal cell membrane of each cell has numerous infoldings and the free surface a striated border. The cells do not show any cytological manifestations of secretion and the lumen of the stomach appears empty (Fig. 2A and B).

The first part of the intestine consists of a small tube which runs from the tubular stomach directly to the ventral surface, then posteriorly before reversing direction (abdominal loop) in the fourth, fifth, or sixth abdominal segment (Fig. 1 and Table 2). In each aphid species studied the stomach lies centrally in the dorsal surface of the aphid and dorsal to the descending intestine, with the first part of the intestine bent either to the right or to the left of the descending intestine. The abdominal loop is connected to the cauda by 'membranes' which presumably keep the loop in position. The first part of the intestine passes into the broader second part of the intestine which runs directly anteriad to the thoracic loop situated in the first, second, or third thoracic segment. The epithelial cells of the first part of the intestine contain some vacuoles and a somewhat spherical nucleus, whereas those of the second part of the intestine are strongly vacuolated and have ovoid-shaped nuclei (Fig. 2C and D). The distal surfaces of these cells are striated and line a stellate-shaped closed or partly closed lumen.

The fourth part of the midgut is the descending intestine which runs from the thoracic loop directly caudad to open into the rectum. In dissections the descending intestine is transparent and dilated forming a sac-like structure with exhibits vigorous peristaltic movements. In contrast the stomach and the first and second parts of the intestine are opaque tubular structures showing slow peristaltic movements. The basement membrane of the foregut, stomach, and first and second parts of the intestine is surrounded by a layer of circular muscle

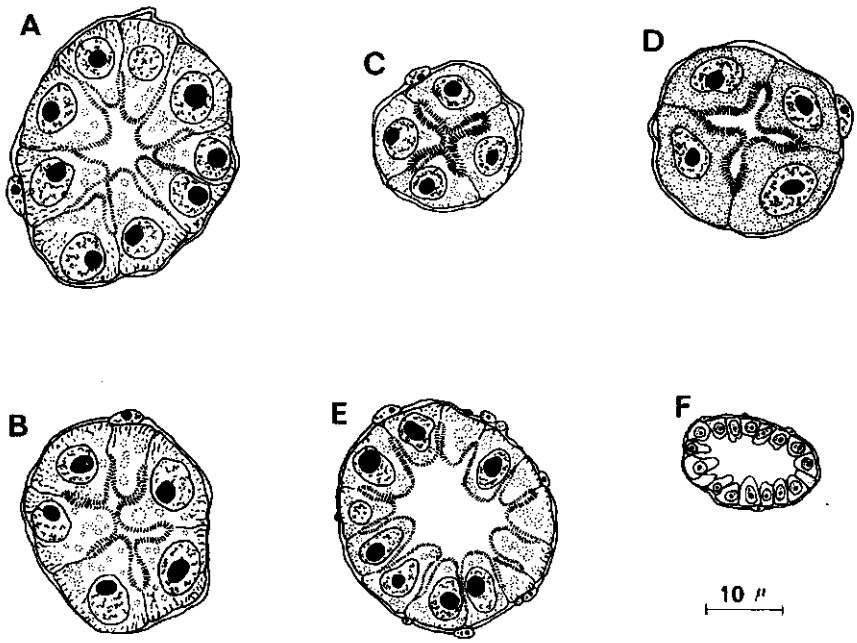

Fig. 2. Transverse sections of the stomach posterior to the oesophageal valve (A) and half-way along the stomach of *Thelaxes dryophila* (B), the first part of intestine (C) and second part of intestine of *Thelaxes suberi* (D), the descending intestine (E) and the rectum of *Glyphina betulae* (F). The position of the sections (A–F) are given in Fig. 1.

fibres, that of the descending intestine by both longitudinal and circular muscle fibres.

Transverse sections of the sac-like descending intestine have 11–13 cells in all the thelaxids investigated. They surround a wide lumen and contain many small vacuoles, ovoid-shaped nuclei, and their luminal surfaces have striated borders (Fig. 2E). Histologically the descending intestine of all thelaxids investigated is identical to that of the species of Callaphididae without a filtersystem (PONSEN, 1982). In the region of the rectum there are dorsal and lateral 'membranes' which connect the descending intestine to the intersegmental membrane and possibly serve to keep the descending intestine in position.

The rectum starts in the seventh abdominal segment and is made up of a single layer of small cuboidal cells (Fig. 2F). It passes into an epidermal invagination of which the cuticular lining is thicker than that of the rectal epithelium. The anal opening is both laterally and dorsally connected by muscles to the integument of the ninth abdominal segment.

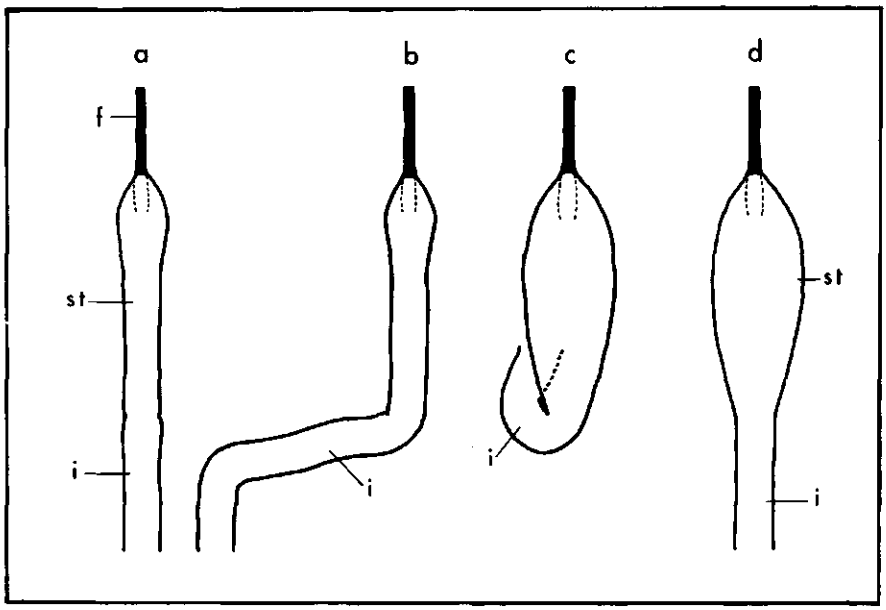

Fig. 3. Diagrams illustrating the junction of the stomach with the intestine in the callaphidids (a), thelaxids (b), and the aphid species mentioned in Table 3 (c-d).

DISCUSSION

Morphologically the digestive system (Fig. 1) of the thelaxids investigated is similar to that of *Hamamelistes* sp., *Sipha* sp., *Tranaphis* sp. (= *Chaitophorus* sp.), and *Hormaphis hamamelidis* FITCH. illustrated by BÖRNER (1938) and LEWIS and WALTON (1958). The digestive system consists of a short foregut, tubular stomach, primitive intestine with two loops, an abdominal and a thoracic one, and a hindgut (BÖRNER, 1952; BÖRNER and HEINZE, 1957). They reported a hindgut in their aphids, but did not describe it. However, in all the thelaxids investigated (Table 2) the hindgut is of endodermal origin and an extension of the midgut and therefore more correctly called a descending intestine (Fig. 1 and 2E).

The descending intestine has, morphologically and histologically, a similar structure to that of the callaphidids without a filtersystem (PONSEN, 1982). In both groups the aphid species investigated have a tubular stomach and lack a hindgut of ectodermal origin. Only in the callaphidids is the ascending intestine coiled in the anterior region of the aphid.

An important difference between the groups is that in the callaphidids without a filtersystem the stomach lies in the ventral surface of the aphid, whereas in the thelaxids it is situated centrally in the dorsal surface of the aphid. Moreover, in the callaphidids without a filtersystem the intestine lies in a direct line with

the tubular stomach (Fig. 3a), whereas in the thelaxids the intestine passes from the tubular stomach to the ventral side of the aphid (Fig. 3b). In other aphid species the transition from the stomach to the intestine is marked by a sharp loop (Fig. 3c), although there are some species in which the intestine runs posteriad from the stomach (Fig. 3d; Table 3).

Summary

The digestive system of *Glyphina* and *Thelaxes* (Table 2) has a short foregut which opens into the stomach by way of a valve (Fig. 1). The stomach has a tubular structure and its diameter is the same as that of the first part of the intestine. The intestine consists of a narrow tube which runs from the stomach to the ventral side of the aphid and terminates in the abdominal loop. From there a broader intestine, the second part, runs directly anteriad to the thoracic loop. The descending intestine runs from the thoracic loop directly caudad to open into the rectum which terminates at the anal opening. A hindgut of ectodermal origin is lacking.

Samenvatting

Het spijsverteringskanaal van *Glyphina* en *Thelaxes* heeft een korte slokdarm die in de maag uitmondt via een oesophageale klep. De maag heeft een buisvormige structuur waarvan de diameter dezelfde is als die van het eerste gedeelte van de darm. Dit darmdeel loopt van de maag direct ventraalwaarts en vervolgens caudaalwaarts om in de abdominale lis over te gaan. Vandaar loopt een wijder darmdeel direct voorwaarts tot in de thorax, buigt zich om en gaat in de neerdalende darm over. De neerdalende darm zet zich caudaalwaarts voort in het rectum dat via de epidermale invaginatie in de anale opening uitmondt. Een einddarm van ectodermale oorsprong ontbreekt.

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