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THE DIGESTIVE SYSTEM OF SOME SPECIES OF CALLAPHIDIDAE WITHOUT A FILTERSYSTEM (HOMOPTERA: APHIDOIDEA)

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INTRODUCTION

Within the family Callaphididae there are a number of species which lack a filtersystem in their alimentary canal (Table 1). According to BÖRNER (1938, 1949, 1952) these species have a long or very long foregut and lack a stomach dilation in the midgut. These morphological features were illustrated by BÖRNER (1938) in a drawing of the digestive system of *Symydobius* sp. and *Drepanosiphum* sp.

The purpose of this study is to investigate in detail the digestive system of a number of species of Callaphididae which lack a filtersystem.

MATERIALS AND METHODS

Individuals of the species listed in Table 2, were fixed in DUBOSQ BRASIL's fluid, embedded in paraplast, and sectioned at 5–10 μ. Sections were stained in EHRLICH's haematoxylin-eosin or in HEIDENHAIN's iron haematoxylin.

The sections were examined under a Wild microscope equipped with a universal phase contrast condensor and fluotar phase objectives. The drawings were made with a Wild drawing tube at a magnification of 600 or 1500 times. The morphology of a digestive system was reconstructed from the drawings of the serial sections of a whole larva.

In order to dissect the digestive system aphids were fixed on self-adhesive tape attached to a glass-plate. Under a dissecting microscope each aphid was covered with a drop of buffer solution (0.15 M SÖRENSEN, pH 7.2) which did not spread on the surface of the adhesive tape. In this drop the aphid was dissected using two very fine sharpened watchmakers forceps.

RESULTS

The most anterior part of the alimentary tract is the food canal of the maxillary stylets. From the stylets the food canal passes 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 by way of a valve. The stomach passes into the intestine which extends forwards and after a number of coils runs posteriad to open into the rectum which terminates at the anal opening (Fig. 1). In both larvae and adults the gut has the same

structure and occupies the same position in the aphid's body cavity. The total length of the gut of *Betulaphis helvetica, Calaphis flava, Drepanosiphum platanoidis,* and *Euceraphis betulae* is about two and a half times that of the aphid's body; the length of the gut was not calculated for other callaphidid species.

The foregut (oesophagus) runs posteriad between the two salivary glands, dorsal to the nervous system, and ventral to the mycetome. It consists of a thin tube made up of a single layer of squamous epithelial cells which secrete the chitinous intima. In dissections the foregut, especially of species in which it is long, shows undulating movements.

The eosophageal 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 epithelial cells. The valve is covered with an intima.

The midgut is the longest part of the alimentary tract and is composed of stomach, ascending intestine, and descending intestine.

The stomach starts in the first, second, third, fourth, or fifth abdominal segment and passes into the intestine in the third, fourth, fifth, sixth, or seventh abdominal segment, respectively (Table 3 and Figs. 1–4). In *Drepanosiphum acerinum* and *D. aceris* the stomach starts in the sixth abdominal segment and terminates beyond the voluminous coil which extends far into the abdomen; in these two species the voluminous abdominal coil is the stomach. The stomach lies in the ventral region of the aphid and within each aphid species the stomach can be situated either to the right or to the left of the descending intestine.

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 ascending intestine. In transverse sections of the fore part of the stomach there are twice as many cells (Table 3) as in the subsequent ascending intestine. The number of cells in each section of the stomach gradually decreases and is equal to the number of cells of in sections of the ascending intestine at the point where the hind stomach passes into the ascending intestine. Both in longitudinal and in transverse sections the epithelial cells of the stomach are smaller than those of the ascending intestine. The stomach wall is made up of triangular cells, with heterogeneous basophilic cytoplasm, small vacuoles and spherical to oval nuclei. The basal cell membrane has numerous infoldings and the free surfaces of the cells have striated borders. The cells are not secreting and the lumen of the stomach appears empty (Fig. 5A and B).

The ascending intestine runs from the tubular stomach to the voluminous abdominal coil passing subsequently into a number of other coils. In *Monaphis antennata* the voluminous abdominal coil is situated in the fifth abdominal segment and in *Calaphis flava* in the sixth or seventh abdominal segment, whereas in the other callaphidid species it is in the seventh segment (Table 3). The abdominal coil of the intestine is connected with the ninth abdominal segment or cauda by 'membranes' which presumably keep the abdominal coil in position. Each callaphidid species has a characteristic number of coils positioned between the prothorax and the fourth abdominal segment. Likewise the

number of cells in transverse sections of the ascending intestine is also characteristic (Table 3; Figs. 2–4). These epithelial cells are strongly vacuolated, have spherical to oval nuclei, and their free surfaces have striated borders which form a stellate-shaped closed or partly closed lumen (fig. 5C and D).

After the last coil the ascending intestine passes into the descending intestine which runs directly caudad to open into the rectum. In dissections the descending intestine is transparent and gradually dilates forming a sac-like structure which exhibits vigorous peristaltic movements. On the other hand the ascending intestine over its entire length, including the stomach, is an opaque tubular structure showing slow peristaltic movements. The basement membrane of foregut, stomach, and ascending intestine is surrounded by a layer of circular muscle fibres, whereas that of the descending intestine by longitudinal and circular muscle fibres.

Transverse sections of the wide region of the sac-like descending intestine have 11–13 epithelial cells in all the species of Callaphididae investigated. As a result of the vigorous peristaltic movements the descending intestine can take several forms (Fig. 6A). When the muscle cells have relaxed the epithelial cells are triangular in shape surrounding a wide lumen containing many small vacuoles and sometimes big ones in the apical region. Each cell has an oval nucleus and its free margin has a striated border (Fig. 6B and C). In the expanded position (balloon-shaped) the epithelium consists of big flattened cells, whereas when the gutwall contracts the basal and apical cell membranes show deep infoldings.

In the region of the rectum there are dorsal and lateral 'membranes' which connect the descending intestine to the intersegmental membrane between the sixth and seventh abdominal tergum. These 'membranes' 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 columnar cells which are quite different from the epithelial cells of the descending intestine (Fig. 5E). The rectum consists of a short tube which 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 with the cauda by muscles. The dorsal rectal sac is innervated by a nerve originating from the medial dorsal nerve which runs alongside the dorsal vessel.

Discussion

The digestive system of callaphidid species without a filtersystem is characterized by a long or very long foregut and the absence of a stomach dilation in the midgut (Börner, 1938, 1949, 1952). Moreover, the coils of the ascending intestine are all situated in the anterior region of the aphid (Figs. 1–4) and a hindgut of ectodermal origin is lacking. Börner (1938) reports the presence of a hindgut in *Symydobius* sp. and *Drepanosiphum* sp., but did not describe it.

However, in all the callaphidid species investigated here (Table 3) the hindgut is of endodermal origin and an extension of the midgut and therefore called a descending intestine.

In dissections of the callaphidid species the descending intestine had the same transparent, sac-like structure (Fig. 6A) showing vigorous peristaltic movements as the hindgut of *Myzus persicae* (PONSEN, 1972). This aphid has a hindgut of ectodermal origin as in *Cryptomyzus ribis, Subsaltusaphis ornata,* and *Eulachnus* sp. (PONSEN, 1977, 1979, 1981).

The descending intestine of *S. ornata,* a callaphidid species with a filtersystem (Table 4), is also transparent and shows vigorous peristaltic movements. Histologically it has a similar structure to the descending intestine of the callaphidid species which lack a filtersystem, although that of *S. ornata* is more tubular. In *S. ornate* the hindgut starts as a closed tube, whereas in the callaphidid species without a filtersystem a hindgut is lacking.

Within the family Callaphididae there is a group of aphids which have a filterchamber (BÖRNER, 1949, 1952). According to WITLACZIL (1884) in *Callipterus tiliae* L. (= *Eucallipterus tiliae* (L.)) (Table 4) the stomach and the anterior part of the tubular midgut are fused with the anterior part of the hindgut. WITLACZIL (1884) was the first to describe this structure which now called a filterchamber. It is interesting to note that the digestive system of the callaphidid species listed in Table 4, is anatomically and histologically identical to that of *S. ornata* (PONSEN, 1979). All species have a very long foregut, a very small stomach encapsulated by the posterior part of the hindgut forming a concentric filtersystem (except *Therioaphis trifolii* and *Thripsaphis cyperi* of which the stomach is encapsulated by the anterior part of the hindgut), an ascending and descending intestine of which the anterior and posterior part of the intestine are fused together forming a parallel filtersystem, a hindgut which starts as a closed tube, and a rectum which terminates at the anal opening.

DIXON (1975) found that second generation *D. platanoidis* adults have a longer gut than first generation aphids. A longer gut in the second generation aphids does not necessarily mean that the stomach starts more anteriorly or that there are more coils in the ascending intestine but rather that the coils are somewhat more voluminous than those of the first generation aphids.

Callipterinella callipterus collected at Ede had a yellow colour with brown markings, and those found in the Pyrenees (France) dark green with black markings. In both collections the stomach starts in the fifth abdominal segment, whereas the configuration of the coils of the ascending intestine is slightly different (Fig. 3 and 4).

Aphids formerly regarded as *Euceraphis punctipennis* (ZETTERSTEDT) are distinguished by BLACKMAN (1977) as two species, *E. punctipennis* and *E. betulae* (KOCH), on the basis of cytological and morphological differences. Besides these differences it appears that in *E. betulae* the stomach starts in the first abdominal segment whereas in *E. punctipennis* it starts in the third abdominal segment (Fig. 2 and 3). On the other hand, there is no difference in configuration

of the three coils of the ascending intestine in the anterior part of the aphid in these species. The aphids were all from one colony.

Summary

The digestive system of the callaphidid species (Table 3) without a filtersystem has a long or very long foregut which opens into the stomach by way of a valve (Figs. 1–4). The stomach has a tubular structure and its diameter is the same as that of the ascending intestine. The tubular stomach passes into the ascending intestine which extends forwards and forms a number of coils in the anterior region of the aphid. From the last coil the ascending intestine passes into the descending intestine which runs directly caudad to open into the rectum which terminates at the anal opening. A hindgut of ectodermal origin is lacking.

Samenvatting

Het spijsverteringskanaal van de Callaphididae zonder filtersysteem heeft een lange of zeer lange slokdarm die in de maag uitmondt via een oesophageale klep (Fig. 1–4). De maag heeft een buisvormige structuur waarvan de diameter dezelfde is als die van de opstijgende darm. Vervolgens gaat de maag over in de opstijgende darm die in het voorste gedeelte van de bladluis een aantal lissen vormt. Na de laatste darmlis gaat de opstijgende darm over in de neerdalende darm die via het rectum in de anale opening eindigt. Een einddarm van ectodermale oorsprong ontbreekt.

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TABLE 1. The structure of the digestive system and its subdivisions in representatives of the family Callaphididae lacking a filtersystem as cited in the literature. The names are corrected according to EASTOP and HILLE RIS LAMBERS (1976).

	Name used by author	Present name	Foregut	Oesophageal valve	Stomach starts in	Filter system	Author
1	*Betulaphis quadrituberculata* (KALT.)	*Betulaphis quadrituberculata* (KLTB.)	very long			–	BÖRNER, 1952
	Betulaphis quadrituberculata (KALTENBACH)	*Betulaphis quadrituberculata* (KLTB.)				+	KUNKEL and KLOFT, 1977
2	*Börnerina depressa* BRAMST.	*Boernerina depressa* BRAMST.	short			–	BÖRNER, 1949, 1952
3	*Calaphis callipterus* (HTG.)	*Callipterinella callipterus* (HTG.)	very long			–	BÖRNER, 1952
4	*Calaphis tuberculata* (v. HEYD.)	*Callipterinella tuberculata* (v. HEYD.)	very long			–	BÖRNER, 1952
5	*Kallistaphis betulicola* (KALT.)	*Calaphis betulicola* (KLTB.)	very long			–	BÖRNER, 1952
6	*Kallistaphis flava* (MORDV.)	*Calaphis flava* MORDV.	very long			–	BÖRNER, 1952
7	*Betacallis comes* (WALK.)	*Clethrobius comes* (WLK.)			III	–	BÖRNER, 1949, 1952
	Clethrobius comes (WALKER)	*Clethrobius comes* (WLK.)	schort			+	KUNKEL and KLOFT, 1977
8	*Betacallis gigantea* (CHOL.)	*Clethrobius giganteus* (CHOL.)			III	–	BÖRNER, 1949, 1952
	Clethrobius giganteus (CHOLODKOVSKY)	*Clethrobius giganteus* (CHOL.)				+	KUNKEL and KLOFT, 1977
9	*Drepanosiphon gracilis* CB.	*Drepanosiphum acerinum* (WLK.)	very long		7	–	BÖRNER, 1938, 1949
10	*Drepanosiphon acerinus* (WALK.)	*Drepanosiphum aceris* KOCH	very long		7	–	BÖRNER, 1938, 1949
11	*Drepanosiphon zimmermanni* CB.	*Drepanosiphum oregonensis* GRANOVSKY	very long			–	BÖRNER, 1952
12	*Drepanosiphum platanoides* SCHRK.	*Drepanosiphum platanoidis* (SCHRANK)	long	+		–	WITLACZIL, 1884; DIXON, 1975
	Drepanosiphum platanoidis (SCHRK.)	*Drepanosiphum platanoidis* (SCHRANK)	very long		7	–	BÖRNER, 1938, 1949
	Drepanosiphon smaragdinus KOCH	*Drepanosiphum platanoidis* (SCHRANK)	very long		7	–	BÖRNER, 1938, 1949
	Drepanosiphum platanoidis (SCHRANK)	*Drepanosiphum platanoidis* (SCHRANK)				+	KUNKEL and KLOFT, 1977
13	*Euceraphis pilosa* NEVS.	*Euceraphis pilosa* NEVS.	very long			–	BÖRNER, 1952
14	*Euceraphis punctipennis* (ZETT.)	*Euceraphis* (?) *punctipennis* (ZETT.)	very long			–	BÖRNER, 1952
15	*Monaphis antennata* (KALT.)	*Monaphis antennata* (KLTB.)	very long			–	BÖRNER, 1952
16	*Phyllaphis fagi* (L.)	*Phyllaphis fagi* (L.)	very long			–	BÖRNER, 1952
	Phyllaphis fagi (L.)	*Phyllaphis fagi* (L.)				+	KUNKEL and KLOFT, 1977
17	*Symydobius oblongus* (v. HEYD.)	*Symydobius oblongus* (v. HEYD.)			III	–	BÖRNER, 1938, 1949, 1952
	Symydobius piceus CB.	*Symydobius oblongus* (v. HEYD.)			III	–	BÖRNER, 1952

+ = present; – = absent
I–III refer to thoracic segments
1–9 refer to abdominal segments

TABLE 2. List of the species of Callaphididae studied, their host plant, and relevant locality data.

	Host plant	Locality
1 *Betulaphis helvetica* H.R.L.	*Betula* sp.	Wageningen, 29.VII.1979
2 *Calaphis flava* MORDV.	*Betula* sp.	Wageningen, 19.V.1980
3 *Callipterinella callipterus* (HTG.)	*Betula* sp.	Ede, 12.VIII.1979
4 *Callipterinella callipterus* (HTG.)	*Betula* sp.	Ax les Thermes (Pyrenees, France), 27.VII.1980
5 *Callipterinella tuberculata* (v. HEYD.)	*Betula* sp.	Wageningen, 20.V.1980
6 *Clethrobius giganteus* (CHOL.)	*Alnus glutinosa*	Wageningen, 21.V.1980
7 *Drepanosiphum acerinum* (WLK.)	*Acer pseudoplatanus*	Bennekom, 1.VIII.1980
8 *Drepanosiphum aceris* KOCH	*Acer campestre*	Wageningen, 28.VIII.1980
9 *Drepanosiphum platanoidis* (SCHRANK)	*Acer pseudoplatanus*	Wageningen, 16.V.1980
10 *Euceraphis betulae* (KOCH)	*Betula* sp.	Wageningen, 16.V.1977
11 *Euceraphis punctipennis* (ZETT.)	*Betula* sp.	Wageningen, 11.IX.1980
12 *Monaphis antennata* (KLTB.)	*Betula* sp.	Ede, 28.IX.1980
13 *Phyllaphis fagi* (L.)	*Fagus sylvatica*	Wageningen, 14.V.1980
14 *Symydobius oblongus* (v. HEYD.)	*Betula* sp.	Wageningen, 19.V.1980

TABLE 3. The structure of the digestive system and its subdivisions in the species of Callaphididae studied.

	Aphid	Total number of aphids		Stomach starts in		Stomach ends in	Number of cells in transverse section of		Coils of ascending intestine in	Voluminous coil of ascending intestine in	Additional coil of ascending intestine in
							Stomach[1]	Ascending intestine			
a	*Euceraphis betulae* (KOCH)	12	wingless	III[2]	(1)	3	10	5–6	II–1	7	–
			wingless	1	(10)	3					
			winged	III[2]	(1)	3					
b	*Phyllaphis fagi* (L.)	11	wingless	1	(7)	3	8	3–4	II–4	7	5 (1)
			wingless	2	(4)						5 (2)
c	*Monaphis antennata* (KLTB.)	10	♀	1	(3)	3	10	5–6	I–III	5	–
			♂	1	(3)	3					
			♀	2	(2)	4					
			♂	2	(2)	4					
d	*Clethrobius giganteus* (CHOL.)	11	wingless	1	(3)	3	12	6–8	II–1	7	–
			wingless	2	(8)	4					
e	*Symydobius oblongus* (v. HEYD.)	15	wingless	2	(2)	4	12	5–7	II–1	7	5 (15)
			wingless	3	(13)	5					
f	*Euceraphis punctipennis* (ZETT.)	10	wingless	3	(5)	5	10	5–6	III–3	7	–
			winged	3	(5)	5					
g	*Calaphis flava* MORDV.	9	wingless	3	(7)	5	8	4–5	II–1	6/7	–
			oviparous	3	(2)	5					
h	*Betulaphis helvetica* H.R.L.	18	wingless	4	(18)	6	8	4–5	II–1	7	–
i	*Callipterinella tuberculata* (v. HEYD.)	15	wingless	4	(15)	6	10	4–5	II–III	7	–
j	*Callipterinella callipterus* (HTG.) (Ede)	11	wingless	5	(11)	7	8	3–5	II–2	7	–
k	*Callipterinella callipterus* (HTG.) (Pyrenees)	14	wingless	5	(13)	7	8	3–4	II–2	7	–
			wingless	6	(1)						
l	*Drepanosiphum platanoidis* (SCHRANK)	16	wingless	5	(16)	7	12	6–8	II–2	7	–
m	*Drepanosiphum acerinum* (WLK.)[3]	11	wingless	6	(6)		12	6–8	II–3		–
			winged	6	(5)						
n	*Drepanosiphum aceris* KOCH[3]	14	wingless	6	(8)		10	4–5	II–2		–
			winged	6	(5)						
			winged	7	(1)						

[1]Maximum number of cells in the beginning of the stomach
[2]Stomach starts half-way the third thoracic segment
[3]In these aphids the voluminous coil represents the stomach situated in the seventh abdominal segement

I–III refer to thoracic segments
I–9 refer to abdominal segments
In brackets number of aphids

TABLE 4. A list of callaphidid species with filtersystems and in which the digestive system is anatomically and histologically identical to that of *Subsaltusaphis ornata* (Theobald). The names are corrected according to EASTOP and HILLE RIS LAMBERS (1976).

1 *Callaphis juglandis* (GOEZE)
2 *Chromaphis juglandicola* (KLTB.)
3 *Ctenocallis setosus* (KLTB.)
4 *Eucallipterus tiliae* (L.)
5 *Hoplocallis pictus* (FERRARI)
6 *Iziphya bufo* (WLK.)
7 *Myzocallis carpini* (KOCH)
8 *Myzocallis castanicola* BAKER
9 *Myzocallis coryli* (GOEZE)
10 *Myzocallis myricae* (KLTB.)
11 *Pterocallis alni* (de GEER).
12 *Pterocallis maculata* (v. HEYD.)
13 *Saltusaphis scirpus* THEOBALD
14 *Subsaltusaphis rossneri* (BÖRNER)
15 *Therioaphis trifolii* (MONELL)
16 *Thripsaphis cyperi* (WLK.)
17 *Tinocallis saltans* (NEVS.)
18 *Tuberculatus querceus* (KLTB.)
19 *Tuberculatus* (*Tuberculoides*) *annulatus* (HTG.)

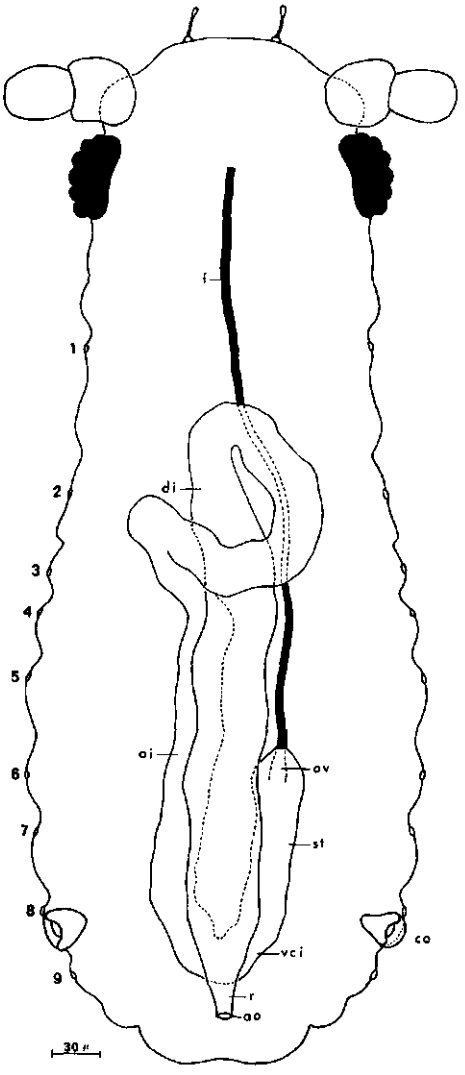

FIG. 1. Dorsal aspect of the digestive system of a one day old *Betulaphis helvetica* larva reconstructed from serial sections showing foregut (f), oesophageal valve (ov), stomach (st), voluminous coil of intestine (vci), ascending intestine (ai), descending intestine (di), rectum (r), and anal opening (ao). In all the callaphidid species investigated (Table 3) the cornicles (co) are outgrowths of the sixth abdominal tergiet, except in *Drepanosiphum acerinum, D. aceris,* and *D. platanoidis,* where they are on the fifth abdominal tergiet. 1–2, meso and metathoracic spiracles; 3–9, abdominal spiracles; the same applies to the other callaphidid species.

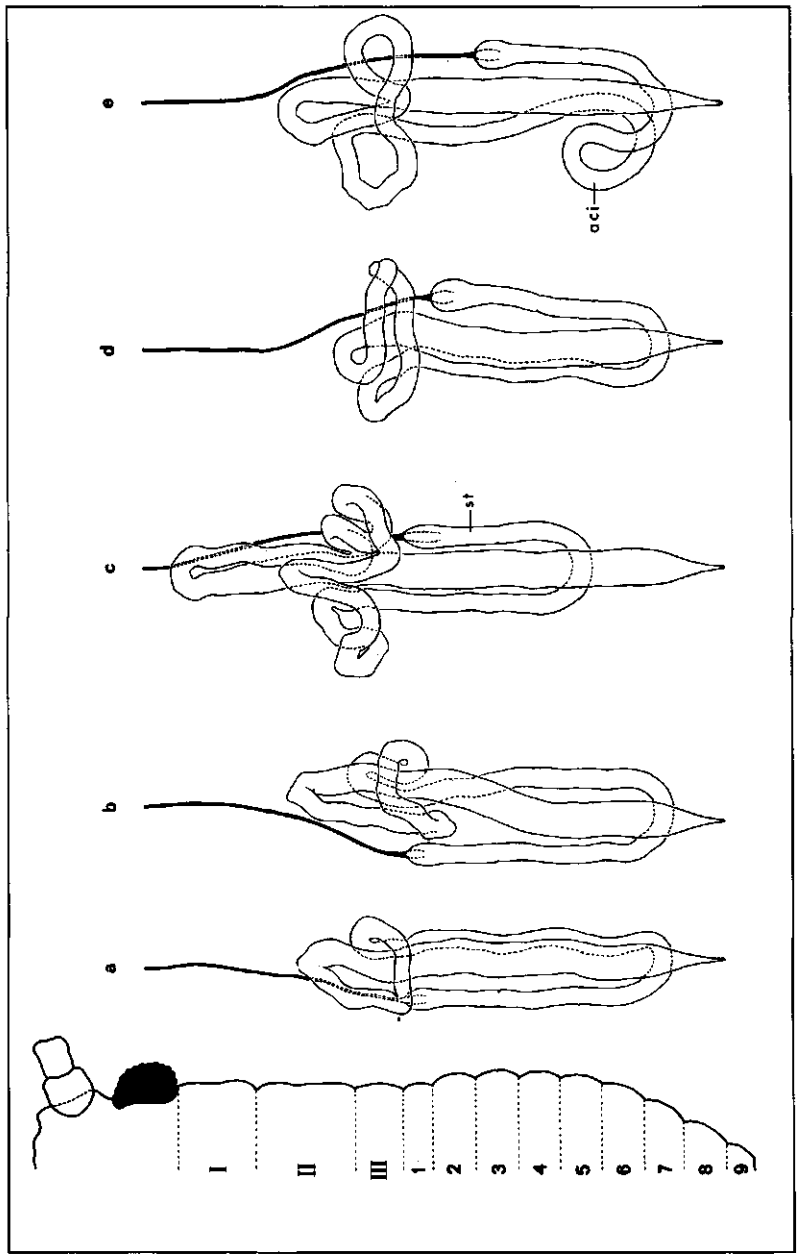

FIG. 2. Semi-schematic representation of the digestive system of *Euceraphis betulae* (a), *Phyllaphis fagi* (b), *Monaphis antennata* (c), *Clethrobius giganteus* (d), and *Symydobius oblongus* (e). I–III, thoracic segments; 1–9, abdominal segments, aci, additional coil of intestine. The letters a–e correspond with those in Table 3.

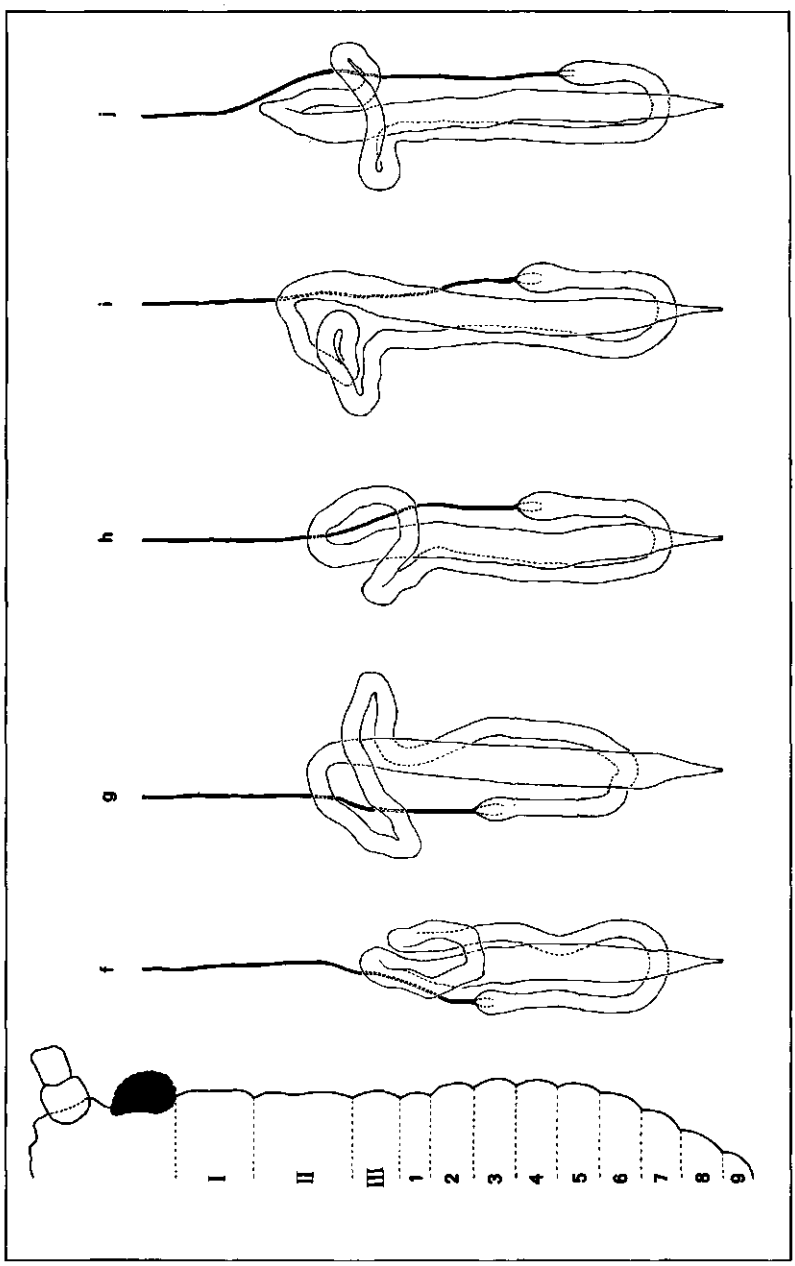

FIG. 3. Semi-schematic representation of the digestive system of *Euceraphis punctipennis* (f), *Calaphis flava* (g), *Betulaphis helvetica* (h), *Callipterinella tuberculata* (i), and *Callipterinella callipterus* (Ede) (j). I–III, thoracic segments; 1–9 abdominal segments. The letters f–j correspond with those in Table 3.

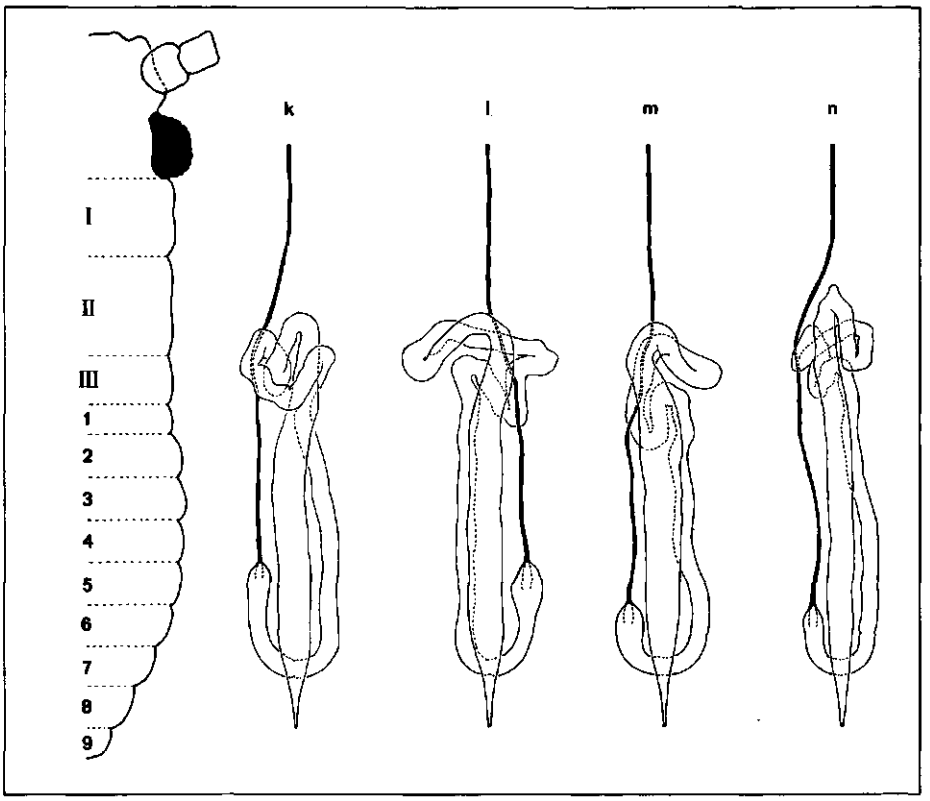

FIG. 4.Semi-schematic representation of the digestive system of *Callipterinella callipterus* (Pyrenees) (k), *Drepanosiphum platanoidis* (l), *D. acerinum* (m), and *D. aceris* (n). I–III, thoracic segments; 1–9, abdominal segments. The letters k–n correspond with those in Table 3.

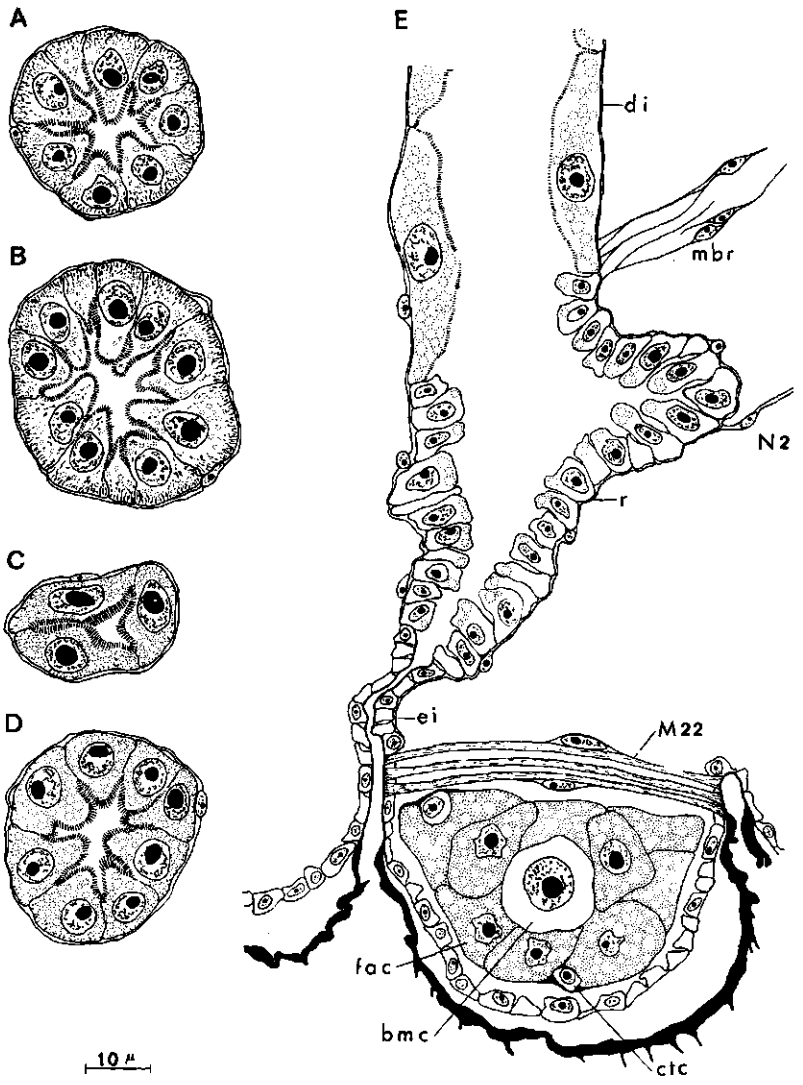

FIG. 5. Transverse sections of the stomach of *Calaphis flava* (A) and *Drepanosiphum platanoidis* (B), the ascending intestine of *Phyllaphis fagi* (C) and *Clethrobius giganteus* (D), and a sagittal section of the rectum of *C. giganteus* (E). bmc, basophilic mesodermal cell; ctc, connective tissue cell; di, descending intestine; ei, epidermal invagination; fac, fat cell; mbr, 'membranes'; M22, retractor muscle fibres of anal opening; N2, branch of medial dorsal nerve; r, rectum.

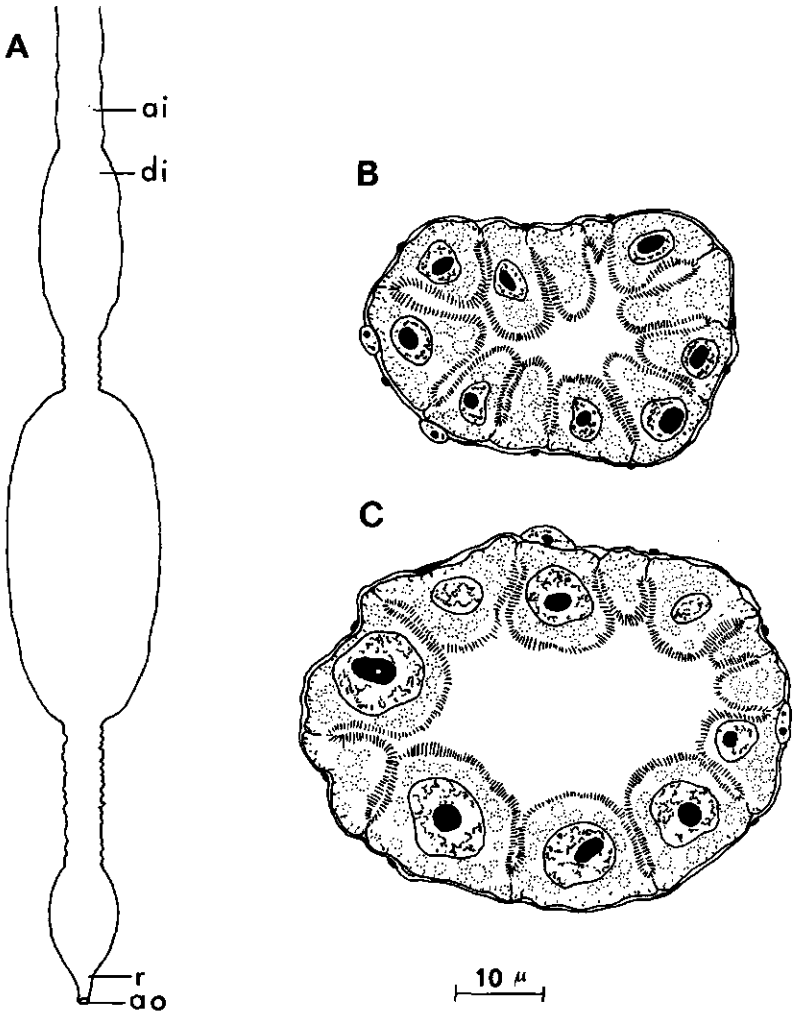

FIG. 6. Schematic representation of the sac-like descending intestine based on dissections of several aphids (A), and transverse sections of the descending intestine of *Symydobius oblongus* (B) and *Monaphis antennata* (C). ai, ascending intestine; ao, anal opening; di, descending intestine; r, rectum.