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A histological description of the salivary gland system of Phylloxeridae (Homoptera, Aphidoidea)

M.B. Ponsen

Laboratory of Virology
Wageningen University

WAGENINGEN UNIVERSITY
University for Life Sciences

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M.B. Ponsen
Hollandseweg 204
6706 KW Wageningen
The Netherlands
E-mail: mbponsenir@hetnet.nl
Phone: 00-31-(0)317-414158

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Summary

The salivary gland system of all species of the Phylloxeridae is a paired organ of which each half is composed of the accessory gland, transparent organ, and principal gland.

The accessory gland is situated at the anterior region of the transparent organ and consists of 2 to 3 cells.

The transparent organ has an irregularly-shaped structure consisting of one type of cells. The total number of cells varies between the several species and asexual morphs.

The principal gland is bilobed and each lobe contains 18 to 20 gland cells of four different types. They are arranged around the end of the principal salivary duct.

The cuticular lumen of the transparent organ which originates in the accessory gland is connected with that of the principal salivary duct. The latter starts in the principal gland and runs forwards partly connected with the transparent organ to unite with the contralateral duct, thus forming the common duct. The latter continues into the afferent duct, salivary pump, efferent duct, and salivary canal formed by the interlocked maxillary stylets.

The very big transparent organ in the phylloxerids is presumably reduced to a small transparent organ in the adelgids and finally evolved to the accessory salivary duct in species of the Aphididae. The transparent organ in the Mindarinae is identical to that in the Adelgidae.

All illustrations in this and previous publications were drawn by the author.

Introduction

The salivary glands of some species of the Phylloxeridae, viz. *Phylloxera florentina* Targioni Tozzetti (Targioni Tozzetti, 1877), *Phylloxera quercus* Boyer de Fonscolombe (Witlaczil, 1886), *Phylloxera punctata* (Lemoine, 1893), *Daktulosphaira vitifoliae* (Fitch) (Krassilstschik, 1893a, b; Grassi et al., 1912; Kunkel, 1966), and *Phylloxera coccinea* (von Heyden) (Kunkel, 1966) consist of one pair of accessory glands and one pair of principal glands. The accessory and principal glands are two separate organs but according to Krassilstschik (1893b) the two glands are connected with each other in the radicicolae of *Daktulosphaira vitifoliae*. The glands are connected with the salivary pump by a duct of which the luminal surface has a cuticular lining (Rilling, 1967). Detailed histological studies on the glands of *Daktulosphaira vitifoliae* have been done by Grassi et al. (1912), Breider (1952) and Rilling (1960, 1967).

The structure of the salivary pump has been described for *Daktulosphaira vitifoliae* (Krassilstschik, 1892; Grassi et al., 1912; Breider, 1952; Rilling, 1960) and all phylloxerid species summarized in Table 1 (Ponsen, 1997).

The sexuales of the Phylloxeridae lack salivary glands (Balbiani, 1874; Lemoine, 1893; Grassi et al., 1912; Ponsen, 1997, 2006).

The purpose of the present study was to investigate the salivary gland system of several species of the Phylloxeridae.

Materials and methods

Specimens of the species were collected from the host plants (Table 3 in Ponsen, 1997). After fixation in Duboscq-Brasil's fluid the aphids were dehydrated in a graded series of ethanol and methyl benzoate, stored in methyl benzoate celluidin (2%) for three days or longer, and then in toluene and finally embedded in paraplast. Serial sections, 5-8 μm thick, were stained in 0.5% methylgreen 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 the aid of a Wild drawing tube.

The morphology of the salivary gland system was reconstructed from the drawings of serial sections of a whole aphid viewed at a magnification of x600. The number of nuclei with their conspicuous big nucleoli, which correspond to the number of cells, were counted at a magnification of x1500.

Salivary gland system

The salivary gland of all species of the Phylloxeridae investigated (Table 1) is a paired organ of which each half is composed of the accessory gland, transparent organ, and principal gland (Figures 1-3). The accessory glands and transparent organs are situated in the pro- and mesothorax one on each side of the stomach and the principal glands in the meso- and metathorax one on each side of the transparent organ. All these glands are connected with the salivary pump by a salivary duct (Figure 4A).

Accessory gland. The accessory gland is situated at the anterior region of the transparent organ (Figures 1-3 and 4B). This gland, named "craniales Läppchen" by Rilling (1967), has already been observed in the gallicolae of *Daktulosphaira vitifoliae*. It consists of 2 to 3 cells (Table 1) each with a spherical to oval nucleus situated at the basal part of the cell. The cytoplasm contains vacuoles and fine granular material. The basal cell membrane has numerous short infoldings (Figures 4C-D).

The cuticular lumen of the transparent organ starts in the accessory gland (Figures 1-4). The cuticular lining of this lumen has a very thick exocuticle similar to that of the epidermis. Before entering the accessory gland the cuticular lumen passes into a cuticular small intercellular canaliculum ending into a cavity. In this cavity the secretory products of the accessory gland cells are collected. The epithelial lining of the cuticular canaliculum consists of 2 to 3 squamous cells, each with a spherical or elongated nucleus (Figures 4C-D).

Histologically, the accessory gland of species of the Phylloxeridae is similar to that of species of the Adelgidae and some species of the Aphididae (Figures 6-8). In all adelgid species the accessory gland consists of 2 cells (Table 3).

Transparent organ. In dissections of living phylloxerid specimens this organ has a transparent structure and consequently named the transparent organ. This organ was named "ghiandola salivare cilindrica" by Grassi et al. (1912) or accessory gland by several authors mentioned in the introduction. The transparent organ has an irregularly-shaped structure as a result of invaginations and evaginations of the basal cell membrane. It consists of one type of cells each with a big spherical to oval nucleus. The lateral cell membranes are difficult to observe. The total number of cells (or nuclei) varies from 8 for winged sexuparous *Moritziella corticalis* to 22 for radicicolous *Daktulosphaira vitifoliae* both between the several species and morphs, but not within a morph as shown for gallicolous *Daktulosphaira vitifoliae* and wingless fundatrigenious *Phylloxera coccinea* (Table 1).

In young larvae the cells are completely filled with vacuoles and granulated material (Figures 4D, G). When the cells enlarge during larval life this material dissolves forming empty irregularly-shaped cavities (Figures 4B, C, E and Figures 1-3). In old larvae and imagines the cells are completely empty except some granulated material along the apical and basal cell membranes. The nuclei start to degenerate by vacuolization and condensation of the chromatin material (Figures 4F, H).

In young larvae the apical cell membrane presents a labyrinthine system of closely packed evaginations which are regularly arranged along a cuticular lumen (Figures 4D, G). During larval life it changes gradually in a loosely scattered structure of short and long evaginations penetrating far into the cells (Figure 4H).

Histologically, the transparent organ of species of the Phylloxeridae is similar to that of

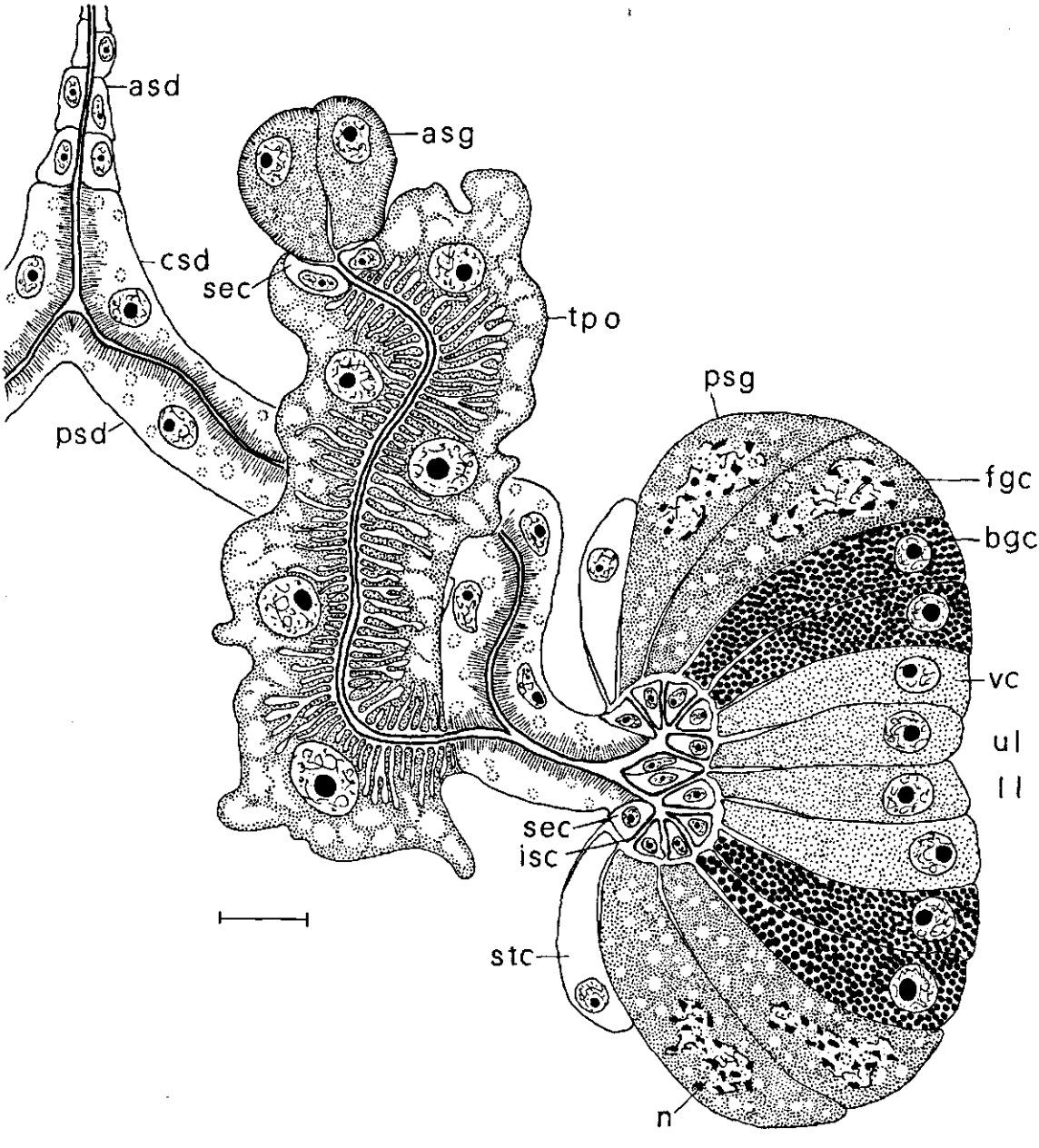

Figure 1 Longitudinal impression of the salivary gland of a fundatrigenious larva of *Aphanostigma piri* reconstructed from transverse serial sections showing the accessory salivary gland (a s g), transparent organ (t p o), principal salivary gland (p s g), principal salivary duct (p s d), common salivary duct (c s d), and the afferent salivary duct (a s d). Each lobe of the principal gland consists of four types of gland cells, viz. fine-granulated cells, big-granulated cells, vacuolated cells, and structureless cells. Both in the transparent organ and principal salivary duct the lateral cell membranes are difficult to observe. Bar represents 10 µm. For list of abbreviations see page 30.

Table 1 Total number of cells of the accessory salivary gland and those of the transparent organ of species of the family Phylloxeridae. The sign ± is followed by the standard deviation of the mean (n = 5). (see Table 3 in Ponsen, 1997).

Aphid	Morph	Accessory salivary gland		Transparent organ	
		Left	Right	Left	Right
Aphanostigma piri (Cholodkovsky)	Wingless fundatrigeniae	2	3	11	11
Aphanostigma ulmifoliae (Aoki)	Fundatrices	2	2	14	17
	Wingless sexuparae	2	2	9	10
Daktulosphaira vitifoliae (Fitch)	Gallicolae	2	2-3	18.6 ± 1.3	18.8 ± 1.9
	Radicicolae	3	2	22	21
	Winged sexuparae	2	3	18	19
Moritziella corticalis (Kaltenbach)	Wingless fundatrigeniae	2	2	8	9
	Winged sexuparae	2	2	8	8
Moritziella castaneivora Miyazaki	Wingless fundatrigeniae	2	3	10	11
Phylloxera caryaecaulis (Fitch)	Fundatrices	2	2	10	11
	Winged sexuparae	2	2	15	14
Phylloxera caryaeseptum (Shimer)	Winged fundatrigeniae	2	2	10	9
Phylloxera coccinea (Heyden)	Fundatrices	3	2	19	21
	Wingless fundatrigeniae	2-3	2	12.4 ± 0.5	13.4 ± 1.1
	Wingless sexuparae	2	3	11	12
Phylloxera devastatrix Pergande	Winged sexuparae	2	2	14	14
Phylloxera punctata (Lichtenstein)	Wingless fundatrigeniae	3	2	15	14
	Brachypterous larvae	3	2	14	16
Phylloxera quercus Boyer de Fonscolombe	Wingless fundatrigeniae	2	3	8	9
Phylloxerina salicis (Lichtenstein)	Wingless fundatrigeniae	2	2	9	9
	Wingless sexuparae	2	2	10	11

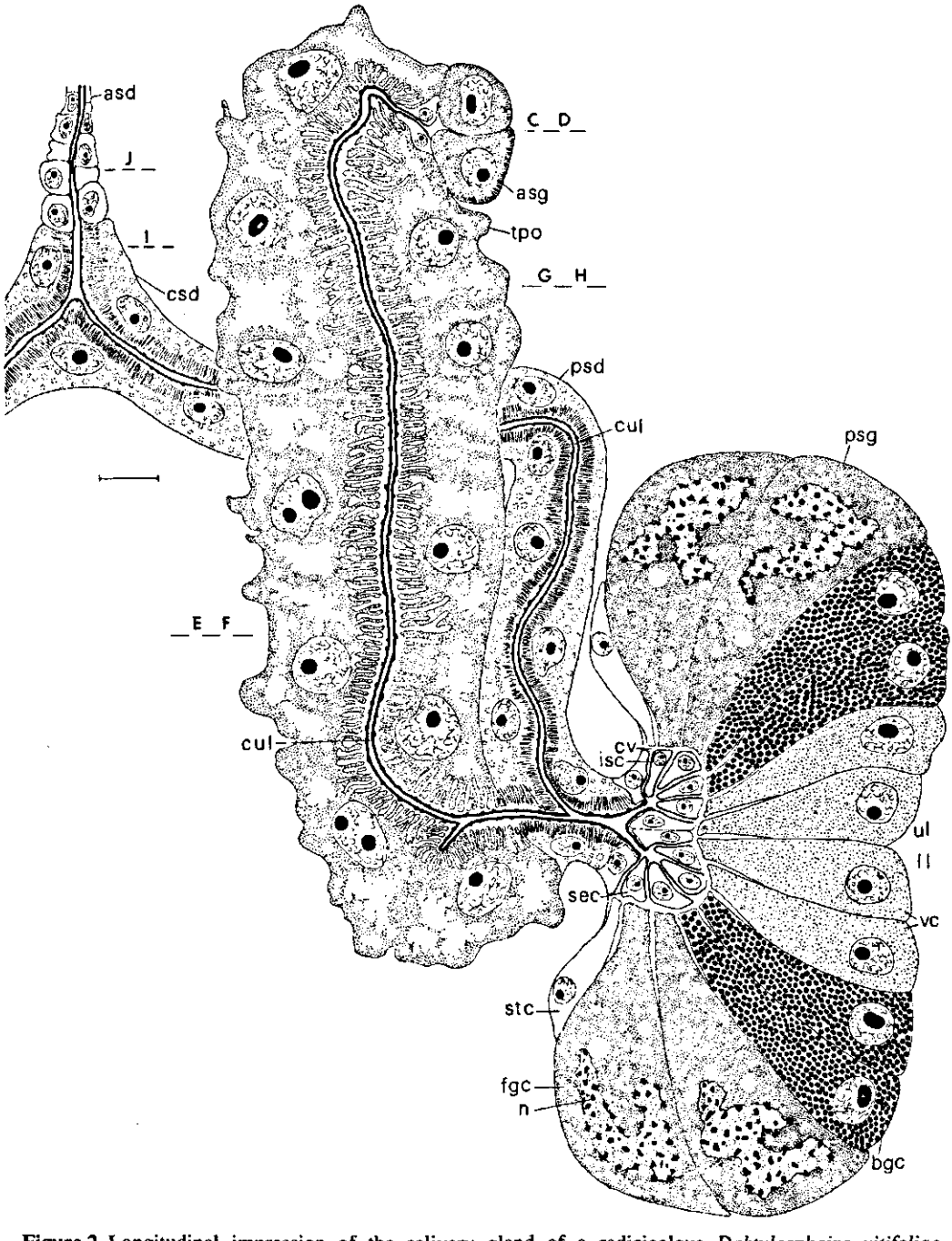

Figure 2 Longitudinal impression of the salivary gland of a radicicolous *Daktulosphaira vitifoliae* reconstructed from transverse serial sections showing the accessory salivary gland (a s g), transparent organ (t p o), principal salivary gland (p s g), principal salivary duct (p s d), common salivary duct (c s d), and the afferent salivary duct (a s d). Each lobe of the principal gland consists of four types of gland cells, viz. fine-granulated cells, big-granulated cells, vacuolated cells, and structureless cells. Both in the transparent organ and in the principal salivary duct the lateral cell membranes are difficult to observe. The dotted lines indicate the plane of the transverse sections C-J in Figure 4. Bar represents 10 μm. For list of abbreviations see page 30.

species of the Adelgidae (Figures 6 and 7). However, in the adelgid species the transparent organ is much smaller; it consists of 5 to 7 cells for the fundatrigeniae and 3 to 4 cells for the remaining asexual morphs (Table 3). Species of the Mindarinae also have a transparent organ identical to that of the Adelgidae (Figure 11).

Principal gland. The principal salivary gland, named "ghiandola salivare bisacca" by Grassi et al. (1912), is composed of two lobes, the upper lobe and the lower lobe (Figures 1-3). Each lobe consists of 18 to 20 bottle-shaped cells which can be distinguished in four distinctly different cell types: 3 to 5 fine-granulated cells, 5 to 6 big-granulated cells, 5 to 6 vacuolated cells, and 4 structureless cells. The total number of cell types is practically constant in each lobe of the principal gland of all asexual morphs and species of the Phylloxeridae investigated (Table 2). They are arranged around the terminal part of the principal salivary duct forming a cavity.

The secretion products of the four types of gland cells are collected in the cavity and transported from there via five cuticular canaliculi to the cuticular lumen of the principal salivary duct (Figures 1-3 and 5A). The exocuticle of the cuticular lining of the lumen of the transparent organ and that of the principal salivary duct is very thick whereas the exocuticle of the cuticular lining of the canaliculi is very thin. The epithelial lining of the cuticular canaliculi consists of small squamous cells, each with an oval to elongated nucleus. The entrance of the cuticular lumen of the principal salivary duct into the principal gland is similar to that of the transparent organ into the accessory gland (Figures 4B-D).

The first type of gland cells are the biggest cells of each lobe. They contain fine granulated material with a diameter of about 0.1 µm. In the apical part of the fine-granulated cells arise vacuoles which during enlargement of the cells increase in size and number. Moreover, in old larvae there extend dense globules of different sizes (Figures 1-3 and 5A).

The most characteristic feature of these cells are the nuclei which during larval life increase in size from "club-shaped" to very big irregularly-shaped structures (Figure 5B). They occupy a large part of the fine-granulated gland cells. The most bizarre shapes are only observed in old larvae and imagines of the gallicolae and radicicolae of *Daktulosphaira vitifoliae* (Figure 5C). Similar shapes have already been reported for the gallicolae of this species (Rilling, 1967).

After hatching the nuclear material starts to condense forming irregularly-shaped particles which increase in number during larval life. In the imaginal stage the nuclear membrane breaks open after which the nuclei disintegrate and the irregularly-shaped particles are released into the cytoplasm (Figure 5A).

The second type of gland cells are the big-granulated cells. They are situated between the fine-granulated gland cells and the vacuolated gland cells (Figures 1-3 and 5A). During larval life they are completely filled with big dense spherical granules with a diameter of about 0.9 µm. They do not show reproduction by fission and do not bear any resemblance to the endosymbionts of the Adelgidae and those of the several subfamilies of the Aphididae (Ponsen, 2006).

The third type of cells are the vacuolated gland cells situated between the biggranulated cells and the vacuolated cells of the opposite lobe (Figures 1-3). They contain granules with a diameter of about 0.2 µm one in each vacuole and between the vacuoles (Figure 5A).

The fourth type of cells are the structureless cells containing homogeneous cytoplasm without any structure. They are the smallest gland cells of each lobe situated on the underside of the fine-granulated cells (Figures 1-3 and 5A).

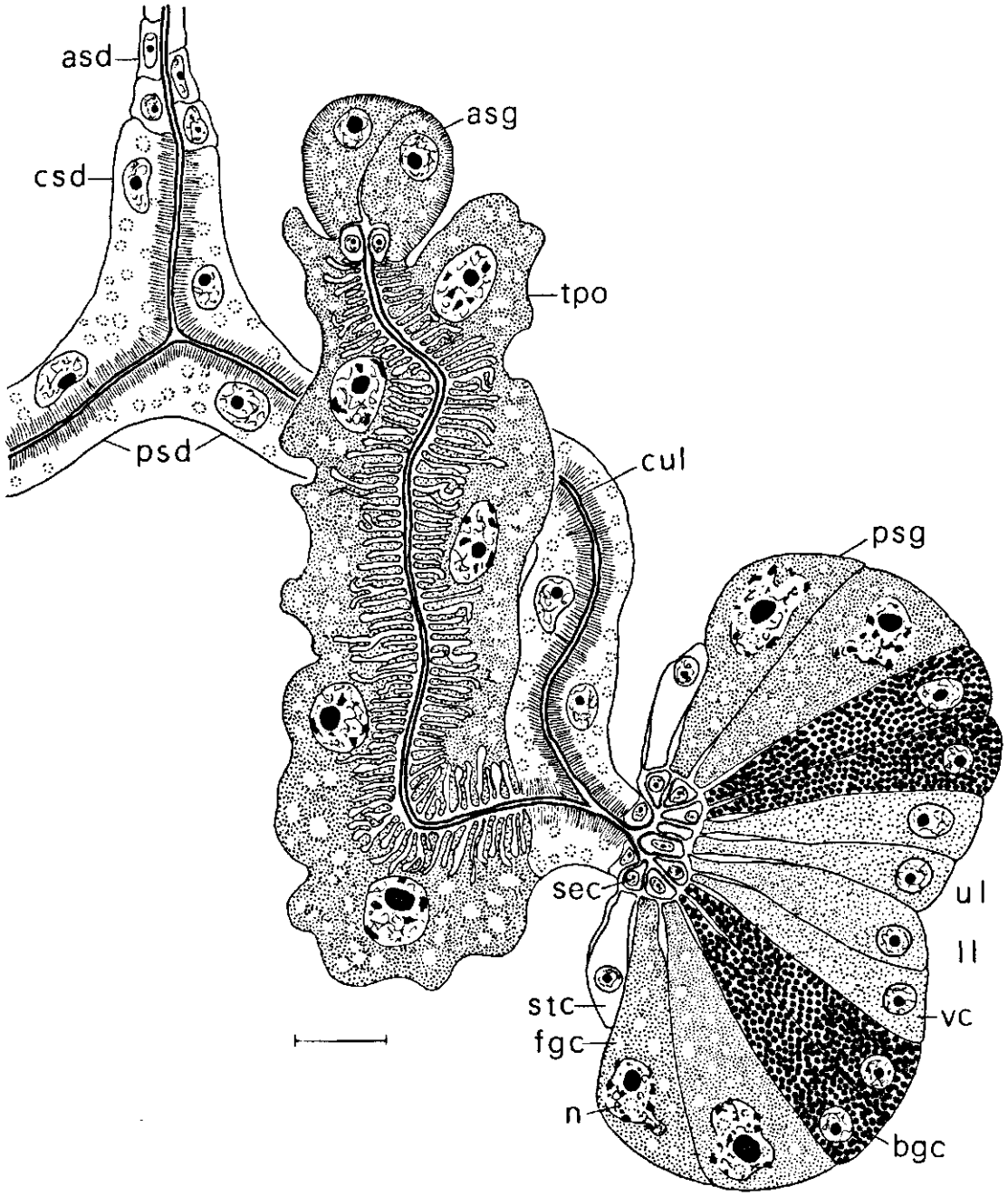

Figure 3 Longitudinal impression of the salivary gland of a larval sexuparous *Moritziella corticalis* reconstructed from transverse serial sections showing the accessory salivary gland (a s g), transparent organ (t p o), principal salivary gland (p s g), principal salivary duct (p s d), common salivary duct (c s d), and the afferent salivary duct (a s d). Each lobe of the principal gland consists of four types of gland cells, viz. fine-granulated cells, big-granulated cells, vacuolated cells, and structureless cells. Both in the transparent organ and in the principal salivary duct the lateral cell membranes are difficult to observe. Bar represents 10 µm. For list of abbreviations see page 30.

Each of the last three cell types has a spherical to oval nucleus located at the basal part of the bottle-shaped cell. The ageing process of these cells starts in the last larval stage with the vacuolization and condensation of the nuclear material.

The topographical position of all four cell types is identical in each lobe of the principal gland (Figures 1-3) of all asexual morphs and species of the Phylloxeridae (Tables 1 and 2).

Probably, in all gland cells of the accessory gland and those of the principal gland the granules migrate to the cell membrane, fuse their own membrane, and release their contents into the intercellular cavity. This secretion process is observed in histological sections of the accessory salivary gland of *Monaphis antennata* (Kaltenbach) as illustrated in Figure 8A.

The arrangement of the gland cells in the principal salivary gland of species of the Adelgidae (Table 3) is similar to that of species of the Phylloxeridae.

Principal salivary duct. The principal salivary duct runs from the principal gland forwards and is connected with the transparent organ. Half-way this organ it runs as a separate duct on the ventral side of the transparent organ to the junction of the suboesophageal and thoracic ganglion to form, together with the contralateral principal salivary duct, the common salivary duct (Figures 1-3). This very short duct runs medio-rostrally beneath the suboesophageal ganglion, and turns downwards to pass into the afferent salivary duct (Figure 17H in Ponsen, 1997).

The cuticular lumen of the transparent organ which starts in the accessory gland, unites with that of the principal salivary duct. Over a short distance it divides into two short cuticular lumens, one to the upper lobe and one to the lower lobe of the principal gland. In each lobe it divides into five very thin cuticular intercellular canaliculi terminating into a cavity (Figures 1-3 and 5A).

The entire tubular salivary duct consists of one type of cells somewhat rectangle inshape of which the lateral cell membranes are difficult to observe. This epithelium contains spherical to oval nuclei and vacuoles of various sizes which increase in number during larval life. Granular material is absent. The apical cell membrane presents a labyrinthine system of closely packed evaginations which are regularly oriented around a cuticular lumen (Figures 4E, F, I and 2). The very thick exocuticle of the cuticular lumen of the common salivary duct passes into a somewhat thin exocuticle of the cuticular lumen of the afferent salivary duct. The latter follows the median line beneath the salivary pump.

Figure 4 Dorsal view of the salivary gland of a wingless fundatrigenious *Moritziella castaneivora* (A) reconstructed from serial transverse sections. 1-2, meso- and metathoracic spiracles; 3-7, abdominal spiracles. Bar represents 30 µm. Longitudinal section of the accessory salivary gland situated at the anterior region of the transparent organ of a wingless sexuparous *Phylloxerina salicis* (B). Transverse sections of the anterior region of the left transparent organ of a winged sexuparous *Phylloxera devastatrix* (C) and that of the right transparent organ of a wingless fundatrigenious young larva of *Moritziella castaneivora* (D) showing the accessory gland; posterior region of the left transparent organ of a winged fundatrigenious old larva of *Phylloxera caryaeseptum* (E) and that of the right transparent organ of a thirdth larval stage wingless fundatrigenious *Phylloxera coccinea* (F) showing the connection with the principal salivary duct; middle region of the transparent organ of a winged sexuparous young larva (G) and that of a gallicolous imago of *Daktulosphaira vitifoliae* (H); the common salivary duct of a winged sexuparous *Daktulosphaira vitifoliae* (I) and the afferent salivary duct of a wingless sexuparous *Phylloxerina salicis* (J). The letters C-J correspond with those given in Figure 2. Bar represents 10 µm. For list of abbreviations see page 30.

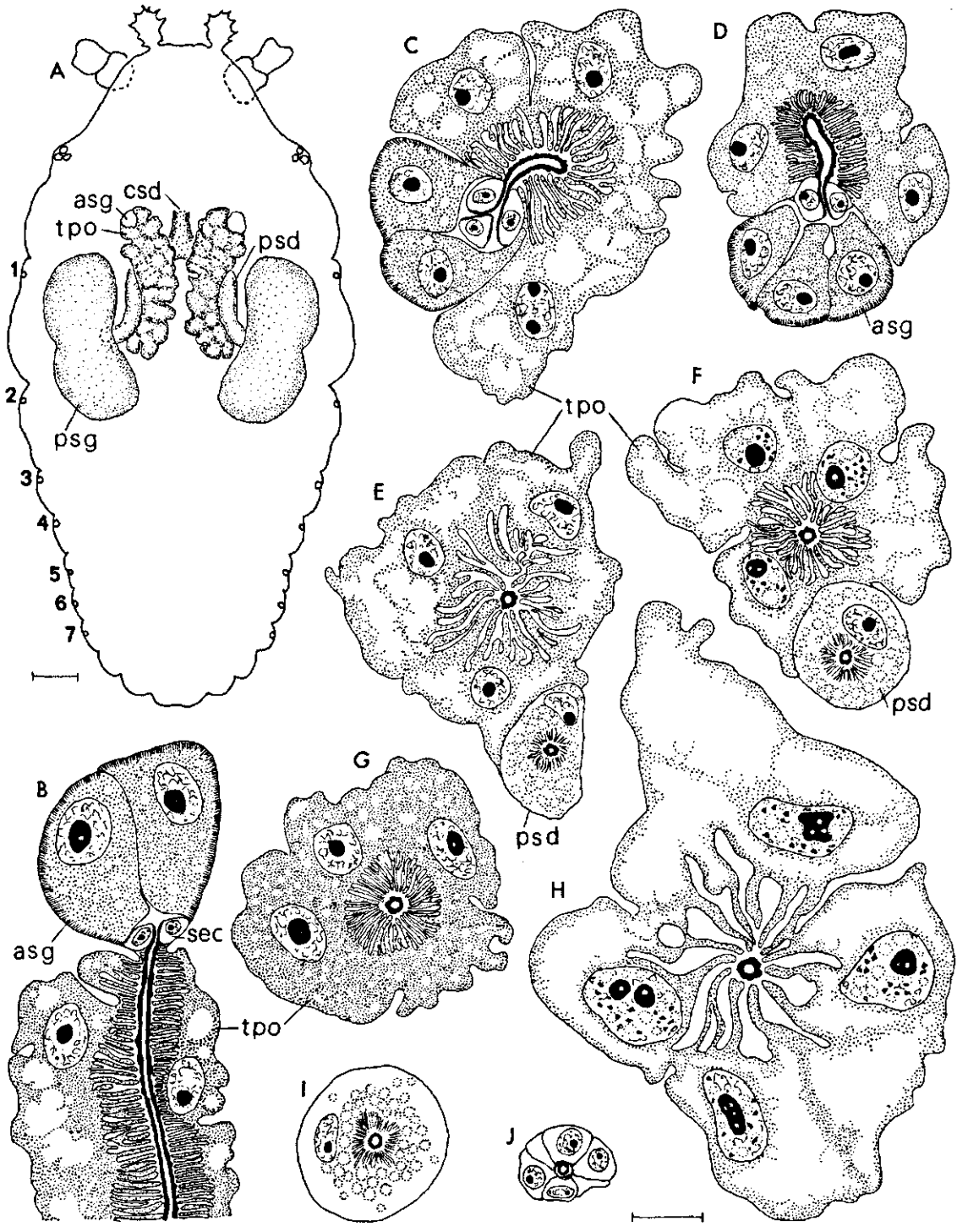
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Table 2 Total number of cells of the principal salivary gland of some species of the Phylloxeridae (see Table 1). Each principal salivary gland is composed of an upper lobe and a lower lobe; each lobe consists of four cell types: fine-granulated (A), big-granulated (B), vacuolated (C), and structureless cells (D) (see Figures 1-3).

Aphid	Morph	Left principal salivary gland								Right principal salivary gland							
		Upper lobe				Lower lobe				Upper lobe				Lower lobe			
		A	B	C	D	A	B	C	D	A	B	C	D	A	B	C	D
Aphanostigma piri	Wingless fundatrigeniae	4	5	6	4	4	6	6	4	5	5	6	4	5	5	5	4
Aphanostigma ulmifoliae	Wingless sexuparae	5	5	6	4	4	5	6	4	4	6	6	4	5	6	5	4
Daktulosphaira vitifoliae	Gallicolae	4	6	5	4	4	6	5	4	5	6	5	4	4	5	6	4
	Radicicolae	4	6	5	4	3	6	5	4	5	5	5	4	4	6	5	4
Moritziella corticalis	Winged sexuparae	4	6	6	4	4	6	5	4	4	5	5	4	5	6	5	4
Moritziella castaneivora	Wingless fundatrigeniae	4	5	5	4	4	5	6	4	4	6	5	4	4	5	5	4
Phylloxera caryaecaulis	Winged sexuparae	4	5	6	4	4	5	5	4	4	6	6	4	4	6	6	4
Phylloxera coccinea	Wingless fundatrigeniae	3	6	5	4	3	6	6	4	4	5	5	4	3	6	6	4
Phylloxera punctata	Brachypterous larvae	4	5	5	4	4	6	6	4	3	6	5	4	4	5	6	4
Phylloxerina salicis	Wingless fundatrigeniae	4	6	6	4	4	6	6	4	4	6	6	4	4	6	5	4
	Wingless sexuparae	3	5	6	4	4	6	5	4	5	6	6	3	5	5	5	4

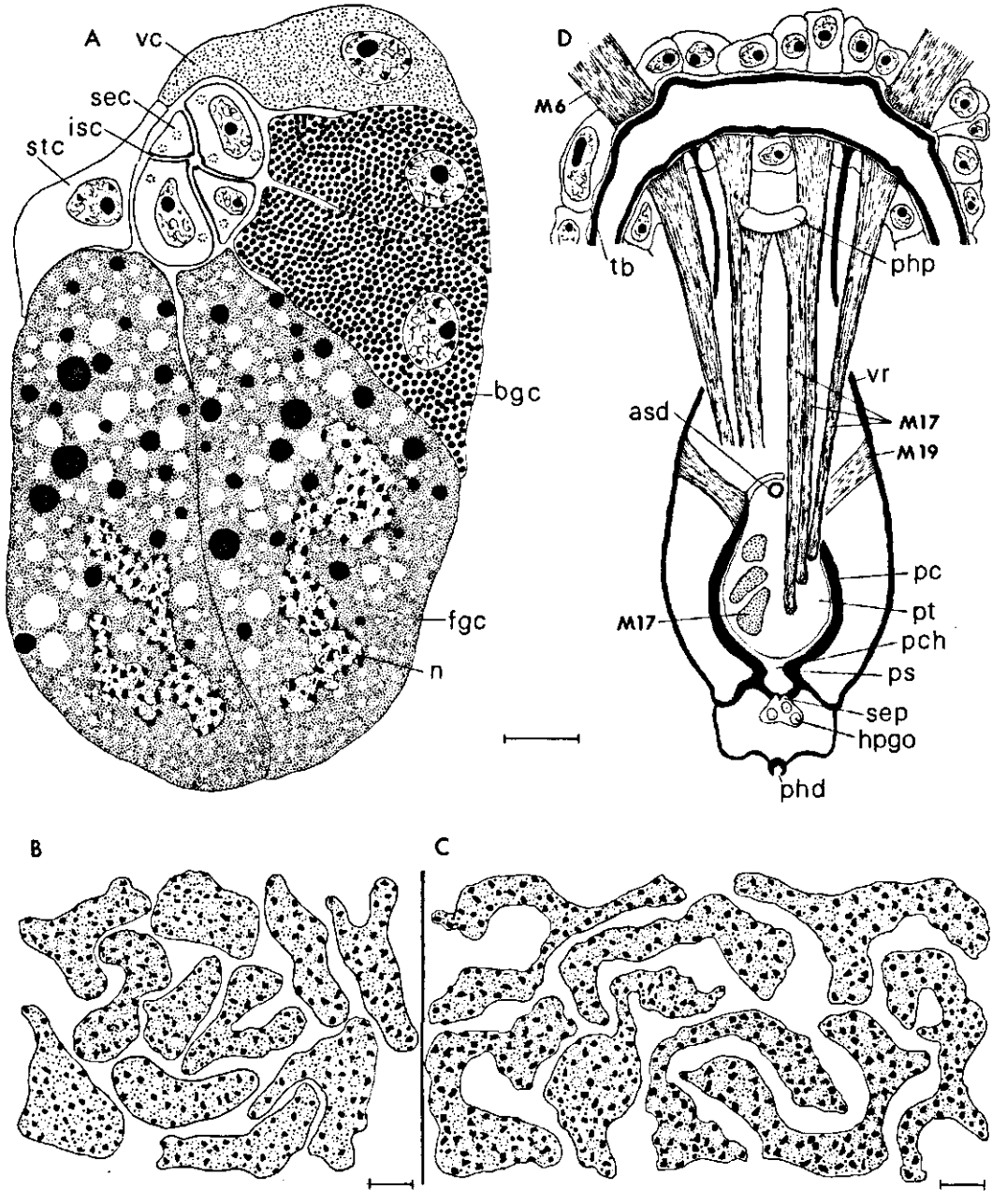

Figure 5 Sagittal section of the lower lobe of the right principal salivary gland of a radicicolous old larva of *Daktulosphaira vitifoliae* showing the four types of gland cells and the squamous cells lining the cuticular intercellular canaliculi at the terminal portion of the principal salivary duct (A). Irregularly-shaped nuclei of the fine-granulated cells of the principal gland of all species of the Phylloxeridae except *D. vitifoliae* (B). The most bizarre shapes of nuclei of the fine-granulated cells of *D. vitifoliae* (C). The salivary pump of a radicicolous *D. vitifoliae* reconstructed from transverse serial sections. Note the three pairs of retractor muscles of the salivary pump piston (D). Bar represents 10 µm. For list of abbreviations see page 30.

Histologically, both the principal salivary duct and the common salivary duct in all species of the Phylloxeridae are similar to that in all species of the Adelgidae (Figure 7) and those of the Aphididae (Figure 8). The accessory salivary duct which only occurs in species of the Aphididae, has the same histological structure as the principal salivary duct and common salivary duct (Figures 8D-L).

Salivary pump. Before entering the pumpchamber at the ventral side of the pumpcylinder the afferent duct turns upwards and then downwards, forming an S-shaped flexure. At the place of entry the opening is controlled by a muscle originating from the middle of the tentorial bar (M20). After leaving the pumpchamber the duct turns upwards and then downwards via a short duct into the pumpstem. At the foot of the pumpstem the duct is provided with two sensillary pores corresponding with the hypopharyngeal gustatory organ (Figures 4 and 17 in Ponsen, 1997).

The duct passes into the efferent salivary duct which runs in the median line on the ventral side of the hypopharynx lip to join the salivary canal. This canal is formed by opposing grooves of the interlocked maxillary stylets (Figures 7F and G in Ponsen, 2006). The epithelial lining of the afferent and efferent duct is similar to that of the epidermis consisting of squamous cells, each with a spherical to elongated nucleus.

The salivary pump lies in the head ventral to the pharyngeal pump. It consists of a tulip-shaped cylinder and pumpstem (Figure 5D). In its open end there fits a U-shaped piston connected with their lips on the edge of the cylinder. Three pairs of muscles are inserted on the flexible dorsal wall of the piston (M17): two pairs originate from the tentorium and one pair from the floor of the pharyngeal pump close to the tentorial bar. On both sides of the pumpcylinder there are muscles (M19) originating from the ventral rods. These rods lead from the tentorial bar to the hypopharynx wall.

Table 3 Total number of cells of the accessory salivary gland and those of the transparent organ of species of the family Adelgidae (see Table 2 in Ponsen, 2006).

Aphid	Morph	Total number of aphids	Accessory salivary gland		Transparent organ	
			Left	Right	Left	Right
Adelges abietis (Linnaeus)	Pseudo-fundatrices	5	2	2	5-6	5-6
	Gallicolae	1	2	2	4	3
Adelges cooleyi (Gillette)	Fundatrices	2	2	2	6-7	7
	Gallicolae	1	2	2	3	4
	Sistens	1	2	2	3	3
	Progrediens	1	2	2	3	4
	Sexuparae	2	2	2	3	3-4
Adelges laricis (Vallot)	Fundatrices	7	2	2	5-7	5-7
	Gallicolae	1	2	2	3	3
	Sistens	2	2	2	3	4
	Progrediens	1	2	2	3	3
	Sexuparae	5	2	2	3-4	3-4
Adelges lapponicus Cholodkovsky	Gallicolae	1	2	2	3	3
Adelges nordmannianae (Eckstein)	Gallicolae	1	2	2	3	3
	Progrediens	1	2	2	4	3
Adelges viridana (Cholodkovsky)	Sexuparae	1	2	2	4	4
Adelges viridis (Ratzeburg)	Gallicolae	1	2	2	3	3
Aphrastasia pectinatae Cholodkovsky	Sistens	1	2	2	4	3
Pineus orientalis (Dreyfus)	Gallicolae	1	2	2	3	4

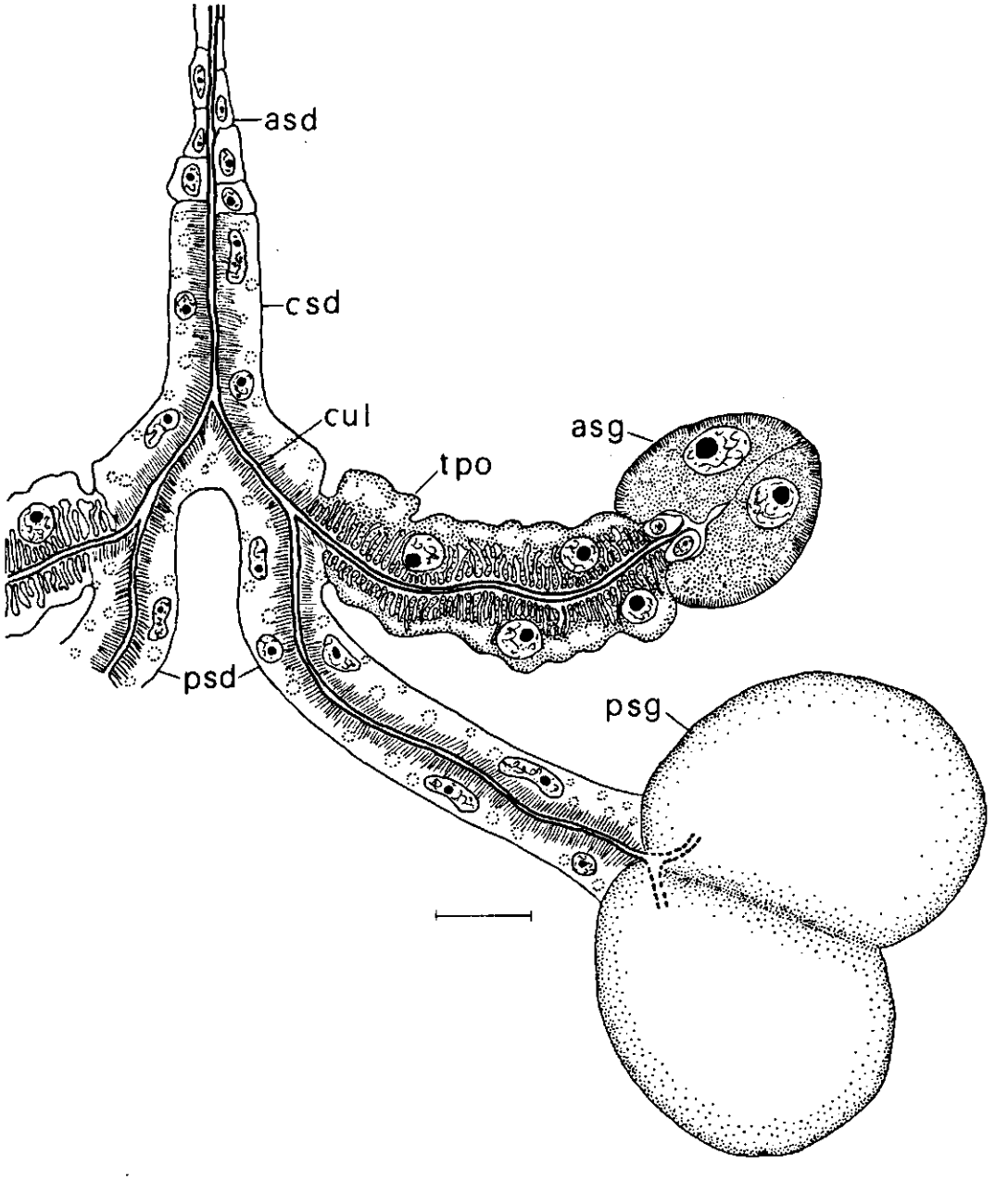

Figure 6 Longitudinal impression of the salivary gland of a wingless progredien larva of *Adelges nordmannianae* reconstructed from transverse serial sections showing the accessory salivary gland (a s g), transparent organ (t p o), principal salivary gland (p s g), principal salivary duct (p s d), common salivary duct (c s d), and the afferent salivary duct (a s d). Bar represents 10 µm. For list of abbreviations see page 30.

Sexuales

In the wingless dwarfish sexuales of *Aphanostigma ulmifoliae*, *Moritziella corticalis*, *Phylloxera coccinea*, *Phylloxera devastatrix*, and *Phylloxerina salicis* (Table 3 in Ponsen, 1997) the mouth parts are lacking and consequently the stylets and the two pairs of retort-shaped organs. Moreover, they have no pharyngeal duct, pharyngeal valve, and gustatory organs. The two pairs of salivary glands, salivary duct, afferent and efferent duct, and the salivary pump with its muscles are lacking. These sexuales also lack the labrum, clypeo-labrum, labium, and hypopharynx (Table 19 in Ponsen, 2006).

Discussion

In all species of the Aphidoidea the salivary gland system is a paired organ of which each half is composed of the accessory gland and principal gland connected with the salivary pump by a duct.

The accessory salivary gland of species of the Phylloxeridae (Table 1; Figures 1-3) is similar to that of species of the Adelgidae (Table 3; Figure 7) and those of the Aphididae (Figure 8), except *Myzus persicae* Sulzer. The release of secretory material from the accessory gland cells of *M. persicae* takes place via intracellular canaliculi inside the gland cells which pass into the cuticular lumen of the accessory salivary duct (Figure 10). In the phylloxerids and adelgids the secretory material of the accessory gland cells is released into a cavity and from there via an intercellular canaliculum to the cuticular lumen of the transparent organ and subsequently to the cuticular lumen of the principal salivary duct (Figures 1-3).

Histologically, the transparent organ in all species of the Phylloxeridae (Table 1) is similar to that in all species of the Adelgidae (Table 3). However, the very big transparent organ in the phylloxerids is reduced to a small transparent organ in the adelgids (Figure 7). In species of the Aphididae (Table 22 in Ponsen, 2006), including *M. persicae* (Figure 10), the transparent organ is evolved to the accessory salivary duct. This duct runs from the accessory gland to the principal salivary duct. The latter starts in the principal gland and passes into the common salivary duct. The accessory salivary duct has the same histological structure as the principal and common salivary duct (Figure 8).

Interestingly, within the Aphididae the species of the Mindarinae (Table 21 in Ponsen, 2006) have a transparent organ identical to that of species of the Adelgidae (Table 3; Figure 7). As in all phylloxerids, the transparent organ of all species of the Mindarinae passes into the principal salivary duct close to the latter's entrance into the principal salivary gland (Figure 11). A similar junction is found in dissections of living specimens of fourth larval stage sexuparous *Mindarus abietinus* Koch (Kunkel, 1966). The salivary glands of Mindarinae males have a degenerated structure showing pycnotic or empty nuclei (Ponsen, 2006).

According to Breider (1952) the accessory gland (= transparent organ) of *Daktulosphaira vitifoliae* serves as a reservoir to store the saliva being produced by the principal gland cells. Working with the same species Rilling (1967) concluded that this organ is a swollen excretory duct of the "craniale Läppchen" (= accessory gland).

Decrease of cytoplasmic material leading to empty irregularly-shaped cavities in the transparent organ of the phylloxerids has also been found in the multinucleated cell. This cell is located in the vicinity of the siphunculus of species of some subfamilies of the Aphididae (Figures 29 and 32, and Table 18 in Ponsen, 2006). The only difference is the presence of an excretory duct in the transparent organ which is lacking in the multinucleated cell.

Each lobe of the principal gland of *Myzus persicae* consists of about 21 gland cells. Each cell is connected with the cuticular lumen of the internal salivary duct via an intercellular canaliculum. The canaliculum terminates in an invagination of the apical cell surface of the gland cell. These invaginations bear a few short, irregularly oriented microvilli (Figure 15 in Ponsen, 1972). In species of the Phylloxeridae, however, 18 to 20 gland cells are arranged around the termination of the principal salivary duct in each lobe of the principal gland (Figures 1-3). The secretory material from the gland cells is released into a

cavity. From this cavity the secretory material is transported via five intercellular cuticular canaliculi which terminate at the end of the cuticular lumen of the principal salivary duct.

The arrangement of the gland cells in the principal salivary gland of species of the Pterocommatinae (Table 24 in Ponsen, 2006) is similar to that of *Myzus persicae* (Figure 10).

According to Rilling (1967) the salivary glands of both gallicolae and radicicolae of *Daktulosphaira vitifoliae* produce two types of saliva, viz. a viscous substance which causes the formation of the salivary sheath to protect the stylet bundle and a watery substance. It is likely that the accessory salivary glands of the phylloxerids which show similarity to the accessory glands of *Myzus persicae*, are responsible for the production of the salivary sheath. The principal glands consisting of four types of gland cells secrete the watery substance to liquify the contents of the parenchyma cells of their host plant. Studies of *Phylloxera coccinea* have shown (Harrewijn et al., 1998) that phylloxerids take their nourishment from parenchyma cells.

Myzus persicae, however, feed in the phloem cells of their host plant (Tjallingii and Hogen Esch, 1993). Their principal glands consisting of eight types of gland cells secrete granules into the lumen of the internal salivary duct where they dissolve in haemolymph pumped up by the myoepithelioid cell situated at the distal end of each principal gland (Figure 13 in Ponsen, 1972). In the principal gland of the phylloxerids such a myoepithelioid cell is lacking.

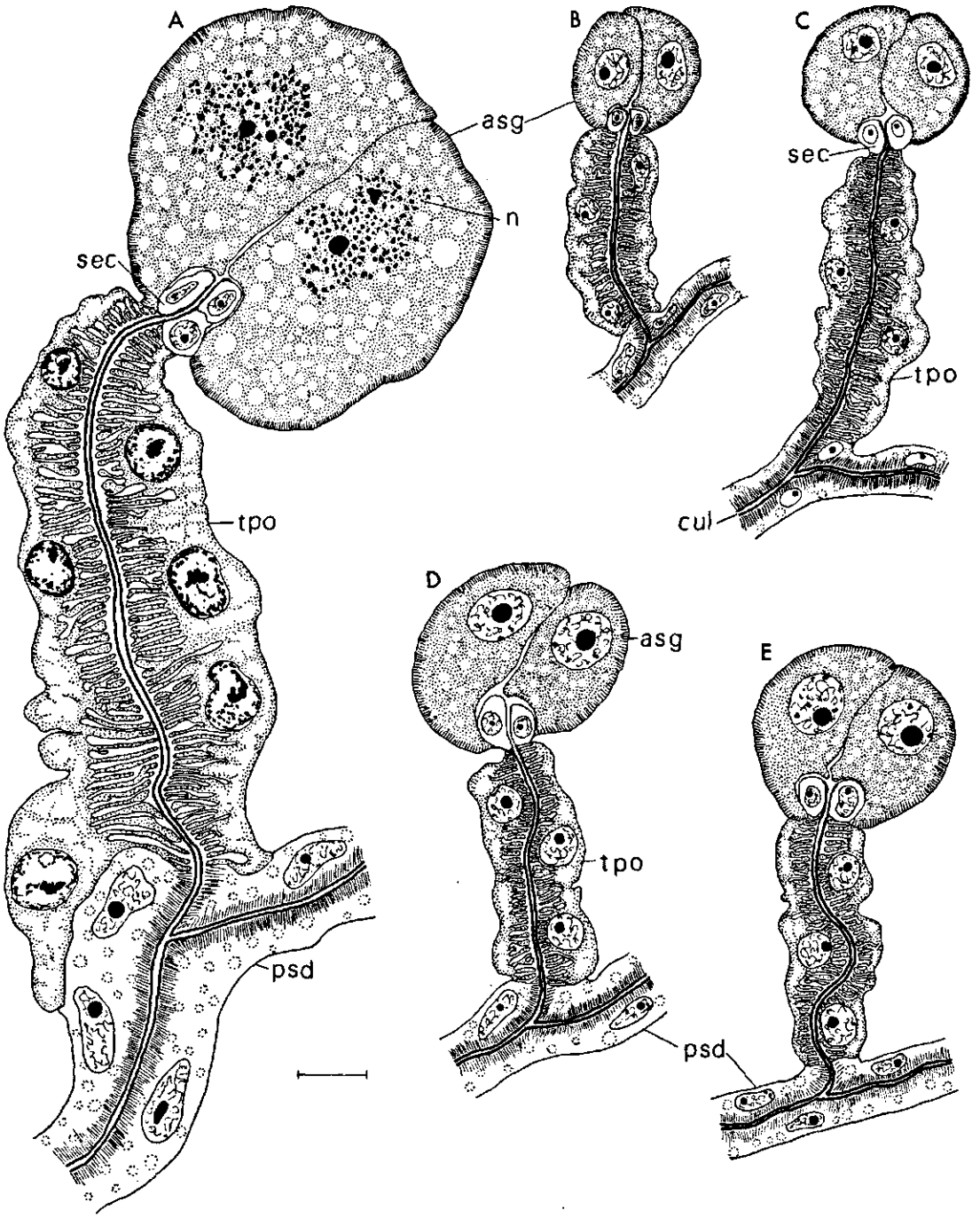

Figure 7 Longitudinal section of the accessory salivary gland and transparent organ of an adult fundatrix of *Adelges laricis* (A), a larval gallicolous *Pineus orientalis* (B), a larval sistens of *Aphrastasia pectinatae* (C), a progredien larva of *Adelges cooleyi* (D), and a larval sexuparous *Adelges viridana* (E). The histological structure of the transparent organ of species of the Adelgidae is similar to that of species of the Phylloxeridae (see Figures 1-3). Bar represents 10 µm. For list of abbreviations see page 30.

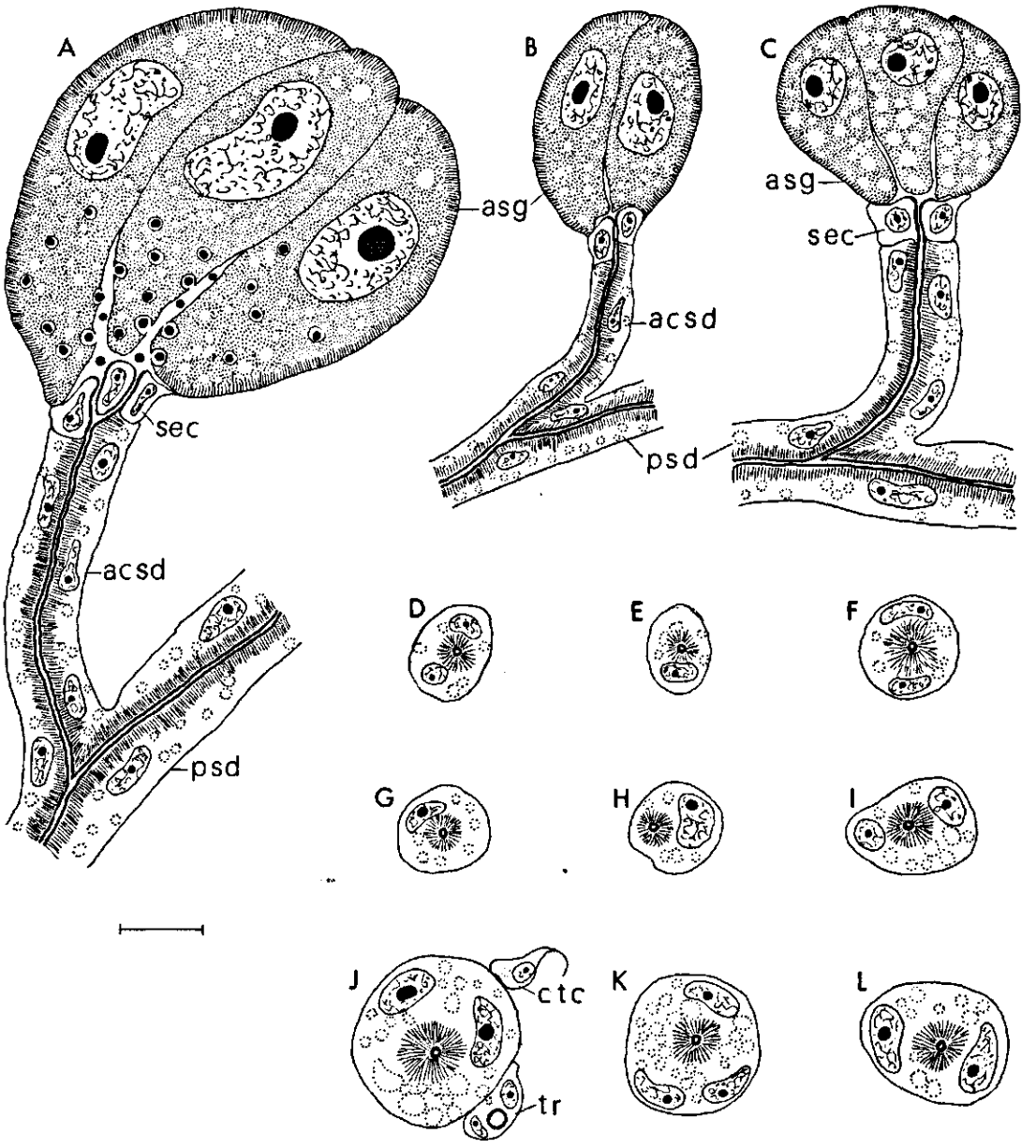

Figure 8 Longitudinal section of the accessory salivary gland and accessory salivary duct of a winged male of *Monaphis antennata* (Kaltenbach) (A), wingless viviparous *Subsaltusaphis ornata* (Theobald) (B) and *Phloeomyzus passerinii* (Signoret) (C). Transverse sections of the accessory salivary duct of a wingless viviparous *Laingia psammae* Theobald (D) and *Periphyllus testudinaceus* (Fernie) (E), and a wingless oviparous *Anoecia* sp. (F); transverse sections of the principal salivary duct of a wingless viviparous *Thelaxes dryophila* (Schrank) (G) and *Israelaphis lambersi* Ilharco (H), and a winged viviparous *Chaitophorus populeti* (Panzer) (I); transverse sections of the common salivary duct of a winged viviparous *Pterocomma salicis* (Linnaeus) (J), winged male of *Greenidea eugeniae* Takahashi (K) and *Calaphis flava* Mordvilko (L). The accessory salivary duct only occurs in species of the Aphididae. Bar represents 10 µm. For list of abbreviations see page 30.

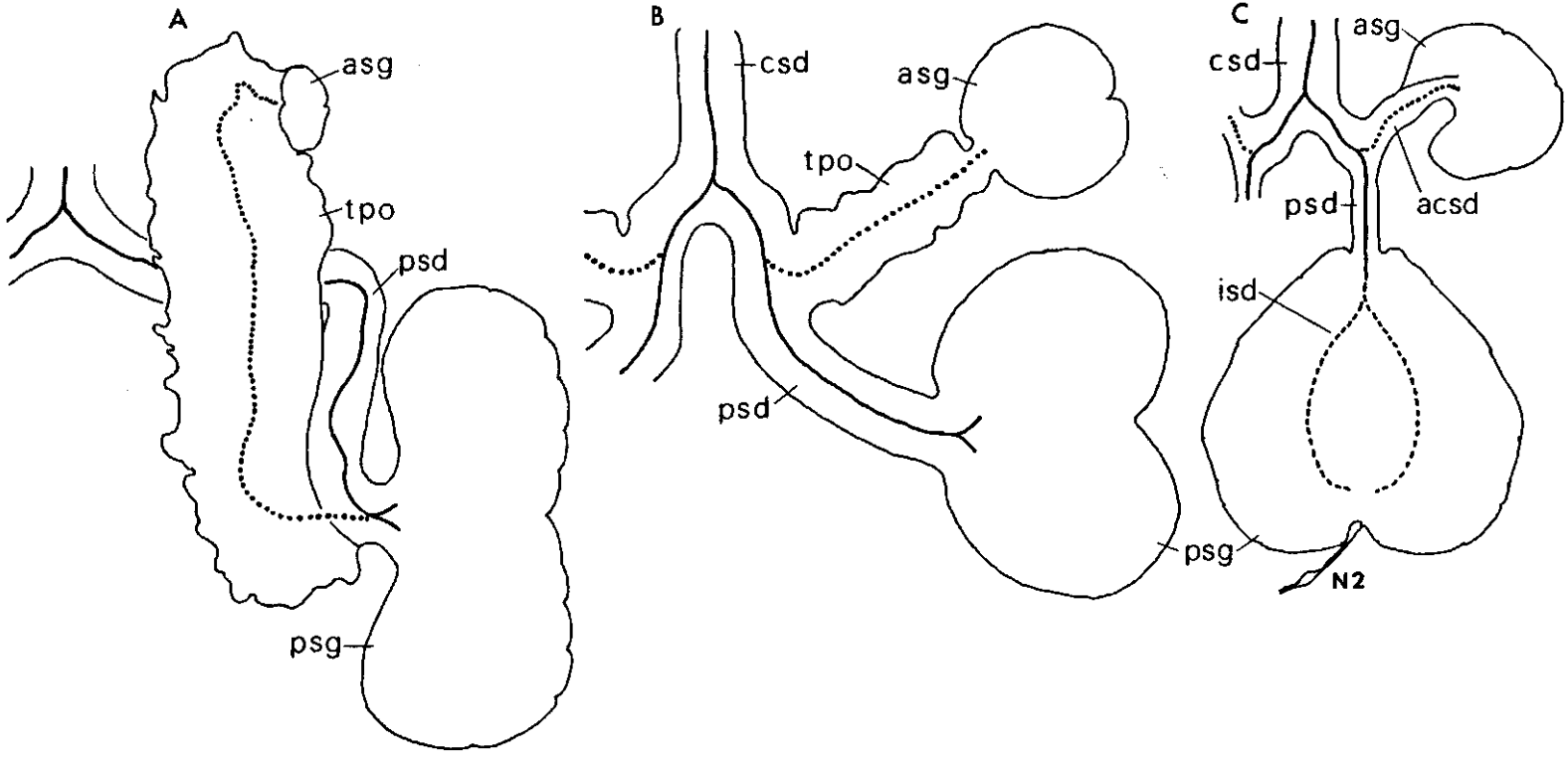

Figure 9 Longitudinal impression of species of the Phylloxeridae (A), species of the Adelgidae (B), and *Myzus persicae* Sulzer (C) (Figure 10). The drawn line represents the cuticular lumen of the principal salivary duct which runs from the principal salivary gland to the cuticular lumen of the common salivary duct. The dashed line represents the cuticular lumen of the internal salivary duct (i s d). The dotted line represents in the phylloxerids (A) and in the adelgids (B) the cuticular lumen of the transparent organ which starts in the accessory salivary gland and terminates into the cuticular lumen of the principal salivary duct. In species of the Aphididae (C) the dotted line represents the cuticular lumen of the accessory salivary duct which starts in the accessory salivary gland and terminates into the cuticular lumen of the principal salivary duct. The very big transparent organ in the phylloxerids (A) is presumably reduced to a small transparent organ in the adelgids (B) and finally evolved to the accessory salivary duct in species of the Aphididae (C). For list of abbreviations see page 30.

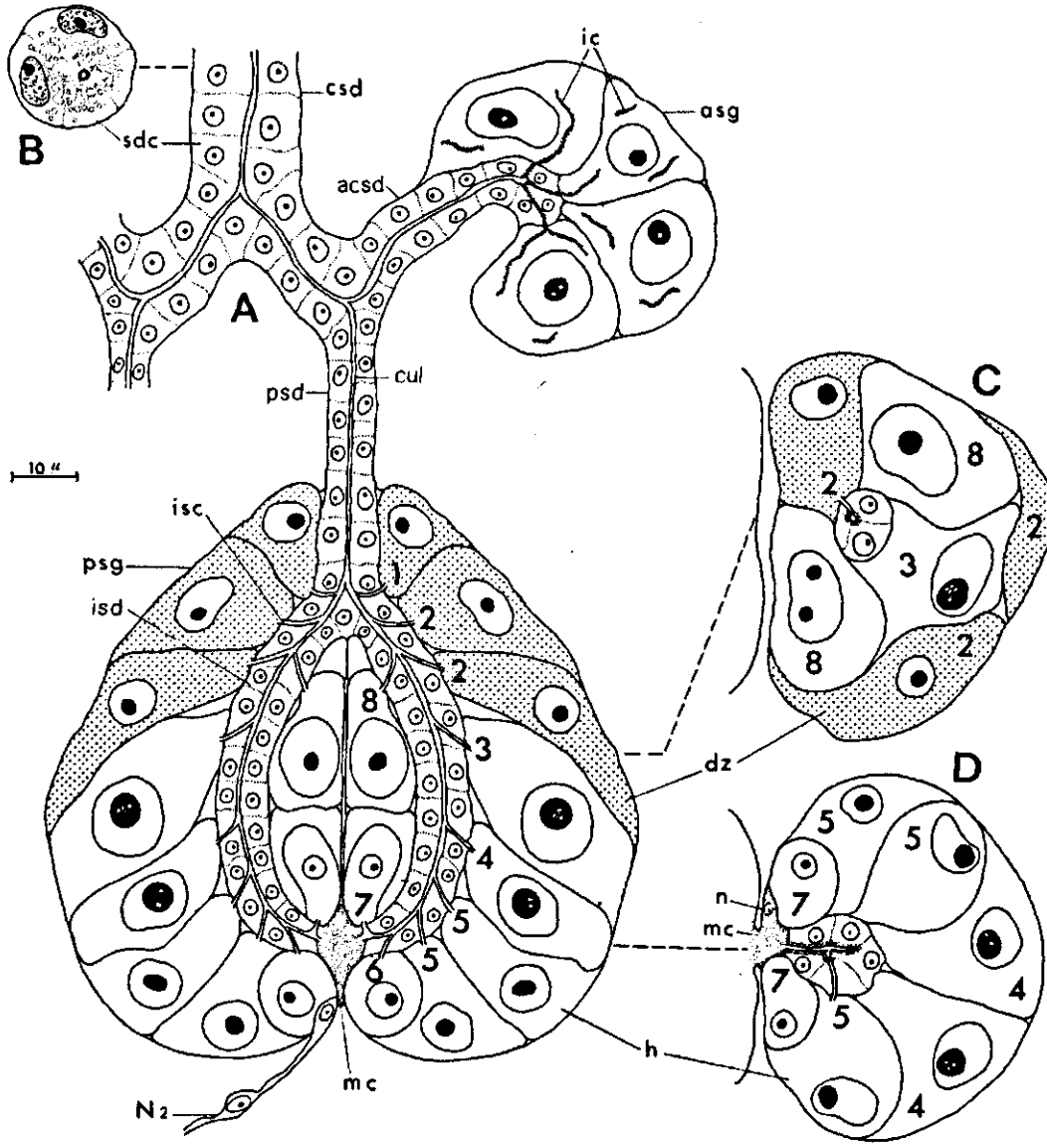

Figure 10 A. Longitudinal impression of the salivary gland of a five days old *Myzus persicae* Sulzer larva reconstructed from transverse serial sections showing the accessory salivary gland (a s g), accessory salivary duct (a c s d), principal salivary gland (p s g), principal salivary duct (p s d), and common salivary duct (c s d). Each lobe of the principal salivary gland is composed of eight types of gland cells situated around the internal salivary duct (i s d). Celltypes 1 and 2 represent the Deckzellen (d z) and celltypes 3-8 the Hauptzellen (h). Notice that the intracellular canaliculi (i c) in the accessory gland cells communicate with the cuticular lumen of the accessory salivary duct. B. Transverse section of the common salivary duct. C. Transverse section of the middle region of the principal gland showing the two separated lobes. D. Transverse section of the posterior region of the principal gland. The two lobes are connected with each other by the myoepithelioid cell (m c) with its eccentrically placed nucleus (n). Bar represents 10 µm. For list of abbreviations see page 30. (see Figure 13 in Ponsen, 1972).

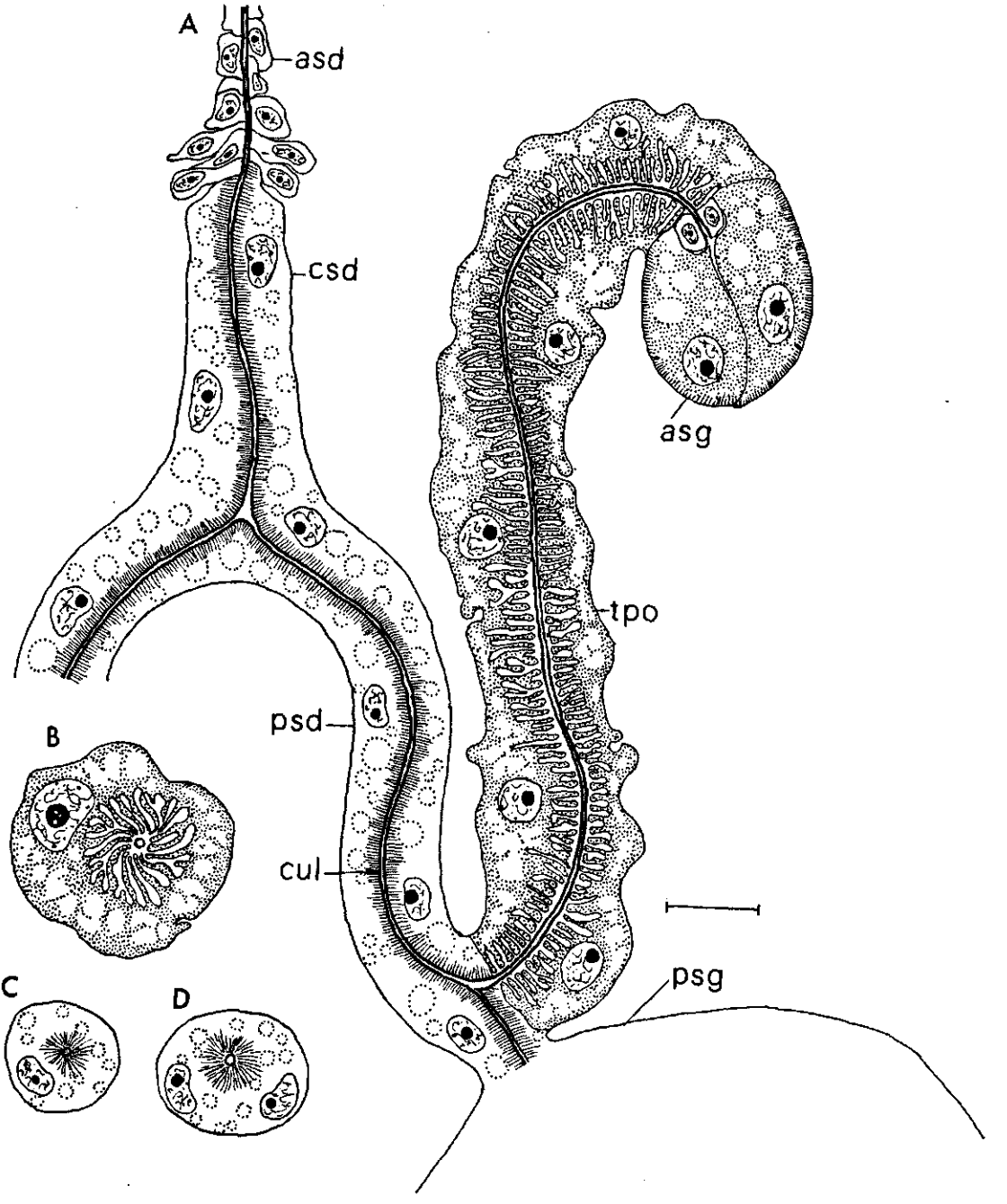

Figure 11 Longitudinal impression of the salivary gland of a larval wingless oviparous (= female sexuales) of *Mindarus obliquus* (Cholodkovsky) (A) reconstructed from transverse serial sections showing the accessory salivary gland, transparent organ, principal salivary gland, principal salivary duct, common salivary duct, and the afferent salivary duct. Transverse sections of the transparent organ (B) and principal salivary duct (C) of a larval winged viviparous (= sexuparous) *Mindarus japonicus* Takahashi, and common salivary duct (D) of a larval winged viviparous (= sexuparous) *Mindarus abietinus* Koch. Bar represents 10 µm. For list of abbreviations see page 30.

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Abbreviations used in figures

a c s d	accessory salivary duct
a s d	afferent salivary duct
a s g	accessory salivary gland
b g c	big-granulated cell
c s d	common salivary duct
c t c	connective tissue cell
c u l	cuticular lumen
c v	cavity
d z	Deckzelle
f g c	fine-granulated cell
h	Hauptzelle
h p g o	hypopharyngeal gustatory organ
i c	intracellular canaliculum
i s c	intercellular secretory canaliculum
i s d	internal salivary duct
l l	lower lobe
m c	myoepithelioid cell
M6	elevator muscle of tentorial bar
M17	retractor muscle of salivary pump piston
M19	retractor muscle of salivary pump wall
n	nucleus
N2	branch of medial dorsal nerve
p c	pumpcylinder
p c h	pumpchamber
p h d	pharyngeal duct
p h p	pharyngeal pump
p s	pumpstem
p s d	principal salivary duct
p s g	principal salivary gland
p t	piston
s d c	salivary duct cell
s e c	squamous epithelial cell
s e p	sensillary pore
s t c	structureless cell
t b	tentorial bar
t p o	transparent organ
t r	trachea
u l	upper lobe
v c	vacuolated cell
v r	ventral rod (chitinous ridge)