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A histological description of the salivary gland system of some aphid species of the Adelgidae and Aphididae (Homoptera, Aphidoidea)

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Contents

Summary

The salivary gland system is a paired organ: each half is composed of the accessory and principal gland.

The accessory gland of the Adelgidae is situated at the anterior region of a transparent organ and that of the Aphididae at the anterior region of the accessory salivary duct. The accessory glands of both families all have the same histological structure.

In the principal glands of species of the Adelgidae the principal salivary duct branches into two short internal salivary ducts. This gland consists of 18-22 bottle-shaped cells of 5 different types of cells. They are arranged around both internal ducts forming a fan-shaped structure.

In species of the Aphididae the principal gland is bilobed and each lobe consists of 18-23 gland cells of 5-8 different types. They are arranged around the internal salivary duct forming a compact structure.

Introduction

In all species of the Aphididae and those of the Adelgidae (summarized in Ponsen, 1972 and 2006) the salivary glands are composed of one pair of accessory glands and one pair of principal glands. All these glands are connected with the salivary pump by a duct.

Cholodkovsky (1905) found that in adult fundatrices of *Chermes lapponicus* (= *Adelges lapponicus* Cholodkovsky) the accessory glands consist of two cells each with one spherical nucleus. The principal glands consist of three big spherical lobes (acini) each with two irregular-shaped nuclei. In *Gilletteella cooleyi* (Gill.) (= *Adelges cooleyi* (Gillette)) each of the three acini has one irregular-shaped nucleus (Kunkel, 1966). The salivary glands of all morphs are similar to each other, except those of the fundatrices which are much bigger (Cholodkovsky, 1905). Each acini is connected with the main duct by a short duct.

The salivary gland cells of the sexuales of *Adelges cooleyi* and *Adelges laricis* are degenerated showing empty nuclei in a spongy cytoplasm (Ponsen, 2006).

The ultrastructure of the salivary glands of *Myzus persicae* (Sulzer) has been studied by Moericke and Wohlfarth-Bottermann (1960, 1963) and Wohlfarth-Bottermann and Moericke (1960). Histological studies on the same organ are described for *M. persicae*, species of the Phylloxeridae and those of the Mindarinae (Ponsen, 1972, S2006, S2012). During larval life the salivary gland cells do not divide but gradually increase in size and the total number of cells remains constant.

The purpose of the present study is to investigate the salivary glands of several aphid species of the Adelgidae and those of the Aphididae.

Table 1 Total number of cells of the principal salivary gland of species of the Adelgidae. Each principal gland is composed of 5 types of bottle-shaped cells forming a fan-shaped structure: Giant cells each with 2-3 nuclei (A), granulated cells each with 2 nuclei (B), granulated cells each with one nucleus (C), structureless cells each with 2 small nuclei (D), and vacuolated cells each with 2 nuclei (E). The letters A-E correspond with the 5 types of cells in Figure 2.

Aphid	Morph	Host plant	Left principal gland						Right principal gland					
			A	B	C	D	E	Total	A	B	C	D	E	Total
Adelges abietis (Linnaeus)	gallicolae	*Picea abies*	3	7	2	2	6	20	3	9	1	3	5	21
Adelges cooleyi (Gillette)	fundatrices	*Picea sitchensis*	3	7	2	2	6	20	3	8	2	1	6	20
	gallicolae	Picea omorika	3	8	3	1	5	20	3	8	2	1	5	19
	gallicolae	*Picea likiangensis* var. *balfourina*	3	7	1	2	6	19	3	8	1	1	6	19
	sistens	*Pseudotsuga menziesii*	3	7	2	1	6	19	3	7	2	1	6	19
	wingless progrediens	*Pseudotsuga menziesii*	3	6	2	1	7	19	3	8	2	1	6	20
	sexuparae	Pseudotsuga menziesii	3	8	2	1	7	21	3	8	2	1	6	20
Adelges laricis (Vallot)	fundatrices	*Picea sitchensis*	3	6	2	2	6	19	3	6	2	2	6	19
	gallicolae	*Picea abies*	3	8	1	2	5	19	3	7	2	2	6	20
	sistens	*Larix decidua*	3	7	2	2	7	21	3	6	2	2	7	20
	wingless progrediens	Larix decidua	3	8	2	2	6	21	3	9	2	2	6	22
		Larix kaempferi	3	8	2	1	7	21	3	7	1	2	7	20
	sexuparae	*Larix decidua*	3	7	2	1	6	19	3	6	2	2	7	20
Adelges lapponicus Cholodkovsky	gallicolae	*Picea abies*	3	7	2	1	6	19	3	8	2	2	6	21

Adelges nordmannianae (Eckstein)	wingless progrediens	*Abies nordmanniana*	3	7	2	1	6	19	3	9	2	2	5	21
Adelges viridana (Cholodkovsky)	sexuparae	*Larix kaempferi*	3	7	2	1	6	19	3	7	2	2	7	21
Adelges viridis (Ratzeburg)	gallicolae	*Picea abies*	3	8	1	2	6	20	3	8	2	2	6	21
Aphrastasia pectinatae Cholodkovsky	sistens	*Abies lasiocarpa*	3	6	1	2	7	19	3	8	1	1	7	20
Pineus orientalis (Dreyfus)	gallicolae	*Picea orientalis*	3	8	1	2	7	21	3	6	2	1	6	18

Materials and methods

Specimens of the species were collected from the host plants (Tables 1 and 2). 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%), and then in toluene and 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 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 glands was reconstructed from drawings of serial sections of a whole aphid viewed at a magnification of x1500.

Table 2 List of aphid species studied, their subfamily and host plant.

Aphid	Subfamily - Tribe	Host plant
Thelaxes dryophila (Schrank)	Thelaxinae	*Quercus robur*
Chaitophorus populeti (Panzer)	Chaitophorinae - Chaitophorini	*Populus alba*
Periphyllus testudinaceus (Fernie)		*Acer campestre*
Calaphis flava Mordvilko	Myzocallidinae - Calaphidini	*Betula* spec.
Clethrobius comes (Walker)		*Alnus glutinosa*
Monaphis antennata (Kaltenbach)		*Betula* spec.
Greenidea eugeniae Takahashi	Greenideinae – Greenideini	*Eugenia jambalana*
Greenidea formosana (Maki)		*Psidium guajava*
Greenidea spec.		*Eugenia jambalana*
Phloeomyzus passerinii (Signoret)	Phloeomyzinae	*Populus* spec.
Anoecia spec.	Anoeciinae	*Cornus* spec.
Plocamaphis amerinae (Hartig)	Pterocommatinae	*Salix* spec.
Pterocomma salicis (Linnaeus)		*Salix* spec.

Adelgidae

The salivary glands of all species of the Adelgidae (see Table 2 in Ponsen, 2006) are composed of the accessory gland, transparent organ, and principal gland. The first two organs are situated one on each side of the suboesophageal ganglion and the principal glands one on each side of the thoracic ganglion.

Accessory gland. The accessory gland is situated at the anterior region of the transparent organ. It consists of two cells each with one nucleus (see Table 3 in Ponsen, S2006). The cytoplasm contains vacuoles and fine granular material. The basal cell membrane has numerous infoldings (Figure 1). This gland is similar to that of species of the Phylloxeridae (Ponsen, S2006) and those of the Aphididae.

Transparent organ. The basal cell membrane of the transparent organ has some invaginations and evaginations showing an irregular-shaped structure. The lateral cell membranes are lacking. The cytoplasm consists of many vacuoles and granules scattered in between them. This material dissolves during larval life forming empty irregular-shaped cavaties. The total number of nuclei varies from 5-7 for the fundatrigeniae and 3-4 nuclei for the remaining asexual morphs (see Table 3 in Ponsen, S2006).

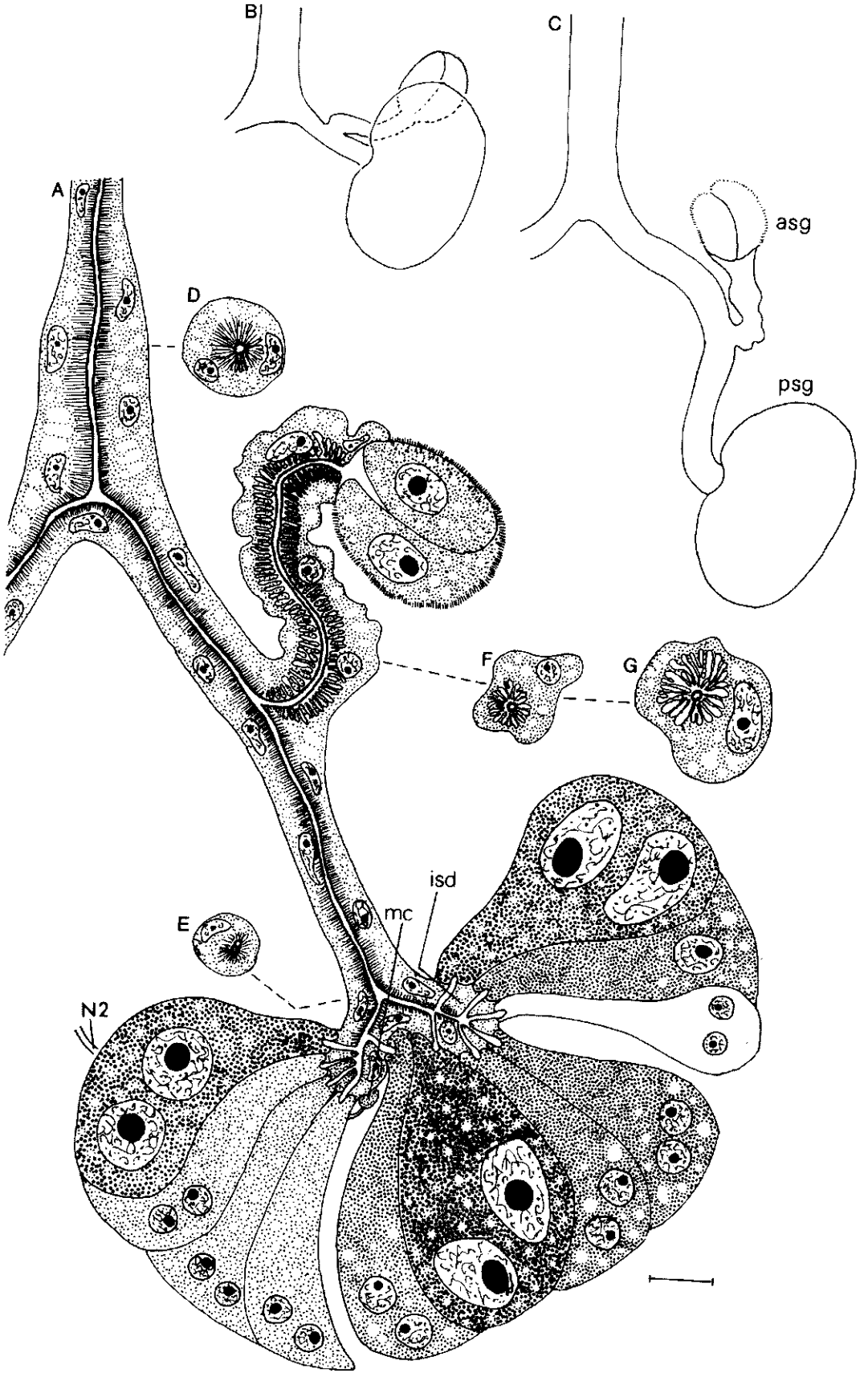
The apical cell membrane presents a labyrinthine system of loosely scattered evaginations arranged along a cuticular lumen. This lumen has a very thick exocuticle and starts in the accessory gland to terminate into the principal salivary duct (Figure 1).

Histologically, the transparent organ of species of the Adelgidae is similar to that of species of the Phylloxeridae and to those of the Mindarinae (Ponsen, S2006, S2012). However, in the adelgid species and species of the Mindarinae the transparent organ is much smaller.

Principal gland. In the principal gland the principal salivary duct branches into two short internal salivary ducts. This gland consists of 18-22 bottle-shaped cells which are so arranged that they form a fan-shaped structure (Figure 1).

The gland cells consist of five types of cells (Table 1 and Figure 2).

Type A: three giant cells situated between the different cell types. The cytoplasm contains many vacuoles surrounded by big granules. Each cell has 2-3 giant spherical to oval nuclei each with 1-2 giant nucleoli. During larval life the nuclear membrane gradually dissolves and the chromatine starts to granulate. The granules release into the cytoplasm forming empty irregular-shaped structures in which big bodies develop. In the imaginal stage these structures fuse to very big bizarre ones which may occupy


B
C
A
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D
psg
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E
N2

the whole cell. In the giant nucleoli develop cavities whereafter they completely dissolved (Figure 3).

Type B: 6-9 granulated cells with some vacuoles in the basal region of the cell; each cell has two spherical nuclei.

Type C: 1-3 granulated cells with some vacuoles in the basal region of the cell; each cell has one nucleus.

Type D: 1-3 structureless cells; each cell has two small nuclei.

Type E: 5-7 vacuolated-granulated cells of which the cytoplasm consists of vacuoles of various sizes and granules scattered in between them. Each cell has two spherical nuclei each with a relatively big nucleolus. During larval life the nuclear material gradually dissolved leaving an empty or shrivelled nucleus. These cells are similar to the "Deckzellen" present in each lobe of the principal gland of species of the Aphididae (Figures 1 and 2).

All the gland cells are connected with the lumen of the internal salivary duct by an intercellular secretory canaliculum. The epithelial lining is similar to that of the principal duct.

The myoepithelioid cell is situated on the end of the left internal salivary duct of the right principal gland and on the end of the right internal salivary duct of the left principal gland (Figure 1). The myoepithelioid cell is innervated by a nerve of the medial dorsal nervous system. This system passes along the dorsal vessel (see page 43).

Salivary duct. The principal salivary duct from both principal glands run to the junction of the suboesophageal and thoracic ganglion where they turn around the junction to fuse with the common salivary duct. This duct runs forwards ventrally to the suboesophageal ganglion and turns downwards to pass into the afferent salivary duct (Figure 1).

The epithelial lining of these ducts is similar to those of the Aphididae.

Figure 1 Longitudinal impression of the salivary glands of a larval gallicolous (A), male (B), and female sexuales (C) of *Adelges cooleyi* reconstructed from transverse serial sections. Transverse sections of the common salivary duct (D), transition of the principal salivary duct in two internal salivary ducts showing two cuticular lumens (E) of a larval sexuparous *Adelges viridana*, transparent organ of a larval gallicolous (F), and an adult pseudofundatrix (G) of *Adelges abietis*. Bar represents 10 μm. For list of abbreviations see page 62.

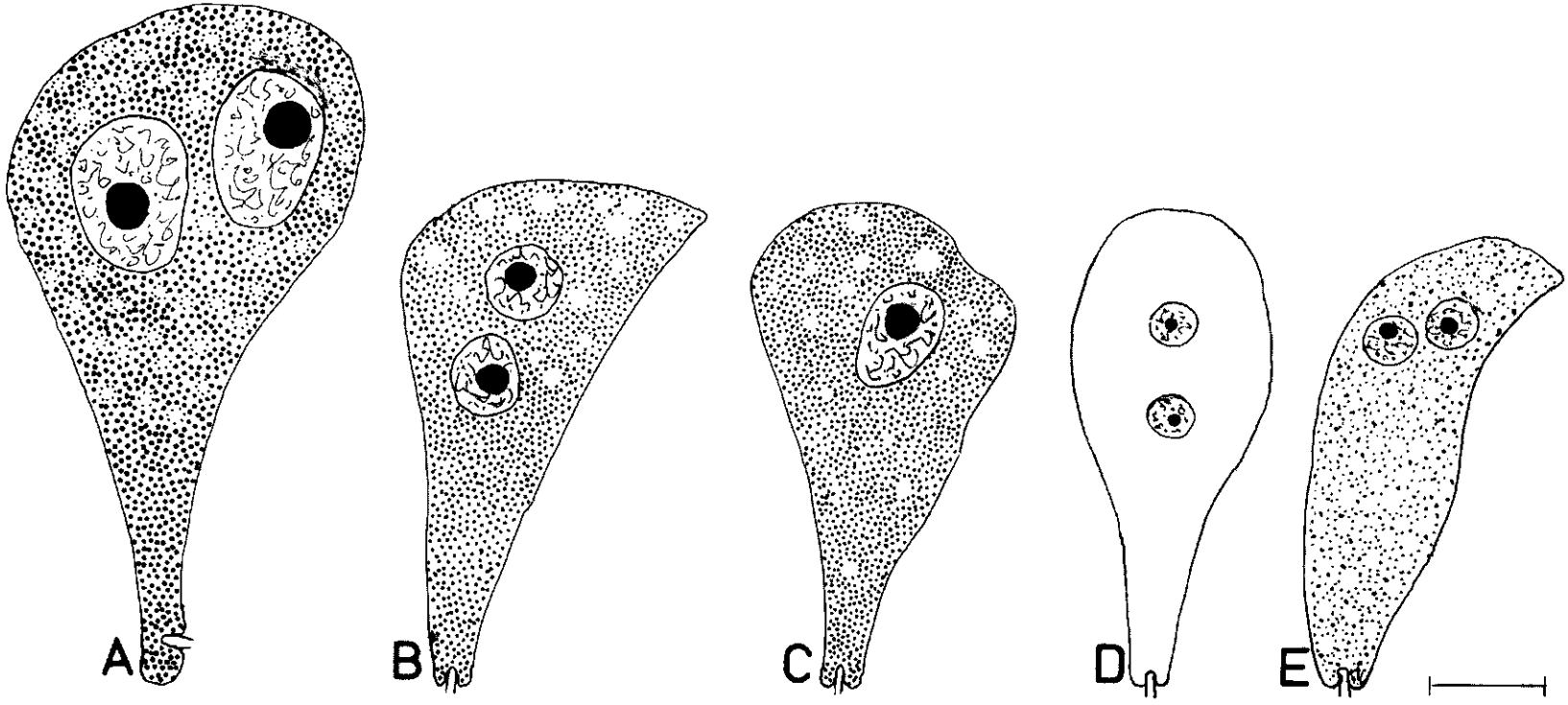


Figure 2 Histological composition of the five types of cells of the fan-shaped principal glands of larvae of the several species of the Adelgidae. The types of cells correspond with those given in Figure 1 and the letters A-E with those in Table 1.

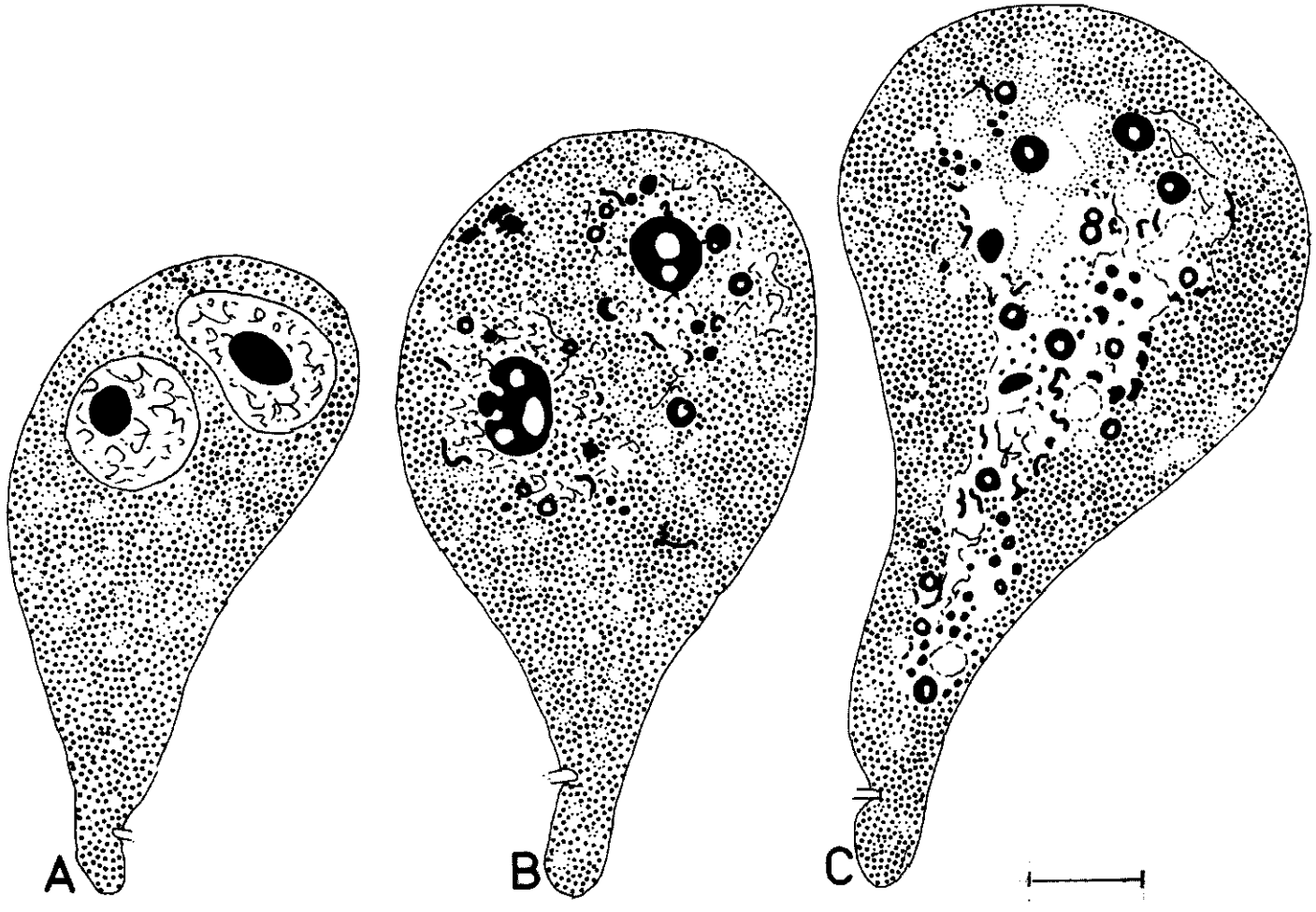


Figure 3 Each giant cell has 2-3 giant spherical to oval nuclei (A). During larval life the nuclear material starts to degenerate by vacuolisation and granulation, and the nuclear membrane gradually dissolves forming irregular-shaped structures. In the giant nucleoli develop cavities where after they completely dissolved (B). These structures fuse to very big bizarre shaped structures and may occupy the whole cell (C). Bar represents 10 μm.

Table 3 The average number and range in parentheses of cells of the accessory salivary gland of species of the seven subfamilies of the Aphididae and that of the spherical nuclei of the accessory salivary duct of *Phloeomyzus passerinii* (see Table 2).

Aphid	Morph	Total number of aphids sectioned	Accessory gland		Accessory duct	
			Left	Right	Left	Right
Greenidea eugeniae	winged viviparous	5	4 (3-4)	3 (2-4)		
	wingless viviparous	4	4 (3-4)	4 (3-4)		
	winged male	5	3 (3-4)	3 (2-4)		
Greenidea formosana	winged viviparous	1	3	3		
	wingless viviparous	3	4	4 (3-4)		
	winged male	4	4 (3-4)	4		
Greenidea spec.	winged viviparous	2	4 (3-4)	4		
	wingless viviparous	2	4	4 (3-4)		
	winged male	9	3 (3-4)	4 (3-4)		
Thelaxes dryophila	wingless viviparous	5	4 (3-4)	4 (3-4)		
Chaitophorus populeti	winged viviparous	2	4	4		
	wingless viviparous	4	4 (3-4)	4 (3-4)		
Periphyllus testudinaceus	wingless viviparous	6	4 (4-5)	5 (4-5)		
Monaphis antennata	wingless oviparous	5	4	4 (3-4)		
	winged male	5	4 (3-5)	4 (3-4)		

Calaphis flava	wingless viviparous	6	4 (3-4)	4 (3-4)		
	wingless oviparous	1	4	4		
	winged male	1	3	4		
Clethrobius comes	wingless viviparous	10	4 (3-4)	4		
Phloeomyzus passerinii	wingless viviparous	9	4 (3-4)	3 (3-4)	14 (12-16)	15 (13-16)
Anoecia spec.	wingless oviparous	4	4 (3-4)	4 (3-4)		
	wingless male	4	4 (3-4)	4 (3-4)		
Plocamaphis amerinae	winged viviparous	5	7 (7-8)	7 (6-8)		
	wingless viviparous	3	7 (5-8)	7 (5-9)		
	winged male	4	7 (6-9)	8 (7-9)		
Pterocomma salicis	winged viviparous	7	6 (4-6)	5 (4-5)		
	wingless viviparous	5	5 (5-6)	6 (4-7)		

Aphididae

Accessory gland. In all aphid species studied (Table 2) the accessory glands are situated one on each side laterally or dorsally to the suboesophageal ganglion. In *Monaphis antennata* one on each side of the tentorial bar ventrally to the protocerebrum.

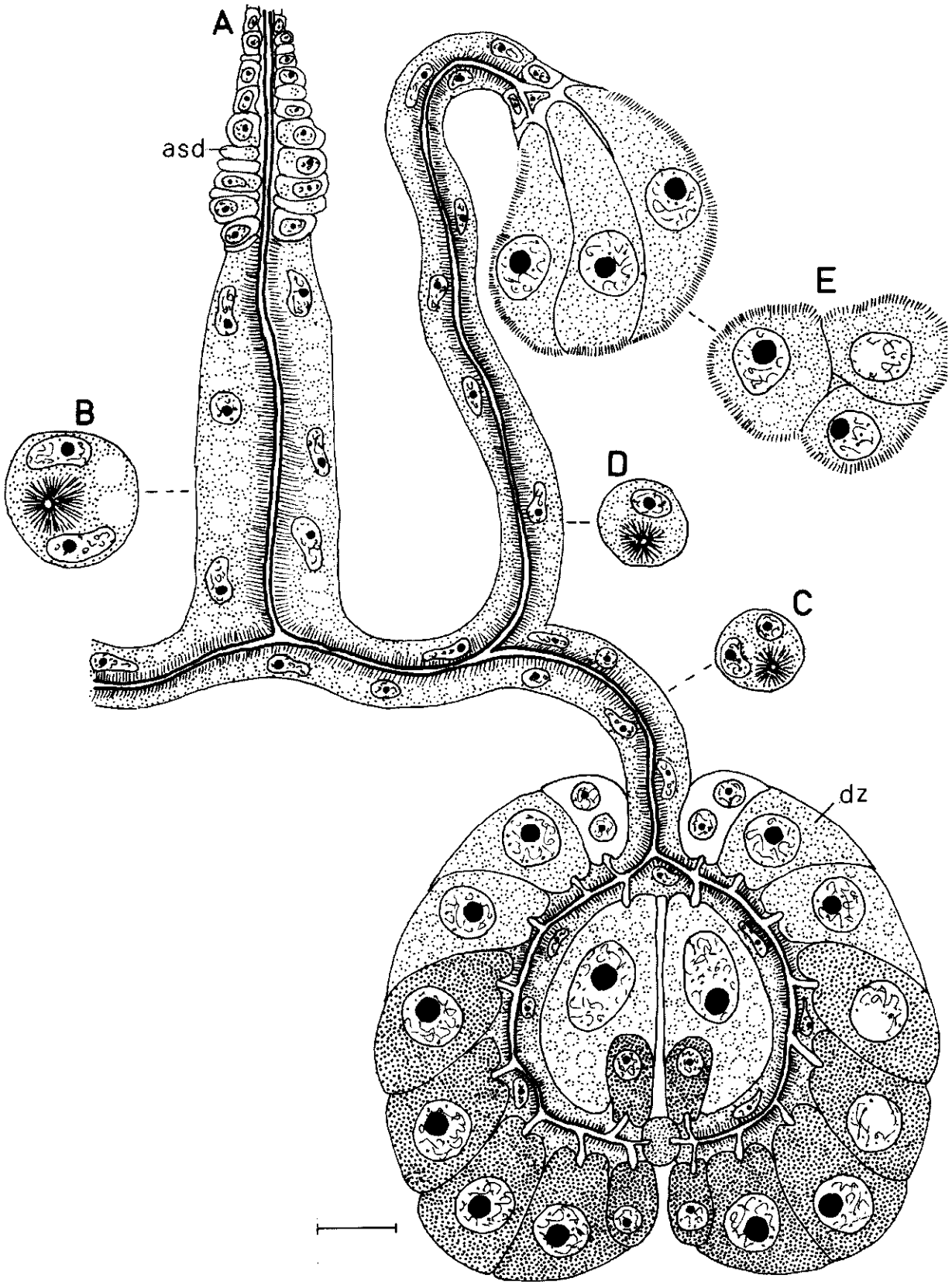
Each gland consists of 3-8 cells which are arranged around the termination of the accessory salivary duct (Table 3). The cuticular lumen of this duct passes into a small intercellular canaliculum ending into a cavity. In this cavity the secretory products of the gland cells are collected. The epithelial lining of the canaliculi consists of squamous cells, each with a spherical or elongated nucleus (Figures 4-16).

The cytoplasm of the accessory glands consists of many vacuoles of various sizes and granules scattered in between them. In *M. antennata*, probably the granules fuse to big ones which migrate to the cell membrane, fuse their own membrane and release their contents into the intercellular cavity. The basal cell membrane is built up of parallel oriented infoldings of several lengths which are clearly visible in sections of *M. antennata* (Figure 9).

Each cell has one nucleus. In young larvae the nuclei are completely intact (Figure 8 in Ponsen, S2006) and during larval life the nuclei start to degenerate by vacuolization and granulation of the chromatine. The nuclear membrane dissolves and the granulated nuclear material is released into the cytoplasm forming an irregular-shaped structure. Minute cavities are formed in the nucleoli.

Principal gland. The principal glands are situated one on each side of the foregut dorsally to the thoracic ganglion. Both principal glands are composed of two lobes: a left and a right lobe. The principal salivary duct branches into two internal salivary ducts forming in each lobe a left and a right part.

Each lobe of the principal gland is composed of "Deckzellen" and "Hauptzellen" which are arranged around the internal salivary duct. The "Deckzellen" are situated in the anterior region of each lobe.


A
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B
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D
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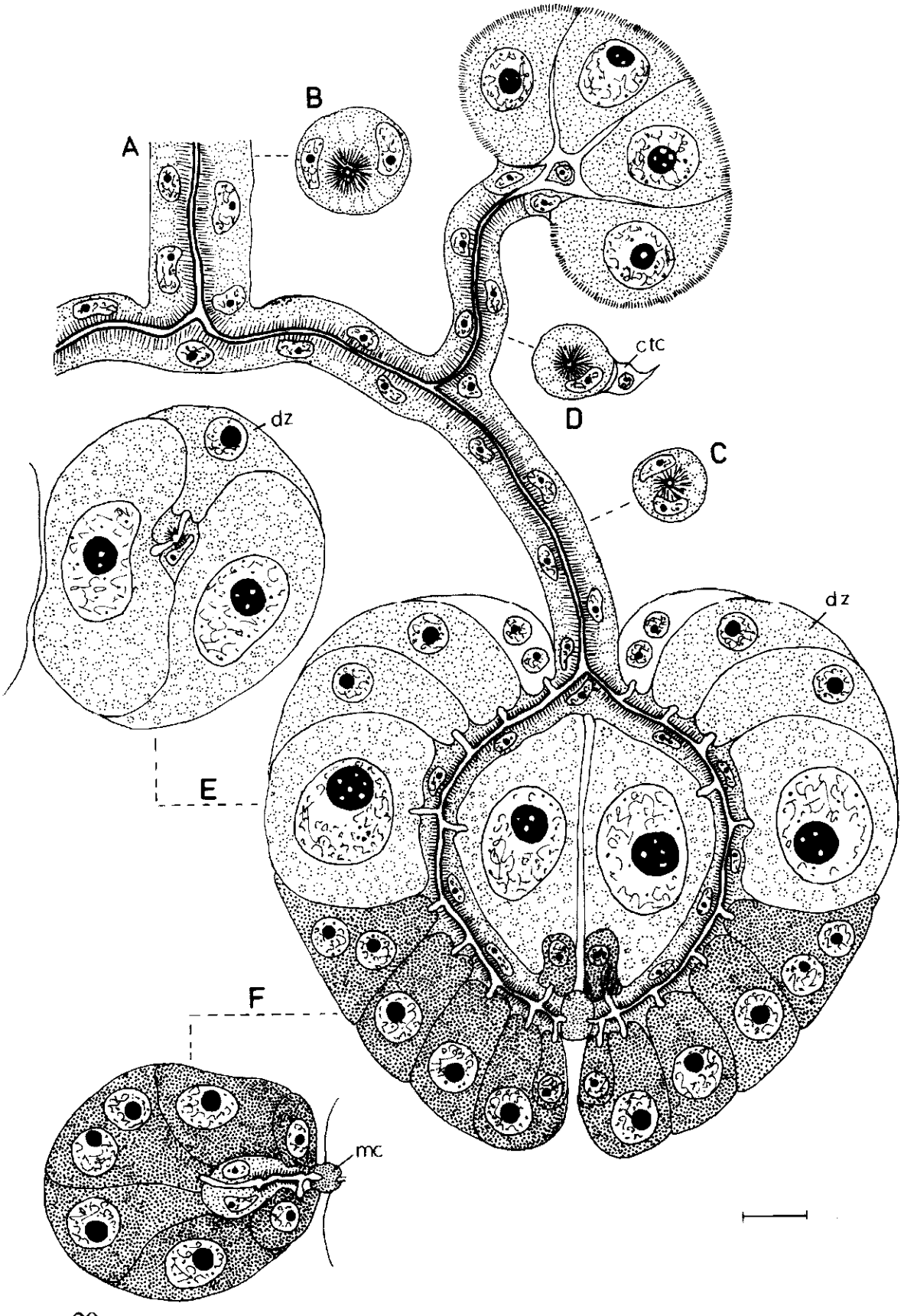
dz

Thelaxinae

In the principal glands of *Thelaxes dryophila* (Figures 4 and 6) the "Deckzellen" consist of two types of cells:
Type A: one structureless cell with two nuclei surrounding the entrance of the principal duct into the principal gland.
Type B: 6-7 cells with vacuoles of various sizes and granules scattered in between them; each cell has one spherical nucleus with a relatively big nucleolus.

The "Hauptzellen" consist of three types of cells:
Type C: 7-9 granulated cells; the cytoplasm consists of numerous granules and each cell has one nucleus.
Type D: two giant cells in each gland: one in the left part of the right lobe and one in the right part of the left lobe. The cytoplasm consists of numerous vacuoles of various sizes and each cell has one relatively big oval nucleus.
Type E: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one spherical nucleus (Table 4).

Figure 4 Longitudinal impression of the salivary glands of a wingless viviparous *Thelaxes dryophila* larva (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), accessory salivary duct (D), and accessory salivary gland (E). Bar represents 10 μm. For list of abbreviations see page 62.


A
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Chaitophorinae

In the principal glands of *Chaitophorus populeti* and *Periphyllus testudinaceus* (Figures 5 and 6) the "Deckzellen" consist of two types of cells:

Type A: one structureless cell with two nuclei surrounding the entrance of the principal salivary duct into the principal gland.

Type B: 6-7 cells with vacuoles of various sizes and granules scattered in between them; each cell has one spherical nucleus with a relatively big nucleolus.

The "Hauptzellen" consist of four types of cells:

Type C: two giant cells beneath the "Deckzellen": one in the right and one in the left part of each lobe. The cytoplasm consists of numerous vacuoles of various sizes and each cell has one giant nucleus.

Type D: 1-2 granulated cells; the cytoplasm consists of numerous granules. Each cell has two spherical nuclei side by side in the basal part of the cell or behind each other.

Type E: 6-8 granulated cells situated in the posterior region of each lobe; each cell has one nucleus.

Type F: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one spherical to oval nucleus (Table 5).

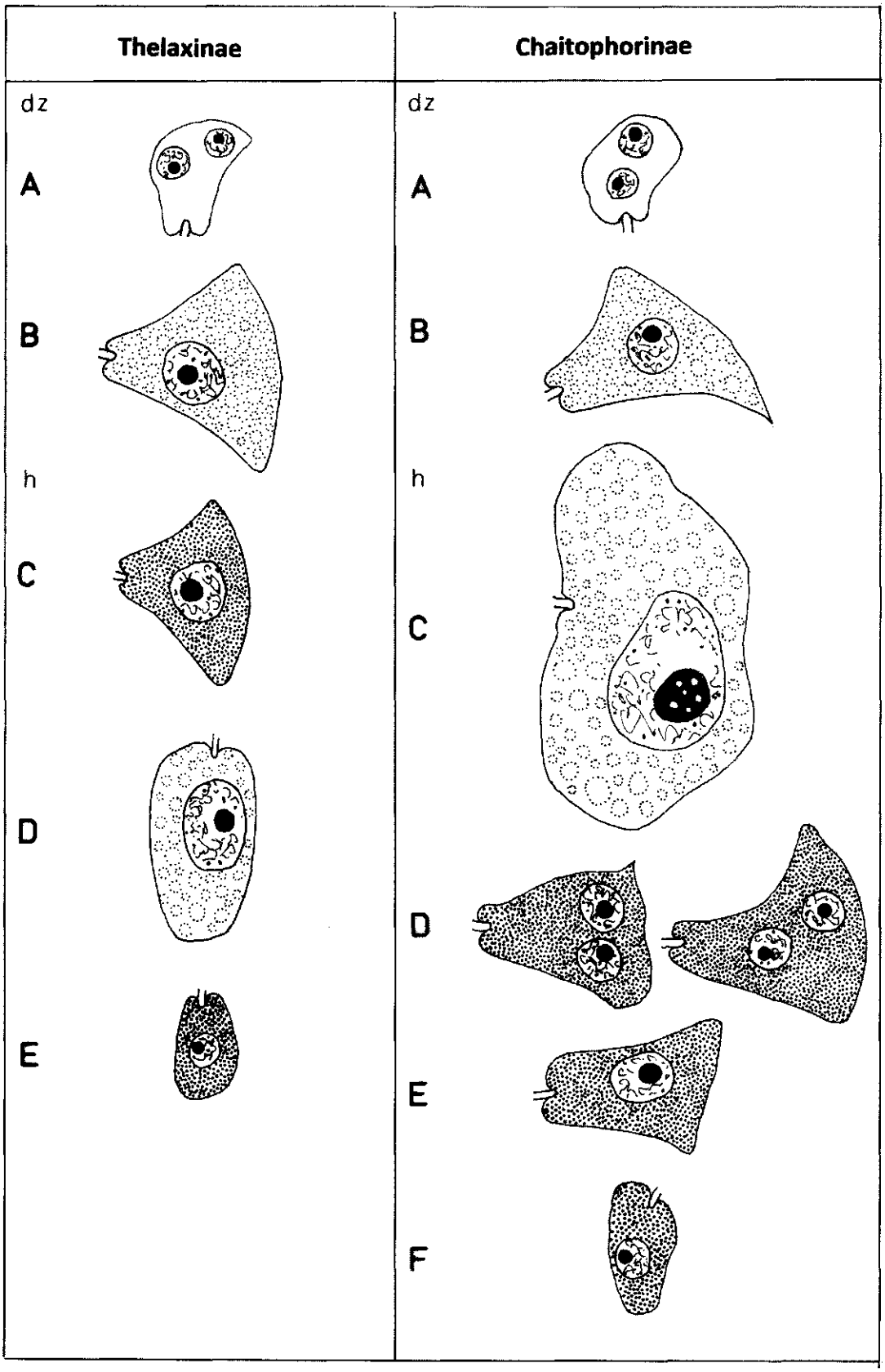
Figure 5 Longitudinal impression of the salivary glands of a wingless viviparous *Periphyllus testudinaceus* larva (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), and accessory salivary duct (D) of a winged viviparous *P. testudinaceus* larva, middle region (E) and posterior region (F) of the principal salivary gland of a winged viviparous *Chaitophorus populeti* larva. Bar represents 10 μm. For list of abbreviations see page 62.

Table 4 Total number of cells of the principal salivary gland of three wingless viviparous larvae of *Thelaxes dryophila*. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of two types of cells: structureless cells (A) and vacuolated cells (B), and the "Hauptzellen" in three types of cells: granulated cells (C), giant cells (D), and small granulated cells (E). The letters A-E correspond with those in Figure 6. See Table 12.

Aphid	Left principal gland										Right principal gland									
	"Deckzellen"				"Hauptzellen"						"Deckzellen"				"Hauptzellen"					
	A		B		C		D		E		A		B		C		D		E	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Thelaxes dryophila	1	1	6	6	9	9	1	1	2	2	1	1	6	6	9	9	1	1	2	2
	1	1	7	7	8	8	1	1	2	2	1	1	6	7	8	7	1	1	2	2
	1	1	6	6	9	8	1	1	2	2	1	1	7	7	8	9	1	1	2	2

Table 5 Total number of cells of the principal salivary gland of *Chaitophorus populeti* and *Periphyllus testudinaceus* larvae. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of two types of cells: structureless cells (A) and vacuolated cells (B), and the "Hauptzellen" in four types of cells: giant cells each with one giant nucleus (C), granulated cells each with two nuclei (D), granulated cells each with one nucleus (E), and small granulated cells (F). The letters A-F correspond with those given in Figure 6. See Table 12.

Aphid	Left principal gland												Right principal gland											
morph	"Deckzellen"				"Hauptzellen"								"Deckzellen"				"Hauptzellen"							
	A		B		C		D		E		F		A		B		C		D		E		F	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Chaitophorus populeti																								
winged viviparous	1	1	7	7	2	2	2	2	8	7	2	2	1	1	7	6	2	2	2	2	7	8	2	2
wingless viviparous	1	1	6	7	2	2	2	2	7	8	2	2	1	1	7	7	2	2	2	2	7	7	2	2
wingless viviparous	1	1	6	6	2	2	1	2	8	8	2	2	1	1	7	6	2	2	2	2	8	7	2	2
Periphyllus testudinaceus																								
winged viviparous	1	1	7	6	2	2	2	2	7	7	2	2	1	1	6	6	2	2	2	2	6	6	2	2
winged viviparous	1	1	7	6	2	2	2	2	7	7	2	2	1	1	7	7	2	2	2	2	6	7	2	2
wingless viviparous	1	1	6	7	2	2	1	1	7	8	2	2	1	1	6	6	2	2	2	2	8	6	2	2


Thelaxinae
Chaitophorinae
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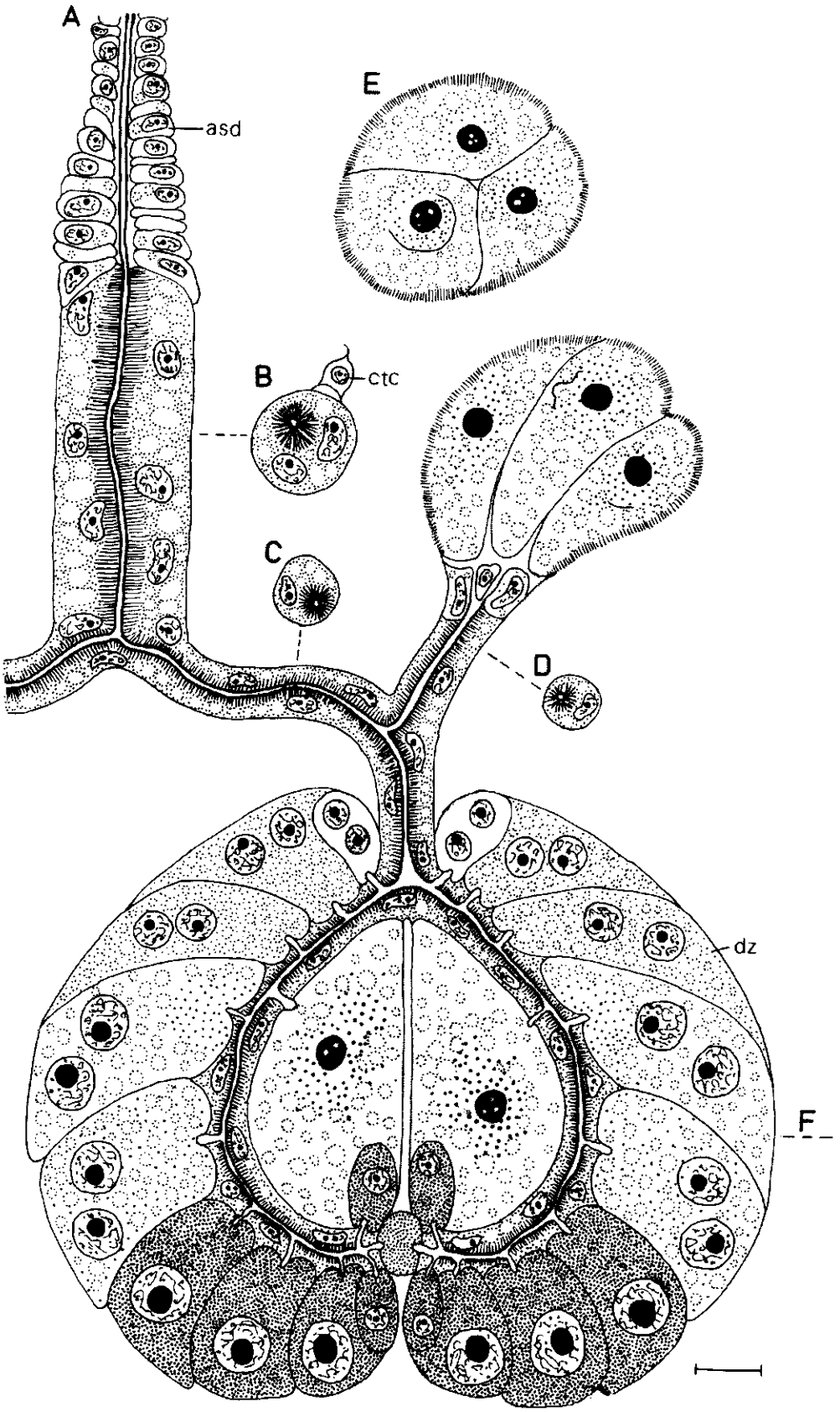
Myzocallidinae (Calaphidini)

In the principal salivary glands of *Calaphis flava*, *Clethrobius comes*, and *Monaphis antennata* (Figures 7, 8, 10, and 11) the "Deckzellen" consist of two types of cells:
Type A: one structureless cell with two nuclei surrounding the entrance of the principal salivary duct into the principal gland.
Type B: 4-6- cells with vacuoles of various sizes and granules scattered in between them; each cell has two spherical nuclei with a relatively big nucleolus.

The "Hauptzellen" of *Calaphis flava* and *Clethrobius comes* consist of five types of cells (Figure 7 and 8):
Type C: two vacuolated cells in each lobe situated beneath the "Deckzellen". The cytoplasm consists of vacuoles and granules in the apical region around the intercellular canaliculum. Each cell has two spherical nuclei side by side in the basal part of the cell or behind each other.
Type D: two vacuolated-granulated cells in the right part of the right lobe and two in the left part of the left lobe. The cytoplasm consists of vacuoles and granules scattered in between them. Each cell has two spherical nuclei.
Type E: 5-8 granulated cells situated in the posterior region of each lobe. The cytoplasm consists of numerous granules and each cell has one big nucleus.
Type F: two giant cells in each gland: one in the left part of the right lobe and one in the right part of the left lobe. The cytoplasm consists of vacuoles and granules scattered in between them. Each cell has one or two giant nuclei of which the nuclear membrane is partly dissolved and the granulated nuclear material is released into the cytoplasm.
Type G: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one nucleus.

Figure 6 Histological composition of the several types of cells in the principal salivary glands of *Thelaxes dryophila* (Thelaxinae), *Chaitophorus populeti*, and *Periphyllus testudinaceus* (Chaitophorinae). The cell types correspond with those given in Figure 4 and 5, and the letters A-E in Table 4 and A-F in Table 5. Bar represents 10 μm. For list of abbreviations see page 62.


A
asd
E
B
ctc
C
D
dz
F

Histologically, the two types of "Deckzellen" and the five types of "Hauptzellen" in the principal glands of the winged males of *Calaphis flava* are identical to those of the wingless viviparous *Calaphis flava* and *Clethrobius comes* (Table 6).

The "Hauptzellen" of *Monaphis antennata* consist of six types of cells (Figures 10 and 11):

Type C: two giant cells in the right part of the right lobe and two in the left part of the left lobe beneath the "Deckzellen". The cytoplasm consists of numerous vacuoles and granules in the apical region around the intercellular canaliculum. Each cell has two giant nuclei of which the granulated nuclear material form an irregular-shaped structure.

Type D: 2-3 granulated cells; the cytoplasm consists of numerous granules and each cell has two nuclei.

Type E: 7-10 granulated cells situated in the posterior region of each lobe; each cell has one nucleus.

Type F: two vacuolated cells: one cell in the left part of the right lobe and one in the right part of the left lobe. Each cell has one or two nuclei of which the granulated nuclear material is partly or completely disappeared with the exception of the relatively small nucleoli.

Type G: two giant vacuolated cells: one cell in the left part of the right lobe and one in the right part of the left lobe. These cells have two nuclei each with one nucleus or one nucleus with two nucleoli. The nuclear membrane is completely dissolved and the fine-granulated nuclear material form an irregular-shaped structure.

Type H: two small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one spherical to oval nucleus.

Histologically, the two types of "Deckzellen" and the six types of "Hauptzellen" in the principal glands of the winged males are identical to that of the wingless oviparous *M. antennata* (Table 7).

Figure 7 Longitudinal impression of the salivary gland of a wingless viviparous larva of *Clethrobius comes* (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), accessory salivary duct (D), and the accessory salivary gland (E) of a winged larval male of *Calaphis flava*. Bar represents 10 μm. For list of abbreviations see page 62.

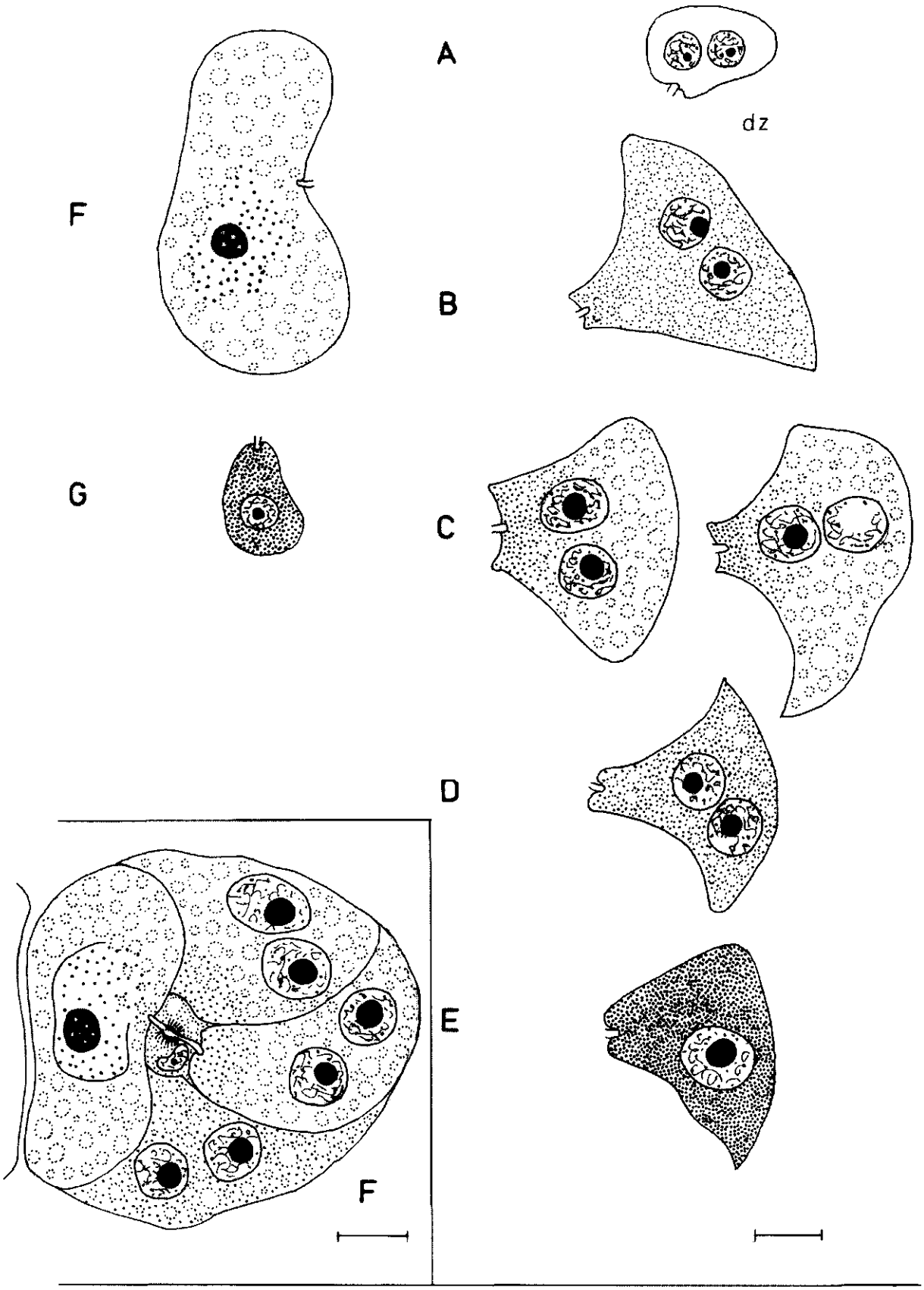

A
dz
F
B
G
C
D
E
F

Figure 8 Histological composition of the two types of "Deckzellen" (A-B) and the five types of "Hauptzellen" (C-G) in the principal salivary glands of larvae of *Calaphis flava* and *Clethrobius comes*. The cell types correspond with those given in Figure 7 and the letters A-G in Table 6. Inset: Transverse section of the middle region of the principal gland of a larval winged male of *Calaphis flava* (F). This section corresponds with letter F in Figure 7. Bar represents 10 μm.

Table 6 Total number of cells of the principal salivary gland of *Calaphis flava* and *Clethrobius comes* larvae. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of two types of cells: structureless cells (A) and vacuolated cells (B), and the "Hauptzellen" in five types of cells: vacuolated cells each with two nuclei (C), vacuolated-granulated cells each with two nuclei (D), granulated cells each with one nucleus (E), giant cells each with one or two nuclei (F), and small granulated cells (G). The letters A-G correspond with those given in Figure 8. See Table 12.

Aphid	Left principal gland														Right principal gland									
morph	"Deckzellen"				"Hauptzellen"										"Deckzellen"				"Hauptzellen"					
	A		B		C		D		E		F		G		A		B		C		D		E		F		G	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Calaphis flava																												
wingless viviparous	1	1	5	4	2	2	2	2	8	8	1	1	2	2	1	1	4	4	2	2	2	2	7	7	1	1	2	2
wingless viviparous	1	1	5	5	2	2	2	2	7	6	1	1	2	2	1	1	5	5	2	2	2	2	6	7	1	1	2	2
winged male	1	1	5	4	2	2	2	2	7	8	1	1	2	2	1	1	6	5	2	2	2	2	7	7	1	1	2	2
Clethrobius comes																												
wingless viviparous	1	1	5	4	2	2	2	2	7	8	1	1	2	2	1	1	4	5	2	2	2	2	7	7	1	1	2	2
wingless viviparous	1	1	5	4	2	2	2	2	7	7	1	1	2	2	1	1	6	6	2	2	2	2	5	6	1	1	2	2
wingless viviparous	1	1	5	5	2	2	2	2	6	6	1	1	2	2	1	1	5	5	2	2	2	2	8	7	1	1	2	2

Greenideinae (Greenideini)

In the principal glands of *Greenidea eugeniae*, *G. formosana*, and *Greenidea* spec. (Figures 12 and 13), the "Deckzellen" consist of one type of cells:

Type A: 5-6 cells with vacuoles of various sizes and granules scattered in between them; each cell has two nuclei of which the nuclear membrane is dissolved and the granulated nuclear material forms an irregular-shaped structure. Each nucleus has one nucleolus.

The "Hauptzellen" consist of six types of cells:

Type B: small structureless cells situated between the "Deckzellen" and the vacuolated cells: two in the right part of the right lobe and two in the left part of the left lobe. Each cell has one relatively big spherical nucleus.

Type C: vacuolated cells situated between the "Deckzellen" and the granulated cells: two in the right part of the right lobe and two in the left part of the left lobe. The cytoplasm consists of numerous vacuoles of various sizes. Each cell has two small spherical nuclei but in some individuals one of the two cells has one big spherical or one big elongated nucleus.

Type D: 2-3 granulated cells situated beneath the vacuolated cells; the cytoplasm consists of numerous granules and each cell has two small spherical nuclei.

Type E: 4-7 granulated cells situated in the posterior region of each lobe; each cell has one big spherical nucleus.

Type F: four giant cells in each gland: two in the left part of the right lobe and two in the right part of the left lobe. The cytoplasm consists of numerous vacuoles of various sizes and granules scattered in between them. Each cell has one giant spherical to oval nucleus of which the granulated nuclear material is loosely scattered around the nucleolus.

Type G: small granulated cells situated one on each side at the end of the internal salivary duct; each cell has one spherical nucleus (Figure 13).

Histologically, the "Deckzellen" and the six types of "Hauptzellen" in the principal salivary glands of the males are identical to those of the winged and wingless viviparous species of the Greenideinae (Table 8).

Table 7 Total number of cells of the principal salivary gland of *Monaphis antennata* larvae. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of two types of cells: structureless cells (A) and vacuolated cells (B), and the "Hauptzellen" in six types of cells: giant cells each with two nuclei (C), granulated cells each with two nuclei (D), granulated cells each with one nucleus (E), vacuolated cells each with one or two nuclei (F), giant vacuolated cells each with one or two nuclei (G), and small granulated cells each with one nucleus (H). The letters A-H correspond with those given in Figure 11. See Table 12.

Aphid	Left principal gland																Right principal gland													
morph	"Deckzellen"				"Hauptzellen"												"Deckzellen"				"Hauptzellen"									
	A		B		C		D		E		F		G		H		A		B		C		D		E		F		G		H	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Monaphis antennata																																
wingless oviparous	1	1	5	4	2	2	2	2	8	8	1	1	1	1	2	2	1	1	4	5	2	2	2	2	10	8	1	1	1	1	2	2
winged male	1	1	4	4	2	2	2	2	7	8	1	1	1	1	2	2	1	1	5	4	2	2	2	3	8	8	1	1	1	1	2	2
winged male	1	1	4	5	2	2	2	2	9	7	1	1	1	1	2	2	1	1	4	4	2	2	3	2	7	7	1	1	1	1	2	2

Phloeomyzinae

In the principal salivary glands of *Phloeomyzus passerinii* the gland cells consist of six types of cells (Table 9; Figure 14):

Type A: 5-6 vacuolated cells in the anterior region of each lobe. They consist of numerous vacuoles and fine granules scattered in between them. Each cell has two small nuclei with granulated nuclear material and a relatively big nucleolus.

Type B: 2-3 vacuolated-granulated cells situated between the first type of cells (A), between the first type of cells (A) and the giant cells (D), and between the giant cells (D) in the right part of the right lobe and in the left part of the left lobe. These cells consist of numerous vacuoles and big granules scattered in between them. Each cell has two small nuclei with granulated nuclear material and a relatively big nucleolus.

Type C: structureless cells situated between the first two types of cells: two in the right part of the right lobe and two in the left part of the left lobe. Each cell has one relatively big oval nucleus.

Type D: three giant cells which cover the entire width of the central region of each lobe (Figures 13D and 14E). The cytoplasm consists of numerous small vacuoles: in the basal region the vacuoles are surrounded by many big granules but less in the apical region. The canaliculum is closed with a microvillar system. Each cell has one or two giant spherical to oval nuclei with granulated nuclear material and a giant nucleolus.

Type E: 6-8 granulated cells situated in the posterior region of each lobe. Each cell has two small spherical nuclei and a relatively big nucleolus. A clear zone without granules surrounds the intercellular secretory canaliculum.

Type F: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one elongated nucleus (Figure 13).

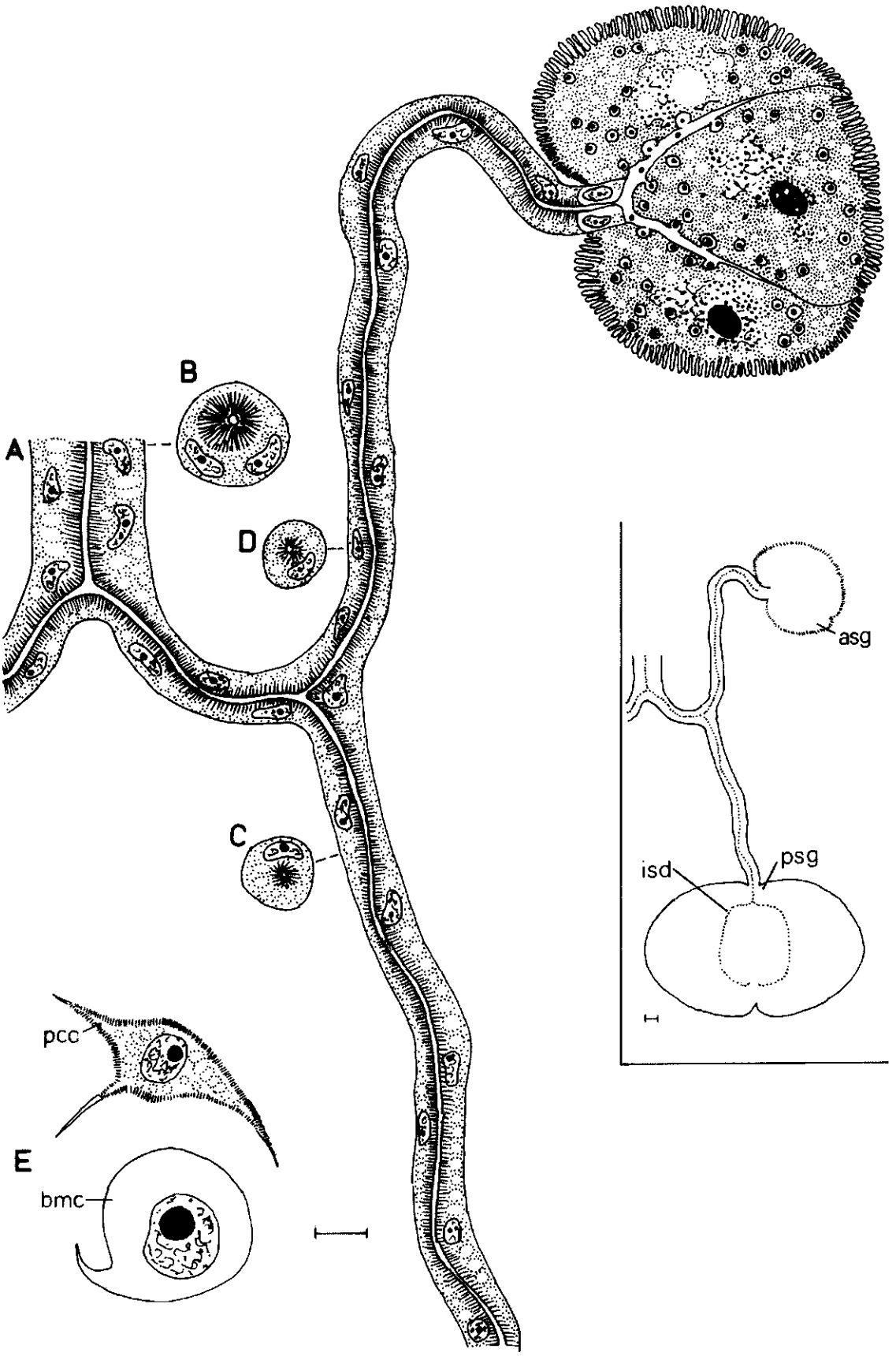

B
A
D
C
asg
psg
isd
pcc
E
bmc

Figure 9 Longitudinal impression of the salivary ducts and accessory salivary gland of a wingless oviparous larva of *Monaphis antennata* (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), accessory salivary duct (D), and a pericardial cell and basophilic mesodermal cell in the environment of the corpus allatum (E) of a winged male of *M. antennata*. Bar represents 10 μm. Inset: Longitudinal impression of the salivary gland showing the accessory gland and the principal gland. The dotted line represents the cuticular lumen of the two internal salivary ducts, principal, accessory, and common salivary ducts (see Figure 10). Bar represents 10 μm. For list of abbreviations see page 62.

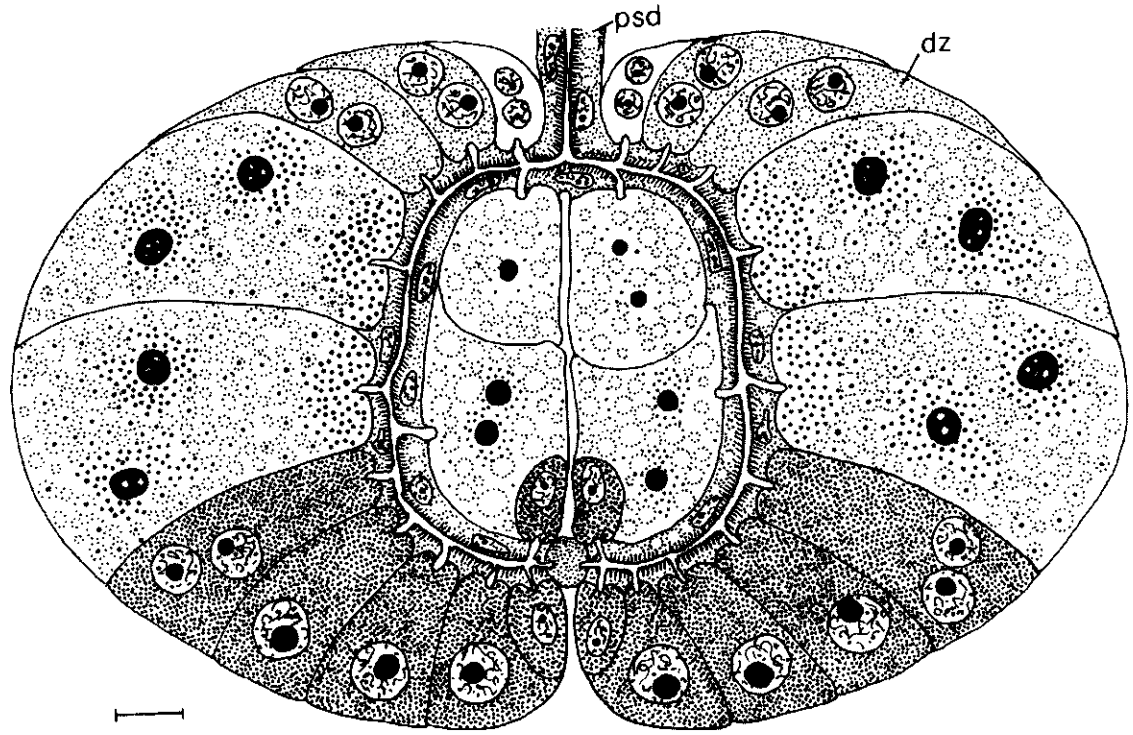


Figure 10 Longitudinal impression of the principal salivary gland of a wingless oviparous larva of *Monaphis antennata* reconstructed from transverse serial sections. Bar represents 10 μm. For list of abbreviations see page 62.

Anoeciinae

In the principal glands of *Anoecia* spec. feeding on *Cornus* spec. (Figure 15) the "Deckzellen" consist of one type of cells:
Type A: 5-6 cells with vacuoles of various sizes and granules scattered in between them; each cell has two small spherical nuclei and a relatively big nucleolus.

The "Hauptzellen" consist of five types of cells:
Type B: structureless cells situated between the "Deckzellen" and the vacuolated cells: two in the right part of the right lobe and two in the left part of the left lobe. Each cell has one relatively big spherical nucleus.
Type C: 4-5 vacuolated cells situated between the "Deckzellen" and the granulated cells. The cytoplasm consists of many vacuoles of various sizes and each cell has one big spherical nucleus.
Type D: 4-7 granulated cells situated in the posterior region of each lobe. The cytoplasm consists of numerous granules and each cell has two small nuclei.
Type E: 4 giant cells in each gland: two in the left part of the right lobe and two in the right part of the left lobe. The cytoplasm consists of vacuoles of various sizes and fine granules scattered in between them. Each cell has one giant spherical to oval nucleus of which the granulated nuclear material is loosely scattered around the giant nucleolus.
Type F: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one spherical to oval nucleus (Figure 18; Table 10).

Histologically, the "Deckzellen" and the five types of "Hauptzellen" in the principal salivary glands of the wingless males are identical to those of the wingless oviparae.

The wingless males of *Anoecia* have a primitive, not degenerated digestive system (Ponsen, 2006). The crenated intestine of the oviparae possesses one and that of the viviparae two additional loops (Ponsen, 1987).

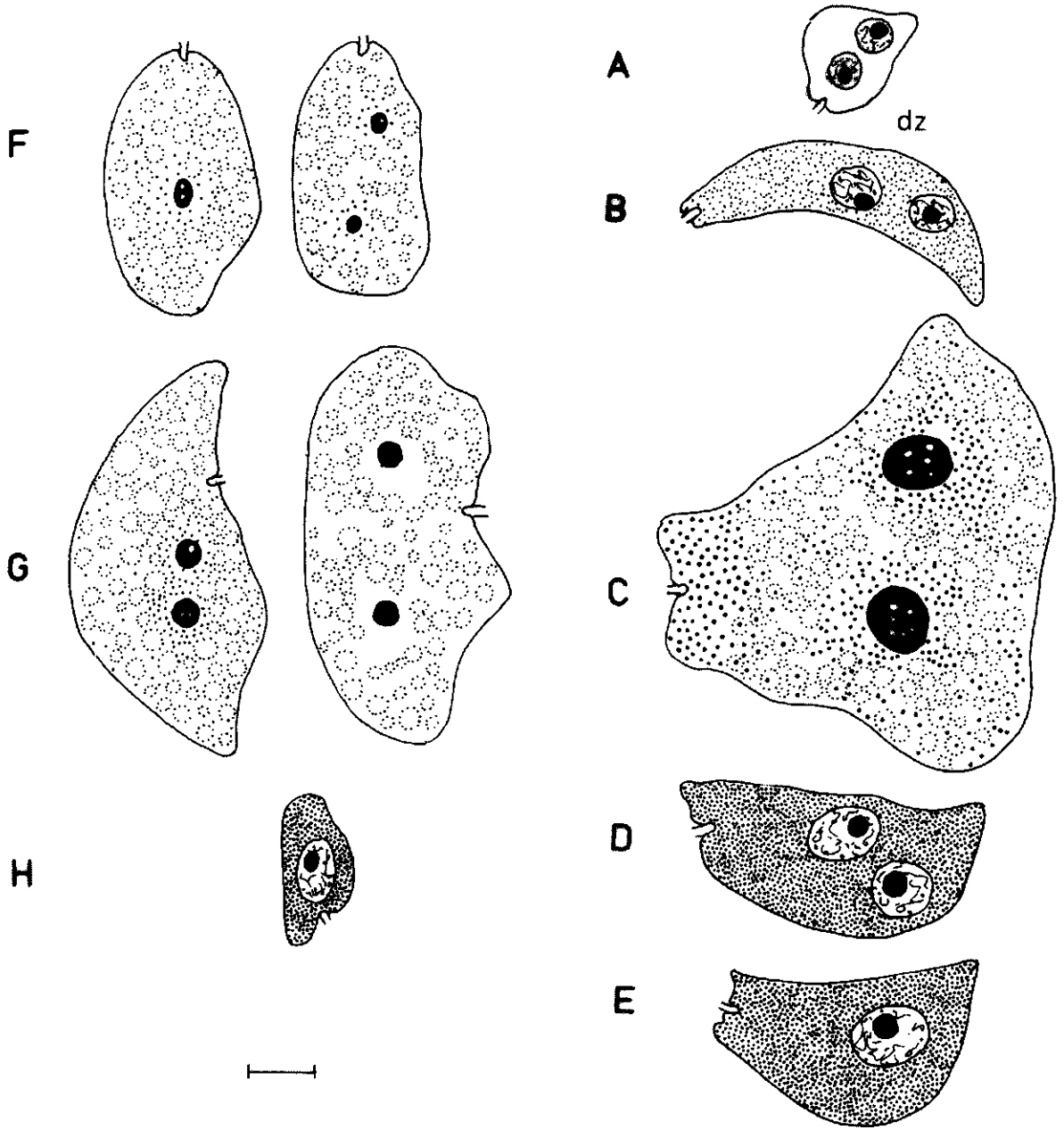
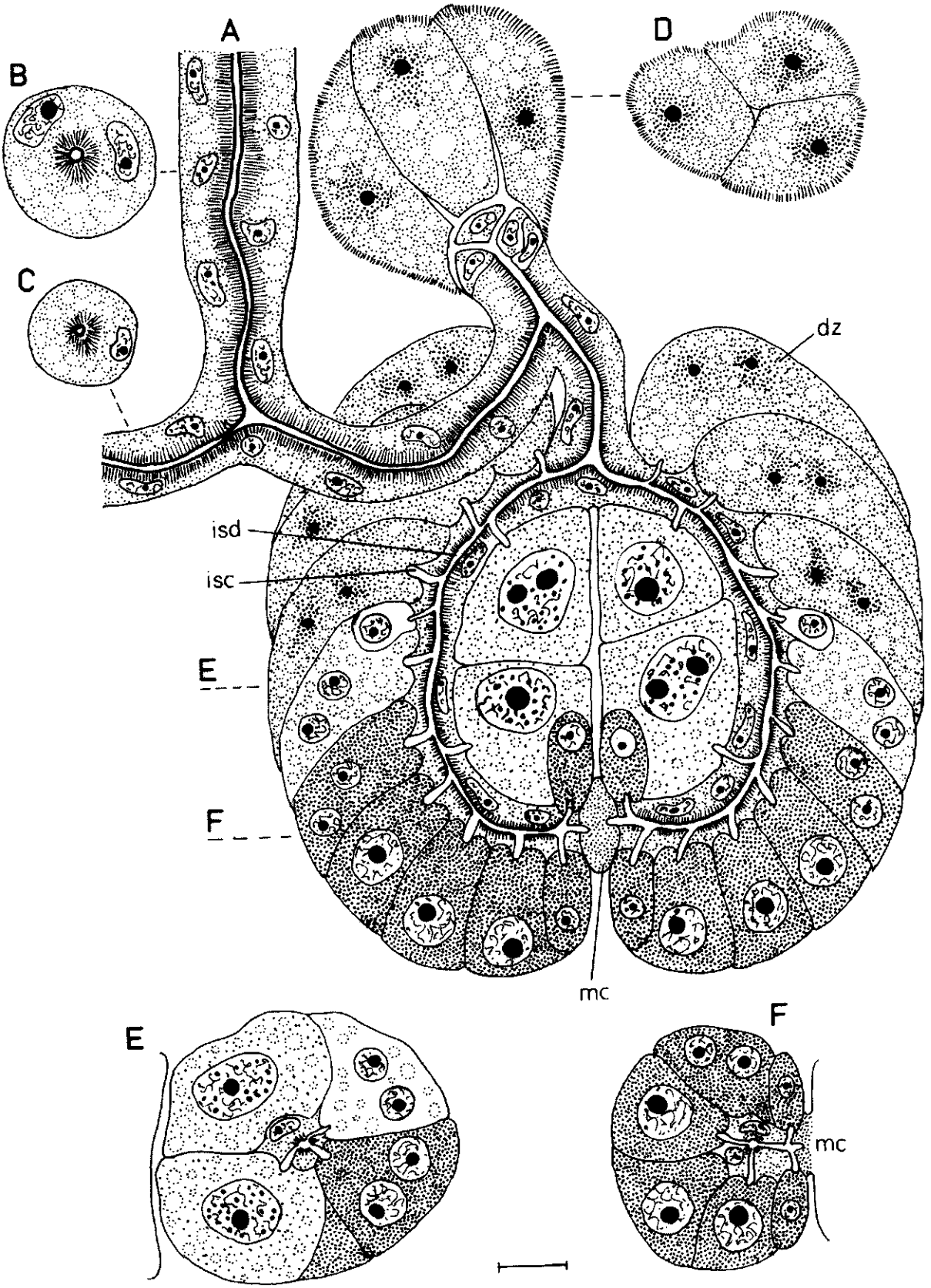

A
dz
B
C
D
E
F
G
H

Figure 11 Histological composition of the two types of "Deckzellen" (A-B) and the six types of "Hauptzellen" (C-H) in the principal salivary gland of a winged larval male of *Monaphis antennata*. The cell types correspond with those given in Figure 10 and the letters A-H in Table 7. Bar represents 10 μm. For list of abbreviations see page 62.


A
B
C
D
dz
isd
isc
E
F
mc
E
F
mc

Pterocommatinae

In the principal salivary glands of *Plocamaphis amerinae* and *Pterocomma salicis* (Figure 16) the "Deckzellen" consist of one type of cells:

Type A: 6-7 cells with vacuoles of various sizes and granules scattered in between them. The apical part of each cell, around the intercellular secretory canaliculum, is a zone of fine granules without any vacuoles. Inside this zone the short canaliculum branches into three canaliculi of which each of them is closed with a microvillar system. This structure is similar to that in the "Deckzellen" of the principal salivary glands in species of the Lachninae (Leonhardt, 1940). Each cell has one nucleus of which the nuclear membrane is dissolved and the granulated nuclear material forms an irregular-shaped structure.

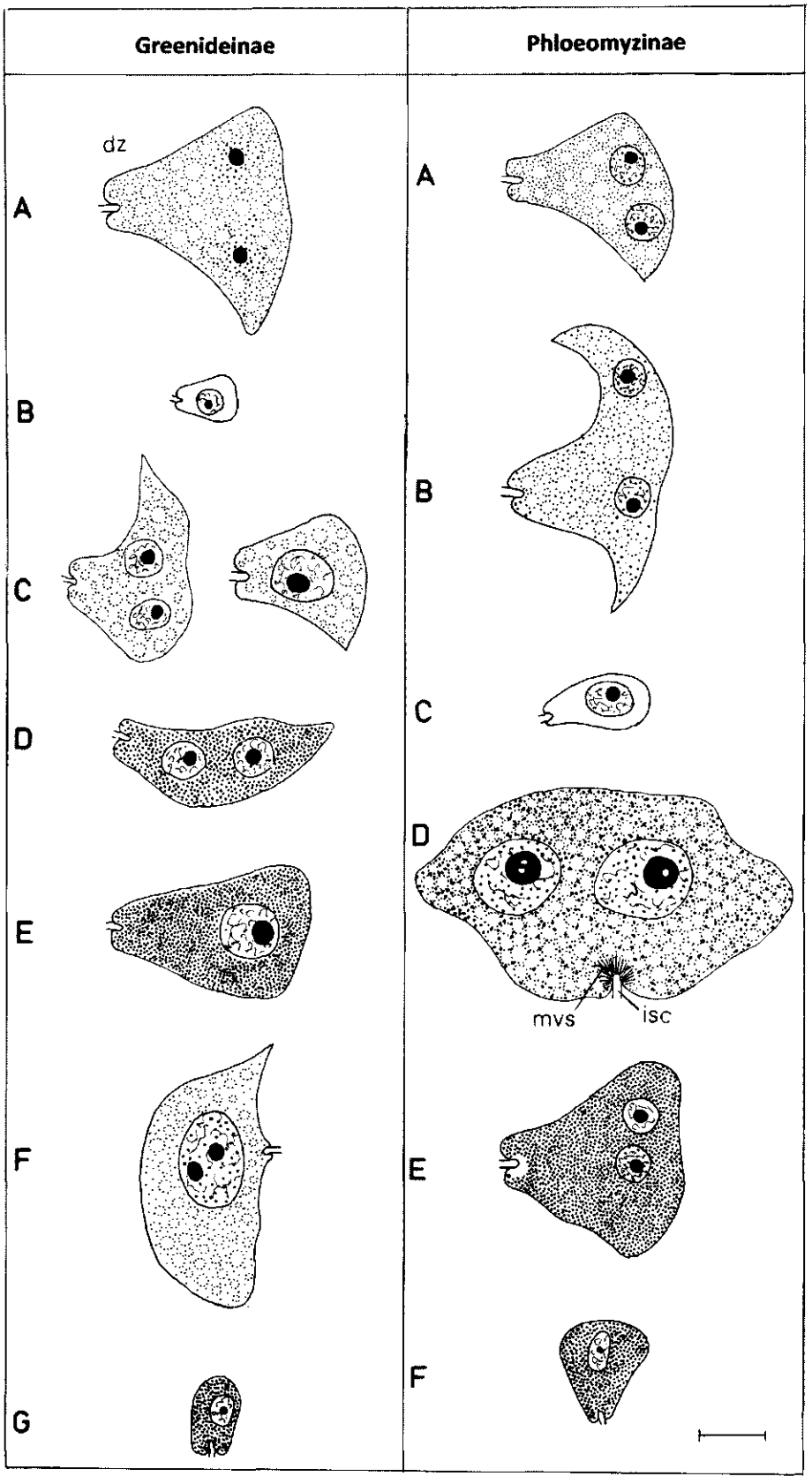
The "Hauptzellen" consist of five types of cells (Figures16, 17G-H, and 18):

Type B: structureless cells situated between the "Deckzellen" and the vacuolated cells: two in the right part of the right lobe and two in the left part of the left lobe. Each cell has one relatively big spherical nucleus.

Type C: vacuolated cells situated between the "Deckzellen" and the granulated cells: two in the right part of the right lobe and two in the left part of the left lobe. The cytoplasm consists of numerous vacuoles of various sizes; each cell has two spherical nuclei. In some individuals one of the two cells has one big spherical or one big elongated nucleus probably a fusion product of two nuclei.

Type D: 7-9 granulated cells situated in the posterior region of each lobe. Thecytoplasm consists of numerous granules and each cell has one spherical to oval nucleus.

Figure 12 Longitudinal impression of the salivary glands of a winged viviparous larva of *Greenidea eugeniae* (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct of a winged male of *G. formosana* (B), accessory salivary duct of a winged viviparous *G. formosana* (C), accessory gland of a winged larval male of *Greenidea* spec. (D), middle region of the principal gland of a winged viviparous larva of *G. formosana* (E), and the posterior region of the principal gland of a winged larval male of *Greenidea* spec. (F). Bar represents 10 μm. For list of abbreviations see page 62.


Greenideinae
Phloeomyzinae
A
dz
B
C
D
E
F
G
A
B
C
D
mvs
isc
E
F

Type E: four giant cells in each gland: two in the left part of the right lobe and two in the right part of the left lobe. The cytoplasm consists of many vacuoles of various sizes and fine granules scattered in between them. Each cell has one giant spherical to oval nucleus of which the granulated nuclear material is scattered around the nucleolus.
Type F: small granulated cells situated one on each side at the end of the internal salivary duct. Each cell has one spherical nucleus (Table 11).

The salivary glands of the males are identical to those of the winged and wingless viviparous species of the Pterocommatinae.

In all aphid species studied (Table 2) the principal salivary gland cell is connected with the cuticular lumen of the internal salivary duct by a short intercellular secretory canaliculum. The epithelial lining of the lumen of the internal duct consists of squamous cells and spherical to elongated nuclei. The lateral cell membranes are lacking and the apical cell membrane consists of a microvillar system.

In all aphid species of the Aphididae investigated the two separated lobes of each principal gland are posteriorly connected with each other by the two internal salivary ducts forming a myoepithelioid cell. This cell is innervated by a branch (N2) of the medial dorsal nervous system which passes along the dorsal vessel (Figure 16). Not in all individuals of the many aphid species studied (Table 2) this nerve (N2) is present, possibly due to damage or to its invisibility.

Salivary duct. The accessory salivary duct runs from the accessory gland to the principal salivary gland where it terminates into the principal salivary duct (Figures 7,15, and 16), to pass either into half way the principal duct (Figures 4 and 5), or to pass into the principal duct near the junction of the suboesophageal and thoracic ganglion (Figures 9 and 12).

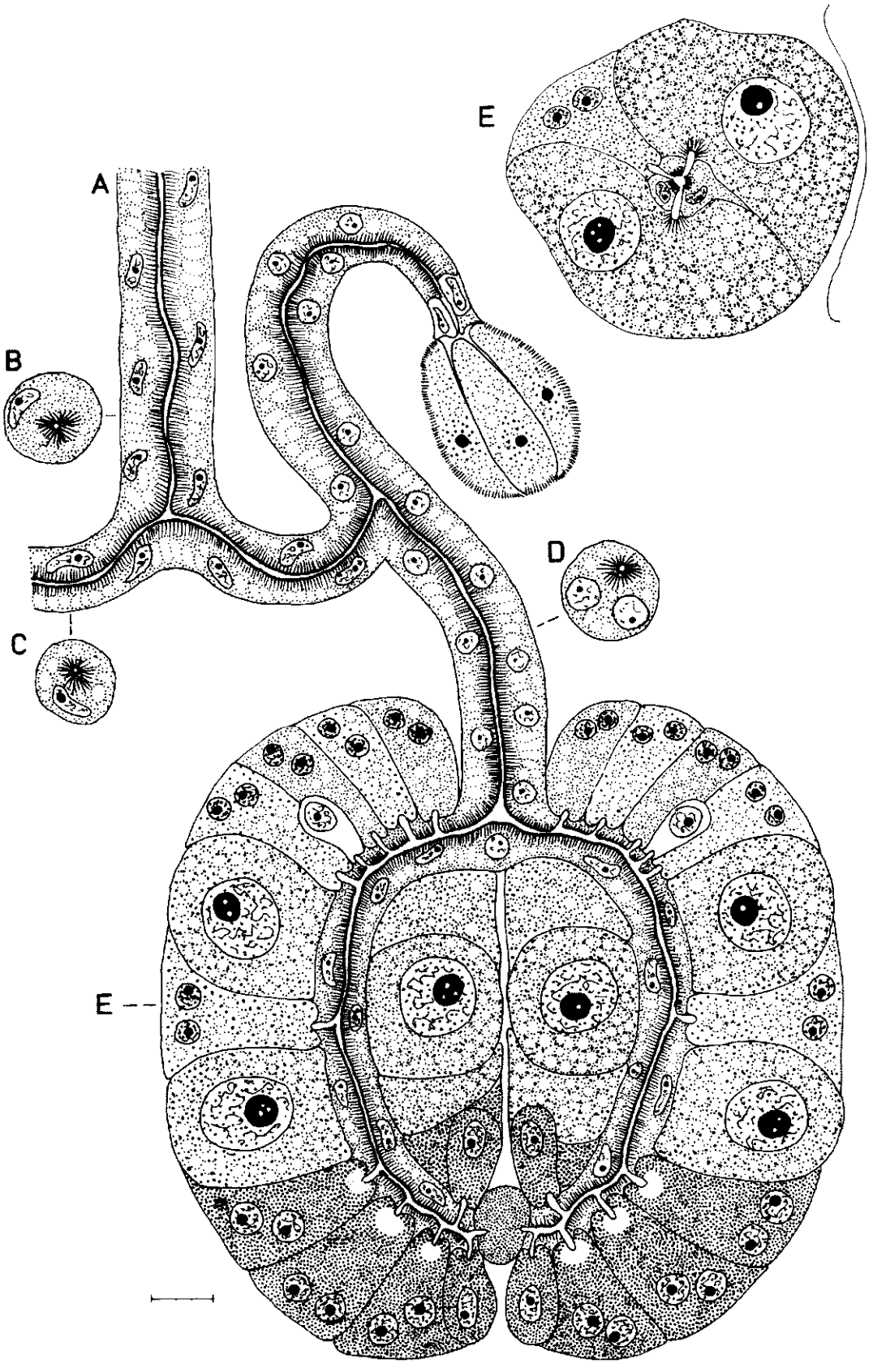
Figure 13 Histological composition of the seven types of cells in the principal salivary glands of three species of the Greenideinae (Greenideini) and the six types of cells in the principal glands of *Phloeomyzus passerinii* (Phloeomyzinae). The cell types correspond with those given in Figures 12 and 14, and the letters A-G in Table 8 and A-F in Table 9. Bar represents 10 μm. For list of abbreviations see page 62.

Table 8 Total number of cells of the principal salivary gland of species of the Greenideinae. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of one type of cells (A) and the "Hauptzellen" in six types of cells: structureless cells (B), vacuolated cells (C), granulated cells each with two nuclei (D), granulated cells each with one nucleus (E), giant cells (F), and small granulated cells (G). The letters A-G correspond with those given in Figure 13. See Table 12.

Aphid	Left principal salivary gland														Right principal salivary gland													
morph	"Deckzellen"		"Hauptzellen"												"Deckzellen"		"Hauptzellen"											
	A		B		C		D		E		F		G		A		B		C		D		E		F		G	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Greenidea eugenia																												
winged viviparous	5	6	2	2	2	2	3	2	6	7	2	2	2	2	6	5	2	2	2	2	2	2	6	7	2	2	2	2
wingless viviparous	5	6	2	2	2	2	2	2	6	7	2	2	2	2	5	6	2	2	2	2	2	2	7	7	2	2	2	2
winged male	6	6	2	2	2	2	2	2	7	6	2	2	2	2	5	6	2	2	2	2	2	2	7	7	2	2	2	2
Greenidea formosana																												
winged viviparous	6	5	2	2	2	2	2	2	5	5	2	2	2	2	5	6	2	2	2	2	2	3	5	4	2	2	2	2
wingless viviparous	5	5	2	2	2	2	2	2	7	7	2	2	2	2	6	5	2	2	2	2	2	3	6	5	2	2	2	2
winged male	5	6	2	2	2	2	2	2	6	7	2	2	2	2	6	6	2	2	2	2	3	2	5	6	2	2	2	2
Greenidea spec.																												
winged viviparous	6	6	2	2	2	2	3	2	5	7	2	2	2	2	6	6	2	2	2	2	2	2	7	5	2	2	2	2
wingless viviparous	5	5	2	2	2	2	2	3	7	6	2	2	2	2	6	6	2	2	2	2	3	3	6	5	2	2	2	2
winged male	6	5	2	2	2	2	2	3	6	7	2	2	2	2	5	5	2	2	2	2	2	2	6	5	2	2	2	2

Table 9 Total number of cells of the principal salivary gland of three wingless viviparous larvae of *Phloeomyzus passerinii*. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) Each lobe consists of six types of cells: vacuolated cells each with two nuclei (A), vacuolated-granulated cells each with two nuclei (B), structureless cells each with one nucleus (C), giant cells each with one or two nuclei (D), granulated cells each with two nuclei (E), and small granulated cells each with one nucleus (F). The letters A-F correspond with those given in Figure 13. See Table 12.

Aphid	Left principal salivary gland												Right principal salivary gland											
morph	A		B		C		D		E		F		A		B		C		D		E		F	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
P. passerinii																								
wingless viviparous	6	6	2	3	2	2	3	3	8	7	2	2	5	6	3	3	2	2	3	3	7	7	2	2
	6	6	2	3	2	2	3	3	6	7	2	2	5	5	3	3	2	2	3	3	7	7	2	2
	6	5	2	3	2	2	3	3	8	7	2	2	6	6	3	3	2	2	3	3	7	7	2	2


E
A
B
D
C
E

In *Phloeomyzus passerinii* the accessory duct runs from the accessory gland into a short duct with elongated nuclei. This duct continues into a broader duct which terminates into the principal gland. It has 12-16 spherical nuclei with a relatively small nucleolus. This tubular duct may have a glandular function (Figure 14; Table 3). The principal duct is connected with the middle of the accessory duct. In Figure 8C in Ponsen (S2006) the "glandular" tubular duct is omitted.

The principal salivary duct from both principal glands runs to the junction of the thoracic and suboesophageal ganglion where they turn around the junction to fuse with the common salivary duct. This duct runs forwards ventrally to the suboesophageal ganglion and turns downwards to pass into the afferent salivary duct (Figures 4, 7, and 15). This duct terminates into the pumpstem of the salivary pump (see Figure 1 in Ponsen, S2012).

The epithelial lining of all three tubular ducts consists of one type of cells of which the lateral cell membranes are lacking. The cytoplasm consists of many vacuoles of various sizes and spherical to elongated nuclei. The apical cell membrane has a microvillar system along the cuticular lumen. This system is built up of parallel oriented infoldings of several lengths which are clearly visible in sections of *M. antennata*.

Figure 14 Longitudinal impression of the salivary glands of a wingless viviparous larva of *Phloeomyzus passerinii* (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), accessory salivary duct (D), and middle region of the principal gland (E) of a wingless viviparous larva of *P. passerinii*. Bar represents 10 μm. For list of abbreviations see page 62.

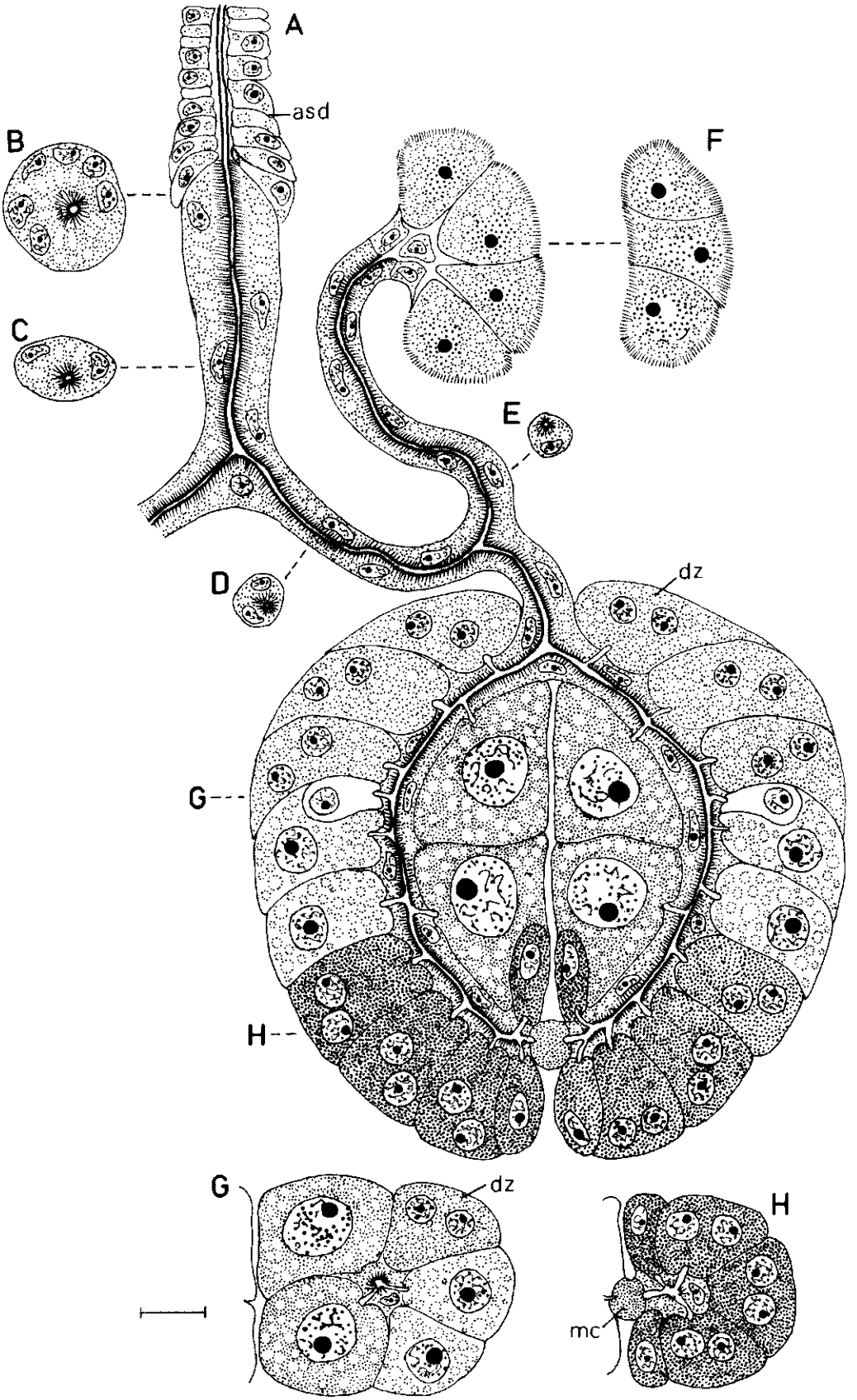
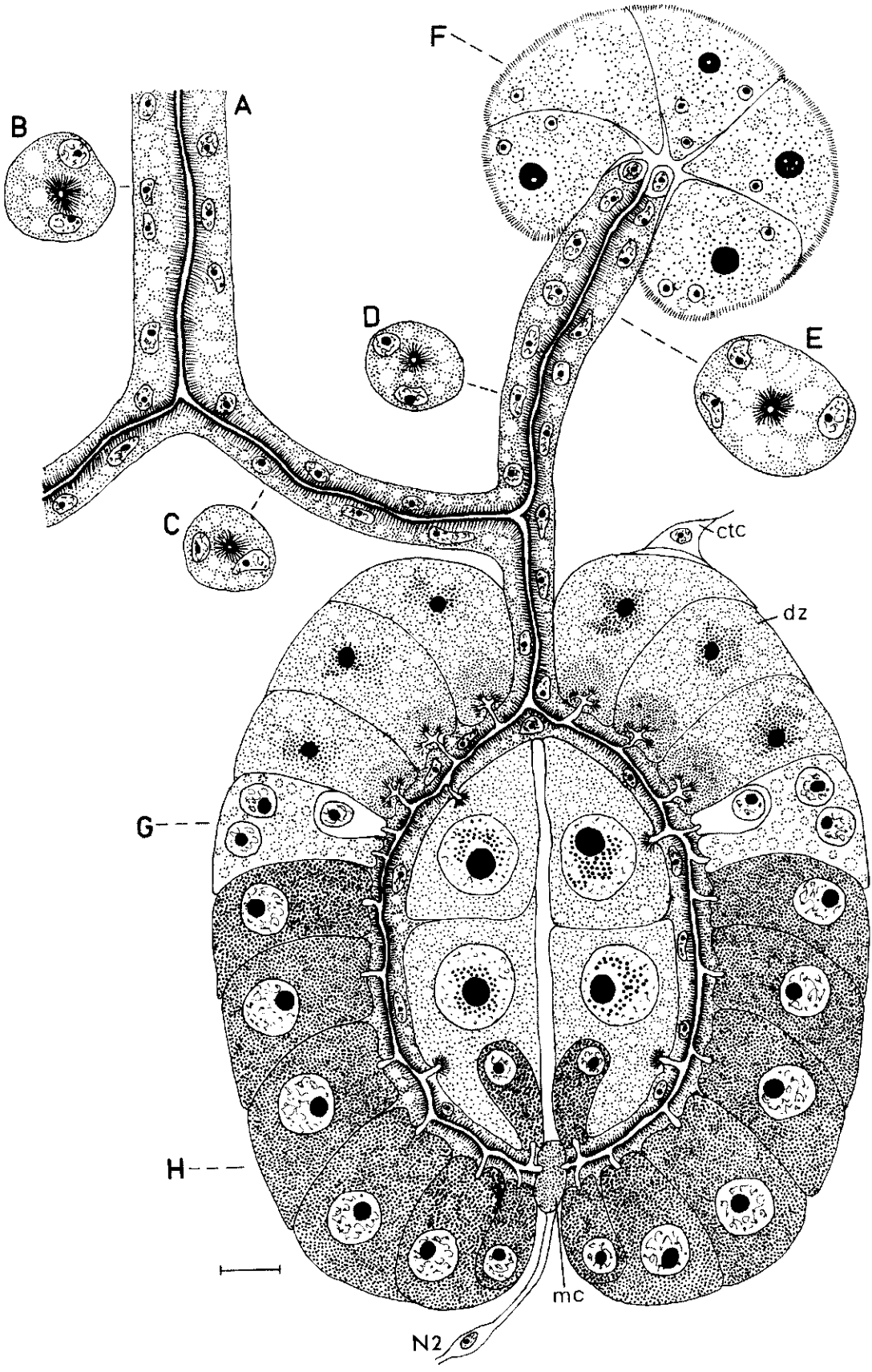

A
asd
B
C
D
E
F
G
H
dz
G
dz
H
mc

Figure 15 Longitudinal impression of the salivary glands of a wingless oviparous larva of *Anoecia* spec. (A) reconstructed from transverse serial sections. Transverse sections of the anterior part (B) and half way (C) the common salivary duct, principal salivary duct (D), accessory salivary duct (E), accessory salivary gland (F), middle region (G), and posterior region (H) of the principal gland of a wingless male of *Anoecia* spec. Bar represents 10 μm. For list of abbreviations see page 62.


A
B
C
D
E
F
G
H
ctc
dz
mc
N2

Discussion

Within the Aphidoidea each family has its own type of salivary glands (Figure 19) (Phylloxeridae, Adelgidae) and in the Aphididae each subfamily, except the Myzocallidinae (Table 2). In the tribe Calaphidini the principal glands of *Calaphis flava* and *Clethrobius* comes have the same configuration (Figure 7). However, the configuration of the principal glands of *Monaphis antennata* are quite different (Figure 10).

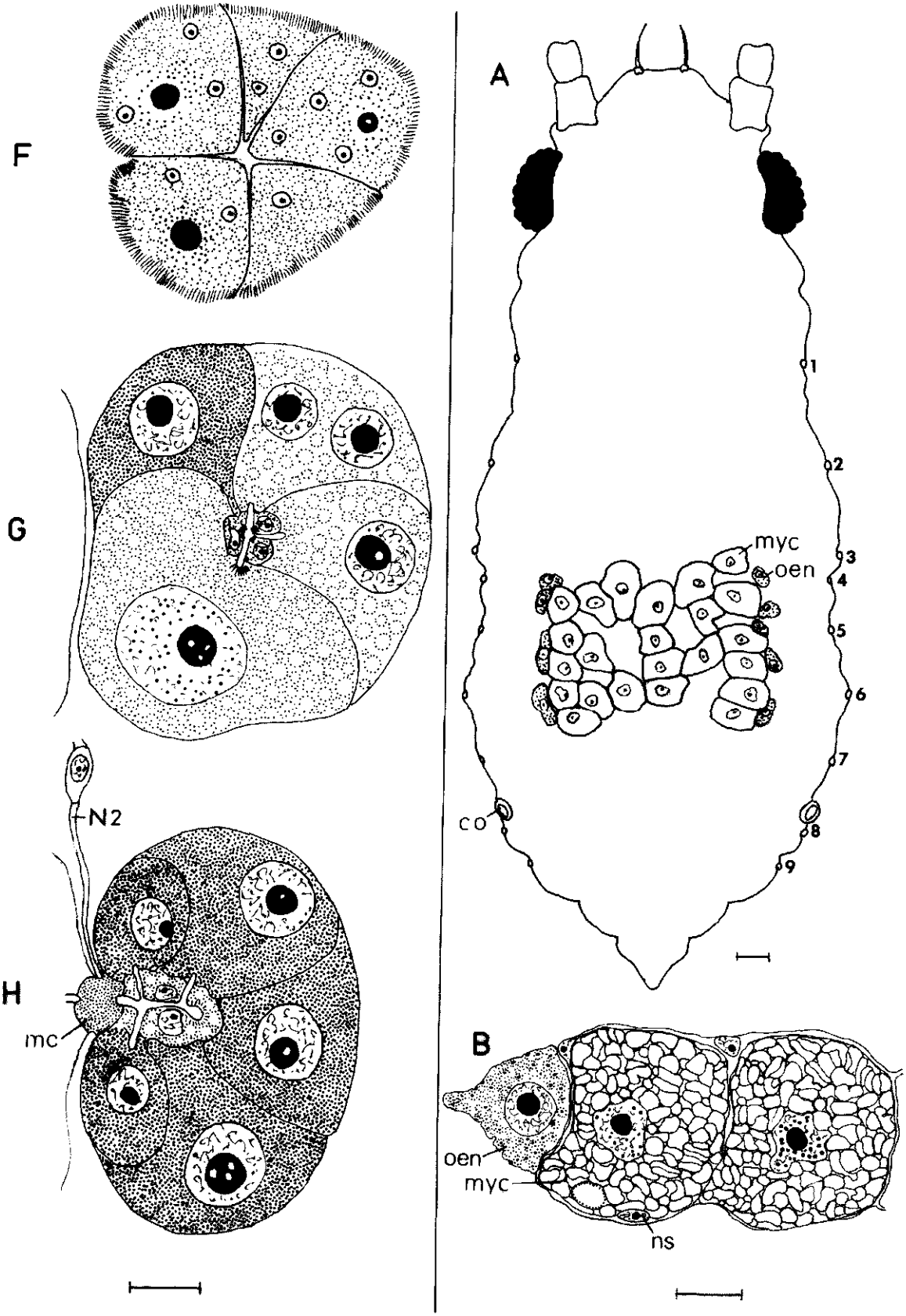
The gland cells of the accessory salivary glands of species of the Adelgidae and those of the Aphididae investigated have a similar histological structure. It is likely that the saliva causes the formation of the salivary sheath which acts as a supporting structure for the movements of the stylets.

On the other hand, the principal glands consist of several types of cells probably corresponding with several types of enzymes and proteins. The saliva serves for the digestion of the food both in the sieve tubes (pre-intestinal) and in the stomach.

Each principal gland of the Adelgidae consists of 19 to 21 cells (Table 2), each lobe of each principal gland of the Phylloxeridae 18 to 20 cells (Table 2 in Ponsen, S2006), and each lobe of each principal gland of the Aphididae 18 to 23 cells (Table 12). The principal glands of the last two families consist of twice as much cells as those of the Adelgidae.

In species of the Adelgidae the bottle-shaped gland cells are connected with two short internal salivary ducts forming a fan-shaped structure (Figure 1). During evolution the two short ducts of each principal gland lengthen to connect subsequently with the myoepithelioid cell forming a closed compact structure as in all species of the Aphididae investigated (see page 11).

Figure 16 Longitudinal impression of the salivary glands of a wingless larval male of *Plocamaphis amerinae* (A) reconstructed from transverse serial sections. Transverse sections of the common salivary duct (B), principal salivary duct (C), accessory salivary duct (D), and after leaving of the accessory gland (E), of a winged viviparous *P. amerinae*. Bar represents 10 μm. For list of abbreviations see page 62.


F
G
H
N2
mc
A
myc
oen
co
1
2
3
4
5
6
7
8
9
B
oen
myc
ns

Electron microscopical studies of the myoepithelioid cell in *Myzus persicae* have been described by Ponsen (1972). Larval aphids injected via the siphunculi with Evans blue (1.5% in 0.85% NaCl) showed that only the myoepithelioid cell and both lumina of the internal salivary ducts were stained intensively blue in contrast to the remaining part of the salivary glands being colourless. In the Adelgidae the myoepithelioid cell is present at the end of the internal salivary duct (page 11; Figure 1) and in the Aphididae between the two internal salivary ducts. Myoepithelial cells are star-shaped cells which embrace the gland cells compressing the secretory portion (Junqueira et al., 1977). These cells are not observed at the basal part of each principal salivary gland cell. From these results can be concluded that the myoepithelioid cell possibly pump up haemolymph from the haemocoel into the lumen of the internal salivary ducts.

The haemolymph of all species of the Phylloxeridae, Adelgidae and Aphididae investigated is characterized by the absence of circulating cells ("haemocytes").

Figure 17 Transverse sections of the accessory salivary gland (F), middle region (G) and posterior region (H) of the principal salivary gland of a winged viviparous *Plocamaphis amerinae* larva. The letters F-H correspond with those given in Figure 16. Bar represents 10 μm. Dorsal view of the mycetome and topographical position of the oenocytes of a wingless viviparous larva of *Subsaltusaphis ornata* (Theobald) reconstructed from transverse serial sections. (A). The mycetome has a thickness of one layer of mycetocytes. The siphuncular elevated pores are situated on the sixth abdominal tergite. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 μm. Transverse section of the mycetome of *S. ornata* (B). Bar represents 10 μm. For list of abbreviations see page 62.

Table 10 Total number of cells of the principal salivary gland of *Anoecia* spec. on *Cornus* spec. Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of one type of cells (A) and the "Hauptzellen" of five types of cells: structureless cells each with one nucleus (B), vacuolated cells each with one nucleus (C), granulated cells each with two nuclei (D), giant cells each with one nucleus (E), and small granulated cells each with one nucleus (F). The letters A-F correspond with those given in Figure 18. See Table 12.

Aphid	Left principal salivary gland												Right principal salivary gland											
morph	"Deckzellen"		"Hauptzellen"										"Deckzellen"		"Hauptzellen"									
	A		B		C		D		E		F		A		B		C		D		E		F	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Anoecia spec.																								
wingless oviparous	6	5	2	2	4	4	5	6	2	2	2	2	5	5	2	2	4	5	6	6	2	2	2	2
	5	5	2	2	4	4	5	5	2	2	2	2	5	5	2	2	4	4	6	7	2	2	2	2
	6	5	2	2	4	4	5	5	2	2	2	2	6	6	2	2	4	4	5	6	2	2	2	2
wingless male	5	5	2	2	4	4	6	6	2	2	2	2	6	6	2	2	4	4	5	6	2	2	2	2
	6	6	2	2	4	4	4	5	2	2	2	2	6	6	2	2	4	4	5	5	2	2	2	2
	5	6	2	2	4	4	6	5	2	2	2	2	6	5	2	2	4	4	4	5	2	2	2	2

Table 11 Total number of cells of the principal salivary gland of *Plocamaphis amerinae* and *Pterocomma salicis* (Pterocommatinae). Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl) of which each lobe consists of "Deckzellen" and "Hauptzellen". The "Deckzellen" consist of one type of cells (A) and the "Hauptzellen" of five types of cells: structureless cells each with one nucleus (B), vacuolated cells each with one or two nuclei (C), granulated cells each with one nucleus (D), giant cells each with one giant nucleus (E), and small granulated cells each with one nucleus (F). The letters A-F correspond with those given in Figure 18. See Table 12.

Aphid	Left principal salivary gland												Right principal salivary gland											
morph	"Deckzellen"		"Hauptzellen"										"Deckzellen"		"Hauptzellen"									
	A		B		C		D		E		F		A		B		C		D		E		F	
	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl	Ll	Rl
Plocamaphis amerinae																								
winged viviparous	6	6	2	2	2	2	8	8	2	2	2	2	6	7	2	2	2	2	8	7	2	2	2	2
wingless viviparous	7	7	2	2	2	2	7	8	2	2	2	2	6	7	2	2	2	2	8	7	2	2	2	2
wingless male	6	7	2	2	2	2	7	8	2	2	2	2	6	6	2	2	2	2	8	7	2	2	2	2
Pterocomma salicis																								
winged viviparous	7	6	2	2	2	2	7	8	2	2	2	2	7	6	2	2	2	2	8	7	2	2	2	2
winged viviparous	6	6	2	2	2	2	8	8	2	2	2	2	6	6	2	2	2	2	7	8	2	2	2	2
wingless viviparous	6	6	2	2	2	2	9	8	2	2	2	2	6	6	2	2	2	2	8	8	2	2	2	2

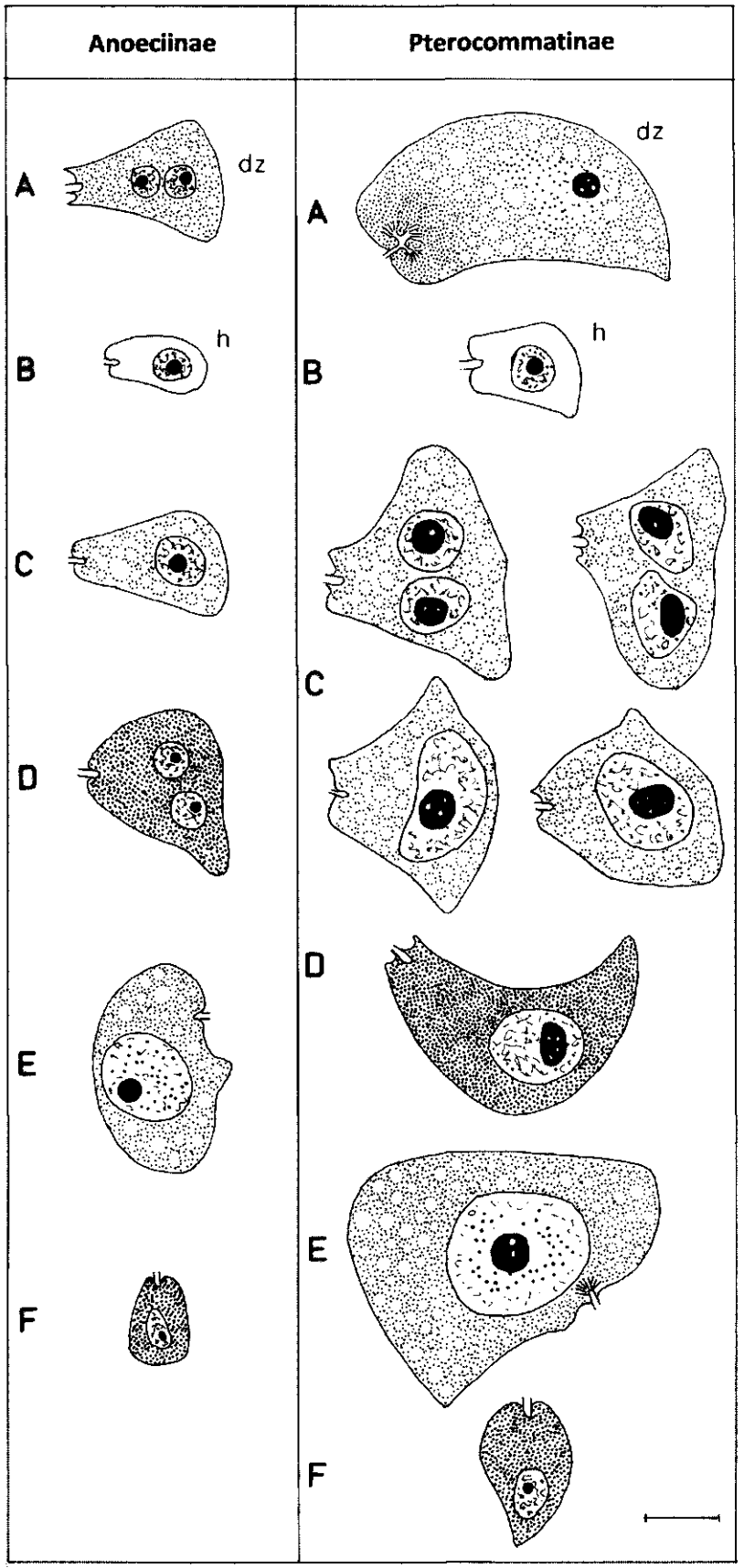

Anoeciinae
Pterocommatinae
A
dz
B
h
C
D
E
F
A
dz
B
h
C
D
E
F

Figure 18 Histological composition of the several types of cells in the principal salivary glands of *Anoecia* spec. (Anoeciinae), *Plocamaphis amerinae* and *Pterocomma salicis* (Pterocommatinae). The cell types correspond with those given in Figure 15 and 16, and the letters A-F in Table 10 and 11. Bar represents 10 μm. For list of abbreviations see page 62.

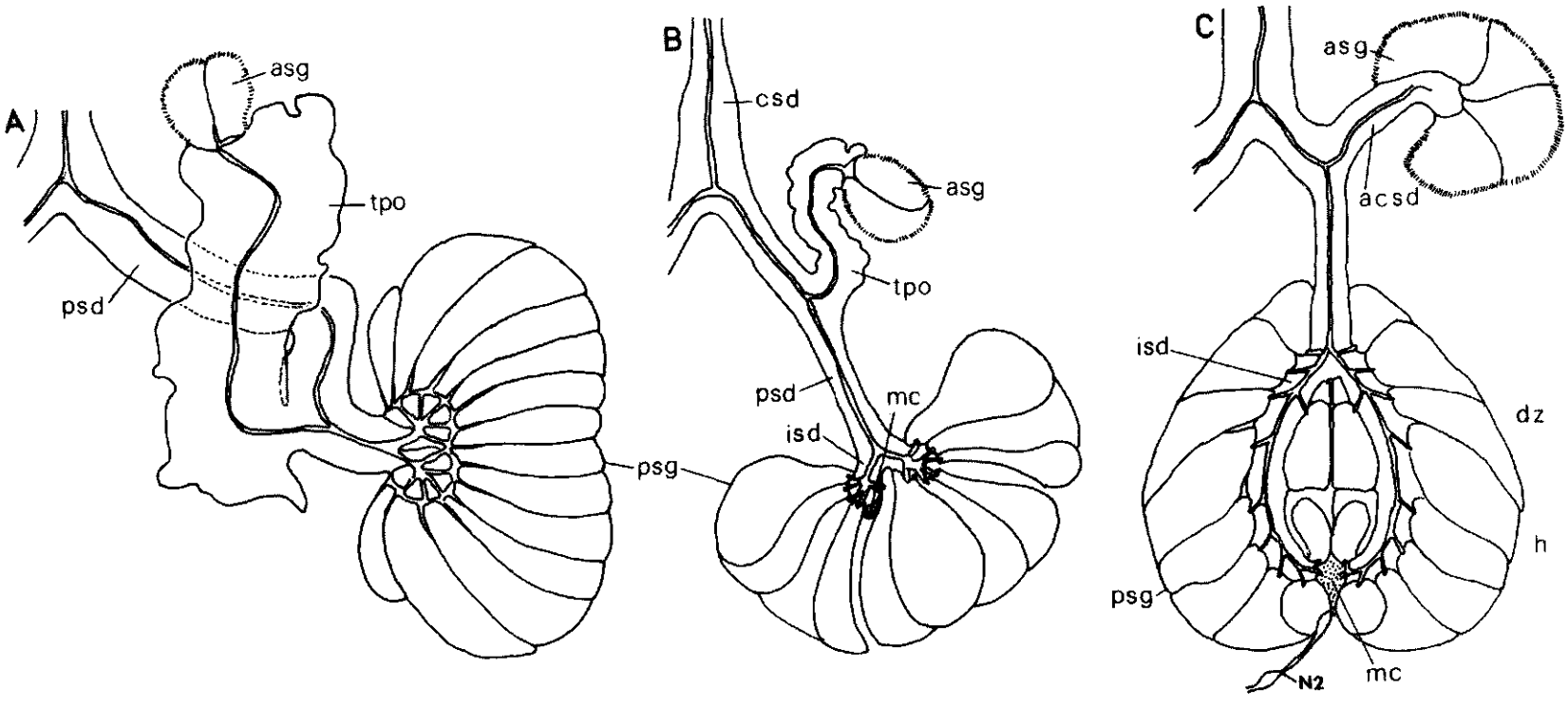


Figure 19 Longitudinal impression of the salivary glands of the Phylloxeridae (A), Adelgidae (B), and Aphididae (C). The nuclei are omitted. For list of abbreviations see page 62.

Table 12 Total number of gland cells of the principal salivary gland of aphid species of seven subfamilies of the Aphididae (see Table 2). Each principal gland is composed of a left lobe (Ll) and a right lobe (Rl).

Aphid	Morph	Left principal gland		Right principal gland		Table
		Ll	Rl	Ll	Rl	
Thelaxes dryophila	wingless viviparous	19	19	19	19	4
	wingless viviparous	19	19	18	18	
	wingless viviparous	19	18	19	20	
Chaitophorus populeti	winged viviparous	22	21	21	21	5
	wingless viviparous	20	22	21	21	
	wingless viviparous	20	21	22	20	
Periphyllus testudinaceus	winged viviparous	21	20	19	19	
	winged viviparous	21	20	20	21	
	wingless viviparous	19	21	21	19	
Calaphis flava	wingless viviparous	21	20	19	19	6
	wingless viviparous	20	19	19	20	
	winged male	20	20	21	20	
Clethrobius comes	wingless viviparous	20	20	19	20	
	wingless viviparous	20	19	19	20	
	wingless viviparous	19	19	21	20	
Monaphis antennata	wingless oviparous	22	21	23	22	7
	winged male	20	21	22	22	
	winged male	22	21	21	20	
Greenidea eugeniae	winged viviparous	22	23	22	22	8
	wingless viviparous	21	23	22	23	
	winged male	23	22	22	23	

Greenidea formosana	winged viviparous	21	20	20	21	
	wingless viviparous	22	22	22	21	
	winged male	21	23	22	22	
Greenidea spec.	winged viviparous	22	23	23	21	
	wingless viviparous	22	22	23	22	
	winged male	22	23	21	20	
Phloeomyzus passerinii	wingless viviparous	23	23	22	23	9
	wingless viviparous	21	23	22	22	
	wingless viviparous	23	22	23	23	
Anoecia spec.	wingless oviparous	21	21	21	22	10
	wingless oviparous	20	20	21	22	
	wingless oviparous	21	20	21	22	
	wingless male	21	21	21	22	
	wingless male	20	21	21	21	
	wingless male	21	21	20	20	
Plocamaphis amerinae	winged viviparous	22	22	22	22	11
	wingless viviparous	22	23	22	22	
	wingless male	21	23	21	21	
Pterocomma salicis	winged viviparous	22	22	23	21	
	winged viviparous	22	22	21	22	
	wingless viviparous	23	22	22	22	

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Abbreviations used in figures

a s d	afferent salivary duct
a s g	accessory salivary gland
b m c	basophilic mesodermal cell
c o	cornicle (siphunculus)
c t c	connective tissue cell
d z	"Deckzell"
h	"Hauptzell"
i s c	intercellular secretory canaliculum
i s d	internal salivary duct
m c	myoepithelioid cell
m v s	microvillar system
m y c	mycetocyte
n s	nucleated sheath
N2	branch of medial dorsal nerve
o e n	oenocyte
p c c	pericardial cell
p s d	principal salivary duct
p s g	principal salivary gland

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