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A histological description of the alimentary tract and related organs of Adelgidae (Homoptera, Aphidoidea)

M.B. Ponsen

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M.B. Ponsen
Hollandseweg 204
6706 KW Wageningen
The Netherlands

Phone: 00-31-(0)317-414158
E-mail: mbponsenir@hetnet.nl

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Contents

Summary	4
Introduction	5
Materials and methods	8
Alimentary tract	10
Stylet bundle	10
Crumena	10
Retort-shaped organ	16
Pharynx	20
Foregut	24
Oesophageal valve	24
Stomach	28
Crenated intestine	28
Descending intestine	30
Rectum	32
Epidermal invagination	32
Anal opening	32
Ovarioles	39
Sexuales	43
Salivary gland system	47
Mycetome	52
Oenocytes	56
Mesodermal tissue	57
Discussion	61
Pharynx	61
Digestive system	61
Rectal organ	76
Oenocytes	76
Haemolymph	78
Multinucleated structure	78
Sexuales	85
Endosymbionts	88
Acknowledgements	96
References	97
Abbreviations used in figures	102

Summary

In all species of the Adelgidae the ectodermal part of the alimentary tract consists of a stylet bundle housing in a crumena, pharyngeal duct, valve, and pump, foregut, and oesophageal valve. The stylets are extruded from bottle-shaped cells situated in retort-shaped organs. The pharyngeal pump is controlled by 12 pairs of muscles as many as that of species of the Phylloxeridae (Aphididae 29). The midgut is the endodermal part of the alimentary tract consisting of a stomach, crenated intestine without any loop or coil, and descending intestine. After hatching the midgut of the sexuales starts to degenerate. The total number of ovarioles is dependent on the total number of stomach cells. The posterior region of the alimentary tract is of ectodermal origin and consists of a very short rectum and epidermal invagination terminating at the anal opening. The latter is controlled by three pairs of anal dorsal muscles and two pairs of anal lateral muscles. Morphologically, each family (Adelgidae and Phylloxeridae) and each subfamily of the Aphididae has its own type of digestive system.

The structure of the salivary pump of adelgid species is similar to that of species of the Aphididae. The adelgid sexuales have degenerated salivary glands.

In all species of the Aphidoidea the haemocytes are lacking. The mesodermal tissue consists of fat cells, basophilic mesodermal cells, and connective tissue cells. Some adelgid species have granulated mesodermal cells but in these species the oenocytes are lacking. These two cell types are absent in the sexuales.

Oenocytes are present in all species of the Aphidoidea, except in some species of the Pemphiginae.

The mycetome of adelgid species consists of mycetocytes harbouring thin rod-shaped endosymbionts. The sexuales have a very small mycetome with degenerated symbionts. Within the Aphididae there are morphologically ten different types of endosymbionts and each subfamily has its own type of endosymbiont. Aphid species with a degenerated midgut have either a degenerated mycetome or no mycetome.

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

Bibliotheek
Plantenfakulteit
Rijksuniversiteit Wageningen
Postbus 8122
6700 ER WAGENINGEN

Introduction

Biological studies, morphological descriptions, and illustrations of species of the family Adelgidae have been produced by Cholodkovsky (1896), Börner (1908), Fluiter (1934), Börner and Heinze (1957), Heinze (1962), Lampel (1968), and Carter (1971) (Table 1). They live exclusively on conifers (Pinaceae) ("Koniferenläuse", "Tannenläuse" – Börner, 1908). The primary host is invariably a *Picea* spp. on which a gall is produced whereas the secondary host is a species of *Abies*, *Larix*, *Pinus*, *Pseudotsuga*, or *Tsuga* but no gall is produced on any member of these genera.

The life cycle of host-alternating species is a two-year one and is made up of six principal morphs, viz. wingless fundatrices, winged gallicolae ("Tannengallläuse"), wingless sistens, wingless progrediens, winged progrediens (= sexuparae), and wingless sexuales. The sexuales, fundatrices, and gallicolae live on the primary host, and the other morphs feed on the secondary host. The two winged morphs maintain the migration cycle from and to the other host. In some adelgid species the life cycle may be shortened by the absence of one or more of the six morphs, and the partial cycle may be confined in some to the primary host, in others to the secondary host. All morphs produce eggs parthenogenetically, except the female sexuales.

When the fundatrix starts feeding in spring gall formation in *Picea* is initiated, but complete gall formation depends on feeding by the gallicolae (Cumming, 1959).

Within the family Adelgidae the digestive system of gallicolous *Adelges abietis* (Witlaczil, 1886; Börner, 1938), progrediens of *Adelges nordmannianae* (Marchal, 1913), fundatrices of *Adelges laricis* (Kunkel, 1966), and *Adelges piceae* adults (Jarial, 1998) consists of a foregut, oesophageal valve, a somewhat dilated stomach, a tubular intestine without a loop or coil, a balloon-shaped hindgut, and an anal opening, but lacks a filter-system and the Malpighian tubules. According to Börner (1952) and Börner and Heinze (1957) the digestive system of the Adelgidae is structurally primitive and similar to that of the Thelaxidae and the Chaitophoridae. Kunkel (1966) has made histological studies of the stomach and oesophageal valve of a fundatrix of *Adelges laricis*. The ultrastructure of the external mouthparts of sistens of *Adelges piceae* has been studied by Forbes and Mullick (1970) and the anterior midgut of *Adelges piceae* adults by Jarial (1998).

The purpose of the present study is to investigate the alimentary tract of the Adelgidae to compare them with the alimentary tract of the Phylloxeridae and several subfamilies of the Aphididae.

The spelling of adelgid names used by the respective authors are corrected both in the text and in the Tables according to Carter (1971) and presented in Table 1. The various generic names of the species of the genus *Adelges*, given by many authors since Linnaeus in 1756, have been compiled by Varty (1956). All aphid names of the Aphididae are corrected according to Remaudière and Remaudière (1997).

Table 1 Names of species belonging to members of the family Adelgidae as used by various authors and corrected by Carter (1971).

Present name	Name used by author	Author
<i>Adelges abietis</i> (Linnaeus)	<i>Chermes abietis</i> Linnaeus	Leuckart, 1859; Mark, 1877; Wülfacil, 1886; Dreyfus, 1894; Fernald and Cooley, 1898; Börner, 1908, 1938; Sulc, 1910; Schneider-Orelli, 1947; Rohlfritsch, 1976
<i>Adelges cooleyi</i> (Gillette)	<i>Chermes abietis</i> Kalt.	Cholodkovsky, 1897, 1900
	<i>Sacchiphantes abietis</i> (Linnaeus)	Profft, 1937; Steffan, 1961, 1962; Kunkel, 1966
	<i>Adelges abietis</i> L.	Meyer, 1951; Plumb, 1953; Kunkel, 1972
	<i>Adelges cooleyi</i> (Gillette)	Anand, 1928; Fluiter, 1934; Cameron, 1936; Cumming, 1959; Polaszek, 1987
<i>Adelges japonicus</i> (Monzen)	<i>Gilletteella cooleyi</i> Gill.	Börner and Heinze, 1957; Kunkel, 1966
	<i>Adelges cooleyi</i> Börner	Fräncke-Grosmann, 1950
	<i>Chermes cooleyi</i>	Chrystal, 1922
	<i>Adelges japonicus</i> (Monzen)	Inouye, 1953
<i>Adelges lapponicus</i> Cholodkovsky	<i>Chermes lapponicus</i>	Cholodkovsky, 1900, 1905
<i>Adelges laricis</i> (Vallot)	<i>Cnaphalodes lapponicus</i> (Chol.)	Steven, 1917
	<i>Chermes laricis</i>	Leuckart, 1859
	<i>Adelges laricis</i>	Schneider-Orelli, 1947; Börner and Heinze, 1957; Kunkel, 1966
	<i>Chermes strobilobius</i> Kalt.	Dreyfus, 1884; Cholodkovsky, 1897, 1900; Sulc, 1910; Rohlfritsch, 1976
<i>Adelges merkeri</i> (Eichhorn)	<i>Chermes coccineus</i>	Cholodkovsky, 1896, 1900
	<i>Adelges strobilobius</i> (Kaltenbach)	Anand, 1928
	<i>Cnaphalodes strobilobius</i> Kaltenbach	Börner, 1908; Nüsslin, 1910; Steven, 1917; Speyer, 1919, 1924
	<i>Adelges</i> (<i>Cnaphalodes</i>) <i>laricis</i> Vall.	Profft, 1937
<i>Adelges nordmannianae</i> (Eckstein)	<i>Dreyfusia merkeri</i>	Eichhorn, 1961
<i>Adelges piceae</i> (Ratzeburg)	<i>Chermes nüsslini</i> Börner	Marchal, 1913
	<i>Dreyfusia nordmannianae</i> Eckstein	Fräncke-Grosmann, 1937b; Profft, 1937
	<i>Dreyfusia nüsslini</i> Börner	Steven, 1917; Chrystal, 1926; Falck, 1928; Schimitschek, 1928; Schneider-Orelli et al., 1929; Kloft, 1955, 1960; Eichhorn, 1961
	<i>Adelges nüsslini</i> (Börner)	Varty, 1956; Wylle, 1958
<i>Adelges prelli</i> (Grosmann)	<i>Chermes piceae</i>	Leuckart, 1859
	<i>Chermes piceae</i> (Ratzeburg)	Nüsslin, 1903, 1908; Dreyfus, 1894; Börner, 1908; Marchal, 1913
	<i>Dreyfusia piceae</i> Ratzeburg	Fräncke-Grosmann, 1937b; Profft, 1937; Kloft, 1955, 1960
	<i>Adelges piceae</i> Ratzeburg	Balch, 1952; Varty, 1956; Forbes and Mullick, 1970; Jarial, 1998
<i>Adelges schneideri</i> (Börner)	<i>Dreyfusia prelli</i> Grosmann	Fräncke-Grosmann, 1937a; Eichhorn, 1961
	<i>Dreyfusia schneideri</i> Börner	Fräncke-Grosmann, 1937b

<i>Adelges segregis</i> (Steffan)	<i>Sacchiphantes segregis</i> Steffan	Steffan, 1962; Heinze, 1962
<i>Adelges tardus</i> (Dreyfus)	<i>Adelges tardus</i>	Kunkel, 1966
<i>Adelges todomatsui</i> (Inouye)	<i>Dreyfusia todomatsui</i>	Eichhorn and Carter, 1978
<i>Adelges tsugae</i> Anmand	<i>Adelges tsugae</i> Anmand	McClure, 1989; Young et al., 1995
<i>Adelges viridana</i> (Cholodkovsky)	<i>Chermes viridanus</i> (Chol.)	Cholodkovsky, 1897, 1900; Gaumont, 1954, 1955
	<i>Pineus</i> (?) <i>viridanus</i> (Cholodkovsky)	Börner, 1908
<i>Adelges viridis</i> (Ratzeburg)	<i>Chermes viridis</i> Ratz.	Blochmann, 1887, 1889; Cholodkovsky, 1897, 1900; Nüsslin, 1910; Steven, 1917; Speyer, 1919
	<i>Sacchiphantes viridis</i> (Ratzeburg)	Profft, 1937; Steffan, 1961, 1962
<i>Aphrastasia pectinatae</i> Cholodkovsky	<i>Aphrastasia pectinatae</i> Chldk.	Nüsslin, 1909; Eichhorn and Carter, 1978
	<i>Aphrastasia pectinatae</i> (Cholodkovsky)	Inouye, 1953
	var. <i>isiharai</i>	
<i>Pineus abietinus</i> n.sp.	<i>Pineus abietinus</i> n.sp.	Underwood and Balch, 1964
<i>Pineus cembrae</i> (Cholodkovsky)	<i>Chermes sibiricus</i> L.	Cholodkovsky, 1890, 1900
	<i>Pineus sibiricus</i> (Cholodkovsky)	Börner, 1908
	<i>Pineus pini</i> (L.)	Marchal, 1913; Steven, 1917
	<i>Chermes orientalis</i> Dreyfus	Becker, 1905
	<i>Pineus orientalis</i>	Profft, 1937; Polaszek, 1987
	<i>Pineus similis</i> (Gill.)	Cumming, 1962
<i>Pineus patchae</i> Börner	<i>Chermes pini</i> Koch	Cholodkovsky, 1900
<i>Pineus pini</i> (Macquart)	<i>Pineus pini</i> (Macquart)	Profft, 1937; Mendel et al., 1994
<i>Pineus pineoides</i> (Cholodkovsky)	<i>Pineus pineoides</i> Cholodk.	Profft, 1937
<i>Pineus pinifoliae</i> (Fitch)	<i>Pineus pinifoliae</i> (Fitch)	Allen and Dimond, 1968
<i>Pineus strobi</i> (Hartig)	<i>Pineus strobi</i> (Hartig)	Doane, 1961; Raske and Hodson, 1964
	<i>Pineus strobus</i> Hartig	Profft, 1937

Materials and methods

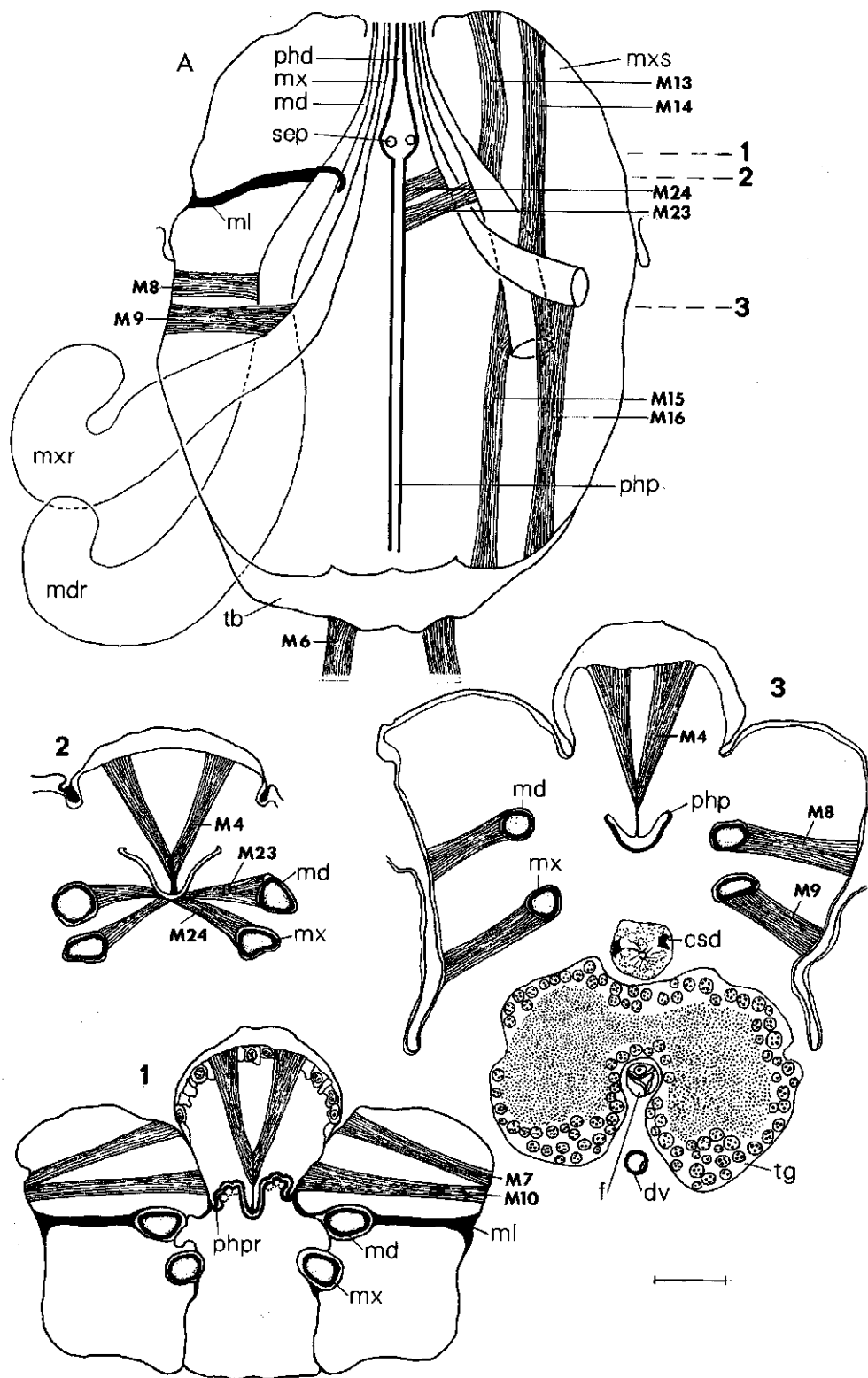
Specimens of the species listed in Table 2, were collected from the host plants and put in Duboscq-Brasil's fluid. After fixation the aphids were dehydrated in a graded series of ethanol and in methyl benzoate, stored in methyl benzoate cellulidin (2 per cent) for three days or longer, and then in toluene and finally embedded in paraplast. Serial sections, 7 and 8 μm thick, were stained in 1 per cent 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 help of a Wild drawing tube.

The morphology of a digestive system was reconstructed from the drawings of serial sections of a whole aphid viewed at a magnification of $\times 600$. The number of nuclei with their conspicuous big nucleoli, which correspond to the number of cells, were counted at a magnification of $\times 1500$. The length of the aphid and that of the digestive system was calculated by multiplying the number of serial sections by the thickness of each section, i.e. 7 or 8 μm .

In order to dissect the digestive system, aphids were placed on double sided self-adhesive tape attached to a black plastic plate. Under a dissecting microscope each aphid was covered with a drop of Levy solution and dissected using watchmaker's forceps.

For electron microscopy the aphids were put one by one in 96 per cent ethanol for 10 seconds to extract the air bubbles from the surface of the cuticle and from the tracheal system. Thereafter they were transferred to 0.1 M cacodylate buffered (pH 7.4) glutaraldehyde (3 per cent) for 2 to 4 hours and then prepared, as described previously by Ponsen (1991).

Figure 1 Oblique section of the musculature of the stylets of a female sexuales of *Adelges cooleyi* (A). Transverse sections of the pharyngeal valve of a male of *Adelges laricis* (1), the pharyngeal pump posterior to the valve of a female sexuales of *Adelges laricis* (2), and half-way the pharyngeal pump of a male of *Adelges cooleyi* (3). The dotted lines indicate the plane of the transverse sections 1-3. Bar represents 10 μm . For list of abbreviations see page 102.



Alimentary tract

In all adelgid species and morphs investigated (Table 2) the ectodermal part of the anterior region of the alimentary tract consists of the stylet-bundle, pharynx, foregut, and oesophageal valve.

The piercing organ of the Adelgidae is the stylet-bundle. It is composed of four stylets: one pair of mandibular and one pair of maxillary stylets (Figures 1A and 7F-G). Each stylet originates from a retort-shaped organ. One pair of retort-shaped organs is situated in the middle region of the head from which the mandibular stylets run parallel to the pharyngeal pump. The maxillary stylets originating from retort-shaped organs situated in the lateral region of the head, cross the mandibular stylets dorsally and run subsequently between the pharyngeal pump and the mandibular stylets. From the retort-shaped organs the stylets are expanded forming hollow chitinous structures but taper gradually to their needle-like form (Figure 1A).

Subsequently the stylets run to the end of the epipharynx where the two maxillary stylets join the pharyngeal duct (p h d) and the efferent salivary duct (e s d) in a chitinous groove of the epipharynx (Figures 2 no. 4 and 4 no. 4). Thereafter the two maxillary stylets become firmly interlocked enclosing dorsally the food canal and ventrally the salivary canal (Figures 2 no. 3, 4 no. 3, and 7F-G). The mandibular stylets are held in a small groove on each side of the middle-groove (Figures 2 no. 4 and 4 no. 4). The stylets are so arranged that they fit snugly into the grooves, being held firmly in position, at the same time having perfect freedom of movement for protraction or retraction.

After leaving the head the mandibular stylets are closely applied to the maxillary pair to form the stylet bundle. The bundle lies in an almost completely enclosed, thick chitinous groove on the ventral face of the labrum (Figures 2 no. 2-1 and 4 no. 2-1). The stylet-bundle soon crosses over into a ventral pouch or crumena (Figure 5 no. 1) which for a short distance is closed by the labrum (Figure 5 no. 2).

The term "crumena" is introduced by Mark (1877) to describe a non-muscular, epidermal invagination housing the very long and flexible stylets of species of the Coccidae. Later on this organ has also been observed in the Psyllidae and Adelgidae (Krassiltschik, 1893; Dreyfus, 1894; "Borstensack" – Börner, 1908), and Aleyrodidae (Weber, 1935; Singh, 1971). According to Weber (1930) the stylet-bundle must be withdrawn into a crumena since species of the above mentioned families possess a very short labium.

As summarized in Table 3 it appears that mainly in all adelgid species the stylet bundle forms a single loop in a figure-eight fashion within the crumena. However, within the crumena of the fundatrices and sistens of some adelgid species there is a double loop of the stylet bundle. According to Steffan (1962a) the stylet bundle of the fundatrices of *Adelges abietis* forms one loop inside the crumena and one loop outside the crumena before entering into the labial groove. Forbes and Mullick (1970) found in larval sistens of *Adelges piceae* the crumena runs posteriad and subsequently makes one loop forming an inverted U-shaped structure containing the stylet bundle. Consequently, in electron microscopical transverse sections of the thorax, there are three sections of the crumena, each with two sections of the stylet bundle inside. In adults the crumena is lacking.

The crumena starts in the midline of the labium at the junction of the suboesophageal and thoracic ganglion where the two salivary ducts unite to the common afferent salivary duct leading to the salivary pump. It runs posteriad ventral to the thoracic ganglion and terminates blindly in the mesothorax half-way or at the end at the thoracic ganglion. In

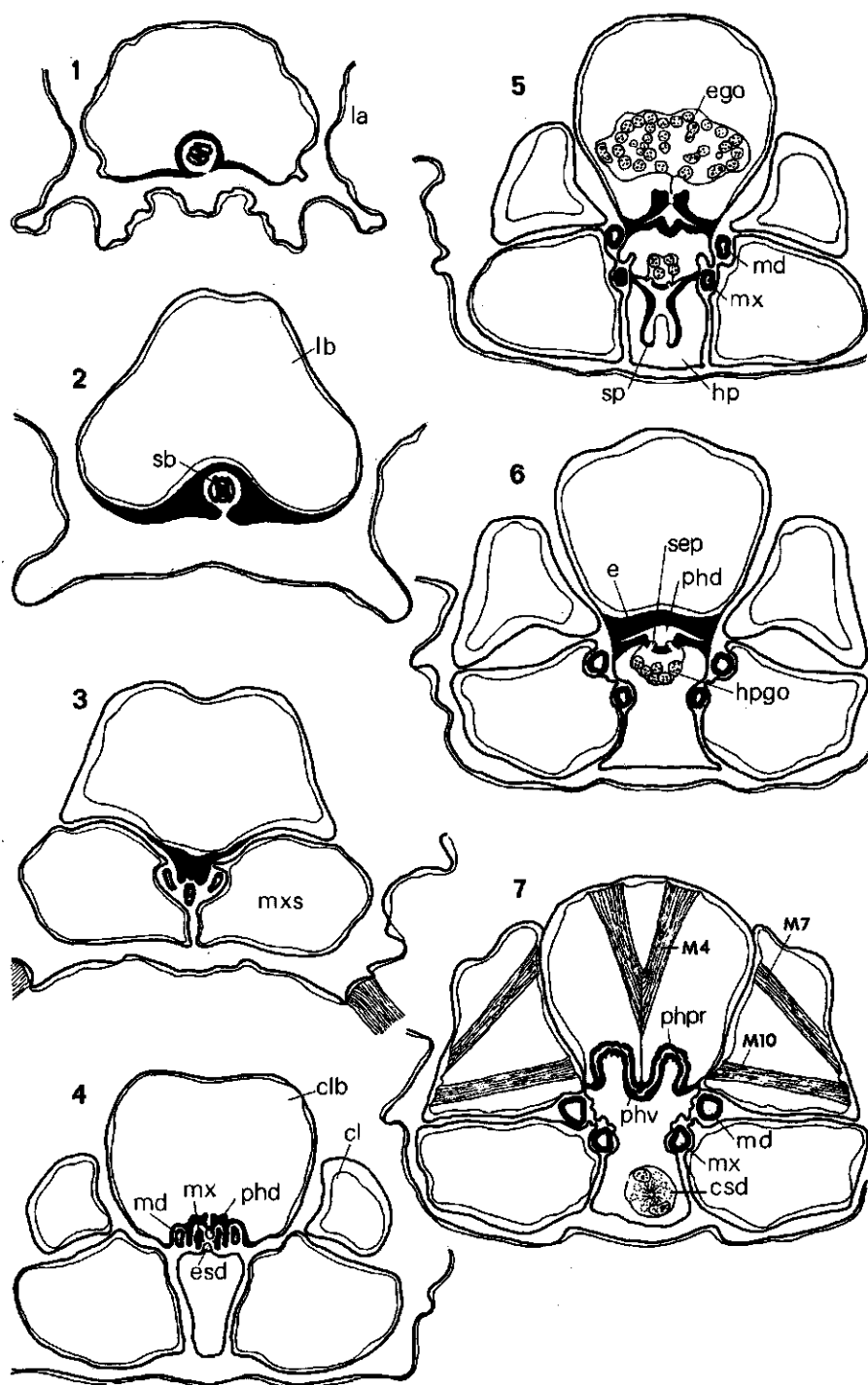


Figure 2 Transverse serial sections 1-7 of the pharyngeal duct and the pharyngeal valve of a larval gallicolous *Adelges abietis*. The sections correspond with the numbers given in Figure 4A. Bar represents 10 µm. For list of abbreviations see page 102.

Table 2 List of species of the family Adelgidae studied, their host plant, morph, and locality data.

Aphid	Morph	Host plant		Locality, data
		Primary	Secondary	
<i>Adelges abietis</i> (Linnaeus)	Pseudo-fundatrices	<i>Picea abies</i>		Wageningen, 17.IV.1997
	Gallicolae	<i>Picea abies</i>		Wageningen, 3.VII.1982
	Gallicolae	<i>Picea abies</i>		Viéville-s/s-les Côtes, Champagne (France), 24.VII.1987
<i>Adelges cooleyi</i> (Gillette)	Gallicolae	<i>Picea engelmannii</i>		Jardin des Plantes, Paris (France), 1.VII.1997
	Fundatrices	<i>Picea sitchensis</i>		Wageningen, 18.IV.1997
	Gallicolae	<i>Picea sitchensis</i>		Hardenberg, 23.VII.1982
	Gallicolae	<i>Picea sitchensis</i>		Wageningen, 14.VIII.1997
	Gallicolae	<i>Picea glauca</i>		Wageningen, 11.VIII.1997
	Gallicolae	<i>Picea omorika</i>		Wageningen, 11.VIII.1997
	Gallicolae	<i>Picea likiangensis</i> var. <i>balfouriana</i>		Parc Floral de la Source, Orléans-Olivet (France), 2.VII.1997
<i>Adelges laricis</i> Vallot	Sistens		<i>Pseudotsuga menziesii</i>	Wageningen, 14.IV.1997
	Wingless progrediens		<i>Pseudotsuga menziesii</i>	Wageningen, 19.V.1997
	Sexuparae		<i>Pseudotsuga menziesii</i>	Wageningen, 19.V.1997
	Sexuales	<i>Picea sitchensis</i>		Wageningen, 27.V.1997
	Fundatrices	<i>Picea sitchensis</i>		Wageningen, 22.IV.1998
	Gallicolae	<i>Picea abies</i>		Prachtice (Czech Republic), 3.IX.1993
	Gallicolae	<i>Picea abies</i>		Wageningen, 8.VIII.1997
	Wingless progrediens		<i>Larix decidua</i>	Wageningen, 2.VII.1993
	Wingless progrediens		<i>Larix kaempferi</i>	Wageningen, 29.V.1997
	Sexuparae		<i>Larix decidua</i>	Wageningen, 28.V.1997
<i>Adelges lapponicus</i> Cholodkovsky	Sexuales	<i>Picea abies</i>		Wageningen, 3.VI.1997
	Gallicolae	<i>Picea abies</i>		Weissensee (Austria), 20.VII.1984
	Gallicolae	<i>Picea orientalis</i>		Wageningen, 15.VII.1982
<i>Adelges nordmannianae</i> (Eckstein)	Wingless progrediens		<i>Abies nordmanniana</i>	Wageningen, 27.V.1997
<i>Adelges viridana</i> (Cholodkovsky)	Sexuparae		<i>Larix kaempferi</i>	Wageningen, 23.VI.1984
<i>Adelges viridis</i> (Ratzeburg)	Gallicolae	<i>Picea abies</i>		Weissensee (Austria), 20.VII.1984
<i>Aphrastasia pectinatae</i> Cholodkovsky	Sistens		<i>Abies lasiocarpa</i>	Ås (Norway), 7.IX.1993
<i>Pinus orientalis</i> (Dreyfus)	Gallicolae	<i>Picea orientalis</i>		Wageningen, 23.VI.1986

larvae the crumena runs in a medial groove of the thoracic ganglion (Figure 6A), but in adults it is situated outside the ganglion. The lumen of the crumena is completely occupied by a very thick endocuticle with deep irregular invaginations (Figure 5 no. 1 and 6C). These invaginations serve to support the stylets together to a bundle. The crumena is not provided with muscles.

Paraplast sections of all asexual adelgid species (Table 2) showed that the stylet bundle extends to the end of the crumena where it turns (Figure 5 no. 11) thus forming a single loop. After leaving the crumena the stylet bundle makes one voluminous loop via a gutter in the anterior part of the labrum (Figure 5 no. 3). Subsequently the stylet bundle runs into the labial groove which is an almost completely enclosed chitinous structure along the ventral surface of the labium (Figure 5 no. 4-13). In the middle labial segment the groove deepens gradually to the centre of the labium and the walls of the groove somewhat lengthen forming an irregular narrow crevice (Figure 5 no. 6). At the end of the last labial segment the groove has a very thick chitinous wall surrounding the stylet bundle provided with two sensillary pores in the dorsal region (Figure 5 no. 13). Outside the head the stylet bundle is held in position by transverse muscles. They are inserted on the cuticular ring of the groove around the bundle and originate from the dorsal wall of the labium (Figure 5 no. 4-12).

According to Forbes and Mullick (1970), the thick-walled groove at the end of the labium (Figure 5 no. 13) is the labial clamp, an efficient vice-like clamping mechanism which firmly grips the stylet bundle to fix the point of stylet insertion, as observed in electron micrographs of *Adelges piceae* sistens. Two nerves enter the clamp proximally and run in a duct to the clamp's distal end. For a very short distance distal to the labial clamp, the stylet bundle lies in an open labial groove (Figure 5 no. 14). A similar clamping device occurs in the labial groove of about eleven species within the Hemiptera, except the aphids, as summarized by Singh (1971).

In all sectioned adelgid larvae (Table 2) the stylet bundle is present within the crumena, but not in that of adults. From this it can be concluded that after withdrawing from the host plant only larvae are able to harbour their stylets within the crumena. Schneider-Orelli (1947) observed that *Adelges abietis* and *Adelges laricis* withdraw their stylet bundle from the crumena by using the labium.

In electron micrographs given by Forbes and Mullick (1970) the maxillary stylets of *Adelges piceae* sistens are interlocked by a series of ridges and grooves to form dorsally the food canal and ventrally the salivary canal between their opposed inner surfaces (Figure 7F). The inner surfaces of the mandibular stylets are contoured to conform to the outer surfaces of the maxillary stylets. In *Adelges tsuga* progrediens the mandibular stylets have deep grooves in which the maxillary stylets lie; these maxillary stylets can be extended from and retracted within the mandibular stylets (Young et al., 1995).

The hollow chitinous structure of each mandibular stylet (Figures 1 no. 1-3, 2 no. 7, 3 no. 8-9, and 4 no. 8) passes gradually into an oval-shaped canal and terminates near the tip of the stylet. In *Adelges piceae* each mandibular canal contains three dendrites (Figure 7F; Forbes and Mullick, 1970), but in *Myzus persicae* (Sulzer) (Figure 7G; Forbes, 1966, 1969), *Acyrtosiphon pisum* (Harris) (Forbes, 1977), *Rhopalosiphum maidis* (Fitch) (Parrish, 1967), *Brevicoryne brassicae* (Linnaeus) (Wensler, 1974), and *Aphis fabae* Scopoli (Tjallingii and Hogen Esch, 1993) two dendrites.

The stylets of the fundatrices are longer than those of the gallicolae of *Adelges abietis* (Fernald and Cooley, 1898); the stylets of the fundatrices and gallicolae are longer than those of the sistens of *Adelges laricis* and *Adelges abietis* (Cholodkovsky, 1900;

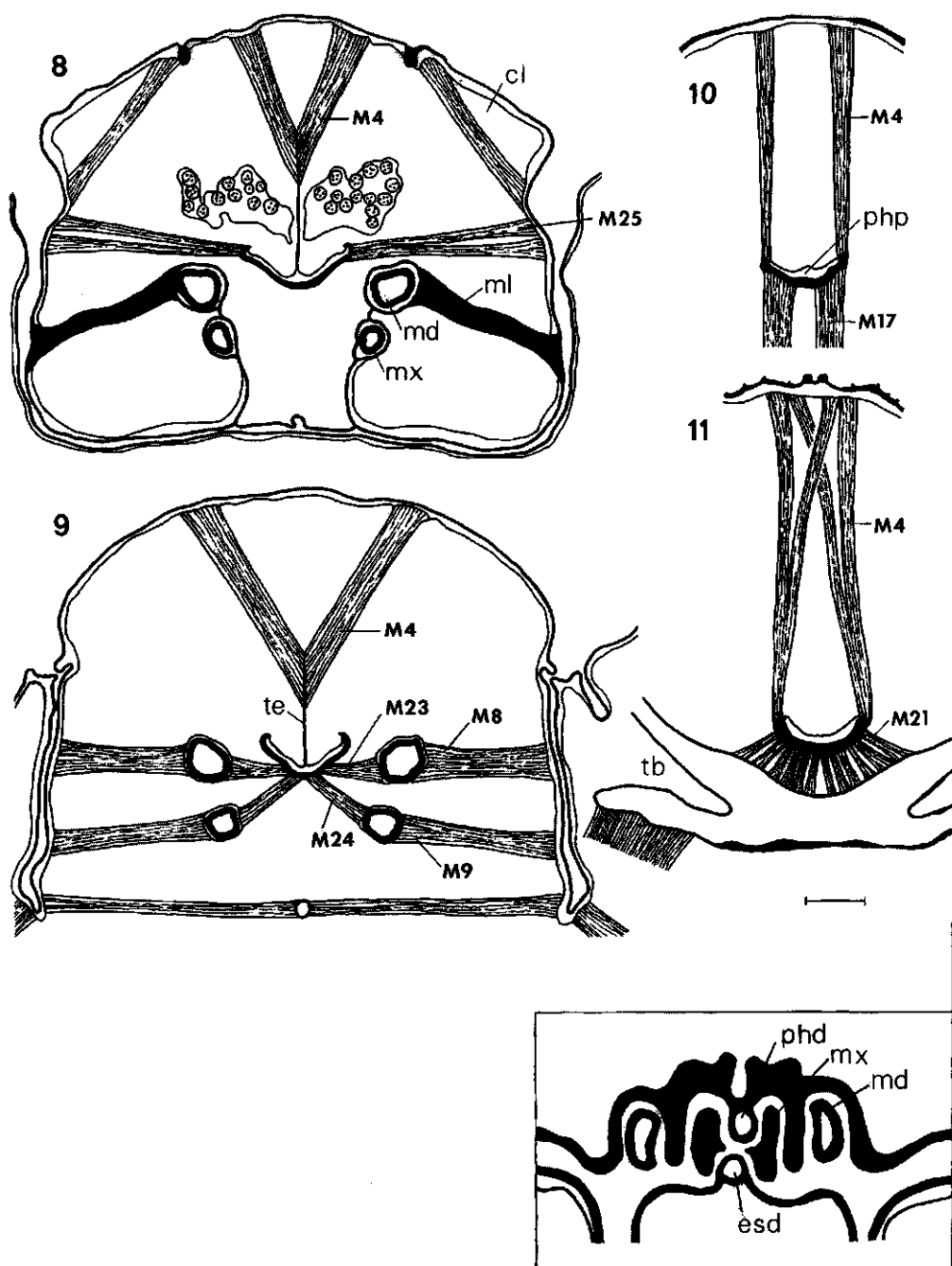


Figure 3 Transverse serial sections 8-11 of the pharyngeal pump of a gallicolous larva of *Adelges abietis*. The sections correspond with the numbers given in Figure 4A. Bar represents 10 μm . Inset: Magnification of transverse section no. 4 in Figure 2 and 4. For list of abbreviations see page 102.

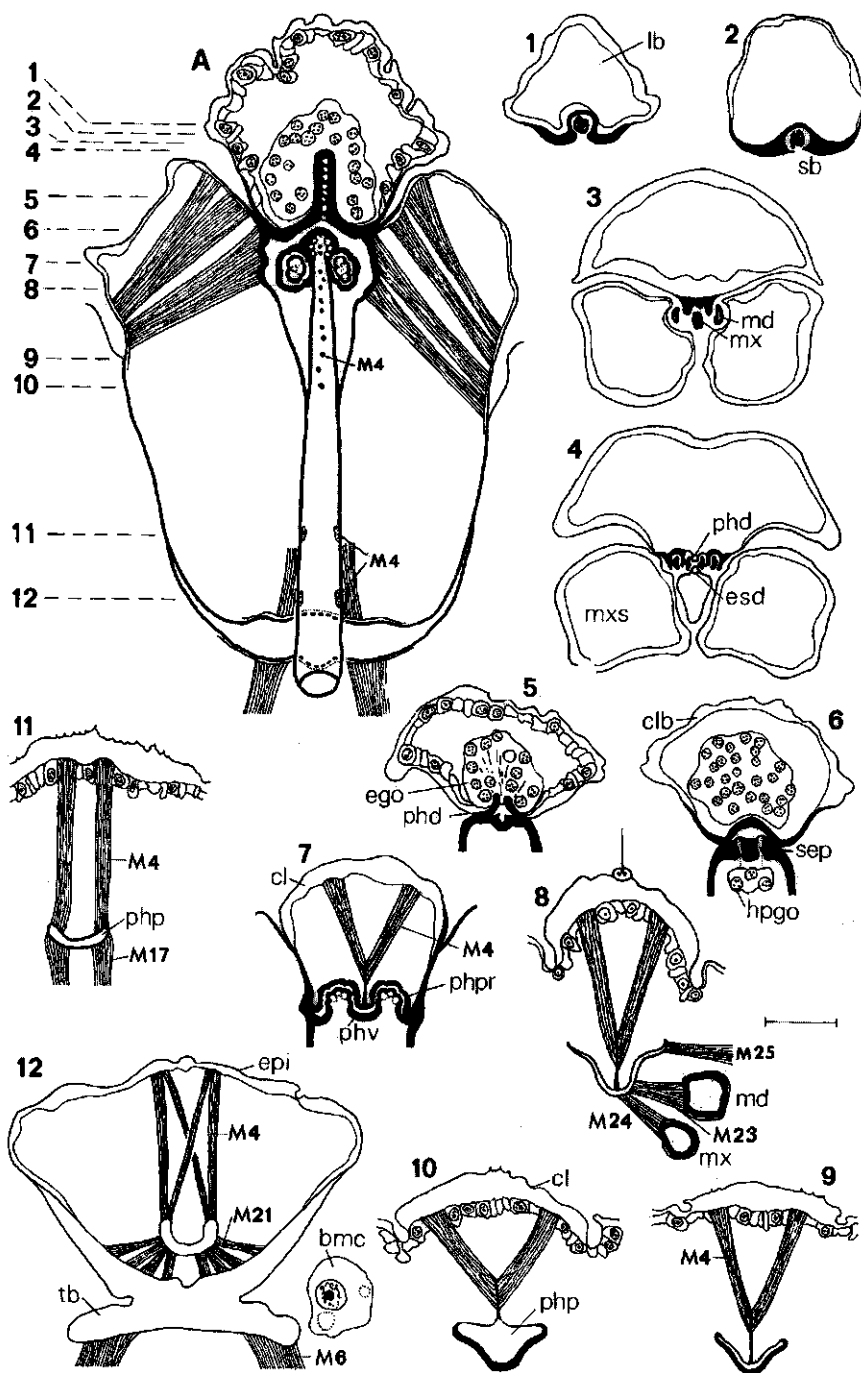


Figure 4 Oblique section of the pharyngeal system of a male of *Adelges laricis* (A). Note the 14 pairs of pharyngeal muscles (M4), the 8 sensillary pores in the epipharynx, and the 6 pores of the pharyngeal valve. The dotted lines indicate the plane of the transverse serial sections 1-12. Transverse serial sections 1-8 taken from a female sexuales of *Adelges laricis* and 9-12 from a female sexuales of *Adelges cooleyi*. See inset in Figure 3. Bar represents 10 µm. For list of abbreviations see page 102.

Schneider-Orelli, 1947); the stylets of the fundatrices are longer than those of the sistens of *Adelges abietis*, *Adelges segregis*, and *Adelges viridis* (Steffan, 1962b); the stylets of the sistens are longer than those of the progrediens of *Adelges piceae* (Marchal, 1913), *Adelges nordmannianae* (Schneider-Orelli et al., 1929), *Aphrastasia pectinatae* var. *ishiharai* (Inouye, 1953), *Adelges merkeri*, *Adelges prelli* (Eichhorn, 1961), *Pineus strobi* (Raske and Hodson, 1964), and *Adelges todomatsui* (Eichhorn and Carter, 1978). The stylet length of the above mentioned adelgids is about 2750 μm for the fundatrices, about 1300 μm for the sistens, and about 1040 μm for the progrediens. Gaumont (1955) stated that the stylets of the sistens of *Adelges viridana* increase in length after each generation from 1780 μm in spring to 2740 μm at the end of June.

In young larvae of the fundatrices of *Adelges abietis* (Fernald and Cooley, 1898) and *Adelges nordmannianae* (Varty, 1956), the sistens of *Adelges nordmannianae* (Schneider-Orelli et al., 1929), *Adelges prelli* (Francke-Grosmann, 1937a), and *Adelges piceae* (Balch, 1952; Varty, 1956), and the sexuparae of *Adelges tsugae* (Young et al., 1995) the length of the stylet bundle is more than three times that of the body. During larval life the stylet bundle of the sistens of *Adelges piceae* (Marchal, 1913), *Adelges prelli* (Francke-Grosmann, 1937a), and *Adelges piceae* (Balch, 1952) and that of the sistens and progrediens of *Adelges nordmannianae*, *Adelges piceae*, and *Adelges schneideri* (Francke-Grosmann, 1937b) does not increase in length. Hence in the adult stage the length of the stylet bundle equals that of the body.

Inside the head there are two muscles attached to the basal end of each stylet: a retractor muscle on the inner side originating from the tentorial bar (M15 and M16) and a protractor muscle (M13 and M14) inserted on the outer side of the stylet and originating from the ventral wall of the maxillary sclerite (Figure 1A). More proximally on the outer side of the stylet another muscle is inserted which originates from the lateral wall of the maxillary sclerite (M8 and M9; Figures 1A, 1 no. 3, 3 no. 9, and 7A). On the inner side there are muscles attached to the pharynx floor (M23 and M24); Figures 1A, 1 no. 2, 3 no. 9, 4 no. 8 and 7B). Just before the pharyngeal valve each mandibular stylet is provided with a lever, a chitinous compact structure to support the mandibular stylets during their operation (Figures 1A, 1 no. 1, and 3 no. 8).

Each stylet originates from a retort-shaped organ (Metschnikov, 1866). The embryonic development of the stylets has been studied for many species of the Hemiptera (Weber, 1930; Heriot, 1934; Pesson, 1944; Newcomer, 1948; Singh, 1971), including the sistens of *Adelges piceae* (Balch, 1952), the fundatrices and gallicolae of *Adelges abietis*, and the fundatrices, gallicolae and sistens of *Adelges viridis* (Steffan, 1961). Each stylet elongates gradually in the form of a watch-spring consisting ultimately of about two and a half coils. After hatching the stylets are uncoiled and protrude into the labial groove. During each moult the old stylet is replaced by a new one.

After hatching of the adelgids studied (Table 2) the stylets are already completely developed. The very long and flexible stylets extend from the retort-shaped organs via the crumena and the labial groove to the tip of the labium. In the first larval stage the retort-shaped organs have a compact structure like a flower-bud (Figure 7A). Each organ consists of two middle epidermal invaginations and on each side one lateral epidermal invagination. The cuticular layer lining of the lateral epidermal invaginations, the common epidermal invagination, and that of the body wall form one continuous layer. These invaginations consist of squamous cells with irregular-shaped nuclei. The two middle invaginations are composed of bottle-shaped cells of which the spherical nuclei are situated at their base (Figure 7A). The distal end of these cells extrude fine, long fibrils which unite to a yellow

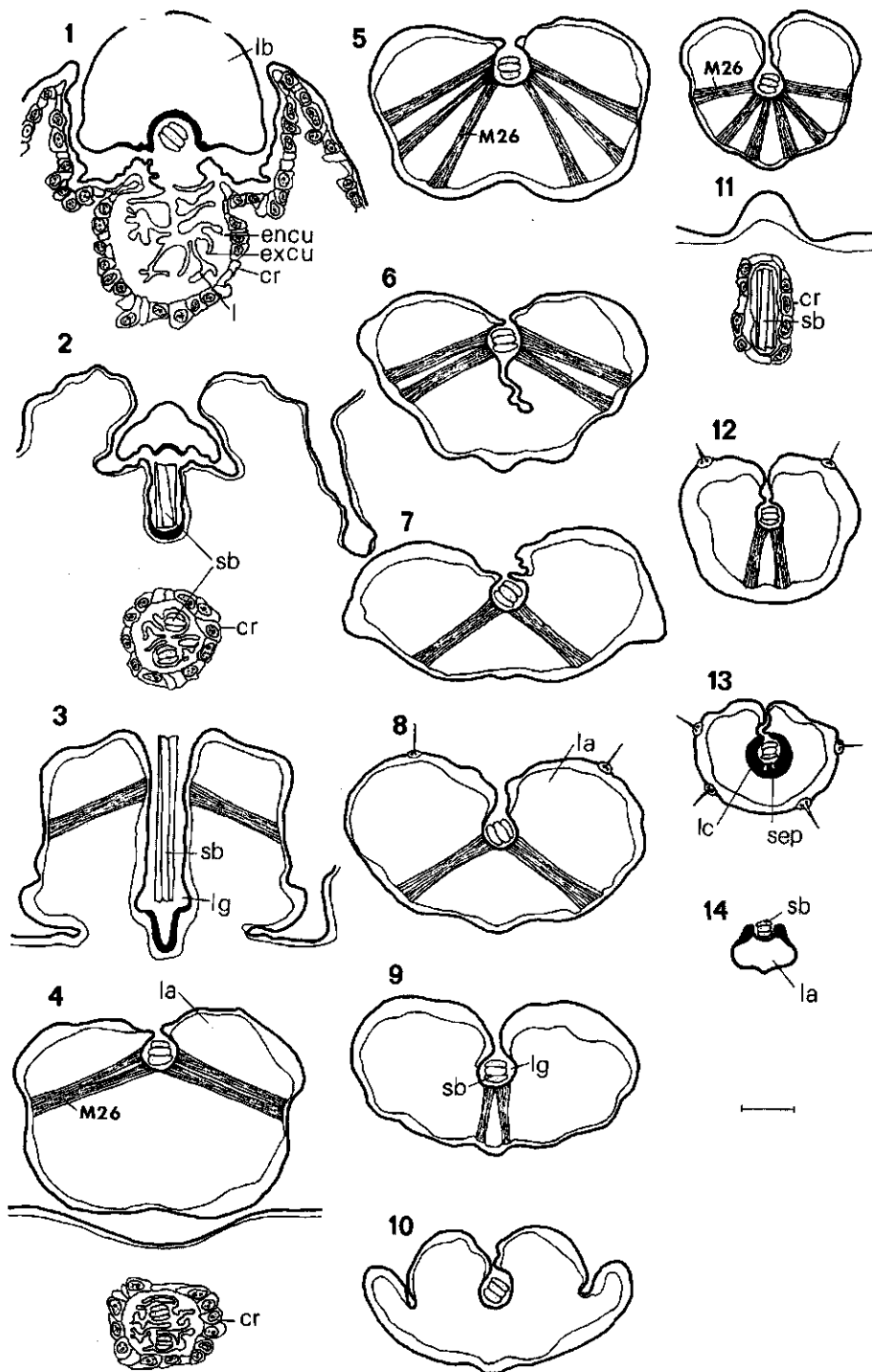


Figure 5 Transverse serial sections 1-14 of the stylet bundle inside the longitudinal labial groove of the rostrum of a gallicolous larva of *Adelges abietis*. Note the nine pairs of transverse labial muscles (M26) and the two sensillary pores (s e p) in the labial clamp (l c). Bar represents 10 μ m. For list of abbreviations see page 102.

chitinous substance forming the new stylet on solidification at each moult. The middle invaginations are a continuation of the lateral invaginations and between them is a space which is in open connection with the body cavity. In this space and in the haemolymph waxy droplets are found. The waxy droplets originate from fat cells. During larval life the retort-shaped organs increase in size and the bottle-shaped cells change gradually into slender cells. At the end of larval life these organs start degenerating and this process continues in the adult stage resulting in shriveled cuticular structures.

The stylets did not moult but are discarded along its entire length from the retort-shaped organs. In the exuviae each hollow part of the stylet is located inside the shedded exocuticle of the common epidermal invagination; the shedded exocuticle of the lateral epidermal invaginations is attached to that of the common epidermal invagination (Figure 7H). The compact part of the very long adelgid stylets are not situated inside the crumena of the shedded skin. They remain behind in the shedded exocuticle of the labial groove and protrude still considerably out of the labium, exceeding the length of the latter two to three times. In the exuviae of aphids without a crumena the stylets extend a very short distance out of the labium. The discarded smooth dark-brown stylets contrast with the transparent

Table 3 List of adelgid species and their morphs of which the stylet bundle lies in a single or double loop inside the crumena according to different authors. The adelgid names used by the respective authors are given in Table 1.

Aphid (present name)	Within the crumena		Author
	Single loop	Double loop	
<i>Adelges abietis</i>	fundatrices	fundatrices	Schneider-Orelli, 1947; Steffan, 1962b
	gallicolae		Cholodkovsky, 1897; Fernald and Cooley, 1898
	sistens		Witlaczil, 1886; Fernald and Cooley, 1898;
<i>Adelges japonicus</i>	fundatrices		Schneider-Orelli, 1947; Steffan, 1962b
<i>Adelges laricis</i>	fundatrices		Schneider-Orelli, 1947
	gallicolae	fundatrices	Inouye, 1953
	sistens		Schneider-Orelli, 1947
	progreiciens		Cholodkovsky, 1897; Speyer, 1919, 1924
<i>Adelges nordmannianae</i>	gallicolae		Speyer, 1924; Schneider-Orelli, 1947
	sistens		
	progreiciens	fundatrices	Speyer, 1919, 1924
	gallicolae		Varty, 1956
	sistens		Schneider-Orelli et al., 1929; Varty, 1956
	progreiciens		Schneider-Orelli et al., 1929
<i>Adelges piceae</i>	sistens		Schneider-Orelli et al., 1929; Varty, 1956
	progreiciens	sistens	Nüsslin, 1908; Balch, 1952
	sexuparae		Marchal, 1913; Varty, 1956
<i>Adelges segregis</i>	sistens		Nüsslin, 1908; Marchal, 1913; Balch, 1952;
<i>Adelges viridana</i>		fundatrices	Varty, 1956
<i>Adelges viridis</i>	sistens		Nüsslin, 1908
		sistens	Steffan, 1962b; Heinze, 1962
<i>Pineus orientalis</i>	sexuparae		Cholodkovsky, 1897
<i>Pineus patchae</i>	fundatrices		Blochmann, 1889; Steffan, 1962b
	gallicolae		Cholodkovsky, 1897
<i>Pineus strobi</i>	sistens		Marchal, 1913
	progreiciens		Cumming, 1962
	sexuparae		

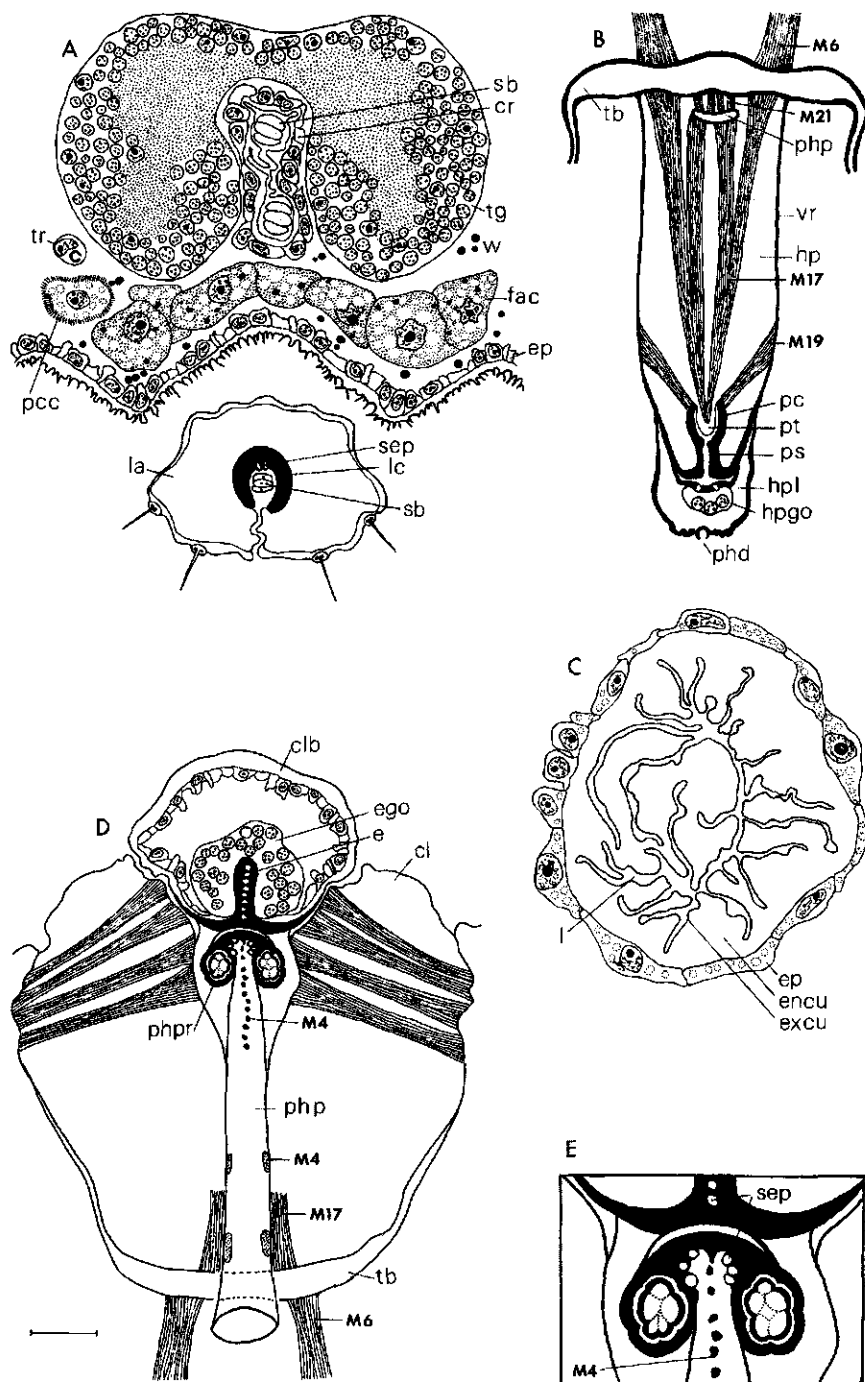


Figure 6 Transverse sections of the thoracic ganglion, crumena, labium with the labial clamp and its two sensillary pores (A), the salivary pump (B) of a gallicolous larva of *Pineus orientalis*, and the crumena of an adult fundatrix of *Adelges cooleyi* (C). Oblique section of the pharyngeal system of a female sexuales of *Adelges cooleyi* (D) and the situation of the three pairs of sensillary pores of the pharyngeal valve by a high magnification (E). Note the 14 pairs of pharyngeal muscles (M4). Bar represents 10 μ m. For list of abbreviations see page 102.

shedded skin. Probably they have another chitinous composition than that of the exuviae.

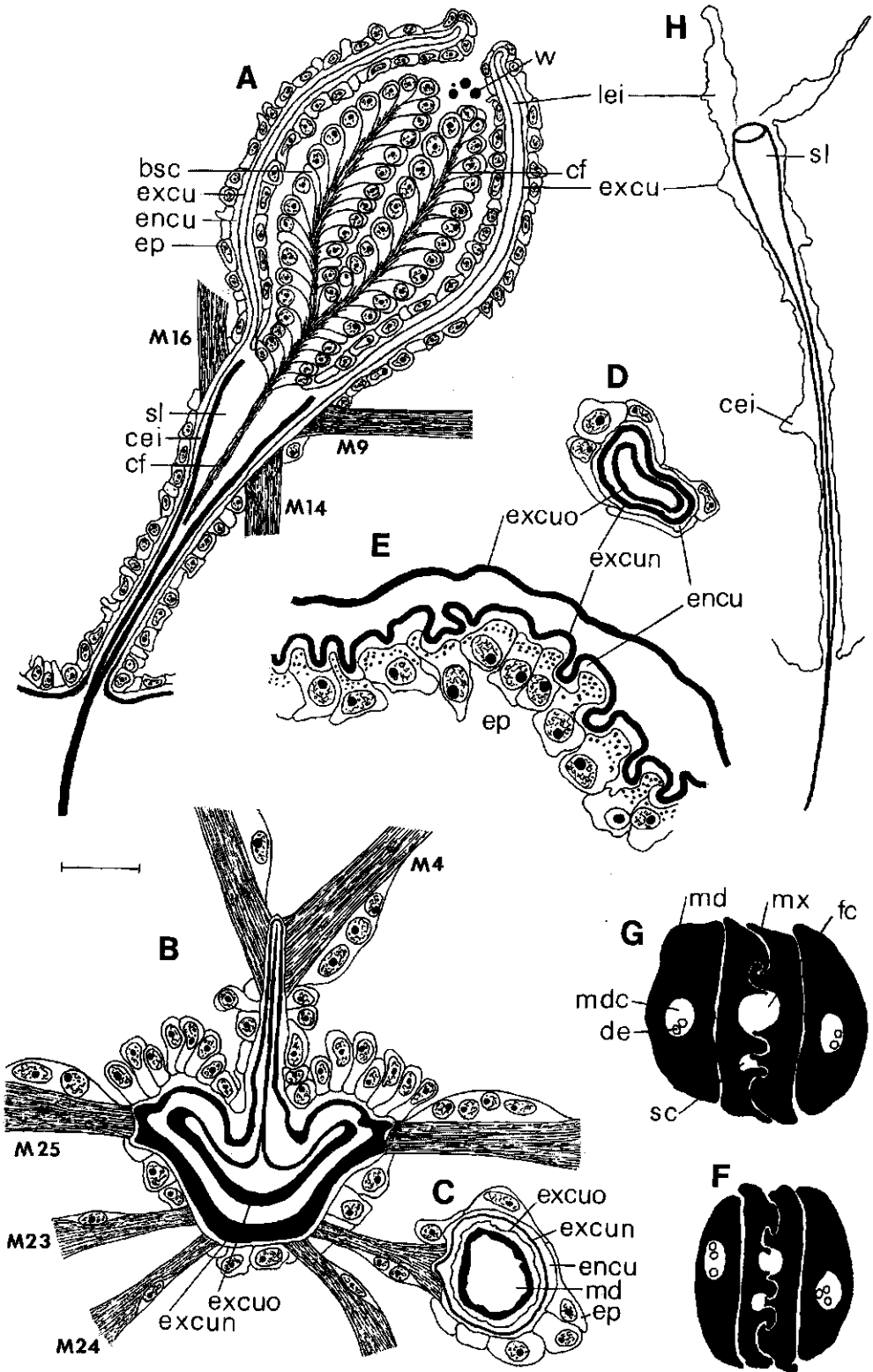
After each larval moult the discarded stylet remains behind inside the common epidermal invagination (Figure 7H) and the stylet bundle in the labial groove of the exuviae. This implies that at each moult the aphids stop their feeding to retract subsequently their stylet bundle from the host plant and after shedding start all over again feeding on the host plant. These findings agree with the fact that at each moult of the fundatrices, gallicolae, progrediens, and sexuparae of *Adelges nordmannianae* (Varty, 1956), the sistens and progrediens of *Pineus strobi* (Raske and Hodson, 1964), and the progrediens and sexuparae of *Adelges tsugae* (Young et al., 1995) the stylet bundle is retracted from their host plant and attached to the shedded skin. Moreover, Young et al. (1995) found no instances of isolated stylets or stylet cuticle within plant tissues. The moulting of the sistens of *Adelges piceae* is preceded by a partial withdrawal of the stylet bundle after which the bundle with the cast skin attached remains inserted in the host plant (Balch, 1952).

It is interesting that in all histological sections the new exocuticle is distinctly present beneath the old exocuticle of the epidermis (Figures 7E, 28D, and 31), internal skeleton (Figure 7D), and pharynx (Figure 7B) during ecdysis. This process of renewing has never been observed inside the hollow structures of the stylets, only the presence of the new stylet has been established (Figure 7C). The old exocuticle of the common epidermal invagination is situated around the old stylet. This implies that each stylet is derived from the bottle-shaped cells in the retort-shaped organ and absolutely not from the squamous cells of the common epidermal invagination (Figure 7A and C).

The pharynx can be divided in three parts, viz. the pharyngeal duct, valve, and pump (Figure 8A). The pharyngeal duct is a continuation of the food canal in the maxillary stylets and is formed by the epipharynx and the hypopharynx lip (Figure 2 no. 4-6 and 4 no. 4-6). The epipharynx is marked by a thick sclerotized plate which also forms the floor of the clypeo-labrum. It reveals a median row of eight sensillary pores (Figures 4A, 6D, 8A, and 9). In the median line of the hypopharynx lip a narrow gutter runs from the food canal to terminate in a cup-shaped structure which connects with that of the valve. This structure in front of the valve is provided with two sensillary pores (Figures 1A, 2 no. 6, and 4 no. 6). The pharyngeal duct does not exert any sucking action, but its function is to taste the acquired plant sap with the sensillary pores and to convey subsequently the plant sap to the pharyngeal pump.

The pharyngeal valve is the connection between the duct and the pump. Both the dorsal and ventral walls of the valve are marked by two cuticular dome-shaped prominences (Figures 1 no. 1, 2 no. 7, 4 no. 7, 6D, and 9) as in species of the Aphididae (Figures 20, 21, and 26B). These structures are reported for *Adelges abietis*, *Adelges piceae*, and *Adelges laricis* and named "Naröiden" by Dreyfus (1894). The dorsal wall of the valve is controlled

Figure 7 Semi-schematic drawing of a retort-shaped organ of a first stage adelgid larva showing the lateral (l e i) and common epidermal invaginations (c e i) and the bottle-shaped cells (b s c) which produce the chitinous fibrils (c f) for the formation of the new stylet (A). Transverse sections of a moulting pharyngeal pump (B), stylet (C), tentorium (D) of a sexuparous *Adelges viridana*, and integument (E) of a winged viviparous *Latgerina orizabaensis* ssp. *mexicana* Remaudière. Inside the head the stylets are hollow structures; outside the head they are compact structures showing the stylet bundle inside the crumena of an *Adelges piceae* sistens (F) and that in the labial groove of *Myzus persicae* (G). The stylets did not moult, but are discarded and each stylet remains behind inside the common epidermal invagination and labial groove of the exuviae. A discarded stylet situated in the transparent exocuticle of the common epidermal invagination of an exuviae of an *Adelges laricis* sistens (H). B-E: bar represents 10 µm. For list of abbreviations see page 102.



by two pairs of divaricator muscles, each pair being attached to a tendon (Figure 8A). The muscles diverge from each side of the tendon (Figure 7B) and are attached bilaterally of the clypeo-labrum. On the lateral side of the valve there is a muscle (lateral pharyngeal valve muscle, M10) inserted which originates from the lateral wall of the clypeus. In a closed position the dome-shaped prominences and the valve fit closely together. On each side of the two tendons there are three sensillary pores (Figures 6D-E, 9, 20, and 21).

The pharyngeal pump extends from the valve across the middle region of the head, through the oesophageal connectives and joins the foregut in front of the tentorial bar (Figure 8A). The movement of the flexible dorsal wall of the pump is controlled by 12 pairs of muscles (Figures 4A, 6D, 8A, and 9). In the anterior region they are attached to 10 short cuticular tendons arising from the midline of the dorsal pump wall (Figure 7B). The muscles diverge from each side of the tendon and have their origin on each side of the mediodorsal line of the wall of the clypeus (Figures 1, 3 no. 8-9, 4 no. 8-10, and 21C). In the middle region of the pump one pair of muscles is attached to the edges of the pharynx floor and originates from the junction of the clypeus and epicranium (Figures 3 no. 10, 4 no. 11, and 8A). Close to the tentorial bar one pair of muscles is inserted on the edges of the floor (Figures 3 no. 11, 4 no. 12, and 8A). Each bundle divides into two muscles which are attached to the midline, one on each side in the middle region of the epicranium. The floor of the pharyngeal pump is a very stout, rigid chitinous structure and is attached by muscles: six pairs of short small muscles originating from the tentorial bar (Figures 3 no. 11 and 4 no. 12; ventral pharyngeal pump muscle, M21), one pair from the piston of the salivary pump (Figures 3 no. 10, 4 no. 11, 6B, and 8A; retractor muscle of salivary piston, M17), and directly after the pharyngeal valve the edges of the pharynx floor are inserted by a muscle originating from the clypeus (Figures 3 no. 8, 4 no. 8, and 7B; lateral pharyngeal pump muscle, M25). The structure of the pharynx, including the muscles of the valve and the pump of all morphs of the Adelgidae investigated (Table 2) are identical to that of the asexual morphs of the Phylloxeridae (Ponsen, 1997).

Only the 10 pairs of muscles that are inserted on the flexible dorsal wall of the pharyngeal pump via a tendon are responsible for the pumping action. Contraction of these muscles pulls the invaginated dorsal wall upwards (Figure 4 no. 10). During this process, the lumen increases in size and the reduced pressure draws plant sap into the pharynx lumen by opening of the pharyngeal valve. When the muscles relax, the dorsal wall springs back (Figures 1 no. 2, 3 no. 8-9, and 4 no. 9) to expel the sap into the foregut and the pharyngeal valve is then closed (Figures 1 no. 1, 2 no. 7, and 4 no. 7).

The epipharyngeal gustatory organ has 14 sensillary pores. Eight pores are arranged in a row in the epipharynx of the pharyngeal duct (Figures 4A, 6D, and 9) as reported for *Adelges abietis* and *Adelges piceae* (Dreyfus, 1894). Six sensillary pores are located in the dorsal wall of the pharyngeal valve, three on each side of the two insertions of the cuticular tendons to which the divaricator muscles of the pharyngeal valve are attached (Figures 4A, 6D-E, and 9). Dreyfus (1894) found two sensillary pores on each side of the pharyngeal valve muscles of *Adelges abietis*. The hypopharyngeal gustatory organ has four sensillary pores: two in the hypopharynx of the pharyngeal duct just anterior to the valve (Figures 1A, 2 no. 6, and 4 no. 6) and two sensillary pores at the foot of the salivary pumpstem (Figures 6B and 8A). The structure of the gustatory organs including the location of the sensillary pores of all adelgid species (Table 2) is identical to that of species of the Phylloxeridae (Ponsen, 1997) and those of the Aphididae (Table 16; Figures 20, 21, and 26B).

As shown in Table 4, the adelgids ingest their food mainly from the cortical parenchyma

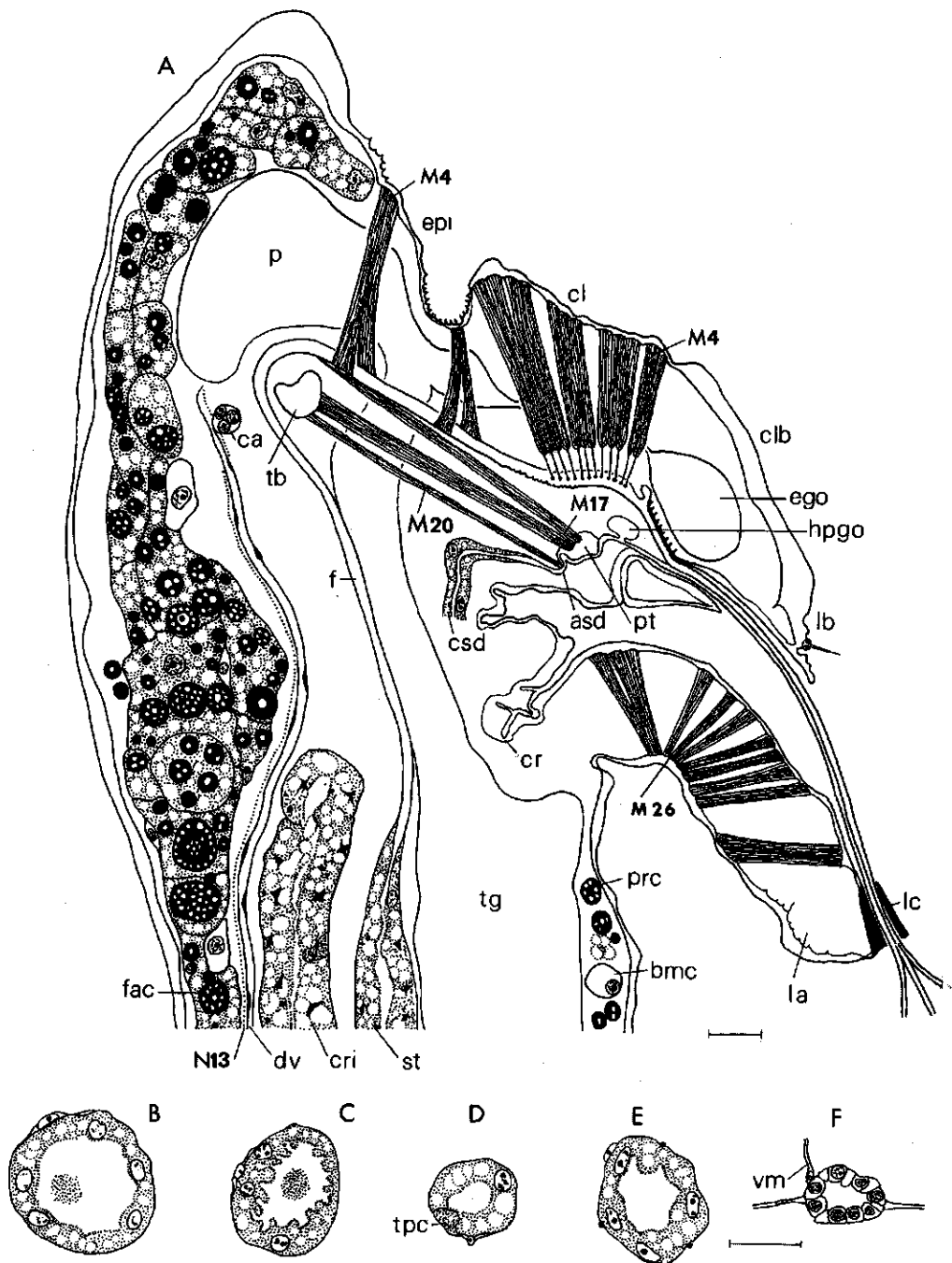


Figure 8 A. Sagittal section of the head of a male of *Adelges laricis* showing the two pairs of pharyngeal valve muscles (M4), the ten pairs of pharyngeal pump muscles (M4), the two pairs of muscles to support the pharynx (M4), and two pairs of salivary pump muscles (M17). The epidermal cell layer is omitted. Transverse sections of the stomach of a female sexuales of *Adelges cooleyi* (B) and *Adelges laricis* (C), the crenated intestine of a male of *Adelges cooleyi* (D), the descending intestine (E) and rectum of a male of *Adelges laricis* (F). Bar represents 10 μ m. For list of abbreviations see page 102.

which they penetrate with their stylets both intercellularly and intracellularly. *Adelges tsuga* feeds not on the cortical parenchyma of *Tsuga canadensis*, but on xylem ray parenchyma cells. On the other hand, *Pineus pinifoliae* and *Pineus strobi* take their nourishment from young sieve cells of the phloem of *Pinus strobi*.

The pharyngeal pump passes into the digestive system which consists of the foregut, midgut, and rectum, and terminates at the anal opening; the midgut is composed of the stomach, crenated intestine, and descending intestine (Figure 10-12). In dissections of living adelgids the foregut, stomach, and crenated intestine are opaque structures which show slow peristaltic movements generated by circular muscles. The crenated intestine has along its entire length a crenated structure and shows some distinct white dots which are the triplets (see page 30). The descending intestine is a smooth transparent structure that shows vigorous peristaltic movements generated by circular and about 20 longitudinal muscles; the latter are external to the circular muscles and are attached to the epidermal invagination on the border with the rectum. In adults the peristaltic movements are very slowly.

The foregut (oesophagus) runs posteriad from the tentorium, between the very small accessory salivary glands in the prothorax, between the principal salivary glands in the mesothorax, and dorsal to the suboesophageal and thoracic ganglia. In larva it runs in a medial dorsal furrow of the suboesophageal ganglion, but in adults it is situated outside the furrow (Figure 1 no. 3). The posterior region of the foregut is invaginated into the lumen of the stomach to form the oesophageal valve (Figure 10-12). The muscularis of the foregut consisting of circular muscles, extends directly into that of the stomach.

Due to the length of the mesothorax the length of the foregut of the winged morphs is about twice as long as that of the wingless morphs (Table 6; Figures 11 and 12).

The foregut is a uniform thin tube made up of simple squamous epithelium of which the nuclei protrude into the narrow lumen. The oesophageal valve consists of two layers of non-muscular epithelium, which form an intravalvular space. The inner layer is a continuation of the foregut, whereas the outer layer is built up of somewhat bent, columnar cells (Figure 13G). The epithelial cells of both the foregut and the valve secrete a chitinous intima showing an achromatic structureless mass with a delicate dark line on the luminal surface.

In ultrathin sections of gallicolous *Adelges nordmannianae* the apical cell membrane of the foregut and that of the valve shows an irregular pattern of invaginations and evaginations (Figure 14A-B). Moreover, the apical cell membrane of the outer layer of the valve has few long, very thin invaginations. The intima consists of an endocuticle and an exocuticle, but lacks the epicuticle. The embryonic cuticle is formed by the epidermis of the embryo inside the egg and during hatching it is shed, but in the foregut and valve it remains inside the lumen.

Inside the epithelial cells of the foregut of *Myzus persicae* there are many rod-shaped virus-like particles which are secreted during the formation of the endocuticle; at each moult these particles are released into the lumen after digestion of the endocuticle whereas the exocuticle remains in the lumen of the foregut (Ponsen, 1987b). In *Adelges nordmannianae* similar particles are never observed both inside the cytoplasm and inside the endocuticle of the foregut.

The foregut runs parallel with the dorsal vessel which starts blindly in the sixth abdominal segment; it extends antieriad as a bottle-shaped structure to pass subsequently into a uniform thin tube in the fourth abdominal segment, dorsal to the descending intestine to terminate at a funnel-shaped mouth (Figures 8 and 10). Half-way above the corpus allatum

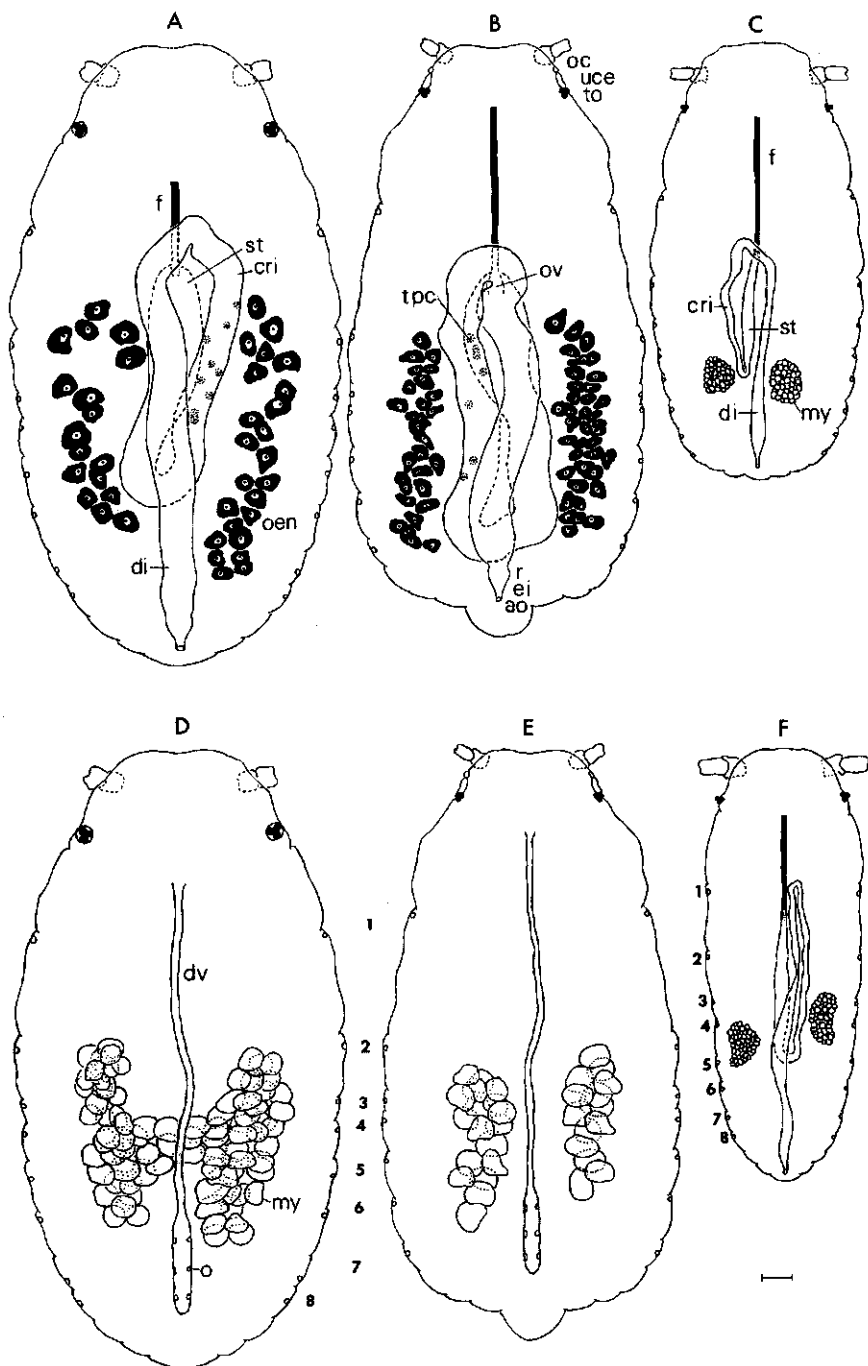


Figure 10 Dorsal view of the digestive system, dorsal vessel with three pairs of ostia, mycetome, and topographical position of the oenocytes of a wingless progredien larva of *Adelges nordmannianae* (A and D), a gallicolous larva of *Pineus orientalis* (B and E), a female sexuales of *Adelges cooleyi* (C) and a male of *Adelges laricis* (F), reconstructed from serial sections. In the sexuales the mycetome is a degenerated organ and the oenocytes are lacking. 1-2, meso- and metathoracic spiracles; *Adelges* has 6 abdominal and *Pineus* 5 abdominal spiracles. Bar represents 30 μm . For list of abbreviations see page 102.

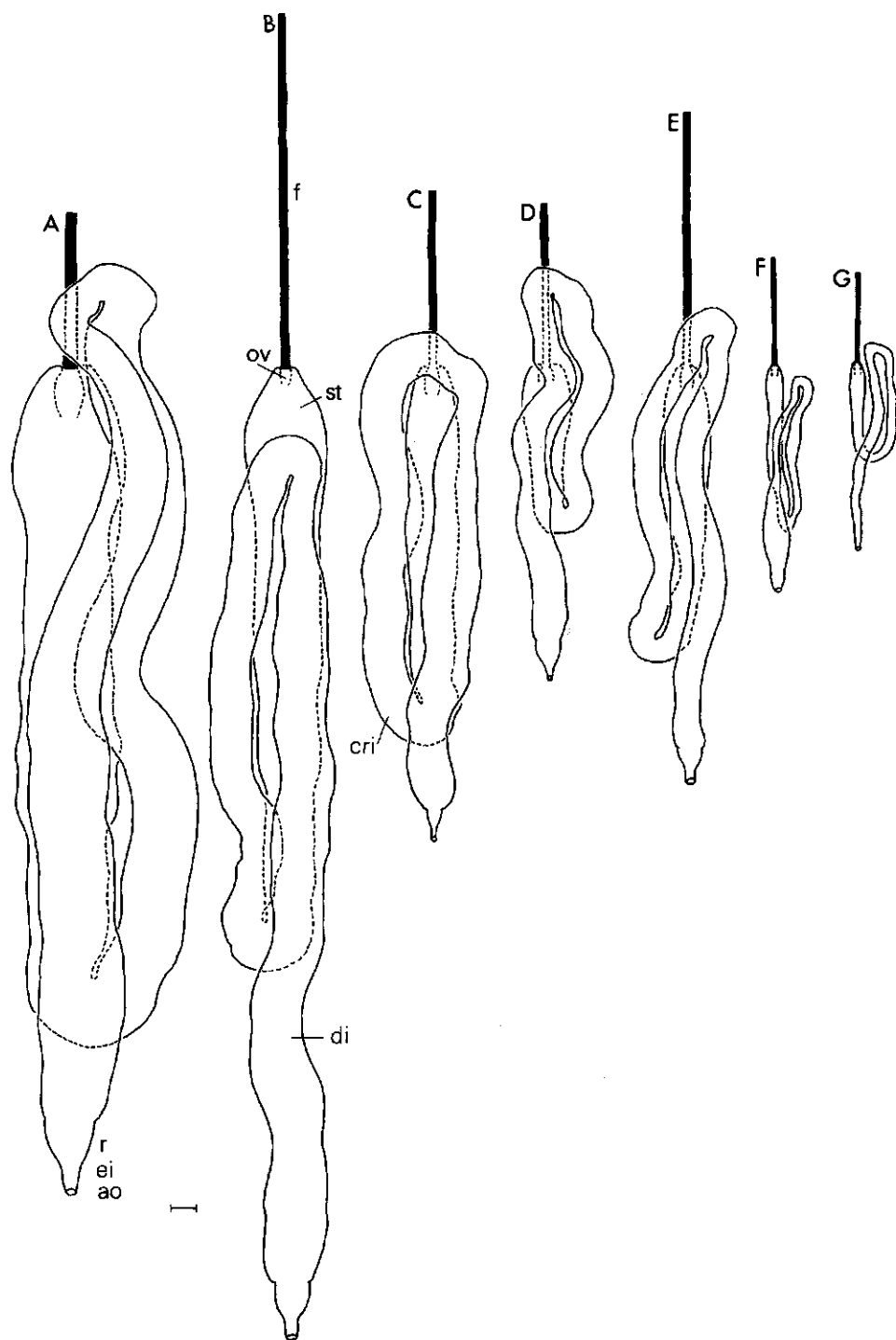


Figure 11 Dorsal view of the digestive system of seven adult morphs of *Adelges cooleyi*, reconstructed from serial sections: fundatrix (A), gallicola (B), sistens (C), progredien (D), sexupara (E), female sexuales (F), and male (G). The sexuales are dwarfish, wingless individuals. Bar represents 30 μ m. For list of abbreviations see page 102.

the ventral wall of the mouth is connected with its ventrolateral sides to this body (Figure 28C). The dorsal wall of the mouth extends further and is attached to the corpora cardiaca. As in *Myzus persicae* (Ponsen, 1997) there are three pairs of ostia occurring laterally in the wall of the bottle-shaped structure (Figure 10). Throughout its length the vessel pulsates vigorously forwards, generated by circular and longitudinal muscles. The innervation of the dorsal vessel takes place by the medial dorsal nerve (N13; Figure 8A). This nerve, originating from the corpora cardiaca, runs alongside the dorsal vessel giving off branches to the wall of this organ, the pericardial cells, and the digestive system (Figure 13D). Many waxy droplets, originating from fat cells are present in the lumen of the dorsal vessel which enter the vessels through the ostia.

The midgut is the endodermal part of the alimentary tract and consists of the stomach, crenated intestine, and descending intestine (Figure 10-12). The majority of all morphs the stomach begins in the meso- or metathorax (in some individuals in the prothorax). It joins the crenated intestine in one of the first six abdominal segments (Table 5). The transition from the stomach to the crenated intestine is marked by a sharp loop, which is situated either to the right or to the left of the stomach.

The stomach lies centrally in the ventral region of the body cavity and ventral to the crenated and descending intestine. It has a tubular or somewhat dilated structure of which the maximum diameter is situated beyond the end of the oesophageal valve. In transverse sections the maximum number of cells varies from 6-8 to decrease gradually to 3-4 cells at the end of the stomach. The stomach consists of two types of cells. The first type of cells is situated in the anterior region of the stomach consisting of about six strongly, basophilic columnar cells with elongated nuclei (Table 6; Figure 13G). They do not show any cytological evidence of secretory activity. The remainder of the stomach is made up of triangular cells (Figure 13A-G). These cells have small vacuoles and granules some of which are situated inside vacuoles. The spherical to oval nuclei contain one or more nucleoli, which have small spherical cavities resembling a spongy structure. The basal membrane of each cell has very long infoldings which extend deeply into the cell; they are about twice as long as those of the crenated intestine (Figure 15). The apical cell membrane consists of a very well-developed striated border, but a peritrophic membrane is absent.

In ultrathin sections of a gallicolous *Adelges nordmannianae* the apical cell membrane presents a labyrinthine system of closely packed irregular invaginations of different dimensions and its luminal surface is lined with extracellular microtubules (Figure 14C). The cells produce a merocrine secretion involving breaking off of parts of the labyrinthine system, which dissolve in the stomach lumen forming an amorphous threadlike mass. They secrete continuously throughout larval life and proceed into the adult stage. The presence of only one type of gland cells in the stomach of the adelgids (Figure 13), viz. merocrine cells, indicates that these species belong to the monophagous aphids. Jarial (1998) found that the cytoplasm of the anterior midgut epithelial cells of *Adelges piceae* contains abundant mitochondria, rough endoplasmic reticulum, free ribosomes, vesicles, and vacuoles, but Golgi complexes are sparse.

The stomach lumen is in open connection with the lumen of the crenated intestine. It is completely filled with solid material and thread-like structures. This material is strictly limited to the lumen of the stomach and does not occur in the lumen of the crenated and descending intestine which shows a clear appearance.

The crenated intestine has a tubular structure and runs from the stomach directly anteriorly without any loop or coil. In one of the thoracic segments it bends to pass subsequently into the descending intestine (Figure 10-12; Table 5). During larval life the

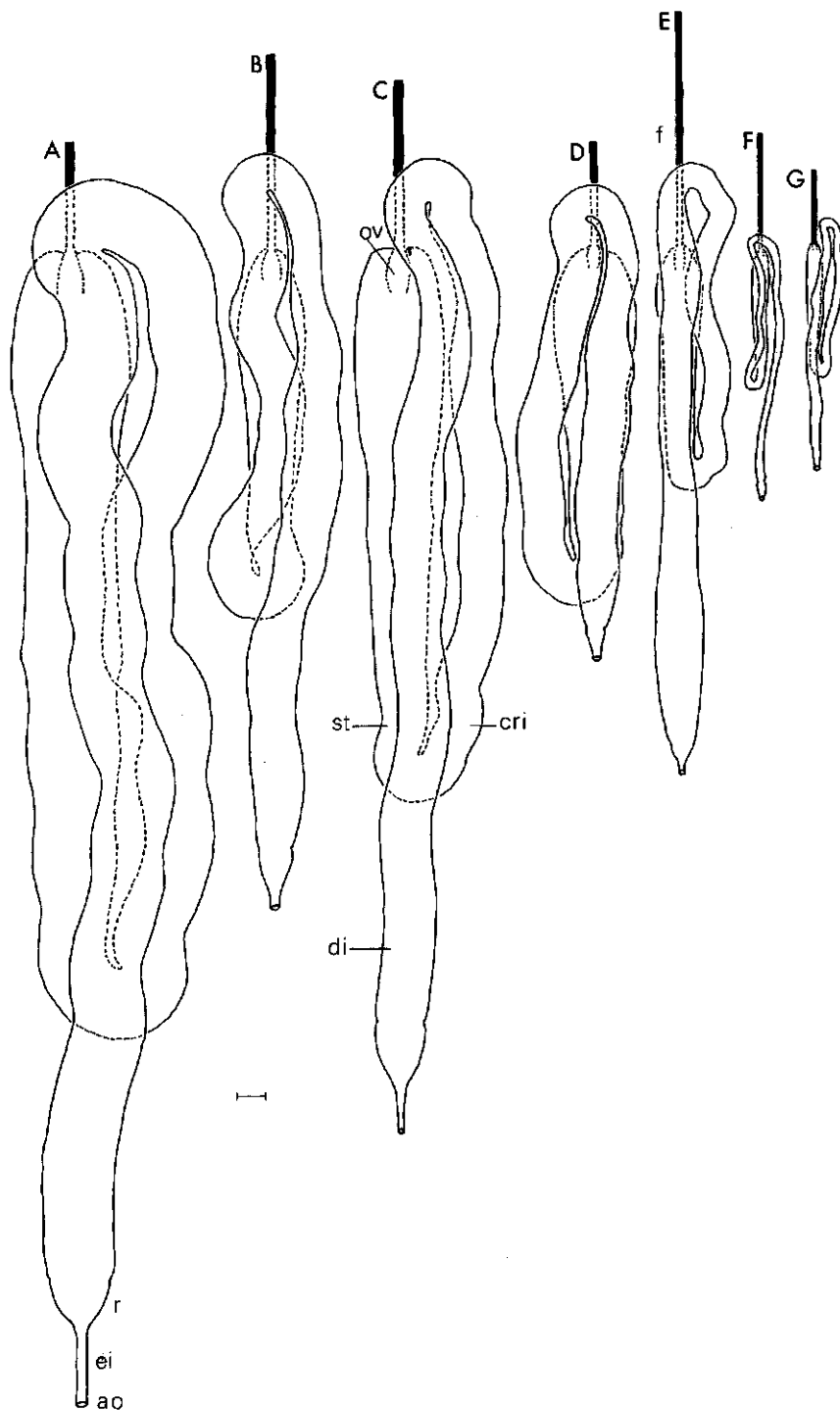


Figure 12 Dorsal view of the digestive system of seven adult morphs of *Adelges laricis*, reconstructed from serial sections: fundatrix (A), gallicola (B), sistens (C), progredien (D), sexupara (E), female sexuales (F), and male (G). The sexuales are dwarfish, wingless individuals. Bar represents 30 μ m. For list of abbreviations see page 102.

entire digestive system retains the same position in the adelgid's body cavity. In some fourth stage larvae and adults the crenated intestine is shifted to the frontal part forming one or two additional loops due to the large number of eggs of different sizes in the body cavity (Table 5).

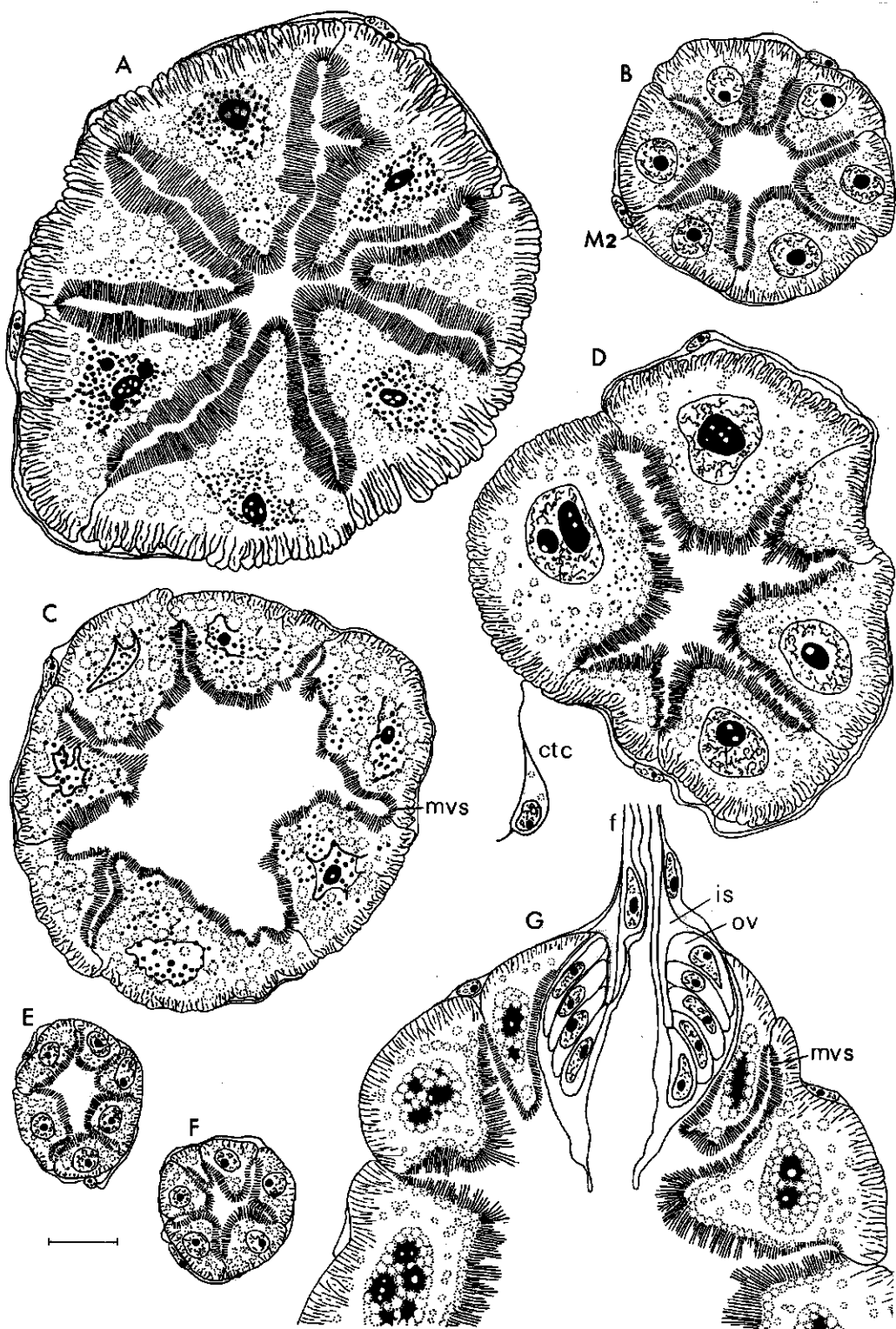
In transverse sections of all asexual morphs of the species investigated (Table 2) the entire crenated intestine consists of 3-4 triangular cells forming a more or less stellate lumen (Figure 15). These cells are strongly vacuolated and have ovoid nuclei. The apical cell membranes of these cells are distinctly striated and in ultrathin sections of *Adelges nordmannianae* gallicolae they present a labyrinthine system of closely packed irregular invaginations of different dimensions; its luminal surface is lined with extracellular microtubules (Figure 14D). The evaginations of this system are all of about the same length and broader than those of the stomach (Figure 14C). The infoldings of the basal cell membrane are about the half of those of the stomach (Figure 13) which can clearly be seen at the transition from the stomach cells to the intestinal cells.

Half-way the crenated intestine, at irregular intervals among the intestinal cells, there are 7 to 10 triplets (Table 6; Figure 10A-B). The majority of the triplets occur singly, occasionally in pairs and rarely in groups of three or four. The triplets consist of three conical-shaped cells of which the middle cell is very large with a large nucleus, whereas the other two are very small each with a relatively small nucleus (Figure 15; Table 6). The triplet cells can clearly be distinguished from the intestinal triangular cells by the presence of numerous minute vacuoles in the cytoplasm, a very thin striated border of the apical cell membrane, and a strongly invaginated basal cell membrane. In ultrathin sections of *Adelges nordmannianae* gallicolae the apical cell membrane consists of short and long evaginations forming a somewhat loose structure; its luminal surface is lined with extracellular microtubules (Figure 14E). All aphid species of the Phylloxeridae (Ponsen, 1997) and those of the Aphididae (Table 15, Figure 15) investigated possess triplets and only in their crenated intestine (Figures 24A-B, 26A, 28A, and 29A).

The third part of the midgut is the descending intestine. It starts in the mesothorax, metathorax, or first abdominal segment (Table 5) and runs directly caudad dorsal to the stomach to open into the rectum (Figures 10A-B, 11, and 12). The transition from the crenated intestine to the descending intestine is marked, in transverse sections, by 1) an abrupt change of strongly vacuolated cells (Figure 15) to the typical cellular structure of the descending intestinal cells (Figure 16A-H); 2) a wide lumen; 3) the presence of longitudinal muscles; and 4) an irregular structure due to the vigorous peristaltic movements. Half-way, on its ventral side, the descending intestine is innervated by a branch of the main abdominal nerve.

The cells contain small vacuoles with an oval nucleus; their basal cell membranes have few infoldings (Figure 16A-H). The area of contact between adjacent cells is shorter than those of the stomach cells and the crenated intestine cells. This cellular arrangement allows

Figure 13 Transverse sections of the stomach of an adult fundatrix of *Adelges abietis* (A), a larval progredien of *Adelges cooleyi* (B), an adult gallicolous *Adelges laricis* (C), a fourth larval stage sexuparous *Adelges viridana* (D), a first larval stage sistens of *Aphrastacia pectinatae* (E), and a larval gallicolous *Pineus orientalis* (F). Longitudinal section of the stomach and oesophageal valve of an adult fundatrix of *Adelges laricis* (G) showing the vacuolization of the nuclei in the first type of cells in the anterior region and the second type of cells in the remaining part of the stomach. The merocrine secretion products are omitted. Bar represents 10 µm. For list of abbreviations see page 102.



considerable dilation of the descending intestine during vigorous peristaltic movements. In the dilated condition the cells are very flat and the oval nuclei are situated parallel to the basal cell membrane. The apical cell membrane has a striated zone which is thinner than that of the crenated intestine. The ultrastructure of this zone of *Adelges nordmannianae* gallicolae shows an irregular pattern of short and broad evaginations with extracellular microtubules on their luminal surface (14 F). Both the epithelial cells of the crenated intestine and those of the descending intestine (Figure 14D-F) did not show any type of secretion as described for the stomach (Figure 14C; see Figure 19-20 in Ponsen, 1991).

Only the luminal surface of the apical cell membrane of the midgut consisting of the stomach, crenated intestine including the triplet cells, and descending intestine (Figure 14C-F) is lined with a single row of extracellular microtubules (Figure 5-8 in Ponsen, 1991). The term extracellular microtubules was introduced by O'Loughlin and Chambers (1972) lying along the luminal surface of the intestine and "hindgut" cells of several aphid species, as summarized in Table 7. Identical extracellular microtubules also occur along the apical cell membrane of the intestinal cells of a coccid, *Planococcus citri* Risso (Foldi, 1973).

The very short ectodermal part of the posterior region of the alimentary tract consists of a rectum, epidermal invagination, and an anal opening (Figures 10A-B, 11, and 12). The rectum is situated in the seventh abdominal segment and consists of small cuboidal cells with spherical nuclei; the apical cell membrane is lined with an intima (Figures 17, 18E, and 19A). The muscular coat of the rectum is connected to the abdominal body wall by dorsal and lateral visceral muscles.

The epidermal invagination is a thin tube forming an S-shaped flexure (Figure 17). The cellular structure is similar to that of the foregut (Figure 25C). The cuticular layer lining of the rectum, the epidermal invagination and that of the body wall form one continuous layer. The invagination opens to the exterior via the anal opening which is situated dorsal to the cauda, between the eighth and ninth abdominal tergites (Börner, 1908; Nüsslin, 1909; Annand, 1928; Varty, 1956).

In all asexual adelgid morphs (Table 2) the anal opening excretes honeydew. The anus is opened by three pairs of dorsal muscles; they arise at the junction of the eighth and ninth tergites and inserted on the edges of the dorsal wall of the epidermal invagination. Two pairs of ventral muscles close the anus; they originate at the junction of the seventh and eighth sternites and are inserted on the ventrolateral walls of the anus (Figure 18A-D and Figure 12B in Ponsen, 1991).

In ultrathin sections of *Adelges nordmannianae* gallicolae the apical cell membrane of the rectum shows deep irregular invaginations (Figure 14G) unlike that of the epidermal invagination (Figure 14H). The intima of the epidermal invagination consists of an endocuticle, an exocuticle, and an epicuticle, but that of the rectum lacks the epicuticle. The endocuticle of the epidermal invagination has a lamellate structure whereas that of the rectum is an amorphous mass similar to that of the foregut and oesophageal valve (Figure 14A-B). The exocuticle of the rectum and that of the epidermal invagination is shed at each moult with the rest of the exuviae.

All the epithelial cells of the digestive system are interconnected by thin septa running perpendicularly between the neighbouring lateral cell membranes forming a septate junction (Figure 14A-H). Moreover, only the apical part of the lateral cell membranes of the ectodermal part of the digestive system, viz. foregut, oesophageal valve, rectum, and epidermal invagination have a zonula adhaerens consisting of dense fine filamentous

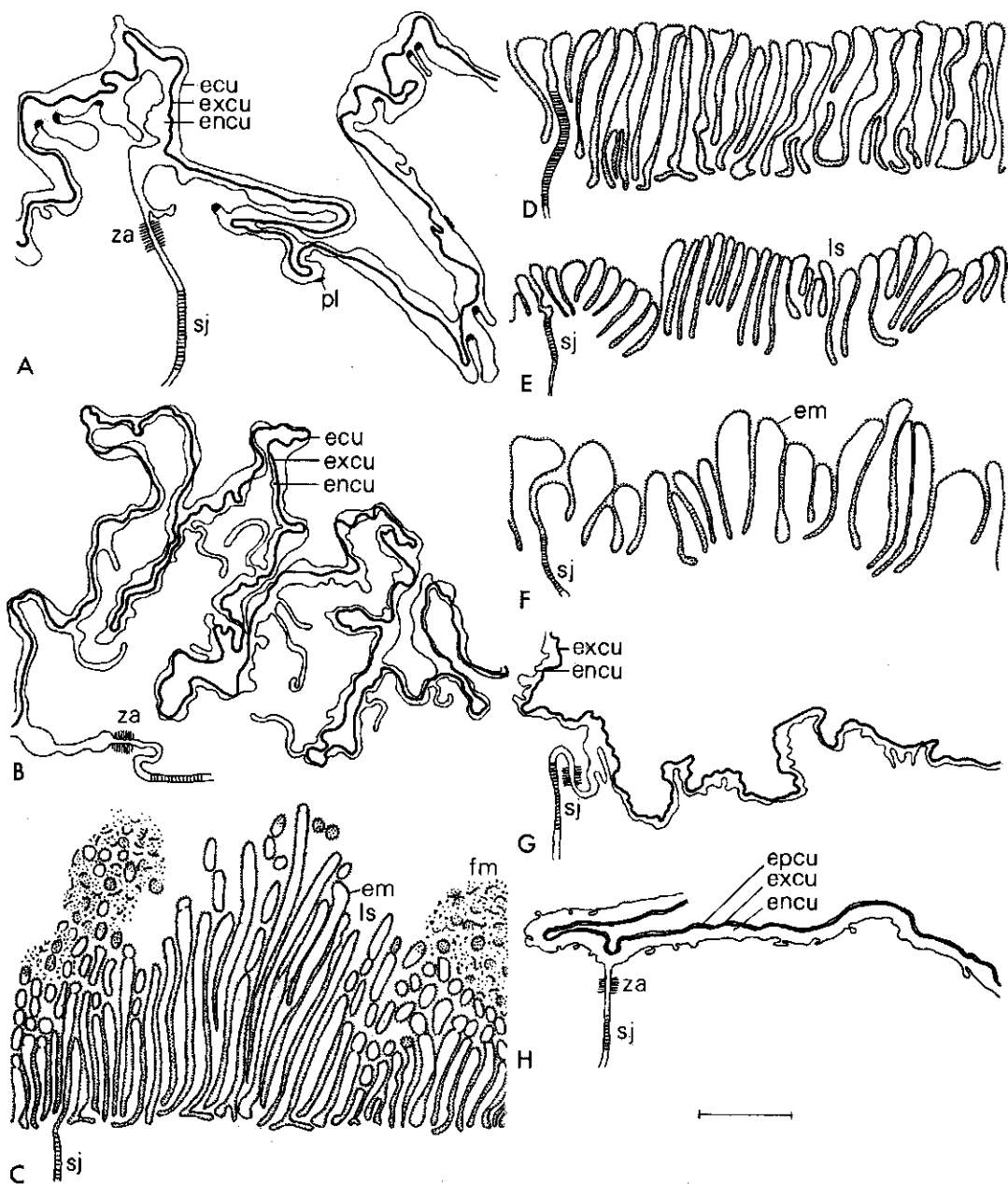


Figure 14 Schematic representation of the apical cell membrane of the digestive system of a first stage gallicolous larva of *Adelges nordmannianae*: foregut (A), outer layer of the oesophageal valve (B), stomach (C, merocrine secretion), crenated intestine (D), triplet cell (E), descending intestine (F), rectum (G), and epidermal invagination (H) taken from electron microscopical photographs. Note: the zonula adherens (z a) only occurs in the radial cell membrane of the ectodermal part of the digestive system and the extracellular microtubules (e m) only on the luminal surface of the apical cell membrane of the endodermal part of the digestive system. Bar represents 0.5 μ m. For list of abbreviations see page 102.

Table 4 Species of the Adelgidae and their morphs, their host plants, the course of the stylets (+), and source of food supply (+) according to different authors. The adelgid names used by the respective authors are given in Table 1.

Aphid (present name)	Morph	Host plant	Penetration		Food source		Author
			intracellular	intercellular	parenchyma	phloem	
<i>Adelges abietis</i>	fundatrices	<i>Picea excelsa</i>	+	+	+		Meyer, 1951; Rohlfritsch, 1976
<i>Adelges cooleyi</i>	fundatrices	<i>Picea abies</i>					Plumb, 1953
	progrediens	<i>Pseudotsuga menziesii</i>	+	+	+		Chrystal, 1922
	gallicolae					+	Sopow et al., 2003
	fundatrices	<i>Picea excelsa</i>		+	+		Rohlfritsch, 1976
<i>Adelges laricis</i>	sistens	<i>Abies alba</i>		+	+		Falck, 1928; Francke-Grosmann, 1937b
<i>Adelges nordmannianae</i>	sistens + progrediens	<i>Abies alba</i>	+	+	+	+	Grosmann, 1937b
	progrediens	<i>Abies alba</i>		+	+		Varty, 1956
							Chrystal, 1926;
							Schimitschek, 1928; Francke-Grosmann, 1937b
<i>Adelges piceae</i>	progrediens	<i>Abies alba</i>	+		+		Kloft, 1955, 1960
	sexuparae	<i>Abies alba</i>		+	+		Schimitschek, 1928
	sistens + progrediens	<i>Abies concolor</i>	+	+	+	+	Varty, 1956
	sistens + progrediens	<i>Abies grandis</i>	+	+	+	+	Varty, 1956
	progrediens	<i>Abies grandis</i>		+	+		Chrystal, 1926
	progrediens	<i>Abies nordmanniana</i>		+	+		Chrystal, 1926
	sistens	<i>Abies alba</i>		+	+		Balch, 1952; Francke-Grosmann, 1937b
							Grosmann, 1937b
<i>Adelges prelli</i>	progrediens	<i>Abies alba</i>	+		+		Kloft, 1955, 1960
	sistens	<i>Abies balsamea</i>		+	+		Balch, 1952
	sistens	<i>Abies concolor</i>	+	+	+		Varty, 1956
	sistens	<i>Abies grandis</i>	+	+	+		Varty, 1956
	sistens	<i>Abies procera</i>	+	+	+		Varty, 1956
	sistens	<i>Abies veitchii</i>	+	+	+		Varty, 1956
	fundatrices	<i>Picea orientalis</i>		+	+		Francke-Grosmann, 1937a
	sistens + sexuparae	<i>Abies nordmanniana</i>		+	+		Francke-Grosmann, 1937a

<i>Adelges schneideri</i>	sistens	<i>Abies alba</i>	+	+	Fräncke-Grosmann, 1937b
<i>Adelges tsuga</i>	progreadiens + sexuparae	<i>Tsuga canadensis</i>	+	xylem ray parenchyma	Young et al., 1995
<i>Pineus abietinus</i>	progreadiens	<i>Abies annabillis</i>	+	+	Underwood and Balch, 1964
<i>Pineus pini</i>	progreadiens	<i>Pinus brutea</i>		+	Mendel et al., 1994
	progreadiens	<i>Pinus halepensis</i>		+	Mendel et al., 1994
	progreadiens	<i>Pinus pinea</i>		+	Mendel et al., 1994
<i>Pineus pinifoliae</i>	sistens	<i>Pinus strobus</i>		+	Allen and Dimond, 1968
<i>Pineus strobi</i>	sistens + progreadiens	<i>Pinus strobus</i>	+	+	Raske and Hodson, 1964

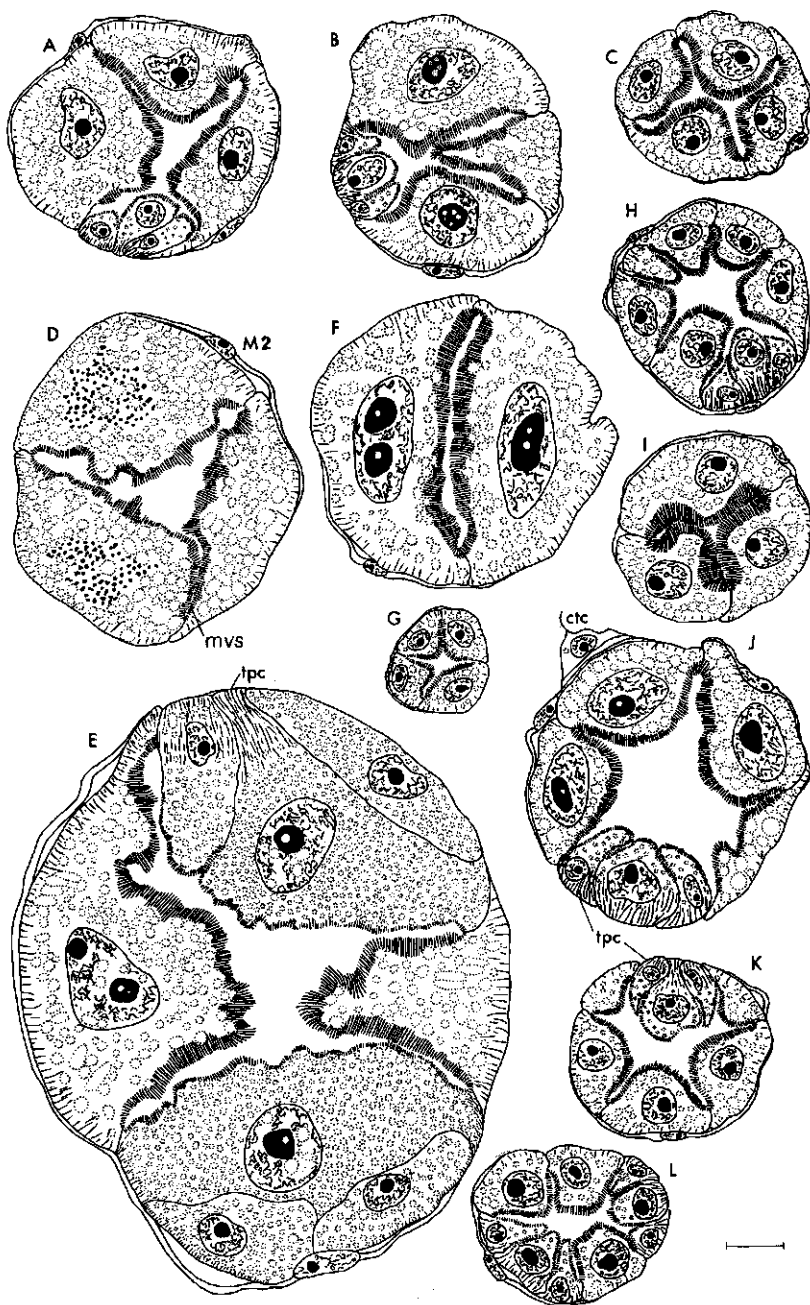


Figure 15 Transverse sections of the crenated intestine of a larval gallicolous *Adelges nordmannianae* (A), *Adelges lapponicus* (B), and *Pineus orientalis* (C), an adult gallicolous (D) and a fourth larval stage fundatrix of *Adelges laricis* (E), a larval sistens of *Adelges cooleyi* (F), a first larval stage sistens of *Aphrastasia pectinatae* (G), a wingless viviparous larva of *Tetaneura ulmi* (Linnaeus) (H), a winged viviparous larva of *Eriosoma ulmi* (Linnaeus) (I), a winged larval male of *Monaphis antennata* (Kaltenbach) (J), a wingless viviparous larva of *Dasyaphis rhusae* (Shinji) (K), and a winged viviparous larva of *Takecallis arundinariae* (Essig) (L). Note: the triplet cells occur only in the crenated intestine of all species of the Aphidoidea. Bar represents 10 μ m. For list of abbreviations see page 102.

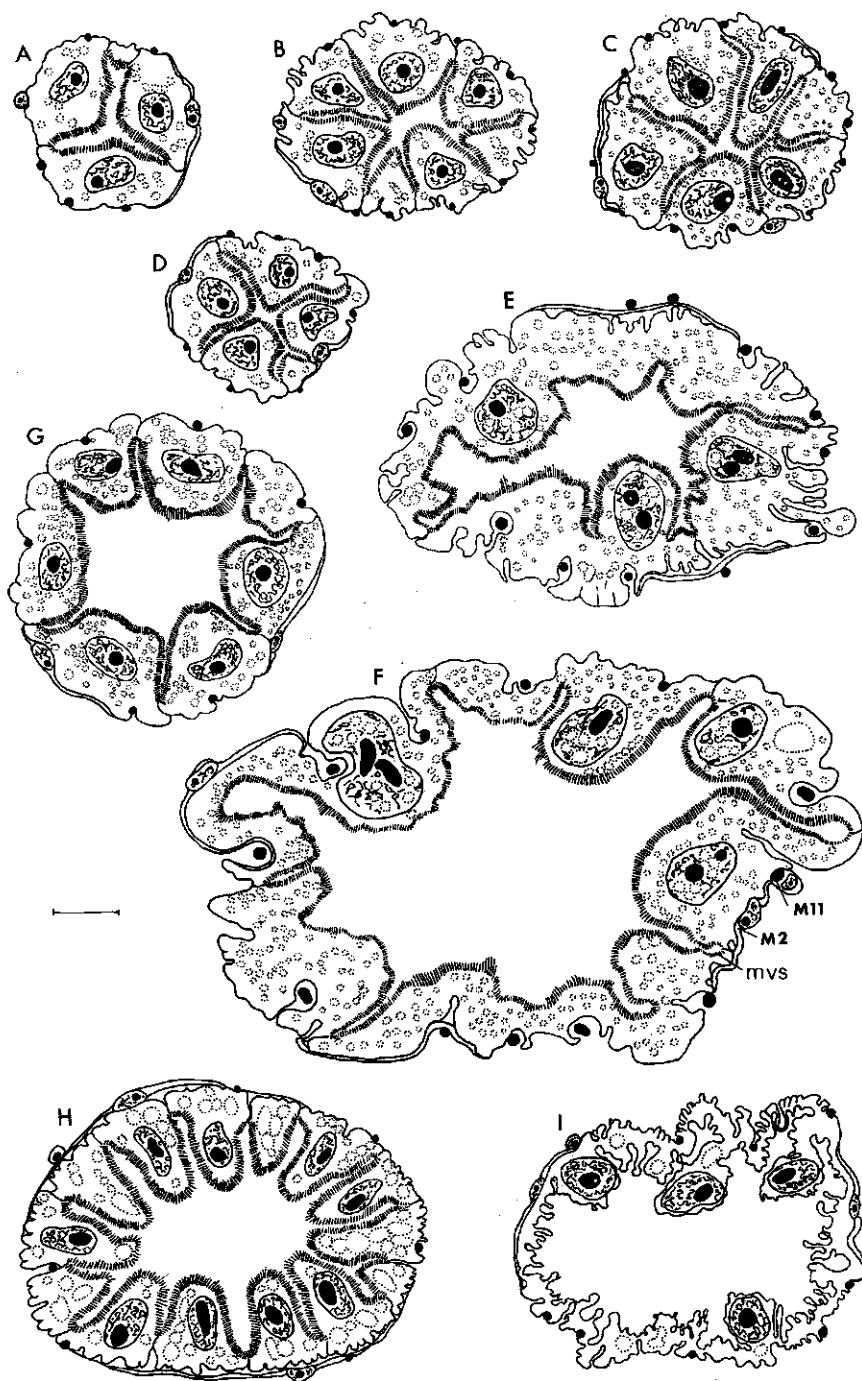


Figure 16 Transverse sections of the anterior (A) and middle region (B) of the descending intestine of a larval gallicolous *Adelges abietis*, a larval sexuparous *Adelges viridana* (C), a larval gallicolous *Pineus orientalis* (D), an adult sistens of *Adelges laricis* (E), an adult fundatrix of *Adelges cooleyi* (F), a wingless viviparous larva of *Cerataphis palmarum* Ghesquière (G) and *Drepanosiphum platanoidis* (Schrank) (H), and a transverse section of the caecal intestine of a wingless viviparous larva of *Lachnus roboris* (Linnaeus) (I). Bar represents 10 μ m. For list of abbreviations see page 102.

material (Figure 14A-B and G-H). Both types of cell attachments in the epithelial cells of the digestive system (viz. septate junction and zonula adhaerens) are also observed in other aphid species (Table 12 and Figure 19-20 in Ponsen, 1991).

All asexual morphs of the Adelgidae have an anal opening and excrete honeydew (Dreyfus, 1894; Fluiter, 1934; Inouye, 1953; Heinze, 1962; Börner and Heinze, 1957). According to Kunkel (1972) it is a liquid-sticky excrement which at the anus is coated by wax filaments. The honeydew excreted by the gallicolae larvae of *Adelges cooleyi* (Cumming, 1959) and *Adelges abietis* (Kunkel, 1972) is covered with a waxy pulverulence, so that the droplets do not coalesce inside the galls. Occasionally the cast skins (exuviae) may be filled with honeydew. The adelgids are not attended by ants (Börner and Heinze, 1957). Varty (1956) observed that a black ant stroked an adult *Adelges nordmannianae* fundatrix with its brown antennae and subsequently fed on the honeydew excreted by this adelgid.

The ageing process of the cells starts in the last larval stage with the vacuolization of the chromatin material in the nuclei (Figure 13G, 15E, and 16E-F). This process continues gradually in the adult stage after which the chromatin undergoes one of the following four changes: 1) the chromatin gets completely dissolved leading to empty nuclei sometimes with a nucleolus still inside (Figures 8B, 13C, and 25F); 2) the chromatin starts to condense to dark stellate-shaped structures (Figures 13G and 23C-E); 3) the chromatin granulates and the nuclear membrane breaks open followed by the release of the granules into the cytoplasm (Figures 13A, 15D, and 18D); 4) fragmentation of the nuclei followed by dissolution of the chromatin (Figures 13C and 31).

Ovarioles

Within each larval and adult stage of each morph the total length of the digestive system is about one and a half that of the aphid's body length (Table 6). The length of the stomach of the fundatrix is about half that of the aphid and in the remaining morphs the length of the stomach is about one third of that of the aphid. The descending intestine is even as long as the crenated intestine and about half the length of the body. After birth cell division in the digestive system ceases and during larval growth the digestive system and its cells increase in size proportionally with the aphid.

During one life cycle the length of the successive morphs after the fundatrix decreases gradually and proportionally the length of the digestive system (Figures 11 and 12), but the total number of cells remains practically constant (Table 6). This implies that during one life cycle the cells of the midgut become gradually smaller up to the sexuales in which they are degenerated (Figures 8A-E and 19A). The length of the midgut of the fundatrix is about twice as long as that of the asexual morphs, and the total number of cells is about twice as much as that of the asexual morphs (Table 6). This is in agreement with the large number of ovarioles in the fundatrix varying between 101 and 119, whereas in the remaining asexual morphs the ovarioles vary between 4 and 42 for *Adelges cooleyi* and between 1 and 46 for *Adelges laricis*, respectively (Table 8). The total number of ovarioles correlates with

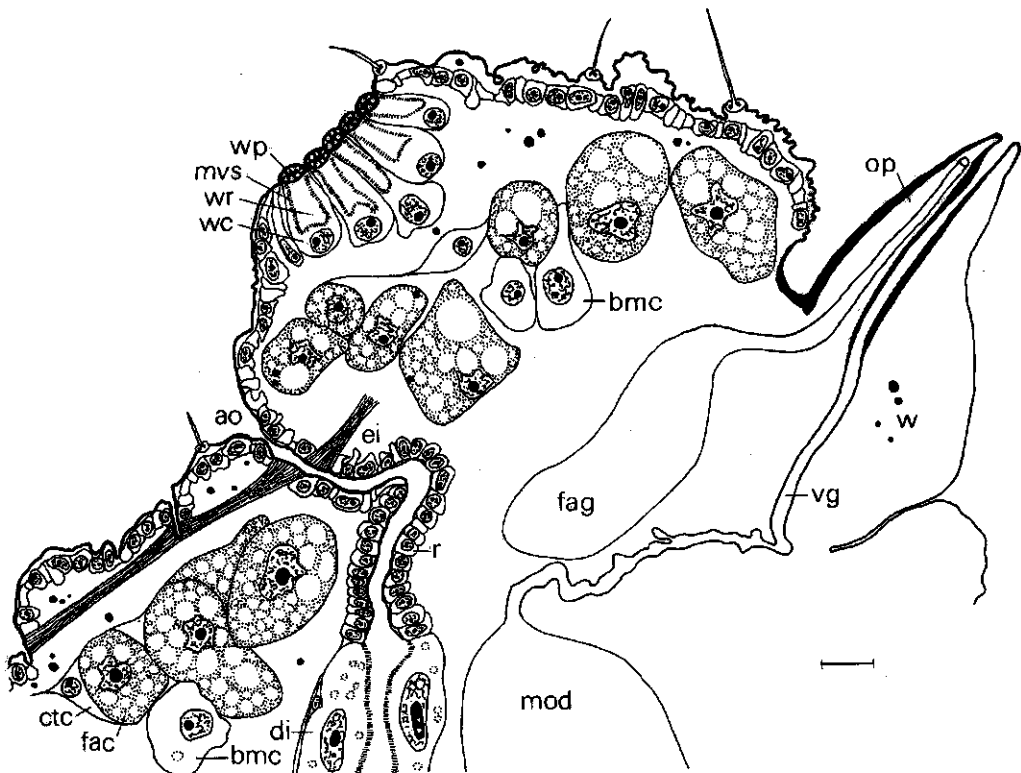


Figure 17 Median longitudinal section of the rectum and epidermal invagination of a wingless fourth larval stage progrediens of *Adelges nordmannianae*. Bar represents 10 μ m. For list of abbreviations see page 102.

the total number of eggs produced per morph, as shown in Table 9. The fundatrix of both adelgid species has the highest number of ovarioles (Table 8) and consequently the egg number (Table 9). Moreover, the variation in both ovariole number and egg number within each morph is also found in several aphidid species, as summarized by Dixon (1998). In the successive morphs after the fundatrix of *Adelges cooleyi* the total number of ovarioles decreases (Table 8), and also the total number of eggs per morph (Table 9). In *Adelges laricis* the sistens have very many ovarioles and consequently many eggs in contrast with the gallicolae, progrediens, and sexuparae. From this it can be concluded that the total number of ovarioles is dependent on the size of the midgut, and especially on the total number of stomach cells. A similar decrease in ovariole number per individual during one life cycle has already been found in other adelgid species (Table 10) as well as in *Phylloxera vastatrix* Planchon (= *Daktulosphaira vitifoliae* (Fitch)), *Phylloxera quercus* Boyer de Fonscolombe (Balbiani, 1884), and *Phylloxera glabra* (von Heyden) (Polaszek, 1987).

Table 5 The position of the midgut and its subdivisions in the body cavity of species of the Adelgidae. The adelgids have three thoracic segments (I-III) and nine abdominal segments (1-9). In parentheses the number of fourth stage larvae and adults of the total number of aphids sectioned.

Aphid	Total number of aphids sectioned	Morph	Host plant	Stomach starts in	Stomach ends in	Number of aphids with an additional loop in crenated intestine	Descending intestine starts in
<i>Adelges abietis</i>	8 (8)	pseudofundatrices gallicolae	<i>Picea abies</i>	II	2-4	4	II
	17	gallicolae	<i>Picea abies</i>	II	4-5		III-1
<i>Adelges cooleyi</i>	13	gallicolae	<i>Picea engelmannii</i>	II	4		II
	5 (5)	fundatrices	<i>Picea sitchensis</i>	II	3-4	2	II-III
	15 (6)	gallicolae	<i>Picea sitchensis</i>	II	3-5	2	III-1
	7 (7)	gallicolae	<i>Picea glauca</i>	II	3	4	III-2
	10 (7)	gallicolae	<i>Picea omorika</i>	II	2-4		III-1
	10 (1)	gallicolae	<i>Picea likiangensis</i> var. <i>balfouriana</i>	II	4-6		III-1
	7 (7)	sistens	<i>Pseudotsuga menziesii</i>	II-III	3-4	3	III-1
	10 (8)	progrediens	<i>Pseudotsuga menziesii</i>	II-III	2-4		II-III
	9 (4)	sexuparae	<i>Pseudotsuga menziesii</i>	II-III	2-4		III-1
	21	female sexuales	<i>Picea sitchensis</i>	II-III	2-4		III-1
	5	males	<i>Picea sitchensis</i>	II	2-3		III
<i>Adelges laricis</i>	9 (9)	fundatrices	<i>Picea sitchensis</i>	I-II	3-4		II
	16 (13)	gallicolae	<i>Picea abies</i>	II	2-3		II-III
	8 (8)	sistens	<i>Larix decidua</i>	II	2-3		II
	10 (2)	progrediens	<i>Larix decidua</i>	II	3-5		II-III
	8 (6)	progrediens	<i>Larix kaempferi</i>	II-III	4-5		III
	11 (7)	sexuparae	<i>Larix decidua</i>	II	2-4		III
	2	female sexuales	<i>Picea abies</i>	II	3		II
	11	males	<i>Picea abies</i>	II	1-3		II
<i>Adelges lapponicus</i>	12 (1)	gallicolae	<i>Picea abies</i>	II	3-5		III-1
<i>Adelges nordmannianae</i>	8	gallicolae	<i>Picea orientalis</i>	II	4-6		III
	10 (1)	progrediens	<i>Abies nordmanniana</i>	I-II	2-4		III
<i>Adelges viridana</i>	13	sexuparae	<i>Larix kaempferi</i>	II-III	4-6		III
<i>Adelges viridis</i>	9 (4)	gallicolae	<i>Picea abies</i>	II	3-5		II-III
<i>Aphrastasia pectinatae</i>	10	sistens	<i>Abies lasiocarpa</i>	I-II	2-4		II
<i>Pineus orientalis</i>	18 (5)	gallicolae	<i>Picea orientalis</i>	II	2-4		II

Table 6 Average length and average number of cells of the digestive system of two imaginal species of the Adelgidae. The values are given in μm . The sign \pm is followed by the standard deviation of the mean ($n = 3$).

Aphid Morph	Body length	Foregut length	Stomach			Crenated intestine			Descending intestine		Midgut		
			length	1 st type of cells	2 nd type of cells	length	cells	triplets	length	cells	length	cells	
<i>Adelges cooleyi</i>													
fundatrices	1621 ± 81	203 ± 20	805 ± 17	8 ± 1	138 ± 3	920 ± 52	52 ± 3	8 ± 1	984 ± 29	84 ± 2	2709 ± 51	282 ± 4	
gallicolae	1869 ± 141	435 ± 5	733 ± 112	5 ± 1	46 ± 5	760 ± 147	38 ± 3	8 ± 1	1016 ± 105	45 ± 4	2509 ± 333	134 ± 6	
sistens	987 ± 28	229 ± 32	389 ± 54	5 ± 1	45 ± 6	637 ± 156	38 ± 5	8 ± 1	411 ± 65	48 ± 5	1437 ± 233	136 ± 1	
progrediens	750 ± 92	193 ± 21	293 ± 83	4 ± 1	44 ± 4	440 ± 70	43 ± 8	8 ± 1	383 ± 57	42 ± 5	1117 ± 164	133 ± 2	
sexuparae	1019 ± 82	328 ± 56	331 ± 59	5 ± 1	46 ± 4	488 ± 105	41 ± 2	8 ± 1	445 ± 69	47 ± 3	1264 ± 205	139 ± 2	
female sexuales	523 ± 29	145 ± 15	149 ± 16	—	—	250 ± 77	—	8 ± 1	245 ± 64	—	644 ± 67	—	
males	411 ± 23	114 ± 21	117 ± 8	—	—	159 ± 11	—	5 ± 1	189 ± 28	—	464 ± 23	—	
<i>Adelges laricis</i>													
fundatrices	1763 ± 171	123 ± 23	832 ± 69	7 ± 1	119 ± 3	1069 ± 99	66 ± 1	8 ± 1	1029 ± 97	76 ± 10	2931 ± 243	269 ± 7	
gallicolae	1053 ± 65	203 ± 44	331 ± 12	7 ± 2	72 ± 3	552 ± 16	55 ± 2	9 ± 2	627 ± 24	70 ± 6	1509 ± 47	203 ± 3	
sistens	1635 ± 95	216 ± 42	629 ± 78	7 ± 1	95 ± 9	909 ± 80	58 ± 4	8 ± 0	787 ± 73	71 ± 5	2325 ± 200	231 ± 10	
progrediens	789 ± 51	144 ± 21	376 ± 29	6 ± 1	60 ± 7	605 ± 57	55 ± 5	8 ± 1	411 ± 36	36 ± 2	1392 ± 84	157 ± 8	
sexuparae	984 ± 81	288 ± 21	341 ± 90	7 ± 1	49 ± 3	451 ± 140	58 ± 6	8 ± 1	432 ± 108	54 ± 6	1224 ± 132	167 ± 5	
female sexuales	441 ± 61	107 ± 45	154 ± 12	—	—	173 ± 4	—	6 ± 1	261 ± 28	—	588 ± 44	—	
males	427 ± 32	89 ± 18	128 ± 28	—	—	135 ± 41	—	6 ± 1	233 ± 35	—	497 ± 98	—	

Sexuales

The sexuales of *Adelges cooleyi* and *Adelges laricis* are produced by the sexuparae after their flight from the secondary to the primary host (Table 2). They produce about 8 eggs mainly at the end of the needles of old shoots. The eggs of the sexuparae and those of the asexuals are attached to the needles by means of a pedicel. Both eggs, larvae, and exuviae are hidden under the spread wings of the dead sexupara which remains attached to the needles. They are covered by wax filaments secreted by their mother. The smooth and transparent larvae moult and do not grow during their larval development. After the last moult the adults leave their dead mother. *Adelges prelli* larvae leave early the protecting wings of the mother and wander to young needles of *Picea orientalis* (Francke-Grosmann, 1937b). *Adelges cooleyi* larvae stay under their mother's wings as long as possible and then settle in a row along the same needle (Cumming, 1959). The larval sexuales of *Adelges laricis*, *Adelges viridis* (Speyer, 1919), and *Adelges cooleyi* (Annand, 1928; Cameron, 1936) moult four times. The larvae do not grow during their larval instars and after the last moult the adults are wingless, dwarfish individuals with well-developed mouthparts (Table 11). Moreover, Blochmann (1887) found that the sexuales of *Adelges viridis* have an alimentary tract and are consequently able to feed. First the males hatch and later on the female sexuales; the active males are somewhat smaller than the plump females. After mating the male dies first followed by the female after she has laid only one egg which overwinters.

The alimentary tract of the sexuales of *Adelges cooleyi* and *Adelges laricis* starts with the food canal which is formed by the interlocked maxillary stylets. These stylets are partly enveloped by the mandibular stylets forming the stylet bundle (Figures 4 and 8A). Each stylet originates from a retort-shaped organ of which the cells possess well-developed nuclei so that the bottle-shaped cells can produce a new stylet during each moult (Figures 1A and 7A). The course of each stylet to the end of the labrum (Figure 4) is similar to that of the asexual adelgid species (Figure 2-3). The stylet bundle crosses over into the labial groove (Figure 8A), but not via a crumena. The crumena of the sexuales is very small in contrast with the well-developed crumena of the asexual adelgid morphs (Figures 5 and 6A, C). In all sectioned sexuales the stylet bundle was absent inside the crumena. In the sexuales of *Pineus orientalis* (Marchal, 1913), *Adelges laricis* (Speyer, 1924), and *Adelges nordmannianae* (Schneider-Orelli et al., 1929; Varty, 1956) the stylet bundle forms one single loop inside the crumena. The stylets of the female sexuales are somewhat longer than those of the males (Schneider-Orelli et al., 1929).

The food canal leads into the pharyngeal duct which is separated from the pharyngeal pump by a valve (Figure 8A). The dorsal wall of the pharyngeal valve is controlled by two pairs of muscles (Figures 1 no. 1 and 4 no. 7) and the flexible dorsal wall of the pump by 10 pairs of muscles (Figure 4A). These muscles are attached to short cuticular tendons (Figures 1 no. 2-3, 4 no. 8-10, and 8A). Moreover, there are two pairs of muscles inserted on the edges of the pharynx floor (Figures 4 no. 11-12 and 8A).

The epipharyngeal gustatory organ has 14 sensillary pores and the hypopharyngeal gustatory organ four sensillary pores. Both the musculature of the stylets, and the structure of the pharynx including the muscles of the valve and the pump (Figures 2 and 3), and the structure of the gustatory organs including the position of the sensillary pores of the sexuales of *Adelges cooleyi* and *Adelges laricis* are identical to those of all asexual morphs of adelgid species investigated (Table 2).

Both the length of the sexuales and that of their digestive system are half of those of the sexuparae (Table 6; Figure 10-12). The digestive system consists of the foregut, midgut, and rectum. The foregut is a continuation of the pharyngeal pump and passes in the mesothorax or metathorax into the stomach with a very small oesophageal valve (Table 5). The tubular stomach passes with a sharp loop into the crenated intestine, which in turn leads into the descending intestine terminating at the rectum (Figures 10, 11, 12, and 19A).

The epithelium of the midgut has no distinct lateral cell membranes and consists of vacuoles of different dimensions (Figures 8A-E and 19A). The nuclei are empty or irregular with condensed chromatin material. The apical cell membranes of the midgut cells have no distinct microvillar system. The stomach lumen contains a small ball of granular material (Figure 8B-C). The triplet cells are somewhat shrivelled and filled with very fine granulated material (Figure 8A and D). The degenerated midgut cells of the adelgid sexuales are similar to that of the sexuales of the Phylloxeridae (Figure 15E-K in Ponsen, 1997).

The rectum continues into an epidermal invagination, which is a straight duct and in open connection with the exterior (Figure 19A). The epithelial cells of these three organs have well-developed nuclei so that the sexuales can moult during their larval life (Figures 8F and 19A). The cuticular layer lining the rectum, epidermal invagination, and that of the body wall form one continuous layer. The anal opening is situated in a somewhat terminal position (Figure 19A) and controlled by two pairs of anal dorsal muscles and two pairs of anal lateral muscles (Figure 19B-C). The musculature of the anal opening of the sexuales is similar to that of all adelgid asexual morphs (Table 2; Figure 18).

The larval sexuales of *Adelges laricis*, *Adelges viridis*, and *Pineus cembrae* feed in the needles without leaving the shelter of the wings of their dead mother (Cholodkovsky, 1890, 1896, 1897). *Adelges laricis*, *Pineus cembrae* (Börner, 1908), *Adelges cooleyi* (Cameron, 1936), *Adelges prelli* (Francke-Grosmann, 1937a), and *Adelges tsuga* (McClure, 1989) insert their stylets into the plant tissue and suck, but do not excrete honeydew. However, Börner (1928-30) stated that the anal opening of the sexuales excretes honeydew. Varty (1956) reported that first stage larval sexuales of *Adelges nordmannianae* after having settled on a leaf of a new shoot of *Picea orientalis* begins to feed at once and soon excretes a minute globule of honeydew from the anus. Thereafter the adelgid remains on its leaf throughout the four larval stadia.

Figure 18 Transverse sections of the anal musculature of a larval gallicolous *Pineus orientalis* (A), a progredien larva of *Adelges cooleyi* (B), a first larval stage sistens of *Aphrastasia pectinatae* (C), an adult sexuparous *Adelges laricis* (D), and the rectum of a larval sexuparous *Adelges viridana* (E). Note the waxy droplets which originate from fat cells and are released in the haemolymph and into the endocuticle. Bar represents 10 µm. For list of abbreviations see page 102.

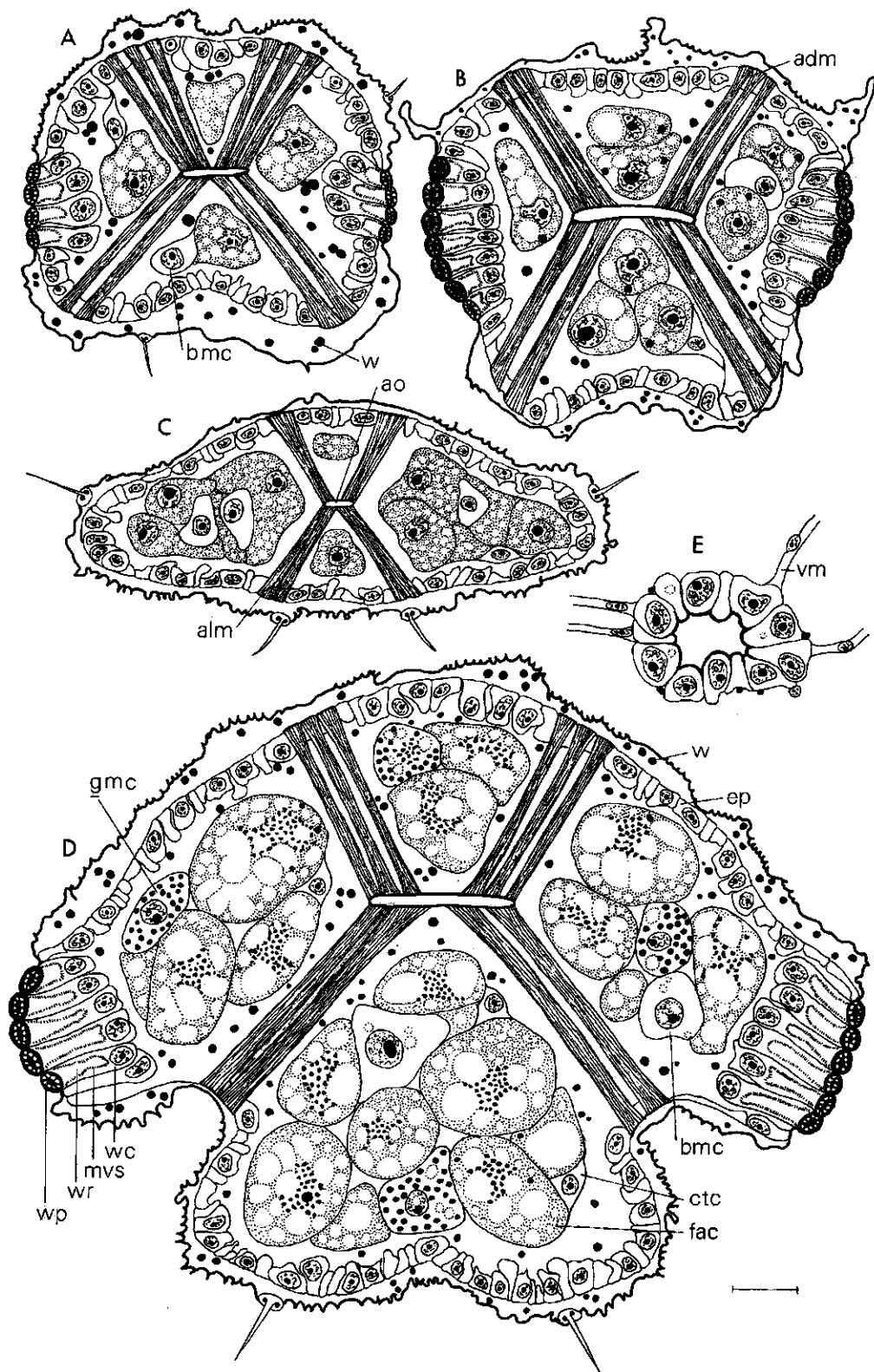


Table 7 Electron microscopical studies of aphid species with (+) or without (-) extracellular microtubules lining the luminal surface of the apical cell membrane of the midgut epithelium, according to different authors. The term extracellular microtubules was introduced by O'Loughlin and Chambers (1972).

Aphid	Midgut					Author
	Stomach	Crenated intestine	Triplet cells	Descending intestine	Caecal intestine	
<i>Aphis craccivora</i> Koch	-	+		+		O'Loughlin and Chambers, 1972
<i>Aulacorthum solani</i> (Kaltenbach)	-	+			+	
<i>Hyperomyzus lactucae</i> (Linnaeus)	-	+			+	
<i>Macrosiphum euphorbiae</i> (Thomas)	-	+			+	
<i>Myzus persicae</i> (Sulzer)	-	+			+	
<i>Rhopalosiphum padi</i> (Linnaeus)					+	Gildow, 1985 Ponsen, 1991
<i>Adelges nordmannianae</i> (Eckstein)	+	+	+	+		
<i>Aphis fabae</i> Scopoli	+	+	+	+		
<i>Drepanosiphum platanoideis</i> (Schrank)	+	+	+	+		
<i>Myzus persicae</i> (Sulzer)	+	+	+		+	
<i>Rhopalosiphum maidis</i> (Fitch)	+	+	+		+	
<i>Subsaltusaphis ornata</i> (Theobald)	+	+	+	+	+	
<i>Uroleucon sonchi</i> (Linnaeus)	+	+	+		+	

Salivary gland system

The salivary glands of all adelgid morphs including the sexuales investigated (Table 2) consist of one pair of accessory glands situated in the prothorax, and one pair of principal glands in the meso- and metathorax. Only the salivary gland cells of the sexuales of *Adelges cooleyi* and *Adelges laricis* are degenerated showing empty nuclei in a spongy cytoplasm.

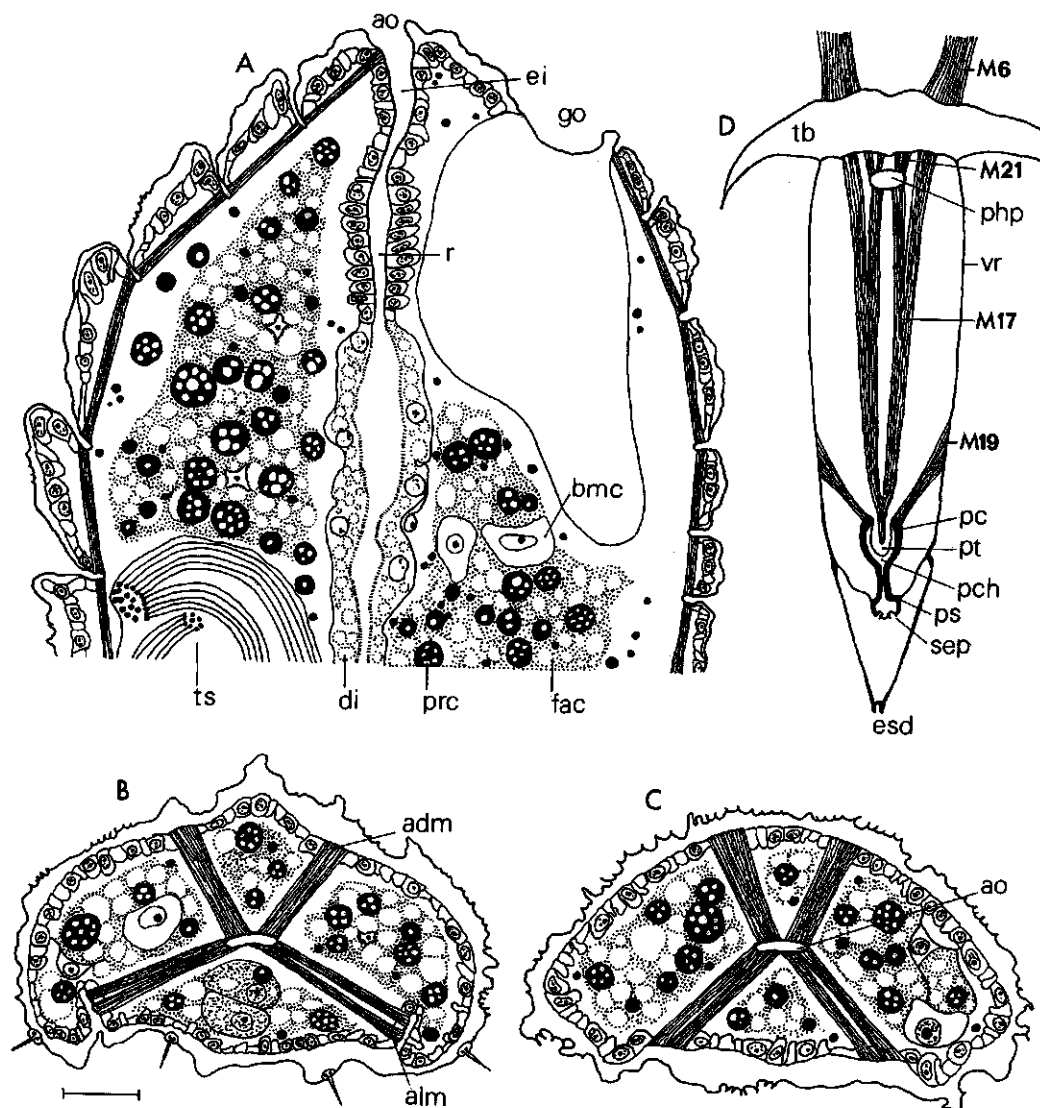


Figure 19 Median longitudinal section of a male of *Adelges laricis* (A). Anal opening in ventral position. Transverse sections of the anal musculature of a female sexuales of *Adelges laricis* (B) and a male of *Adelges cooleyi* (C), and the salivary pump of a female sexuales of *Adelges cooleyi* (D). Note: the fat cells and haemolymph of the sexuales contain protein crystals with one or more cavities (p r c). Bar represents 10 μ m. For list of abbreviations see page 102.

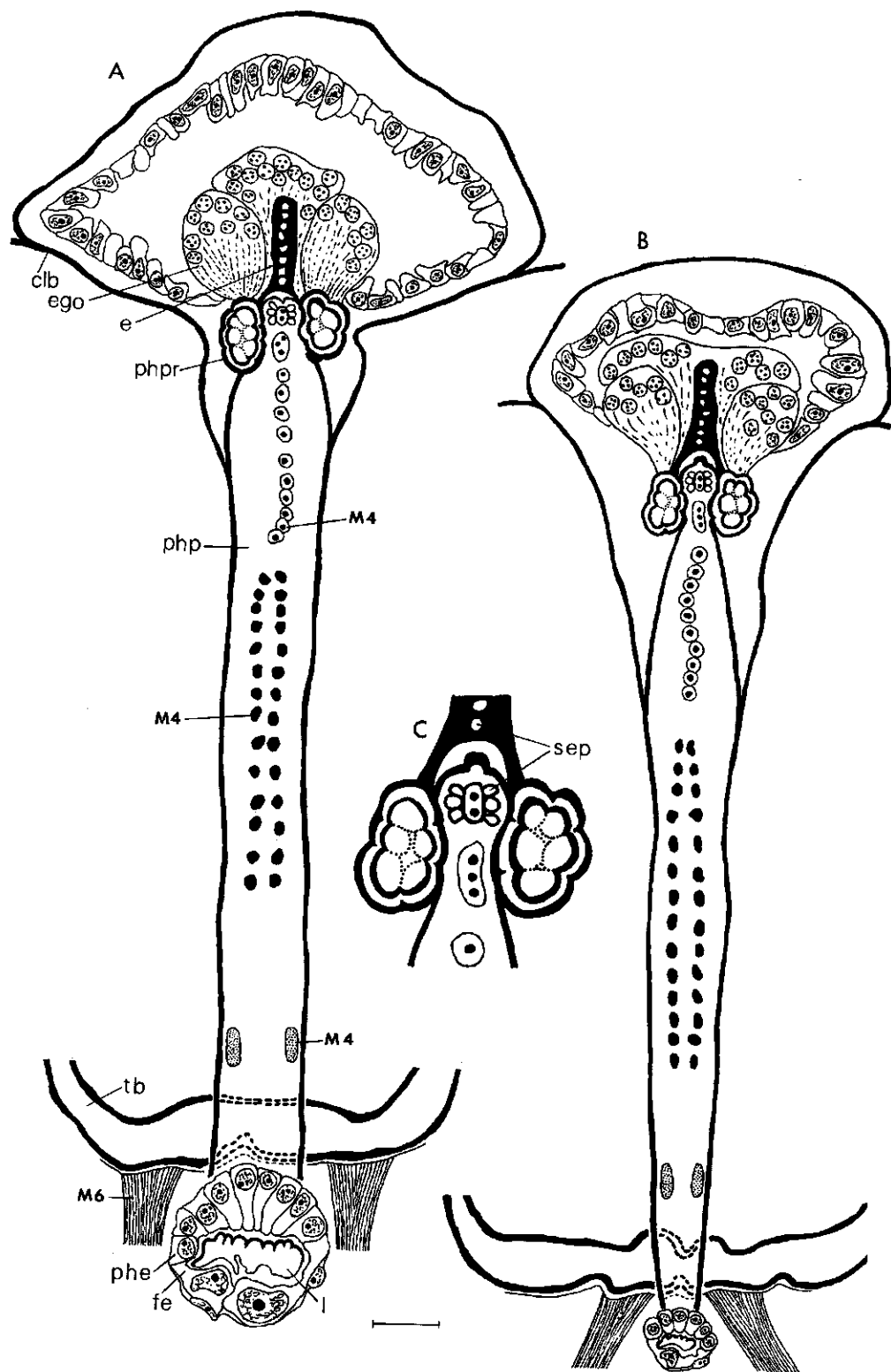
Salivary glands have been observed in *Adelges abietis* (Mark, 1877; Wiltaczil, 1886), the fundatrices of *Adelges lapponicus* (Cholodkovsky, 1905), *Adelges abietis* (Plump, 1953), *Adelges abietis*, *Adelges tardus* (Kunkel, 1966), the gallicolae of *Adelges abietis* (Plump, 1953), *Adelges cooleyi*, *Adelges tardus* (Kunkel, 1966), and the sistens and progrediens of *Adelges nordmannianae*, *Adelges piceae*, and *Adelges schneideri* (Francke-Grosmann, 1937c). Moreover, Cholodkovsky (1905) found that the salivary glands of all morphs, including the sexuales, of *Adelges lapponicus* are similar to each other, but the glands of the fundatrices are much bigger than those of the other morphs.

The salivary glands of the fundatrices of *Adelges abietis*, *Adelges laricis* (Rohfritsch, 1976), the sistens of *Adelges nordmannianae* (Falck, 1928) and *Adelges piceae* (Balch, 1952), the progrediens of *Adelges nordmannianae* (Chrystal, 1926) and the progrediens and sexuparae of *Adelges tsuga* (Young et al., 1995) secrete in the parenchyma a substance forming a sheath around the stylets which varies in thickness along its path. Plump (1953) found that in contrast to the fundatrices the gallicolae of *Adelges abietis* do not form stylet sheaths in the cortical tissue of their host plant (Table 4). From the presence of two pairs of salivary glands, Francke-Grosmann (1937c) concluded that adelgids probably produce two types of saliva, one which causes the formation of the salivary sheath to protect the stylet bundle, and the other a hypothetical enzymatic substance to liquify the parenchyma cells of their host plant.

The ducts from both lateral glands fuse to a single one which runs further ventrally around the junction of the suboesophageal and thoracic ganglion to form the common salivary duct. This duct runs forwards ventrally to the suboesophageal ganglion and turns downwards to the hypopharynx where it passes into the afferent salivary duct (Figure 8A). Before entering the pumpchamber the afferent salivary duct turns upwards and then downwards, forming an S-shaped flexure. At the site of entry the opening is controlled by a muscle (M20) originating from the middle of the tentorial bar (Figure 8A). After leaving the pumpchamber the duct turns upwards and then downwards into the pumpstem. At the foot of the pump stem the duct is somewhat dilated and provided with two sensillary pores corresponding with the hypopharyngeal gustatory organ (Figures 2 no. 6, 4 no. 6, 6B, and 19D). The duct passes into the efferent salivary duct and runs in the median line on the ventral side of the hypopharynx lip (Figure 8A) to terminate in the salivary canal enclosed by the maxillary stylets (Figures 2 no. 4, 4 no. 4, and 7F-G).

The salivary pump lies in the hypopharynx beneath the pharyngeal pump (Figure 8A). In transverse sections it appears as a chitinous tulip-shaped cylinder and a pump stem (Figures 6B and 19D). In its open end there fits a U-shaped piston connected with their lips on the edge of the cylinder. Two pairs of muscles are inserted on the flexible dorsal wall of the piston (M17): one pair originates from the tentorium (Figures 6B, 8A, and 19D) and another pair from the floor of the pharyngeal pump close to the tentorial bar (Figures 3 no. 10, 4 no. 11, and 6B). On both sides of the pump cylinder there are muscles (M19) originating from the ventral rods (chitinous ridges) (Figure 19D). These rods lead from the tentorial bar to the hypopharynx wall.

Figure 20 Oblique sections of the pharyngeal system of a larval wingless viviparous *Aphis fabae* Scopoli (A), a larval winged viviparous *Eucallipterus tiliae* (Linnaeus) (B), and the situation of the three pairs of sensillary pores of the pharyngeal valve at a high magnification (C). Note the 31 pairs of muscles of the pharynx (M4). Bar represents 10 µm. For list of abbreviations see page 102.



The structure of the salivary pump including the muscles, ducts, and sensillary pores of all adelgid species (Table 2) is identical to that of species belonging to all subfamilies of the Aphididae (Table 15). Only in the asexual morphs of the phylloxerid species the dorsal wall of the piston is inserted with three pairs of muscles: two pairs of muscles originate from the tentorium and one pair from the floor of the pharyngeal pump. In the sexuales of the Phylloxeridae (Ponsen, 1997) and in the males of *Stomaphis quercus* (Linnaeus) (Table 19) the salivary glands and the salivary pump are lacking.

Table 8 The average number and range of ovarioles in the several morphs of *Adelges cooleyi* and *Adelges laricis*. The sign \pm is followed by the standard deviation of the mean. Number of sexuales in parentheses.

Aphid Morph	Total number of aphids sectioned	Average number of ovarioles	Range	
<i>Adelges cooleyi</i>				
fundatrices	3	108.3 \pm 9.5	101 – 119	
gallicolae	10	32.5 \pm 5.4	24 – 42	
sistens	7	11.4 \pm 1.9	9 – 15	
progreiciens	10	6.5 \pm 0.9	5 – 9	
sexuparae	9	6.8 \pm 2.0	4 – 9	
sexuales	26			1 ovariole + egg (1) 1 ovariole + egg + 1 degenerated ovariole (6) 2 degenerated ovarioles (14) 2 testes + 4 degenerated ovarioles (2) 2 testes (3)
<i>Adelges laricis</i>				
fundatrices	3	109.7 \pm 6.7	104 – 117	
gallicolae	9	7.2 \pm 2.8	4 – 13	
sistens	8	40.4 \pm 4.1	34 – 46	
progreiciens	9	3.4 \pm 1.7	1 – 6	
sexuparae	13	2.6 \pm 1.2	2 – 6	
sexuales	13			1 ovariole + egg (2) 2 testes + 4 degenerated ovarioles (8) 2 testes (3)

Table 9 Total number of eggs per individual of *Adelges cooleyi* and *Adelges laricis* according to different authors. The adelgid names used by authors are given in Table 1. The primary host is a *Picea* species, the secondary host a species of *Abies*, *Larix*, or *Pseudotsuga*.

Aphid	Host plant	Fundatrices	Gallicolae	Sistens	Progrediens	Sexuparae	Female sexuales	Author
<i>Adelges cooleyi</i>	<i>Picea sitchensis</i>	300 – 500				10 – 25	1	Chrystal, 1922
	<i>Pseudotsuga menziesii</i>		100 – 150	30 – 60				Fluiter, 1934
	<i>Pseudotsuga douglasii</i>			60				Cameron, 1936
	<i>Picea sitchensis</i>	300 – 500				10 – 12		
	<i>Pseudotsuga douglasii</i>		100 – 150					
	<i>Picea sitchensis</i>	350				15 – 20	1	Fräncke-Grosmann, 1950
	<i>Pseudotsuga menziesii</i>		80 – 100					
	<i>Picea sitchensis</i>	± 350				15 – 21	1	Börner and Heinze, 1957
	<i>Pseudotsuga douglasii</i>		80 – 100					
<i>Adelges laricis</i>	<i>Picea</i> sp.	90 – 352				5 – 20		Cumming, 1959
	<i>Pseudotsuga menziesii</i>		28 – 103	6 – 52	3 – 25			
	<i>Picea excelsa</i>							
	<i>Larix</i> sp.		18 – 20			5 – 10	1	Cholodkovsky, 1897
	<i>Picea abies</i>							
	<i>Larix europaea</i>		18 – 20	150		5 – 10	1	Börner, 1908
			20	150		10	1	Nüsslin, 1910
	<i>Picea</i> sp.						1	Steven, 1917
	<i>Abies</i> sp.		20 – 30	35 – 50				
	<i>Picea</i> sp.	50 – 100				5 – 10	1	Speyer, 1919
	<i>Larix europaea</i>		20 – 40	35 – 50				
	<i>Picea mariana</i>	200					1	Annam, 1928
	<i>Larix</i> sp.		40	200	20 – 50			
	<i>Larix kaempferi</i>			63				Inouye, 1953
	<i>Picea excelsa</i>	± 150				10 – 20		Börner and Heinze, 1957
	<i>Larix europaea</i>			± 150				

Mycetome

Witlaczil (1886) was the first who reported the presence of a pseudovitellus (= mycetome) both in the eggs and in the larvae of gallicolous *Adelges abietis*. It consists of two longitudinal rows of cells with fine granular material, one on each side of the digestive system. The term mycetome is introduced by Sulc (1910) and he found in the mycetocytes of gallicolous *Adelges abietis* and *Adelges laricis* cummin-shaped symbionts with a diameter of 1-2 μm ; they multiplied by transversal fission. The mycetome of six out of the nine adelgid species investigated by Profft (1937) consisted of both mycetocytes with spherical symbionts and those with oval-shaped symbionts; in the remaining three species only minute thread-like symbionts were found in the mycetocytes.

In young larvae of all asexual adelgid morphs (Table 2) the mycetome consists of two longitudinal masses of mycetocytes, one on each side of the digestive system (Figure 10D). They run from the metathorax to the sixth abdominal segment; in the fourth and fifth

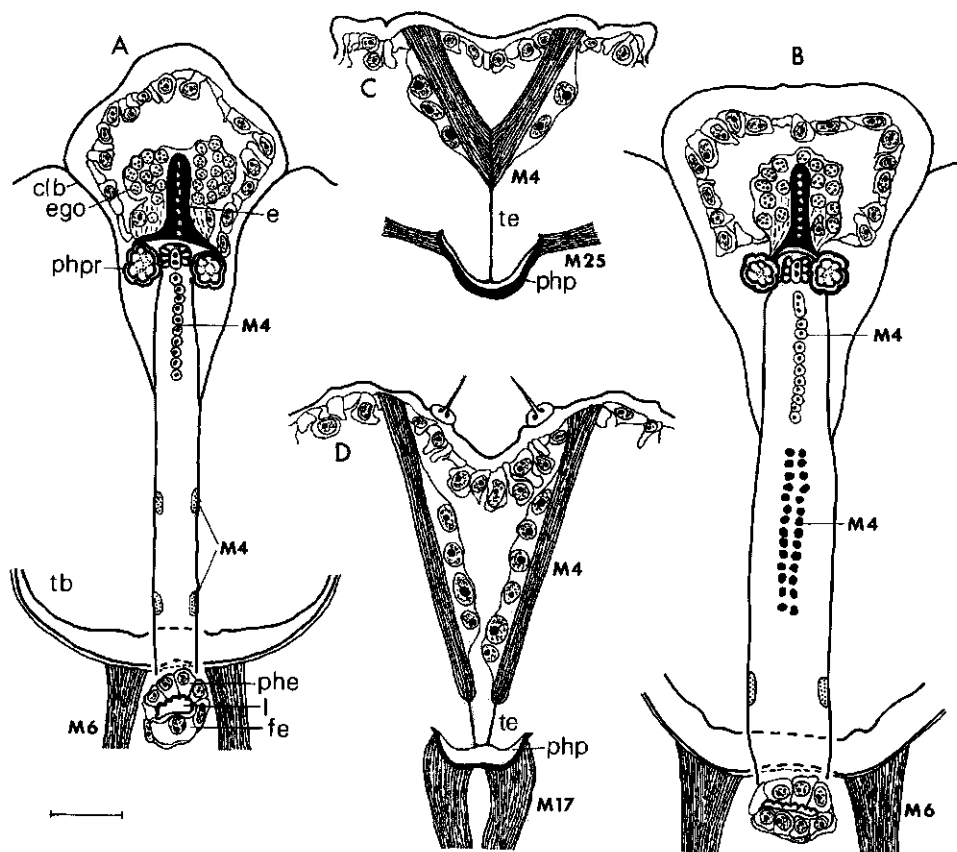


Figure 21 Oblique sections of the pharyngeal system of a larval winged viviparous *Lizerius tuberculatus* (Blanchard) (A) and a larval wingless viviparous *Mindarus obliquus* (Cholodkovsky) (B). Note the 14 and 31 pairs of muscles (M4) of the pharyngeal valve and pump. Transverse sections of the pharyngeal pump with one cuticular tendon of a wingless oviparous larva (C) and that with two tendons of a winged viviparous larva of *Mindarus abietinus* Koch. Bar represents 10 μm . For list of abbreviations see page 102.

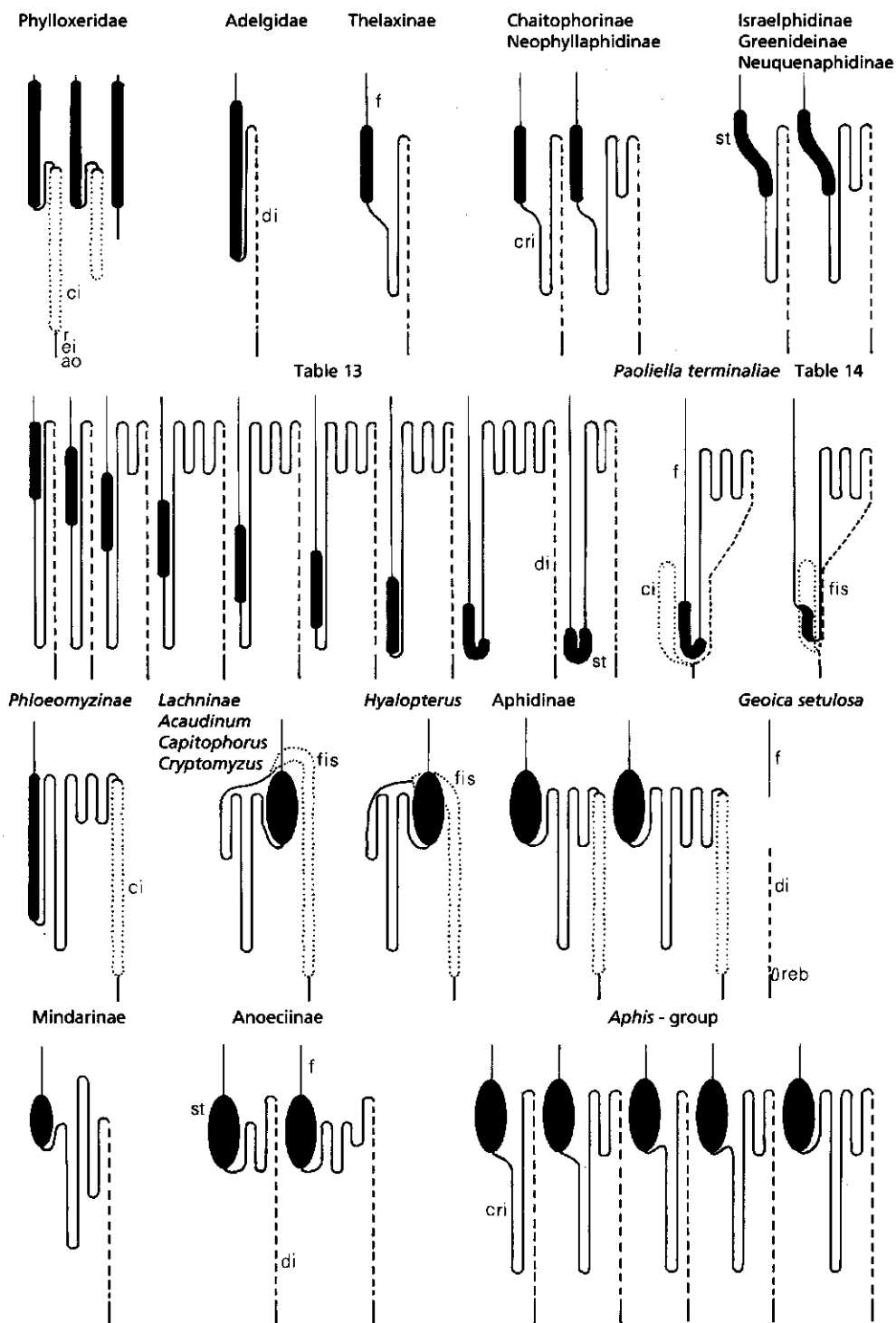


Figure 22 Diagrams illustrating the existing forms of the digestive system within the Aphidoidea. The dashed line represents the descending intestine, and the dotted line the caecal intestine (see Table 15). For list of abbreviations see page 102.

abdominal segment they join thus forming a bridge dorsally of the digestive system. In *Pineus orientalis* the two longitudinal masses are not connected with each other (Figure 10E). The total number of mycetocytes of a wingless progredien larva of *Adelges nordmannianae* is 85 and that of a gallicolous larva of *Pineus orientalis* 31.

The mycetome is enclosed by a nucleated sheath. The scanty cytoplasm of the mycetocytes is completely filled with thin rod-shaped symbionts (Figure 35C). In ultrathin sections of *Adelges nordmannianae* they show an ellipsoid-shaped structure multiplying by constriction of the circular centre. Each mycetocyte has an irregularly shaped nucleus due to the pressure of the multiplying symbionts. Scattered among the symbionts there are spiral-like bodies which show a filamentous structure at high magnification (Figure 38). The much smaller nuclei of the sheath are projected into the mycetocytes.

During larval life the mycetocytes increase in size, whereas the size of the symbionts remains constant. The mycetome gradually disintegrates in clusters of mycetocytes or in single mycetocytes, and parts of the nucleated sheath remains connected with the separated mycetocytes. The cell wall of some mycetocytes breaks open and this process continues in the adult stage. The symbionts liberate into the haemolymph and are distributed throughout the body cavity. Some of them enter into the posterior pole of the oocytes inside the telotrophic ovarioles where they multiply.

Both in the female sexuales and males of *Adelges cooleyi* and *Adelges laricis* the mycetome consists of two small organs, one on each side of the digestive system situated in the first and second or second and third abdominal segment (Figure 10C and F). Each organ consists of very small mycetocytes of which the nuclei are empty or irregular with condensed chromatine (Figure 35D and E). The cytoplasm is somewhat vacuolized and filled with fibrous material quite different from the symbionts of the asexual adelgids. Histologically the mycetocytes of the adelgid sexuales as well as their midgut and salivary glands show degeneration symptoms.

Lampel (1959), working with *Pemphigus bursarius* (Linnaeus) and *Pemphigus spyrothecae* Passerini found that during embryonal development of the sexuales in the sexuparae the symbionts from the sexuparae only invade the female sexuales. This implies that after hatching the males lack a mycetome. The sexuales of the Pemphiginae are dwarfish, wingless individuals characterized by the absence of mouthparts.

Table 10 The average number of ovarioles per individual in the several species of the Adelgidae according to different authors. The adelgid names used by authors are given in Table 1.

Aphid (present name)	Fundatrices	Gallicolae	Sistens	Progrediens	Sexuparae	Author
<i>Adelges abietis</i>	40 – 48 30	10 – 30 10 – 20	– –	– –	– –	Leuckart, 1859 Cholodkovsky, 1900
<i>Adelges laricis</i>	– 24	– –	– 10	6 2 – 6	4 – 5 6 – 7	Leuckart, 1859 Cholodkovsky, 1900
<i>Adelges lapponicus</i>	20 – 40 20 – 36	20 – 30 4 – 12	2 – 3 –	2 – 3 –	2 – 6 –	
<i>Adelges nordmannianae</i>	–	–	–	5 – 8	–	Marchal, 1913
<i>Adelges piceae</i>	–	–	–	6 – 8	–	Leuckart, 1859
<i>Adelges viridana</i>	–	6 – 8	–	–	–	Cholodkovsky, 1900
<i>Adelges viridis</i>	–	20	6	–	4 – 6	
<i>Pineus cembrae</i>	–	–	8	6	8	
<i>Pineus pini</i>	–	–	6 – 8	4	4	
<i>Pineus pini</i>	–	18 – 20	–	–	2 – 6	Marchal, 1913

Oenocytes

The oenocytes only occur in a number of adelgid species and its morphs (Table 12). They are situated in the body cavity between the mesodermal tissue and the internal organs of the thorax and the first seven abdominal segments (Figure 10A-B). The majority of them occur as single cells, but sometimes in clusters of 2-3 cells intimately attached to each other.

During larval life the oenocytes gradually increase in size. They contain vacuoles and granules in vacuoles; each oenocyte has a somewhat irregularly-shaped nucleus which decreases in size due to the production of granules which are released into the cytoplasm (Figure 35C). They become encapsulated in vacuoles and transported to the cell membrane to be released subsequently into the haemolymph by membrane fusion. In the imaginal stage the nuclear chromatin and sometimes the nucleolus have completely disappeared, but the oenocyte is still intact (Figures 31, and 34-37).

In a wingless progredien larva of *Adelges nordmannianae* there are 41 oenocytes and in a gallicolous larva of *Pineus orientalis*, 67; the latter are smaller than the former (Figure 10A-B). During one life cycle of *Adelges cooleyi* the total number of oenocytes decreases gradually in the successive morphs after the fundatrix has developed (Table 12). In the sexuales of both the adelgids (Figure 10C and F) and the phylloxerids (Ponsen, 1997) the oenocytes are lacking.

Mesodermal tissue

The larval mesodermal tissue forms a continuous sheet situated in the body cavity against the epidermis. In the dorsal region of the head the sheet has a thickness of about 3-4 cell layers and in the lateral and ventral region it is a single layer of cells. Both the thorax and abdomen the mesodermal tissue consists of about 1-3 cell layers with offshoots of fat cells between the various organs and inside all appendages (Figures 6A, 17, 18, 26C, 28C-D, 30, 31, 32, and 34).

Histologically the mesodermal tissue consists of four distinct types of cells which increase in size during larval life. Most numerous are the fat cells, characterized by the presence of many various-sized vacuoles filled with a yellow oil-like substance. Due to the pressure of the lipid vacuoles the spherical nuclei gradually transform into various shapes, from polygonal to stellate or flattened and displaced to one side of the cell. Moreover, waxy droplets arise in the cytoplasm of the fat cells and are released by the cell membrane into the haemolymph and from there to the endocuticle of the epidermis (Figures 17 and 18). During the growth proceeds the compact structure of the fat body disintegrates in single spherical cells which disperse between the several organs, eggs, mycetocytes, and oenocytes.

Both the granulated and the basophilic mesodermal cells are individually dispersed among the fat cells, but in the appendages these polygonal cells are lacking (Figures 17, 18, and 28C-D). The basophilic mesodermal cells are present in all adelgid species and its morphs; the granulated mesodermal cells only occur in those adelgid species and its morphs where the oenocytes are lacking (Table 12). In very young larvae the granulated mesodermal cells contain some granules and vacuoles in their cytoplasm (Figure 28C-D) which increase in number during larval life without deformation of the spherical nuclei (Figure 18D). The basophilic mesodermal cells have a structureless homogeneous basophilic cytoplasm and a distinct spherical nucleus. Similar cells have been shown in the fat body of *Adelges viridis* (Profft, 1937).

The fourth type of cells are the much smaller connective tissue cells. These spindle-

Table 11 List of species of the Adelgidae of which the sexuales are wingless, dwarfish individuals with well-developed mouthparts, and the female sexuales lay but one egg, as cited in the literature. The adelgid names used by the various authors are given in Table 1.

Aphid (present name)	Host plant	Author
<i>Adelges cooleyi</i>	<i>Picea sitchensis</i>	Chrystal, 1922; Cameron, 1936; Francke-Grossmann, 1950; Börner and Heinze, 1957
	<i>Picea</i> sp.	Annand, 1928
<i>Adelges laricis</i>	<i>Picea excelsa</i>	Cholodkovsky, 1896, 1897; Speyer, 1924
	<i>Picea abies</i>	Börner, 1908; Nüsslin, 1910; Steven, 1917; Speyer, 1919
	<i>Picea mariana</i>	Annand, 1928
<i>Adelges nordmannianae</i>	<i>Picea orientalis</i>	Marchal, 1913; Steven, 1917; Schneider-Orelli et al., 1929; Varty, 1956
<i>Adelges piceae</i>	<i>Picea</i> sp.	Nüsslin, 1903
<i>Adelges prelli</i>	<i>Picea orientalis</i>	Francke-Grossmann, 1937a
<i>Adelges viridis</i>	<i>Picea</i> sp.	Blochmann, 1887; Cholodkovsky, 1897; Nüsslin, 1910; Steven, 1917; Speyer, 1919
<i>Pineus cembrae</i>	<i>Picea excelsa</i>	Cholodkovsky, 1890; Börner, 1908
<i>Pineus orientalis</i>	<i>Picea orientalis</i>	Marchal, 1913; Steven, 1917

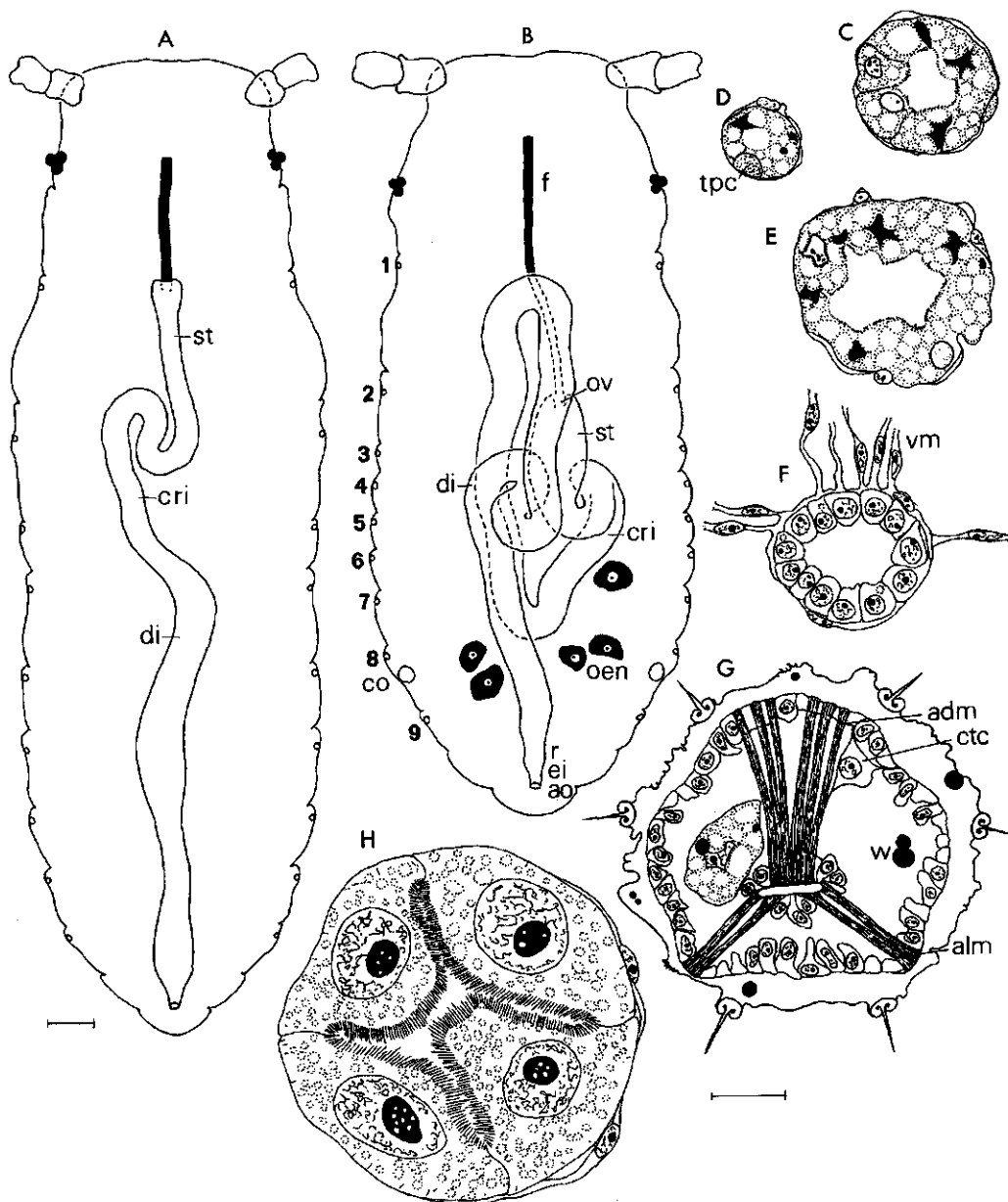


Figure 23 Dorsal view of the digestive system and topographical position of the oenocytes of a male of *Mindarus abietinus* Koch (A) and a wingless viviparous larva of *Mindarus obliquus* Cholodkovsky (B) reconstructed from serial sections. In the males the mycetome and oenocytes are lacking. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 μ m. Transverse sections of the stomach (C), crenated intestine (D), and descending intestine (E) of a male of *Mindarus japonicus* Takahashi, the rectum of a male of *Mindarus obliquus* (F), the anal musculature of a male of *Mindarus abietinus* (G) (anal opening in ventral position), and the crenated intestine of a winged viviparous *Mindarus japonicus* (H). Bar represents 10 μ m. For list of abbreviations see page 102.

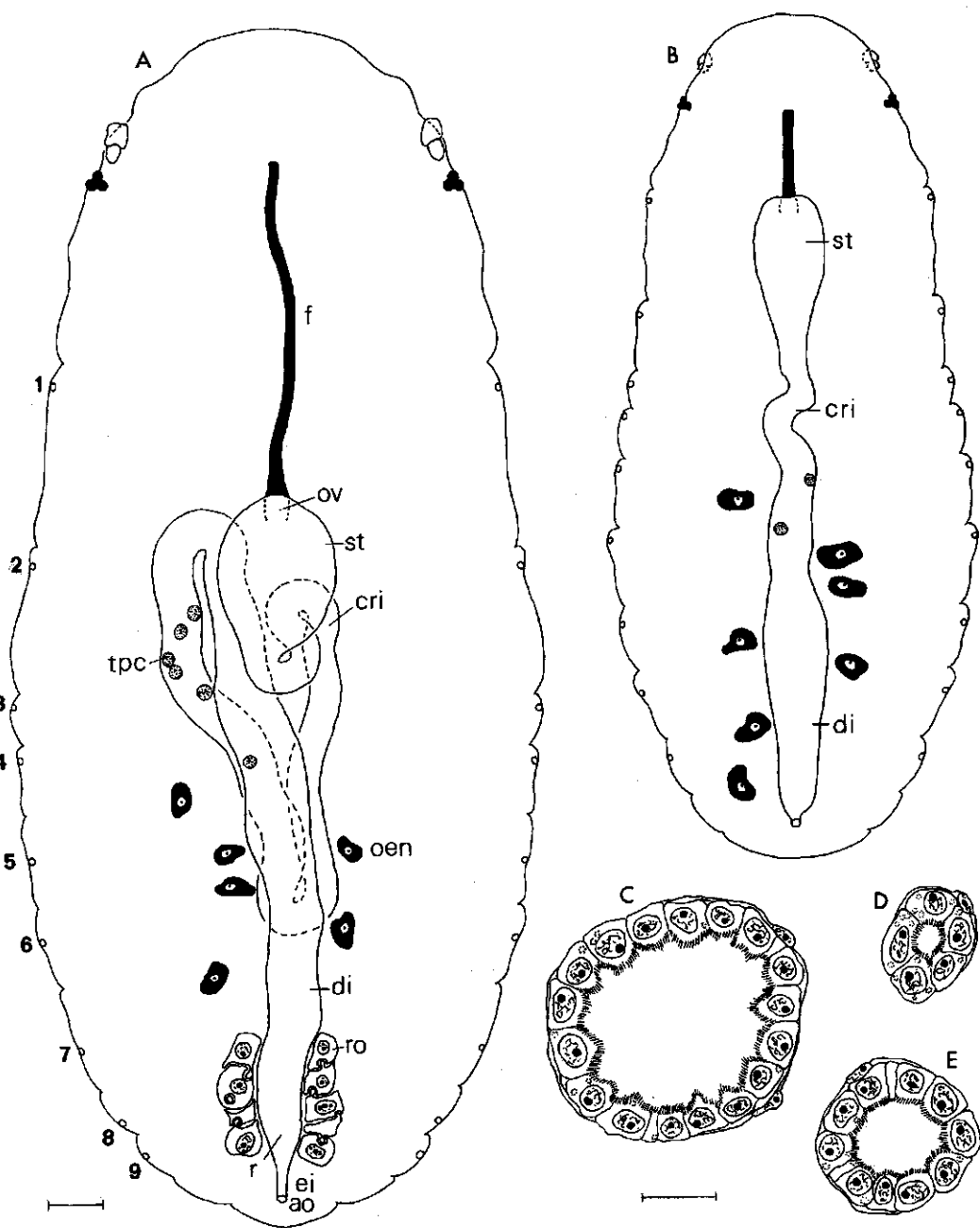


Figure 24 Dorsal view of the digestive system and topographical position of the oenocytes of an embryonic wingless viviparous (A) and an embryonic male (wingless exule) of *Forda formicaria* von Heyden (B) reconstructed from serial sections. Note the rectal organ (ro) which surrounds the posterior end of the descending intestine and rectum is lacking in the males. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 µm. Transverse sections of the stomach (C), crenated intestine (D), and descending intestine (E) of an embryonic male of *Forda formicaria*. Bar represents 10 µm. For list of abbreviations see page 102.

shaped or stellate cells with their proportionally large, spherical nuclei are mainly distributed along the surface of the fat body, but are also present in the haemocoel (Figures 13D, 17, 18, 28C-D, 30A, 32, and 34). Their tapering processes form a network of delicate membranes to support the mesodermal tissue and to keep the several organs in position.

In the haemolymph of all adelgid species investigated (Table 2) the haemocytes are lacking.

In the sexuales of *Adelges cooleyi* and *Adelges laricis* the fat cells and the haemolymph contain numerous protein crystals with cavities of various dimensions (Figures 8A and 19A-C); the waxy droplets present in all asexual morphs (Figures 6A and 18) are absent in the sexuales. The basophilic mesodermal cells are evenly dispersed individually among the fat cells, but the oenocytes and granulated mesodermal cells are lacking (Table 12).

Discussion

In all aphid species investigated (Table 15) the ectodermal part of the anterior region of the alimentary tract consists of the stylets, pharynx, foregut, and the oesophageal valve. The pharynx consists of the pharyngeal duct, valve, and pump. The majority of species of the Aphididae the last two pharyngeal parts are controlled by 31 pairs of muscles (Figures 20, 21B, and 26B). The dorsal wall of the pharyngeal valve has two pairs of muscles, each pair being attached to a tendon (Figures 1 no. 1, 2 no. 7, and 4 no. 7). The movement of the flexible dorsal wall of the pharyngeal pump is controlled by 27 pairs of muscles. In the anterior part they are attached to 13 long tendons arising from the midline of the dorsal pump wall. The muscles diverge from each side of the tendon (Figure 21C). Within some species the total number of long tendons varies from 13 to 16 for *Geoica utricularia* (Passerini) and *Pterocomma populeum* (Kaltenbach), from 13 to 18 for *Plocamaphis amerinae* (Hartig) and *Trama rara* Mordvilko, from 13 to 20 for *Anoecia* (Figure 26B), and 30 to 37 for wingless oviparous *Stomaphis quercus*. The middle part of the pump is provided with short tendons placed in 14 pairs, each of them inserted with one muscle (Figure 21D). In the posterior part of the pump two pairs of supporting muscles are attached to the edges of the dorsal wall (Ponsen, 1972).

On the other hand, in the Phylloxeridae (Ponsen, 1997) and Adelgidae (Figure 9) there are 14 pairs of muscles to control the pharyngeal valve and pump: two pairs of muscles, each pair attached to a tendon to open the valve (Figures 1 no. 1 and 2 no. 7), 10 pairs of muscles inserted on 10 tendons arising from the midline of the flexible dorsal pump wall (Figures 1 no. 2-3 and 3 no. 8-9), and 2 pairs of supporting muscles attached to the edges of the dorsal wall of the pharyngeal pump (Figures 3 no. 10-11 and 4 no. 11-12). Species of the last two families take their nourishment from non-vascular tissue cells by intracellular penetration (Harrewijn et al., 1998; Table 4) and those of the Aphididae from phloem by intercellular penetration (Kidd, 1976; Tjallingii and Hogen Esch, 1993).

In species of the Aphididae (Table 15) the 13 pairs of pharyngeal muscles with long tendons pump up their food from the phloem to the pharyngeal pump and from there to the stomach by the 14 pairs of pharyngeal muscles with short tendons (Figures 20, 21B, and 26B). However, in the asexual morphs of the Phylloxeridae and those of the Adelgidae the 14 pairs of pharyngeal muscles with short tendons are lacking (Figures 8 and 9). Hence the 10 pairs of muscles with long tendons have to pump up the food from the parenchyma tissue to the pharyngeal pump and from there to the stomach. These data correspond with the fact that the pharyngeal pump of phloem feeders is about one and a half times as long as that of the parenchyma feeders.

The 10 pairs of muscles with long tendons of the phylloxerids pump up the food from the parenchyma tissue via very short stylets whereas those of the adelgids via extremely long stylets housing in a crumena (Figure 5). *Stomaphis quercus* has also very long stylets and 30-37 pairs of muscles with long tendons to pump up the food from the phloem to the pharyngeal pump and from there to the stomach by 14 pairs of muscles with short tendons.

The foregut is a very thin, straight tube which runs posteriad from the tentorium to terminate into the oesophageal valve (Figures 10A-B, 11, 12, 22, 23A-B, 24A-B, 26A, 28A, and 29A). The length of the foregut varies from extremely short in all species of the Phylloxeridae (Ponsen, 1997) to very long terminating in the seventh abdominal segment of all species in Table 14 and some species in Table 13. Waxy droplets originating from fat cells are both present in the haemolymph and endocuticle of the epidermis (Figures 6A, 17,

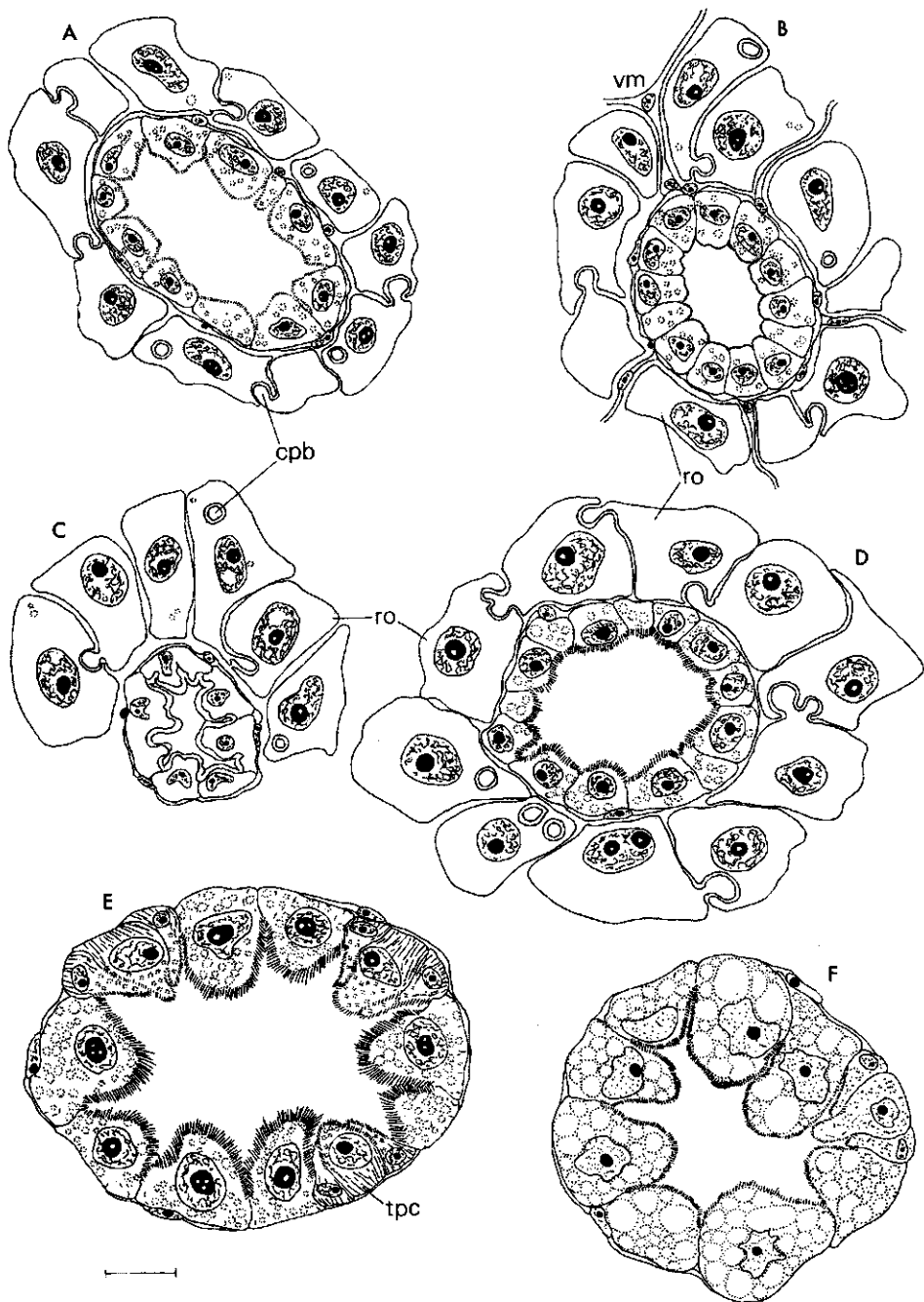


Figure 25 Transverse sections of the descending intestine (A), rectum (B), and epidermal invagination (C) of a wingless viviparous *Fordia marginata* Koch (modified after Ponsen, 1991), and the descending intestine of an embryonic wingless viviparous *Fordia formicaria* von Heyden (D). The polygonal cells of the rectal organ (ro) are interconnected by a cytoplasmic bulge (c p b) which locks in a membrane invagination of the neighbouring cell like pieces of a jigsaw puzzle. Transverse sections of the crenated intestine of a wingless oviparous (E, with three triplets) and a male (F) of *Stomaphis quercus* (Linnaeus). Bar represents 10 μ m. For list of abbreviations see page 102.

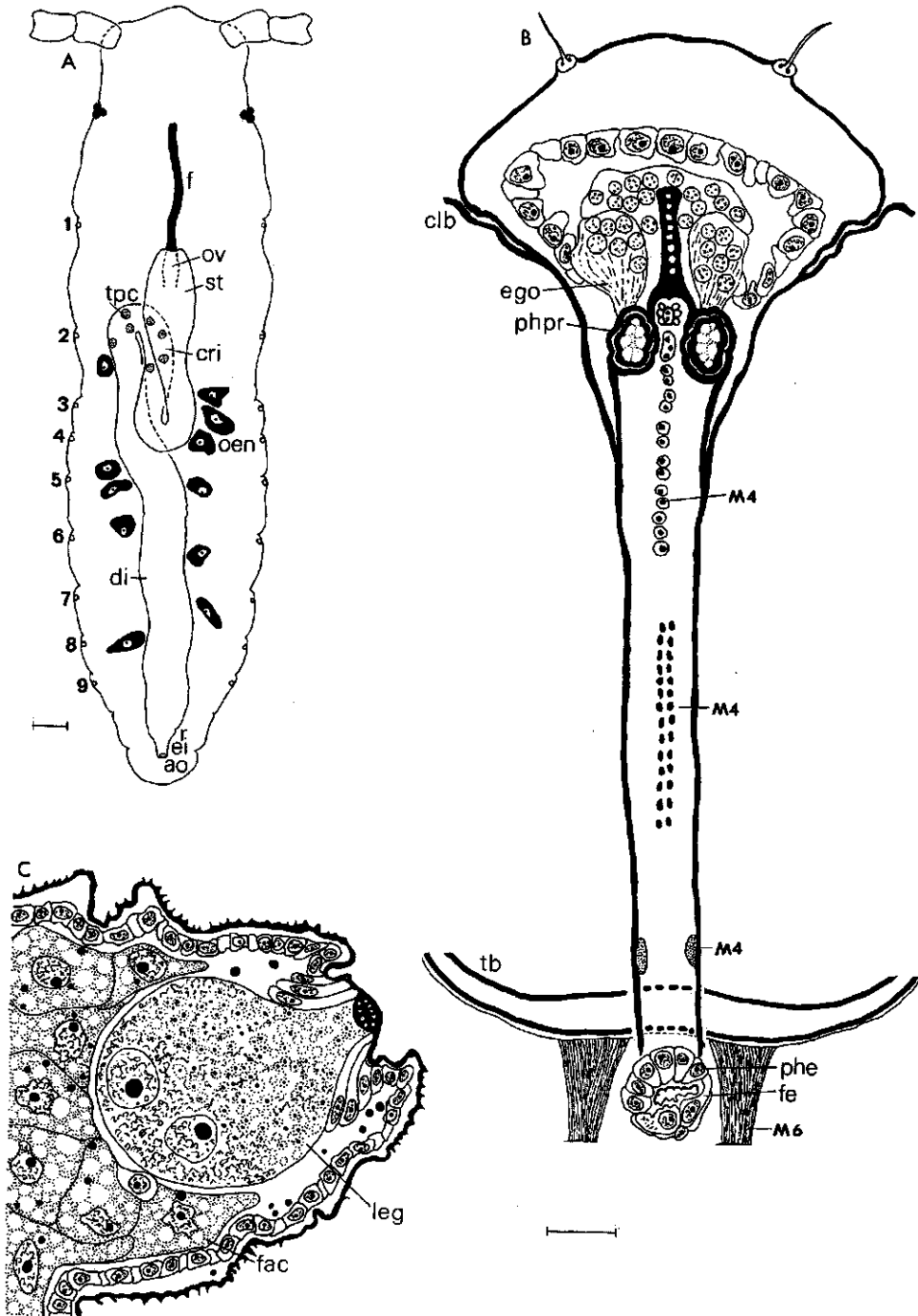


Figure 26 Dorsal view of the digestive system and topographical position of the oenocytes of a male of *Anoecia* sp. (A) reconstructed from serial sections. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 µm. Oblique section of the pharyngeal system of a winged viviparous *Anoecia corni* (Fabricius) (B). Note the 34 pairs of muscles of the pharynx (M4). Transverse section of a lateral epidermal gland of a winged viviparous *Paoliella terminaliae* (Hall) (C). Bar represents 10 µm. For list of abbreviations see page 102.

18, 23G, 30, 31, and 32). In the endocuticle of the foregut and that of the oesophageal valve the waxy droplets are lacking (Figure 13G).

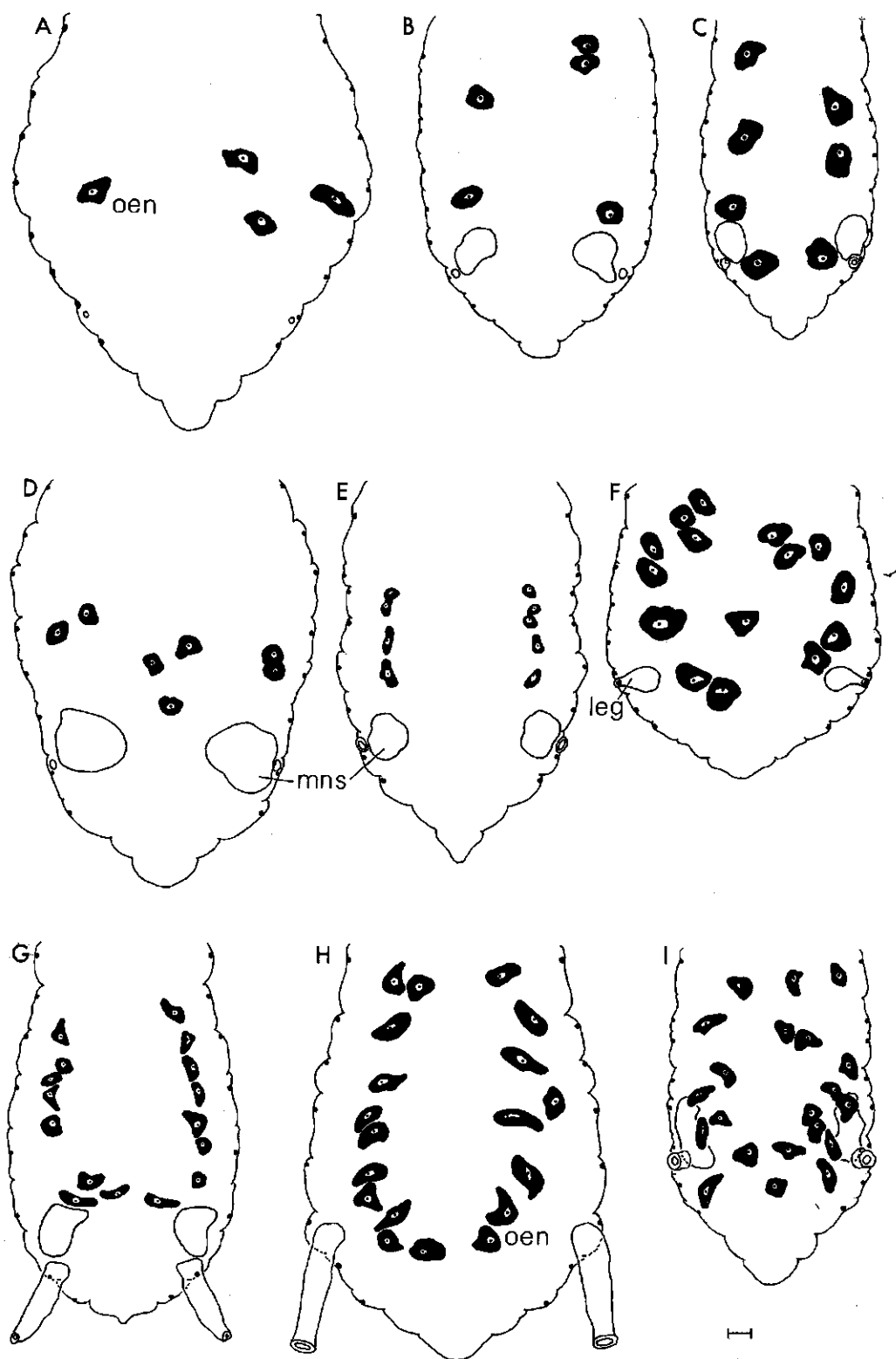
In all aphid species (Table 15) the midgut is the endodermal part of the alimentary tract. It consists of a stomach, crenated intestine, caecal- and/or descending intestine (Figure 22). The stomach of species of the Adelgidae and those of the Phylloxeridae is situated ventrally in the middle region of the body cavity. In species of the subfamilies summarized in Table 13 and 14 the stomach lies either to the left or to the right in the ventral region of the body cavity and ventrally to the two types of intestines. The stomach of *Phloeomyzus passerinii* (Signoret) (Phloeomyzinae) and that of species of the Mindarinae (Table 15; Figure 23B) lies in the central region of the aphid, both dorsally and ventrally of the two types of intestines. Species of the remaining subfamilies have a stomach which lies centrally in the dorsal region of the body cavity and dorsally to the intestines.

Histologically, the tubular stomach of species of the Chaitophorinae, Neophyllaphidinae, Thelaxinae, and those summarized in Tables 13 and 14, is occupied by a single layer of cells which do not show any cytological evidence of secretory activity. The triangular cells of the tubular or more or less dilated stomach of the Adelgidae, Phylloxeridae, Greenideinae, Israelaphidinae, and Neuquenaphidinae produce a merocrine secretion. The stomach of the last three subfamilies bends either to the right or to the left ventral part of the aphid before joining the crenated intestine (Figure 22). In polyphagous species of the Aphidinae and those of the *Aphis*-group the stomach has both cells with a holocrine secretion and cells with a merocrine secretion. Similar secretory cells occur in the stomach of *Phloeomyzus passerinii*. In the remaining species the cells are either triangular or cuboidal and produce a merocrine secretion. This type of secretion is also found in the dilated stomach of species of the Anoeciinae and those of the Mindarinae. The secretion of the stomach cells continues during larval life and proceeds into the adult stage.

The tubular part of the midgut has along its entire length an opaque, crenated structure (Table 15). It has slow peristaltic movements generated by circular muscles as well as the foregut and stomach. From the stomach to the crenated intestine there are four types of transitions (Figure 22). In the first type the intestine runs from the stomach directly posteriorly to the abdominal loop (Greenideinae, Israelaphidinae, Neuquenaphidinae, and Table 13); in the second type it runs from the stomach directly to the ventral part of the aphid and subsequently posteriorly to the abdominal loop (Thelaxinae, Chaitophorinae, and Neophyllaphidinae). The transition from the stomach to the intestine of the third type is marked by a weak loop and that of the fourth type by a sharp loop. In each individual the transition from the stomach to the intestine of the last three types is situated either to the right or to the left of the stomach. Within the *Aphis*-group there are species with one of the last three types of transitions (Figure 22).

The length of the crenated intestine varies from a very short tube for species of the Phylloxeridae to a very long tube for *Phloeomyzus passerinii* (Figure 22). In the crenated

Figure 27 Topographical position of the oenocytes (o e n) of a wingless viviparous *Phloeomyzus passerinii* (Signoret) (A) and *Thelaxes dryophila* (Schrank) (B), winged viviparous *Neophyllaphis grobleri* Eastop (C) and *Anoecia corni* (Fabricius) (D), wingless viviparous *Subsaltusaphis ornata* (Theobald) (E), winged viviparous *Paoliella terminaliae* (Hall) (F), winged male of *Greenidea eugeniae* Takahashi (G), winged viviparous *Drepanosiphum platanoidis* (Schrank) (H) and *Chaitophorus populeti* (Panzer) (I) reconstructed from serial sections. The head, pro- and mesothorax are omitted. The nine species have two pairs of thoracic and seven pairs of abdominal spiracles. Bar represents 30 µm. For list of abbreviations see page 102.



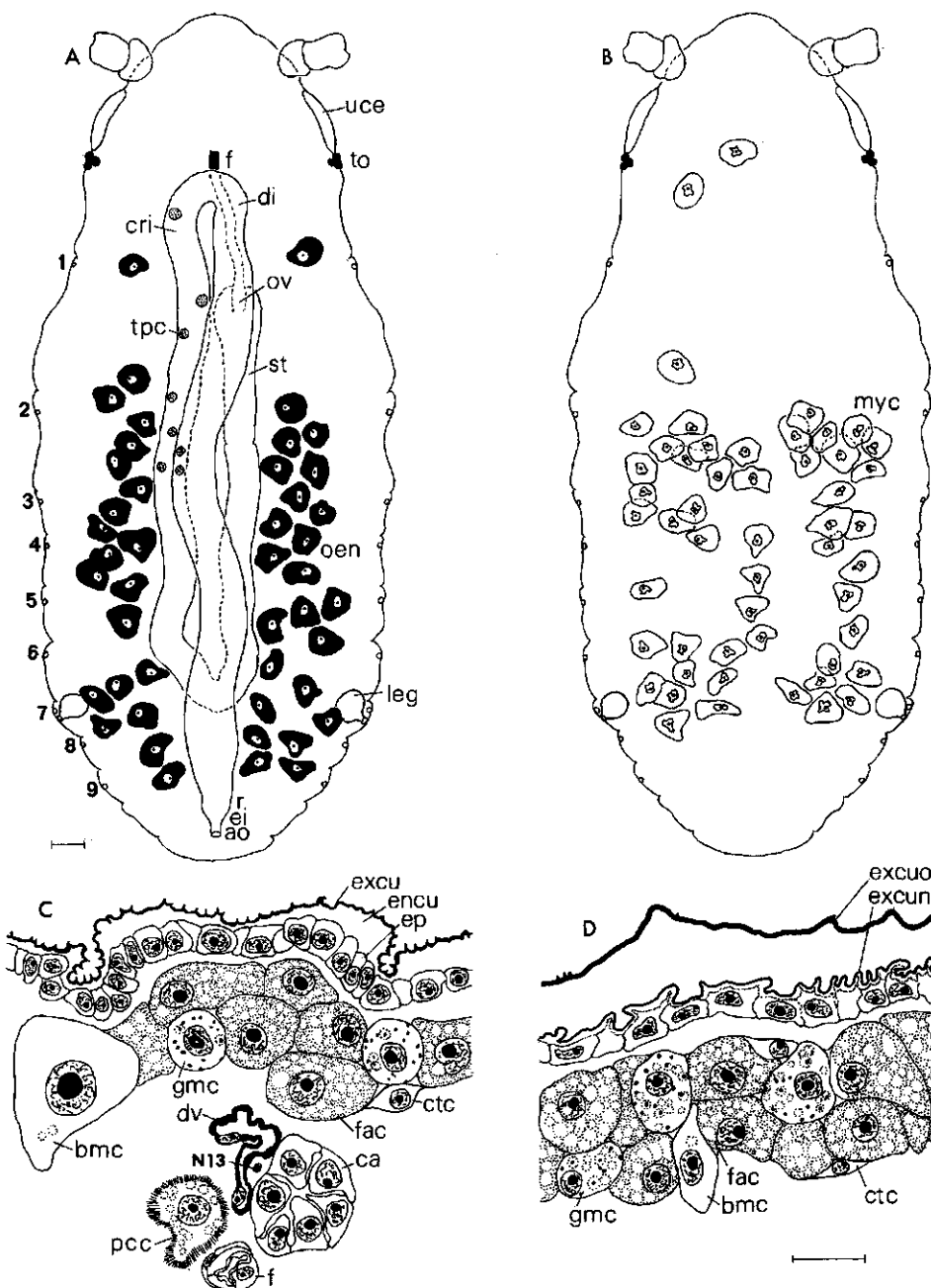


Figure 28 Dorsal view of the digestive system and topographical position of the oenocytes (A) and mycetocytes (B) of a first larval stage of a winged viviparous *Lizerius tuberculatus* (Blanchard) reconstructed from serial sections. This species has no mycetome but the mycetocytes are dispersed throughout the body cavity. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 µm. Transverse sections of the head of a young larval sexuparous *Adelges viridana* (C) and a moulting larval gallicolous *Adelges lapponicus* (D) showing the granulated mesodermal cells (g m c), dorsal vessel (d v), foregut (f), medial dorsal nerve (N13), corpus allatum (ca), and a pericardial cell (p c c). Bar represents 10 µm. For list of abbreviations see page 102.

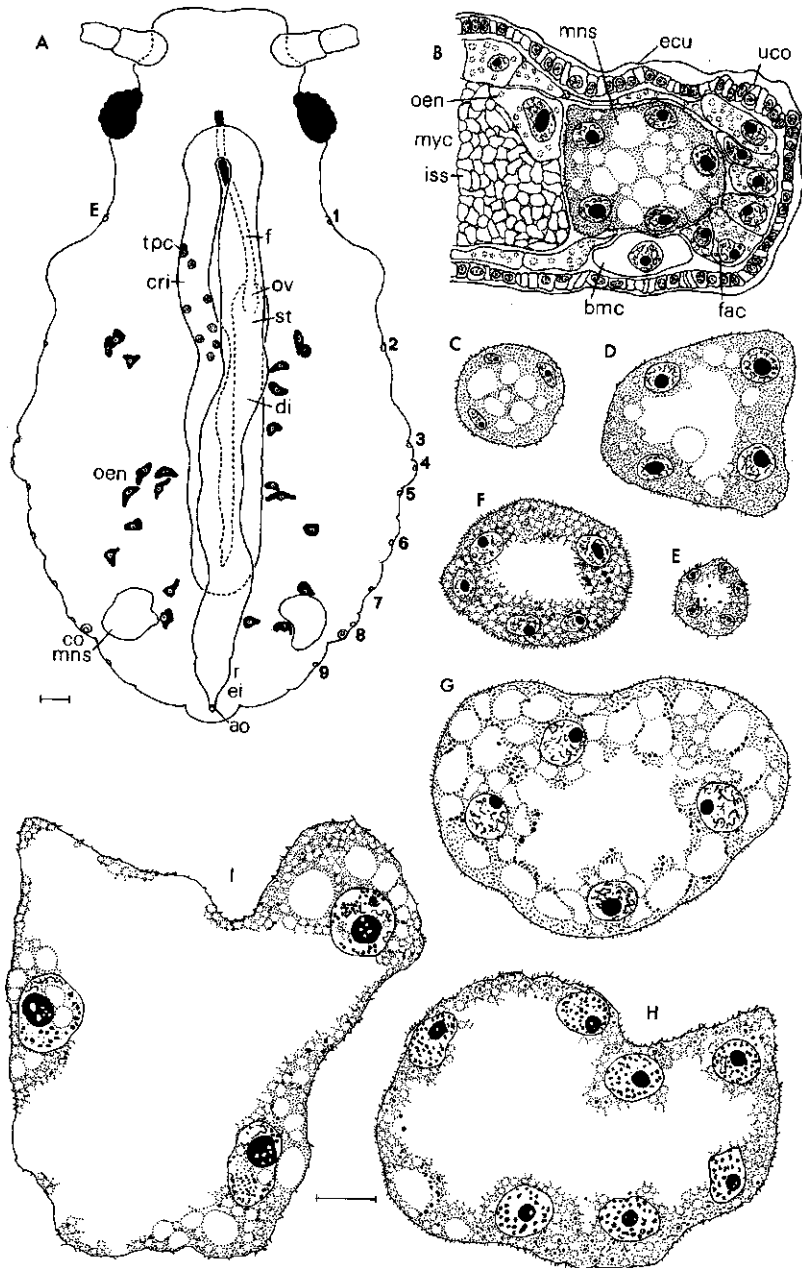
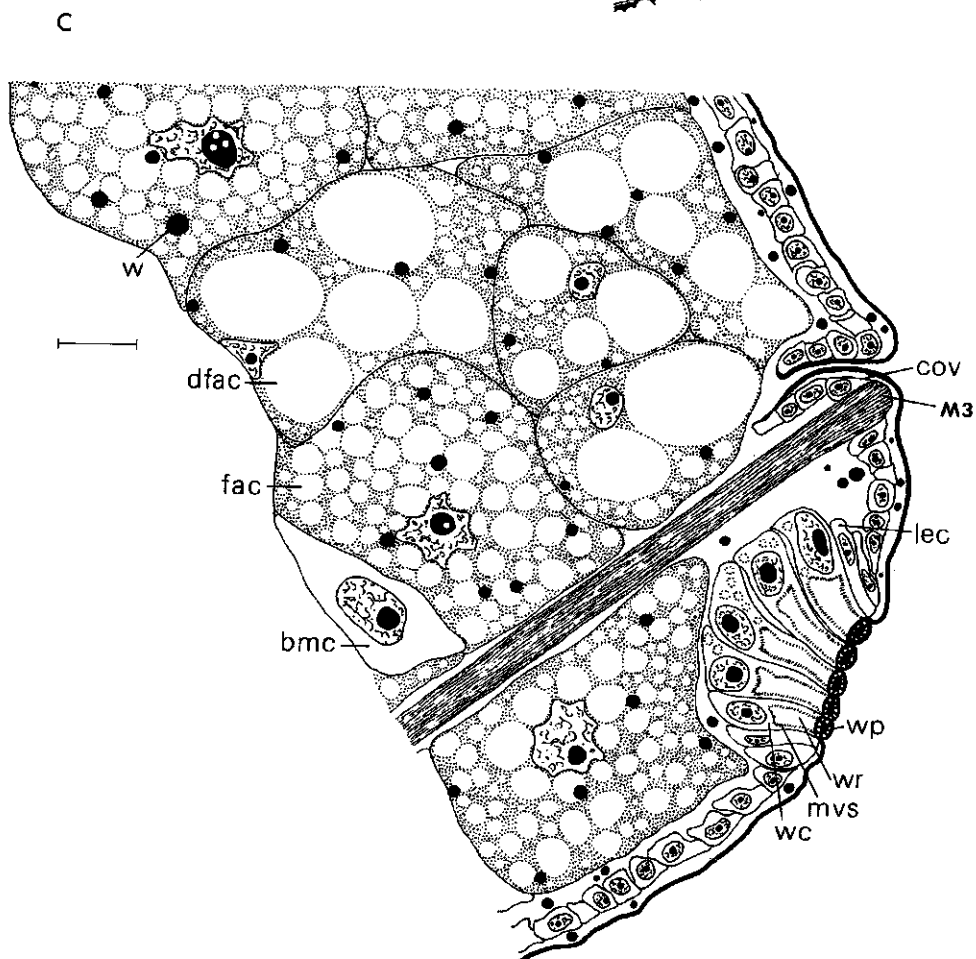
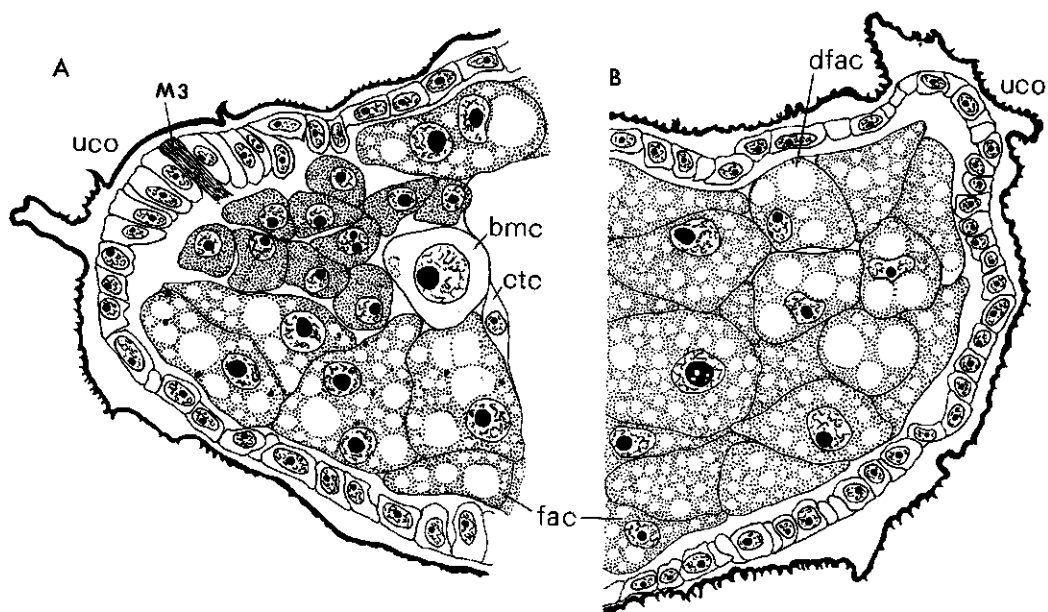


Figure 29 Dorsal view of the digestive system, topographical position of the oenocytes, and that of the multinucleated structure of a winged viviparous larva of *Latgerina orizabaensis*, ssp. *mexicanus* Remaudière (A) reconstructed from serial sections. 1-2, meso- and metathoracic spiracles; 3-9, abdominal spiracles. Bar represents 30 µm. Transverse sections of a multinucleated structure of an embryo in a wingless viviparous *Callipterinella calliptera* (Hartig) (B; the siphuncular valve retractor muscle is omitted), a wingless viviparous *Atheroides serrulatus* Haliday (C), a wingless viviparous *Greenidea formosana* (Maki) (D), a wingless viviparous *Dasyaphis rhusae* (Shinji) (E), and a winged viviparous *Tuberculatus quercus* (Kaltenbach) (F). Transverse sections of a multinucleated structure in a wingless viviparous young larva of *Tinocallis caryaefoliae* (Davis) (G), a winged viviparous *Latgerina orizabaensis* (H), and a winged viviparous young adult of *Neophyllaphis grobleri* Eastop (I). Bar represents 10 µm. For list of abbreviations see page 102.

Table 12 The presence (+) or absence (–) of oenocytes, granulated mesodermal cells, and basophilic mesodermal cells of species of the Adelgidae. The sign ± is followed by the standard deviation of the mean (n = 3).

Aphid	Total number of aphids sectioned	Morph	Oenocytes	Granulated mesodermal cells	Basophilic mesodermal cells
<i>Adelges abietis</i>	8	pseudofundatrices	–	+	+
	30	gallicolae	–	+	+
<i>Adelges cooleyi</i>	5	fundatrices	–	+	+
	42	gallicolae	59.3 ± 8.4	–	+
	7	sistens	51.3 ± 5.9	–	+
	10	progredivens	38.7 ± 2.3	–	+
	9	sexuparae	39.3 ± 3.5	–	+
	26	sexuales	–	–	+
<i>Adelges laricis</i>	9	fundatrices	–	+	+
	16	gallicolae	–	+	+
	8	sistens	–	+	+
	18	progredivens	–	+	+
	11	sexuparae	–	+	+
	13	sexuales	–	–	+
<i>Adelges lapponicus</i>	12	gallicolae	–	+	+
<i>Adelges nordmannianae</i>	8	gallicolae	–	+	+
	10	progredivens	+	–	+
<i>Adelges viridana</i>	13	sexuparae	–	+	+
<i>Adelges viridis</i>	9	gallicolae	–	+	+
<i>Aphrastasia pectinatae</i>	10	sistens	+	–	+
<i>Pineus orientalis</i>	18	gallicolae	+	–	+

Figure 30 Transverse sections of an undeveloped siphunculus (u c o) with a muscle (M3) on sixth abdominal tergite of a wingless oviparous larva of *Anoecia* sp. showing cells of which the cytoplasmic structure is quite others than that of the fat cells (A), an undeveloped siphunculus (u c o) with a muscle (M3) on sixth abdominal tergite of a very young larval wingless oviparous *Mindarus abietinus* Koch showing some small degenerating fat cells (B), and a pore-shaped siphunculus with a muscle (M3) on sixth abdominal tergite of a wingless viviparous old larva of *Mindarus obliquus* (Cholodkovsky) showing big degenerating fat cells (C). Bar represents 10 µm. For list of abbreviations see page 102.



intestine of species of the Adelgidae (Figures 10A-B, 11, and 12), Phylloxeridae, and Thelaxinae the loops and/or coils are lacking whereas in species of the other subfamilies they vary from one to eleven for *Monaphis antennata* (Kaltenbach) (Table 13). The compact structure of the digestive system of species of the Anoeciinae is due to the absence of the voluminous abdominal loop (Figure 22).

The lining of the crenated intestine is composed of a single layer of triangular cells forming a more or less stellate lumen. In transverse sections the total number of cells varies from 3 for species of the Adelgidae to 8 for some species of the Anoeciinae. In the posterior region of the crenated intestine there occur 5-11 groups of three conically-shaped cells (triplet) at irregular intervals among the intestinal cells (Figures 10A-B, 15, 24A, 26A, 28A, and 29A).

The digestive system of *Geoica setulosa* (Passerini) consists of a foregut which is closed at its posterior end and a blindly starting descending intestine. The stomach and crenated intestine are lacking (Figure 22; Figure 13A in Ponsen, 1991).

The species of the tribe Myzocallidini and the subfamily Saltusaphidinae (Table 14) have both a blindly starting intestine or caecal intestine and a descending intestine which is a continuation of the crenated intestine. Both types of intestines pass into the rectum (Figure 22). In dissections they have a smooth transparent structure showing vigorous peristaltic movements generated by circular and longitudinal muscles. Both transparent intestines form a filtersystem: a concentric filtersystem in which the stomach is encapsulated by the caecal intestine, and a parallel filtersystem of which the anterior region of the crenated intestine is fused with the posterior region of the descending intestine. The descending intestine consists of a single layer of triangular cells of which the apical cell membrane presents a labyrinthine system of closely packed irregular invaginations of different dimensions as well as that of the stomach and crenated intestine (Figure 14). The caecal intestine consists of squamous cells of which the apical cell membrane presents irregular finger-like evaginations. Moreover, the luminal surface of the apical cell membrane of the intestinal epithelium is lined with a single row of extracellular microtubule-like structures as well as that of the stomach and crenated intestine (Table 7; Figure 5-8 in Ponsen, 1991). Both the caecal intestine and the descending intestine are of endodermal origin by the absence of a cuticular lining (intima) of the apical cell membranes and consequently a subdivision of the midgut.

In species of the Phylloxeridae (Table 3 in Ponsen, 1997) and those of the subfamilies Aphidinae (except the *Aphis*-group), Lachninae, and Phloeomyzinae (Table 15) the midgut consists of a stomach, crenated intestine, and a smooth transparent intestine (Figure 22). Histologically, the latter is identical to the blindly starting intestine or caecal intestine (Figure 16I). Consequently the term caecal intestine is introduced for this type of intestine although it is a continuation of the crenated intestine and passes into the rectum. The smooth transparent intestine of species of the Adelgidae (Table 2) and that of the other subfamilies of the Aphididae (Table 15) has been named the descending intestine (Figures 16, 24E, 25A and 25D). All aphid species with a caecal intestine have a filtersystem (Table 15; Figure 22), except species of the Phylloxeridae, *Phloeomyzus passerinii*, and *Paoliella terminaliae* (Hall). The species of the Aphidinae (except the *Aphis*-group) may have had a filtersystem by the presence of filterchamber cells in the anterior region of the caecal intestine. A detailed description is given by Ponsen (1991).

The very short ectodermal part of the posterior region of the alimentary tract consists of a rectum and epidermal invagination which opens into the exterior via the anal opening (Figure 22). In two species of the Phylloxeridae the rectum and anal opening are lacking; in

Aphanostigma ulmifoliae (Aoki) the crenated intestine ends blindly and in *Aphanostigma piri* (Cholodkovsky) the caecal intestine (Ponsen, 1997).

The cuticular layer of the cells of both these organs forms one continuous layer with that of the body wall (Figure 17). The anal opening is controlled by two pairs of three dorsal muscles and two pairs of lateral muscles. In species of the Aphididae the three pairs of dorsal muscles are inserted on the middle of the dorsal wall of the epidermal invagination (Figure 23G) and in those of the Adelgidae they are inserted on the edges of the dorsal wall of the epidermal invagination (Figures 18 and 19B-C). In all species of the Phylloxeridae the anal dorsal muscles are lacking (Ponsen, 1997).

Both the asexual morphs of the Phylloxeridae (Harrewijn et al., 1998) and those of the Adelgidae (Table 11) feed mainly in the non-vascular tissue cells, and species of both these

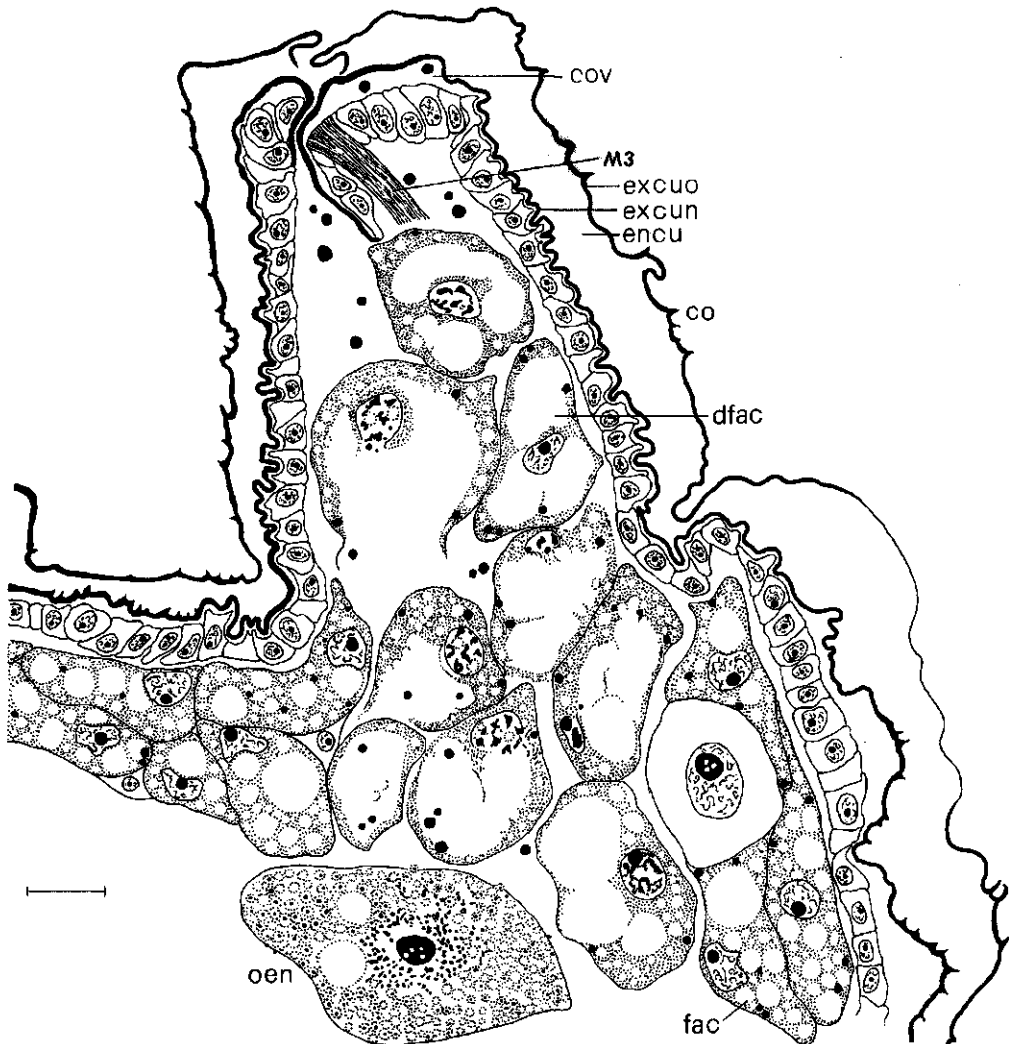


Figure 31 Transverse section of a moulting right siphunculus (cornicle) placed on the sixth abdominal tergite of a winged viviparous larva of *Macrosiphoniella artemisiae* (Boyer de Fonscolombe) (A) showing the degenerating fat cells. Bar represents 10 μ m. For list of abbreviations see page 102.

Table 13 List of species of five subfamilies of the Aphididae in sequence of the starting of the stomach which lies either left or right in the ventral region of the body cavity, total number of loops and/or coils of the crenated intestine, host plant, and locality data. I-III refer to thoracic segments; 1-9 refer to abdominal segments. The mycetome of all these species consists of mycetocytes harbouring irregularly-shaped symbionts which multiply by a budding process (see Figure 22).

Subfamily	Stomach starts in	Total number of loops and/or coils of the crenated intestine	Host plant	Locality, data
Aphid				
Parachaitophorinae				
<i>Parachaitophorus spiraeae</i> (Takahashi)	II	7	<i>Spiraea thunbergii</i>	Mie Pref., Japan, 11.XII.1999
Taiwanaphidinae				
<i>Sensortaphis nothofagi</i> Coitier	III	1	<i>Nothofagus</i> sp.	New Zealand, II.2000
Myzocallidinae – Calaphidini				
<i>Latgerina orizabaensis</i> ssp. <i>mexicanus</i> Remaudière	II – III	1	<i>Alnus</i> sp.	Mexico, V.1999
<i>Boernerina depressa</i> Bramstedt	II	3	<i>Alnus viridis</i>	Haute Savoie, France, 9.VII.1999
<i>Crypturaphis grassii</i> Silvestri	III	7	<i>Alnus cordata</i>	France, 3.VI.1999
<i>Crypturaphis grassii</i> Silvestri	III	7	<i>Alnus cordata</i>	Messina, Sicilia, Italy, 18.VI.1999
<i>Platyaphis fagi</i> Takahashi	III	5	<i>Fagus crenata</i>	Yamagata Pref., Japan, 26.VII.1998
<i>Euceraphis betulae</i> (Koch)	III – I	3	<i>Betula</i> sp.	Wageningen, 16.V.1977
<i>Clethrobios comes</i> (Walker)	1 – 2	5	<i>Alnus glutinosa</i>	Wageningen, 21.V.1980
<i>Clethrobios comes</i> (Walker)	2	5	<i>Alnus incana</i>	Haute Savoie, France, 7.VII.1999
<i>Monaphis antennata</i> (Kaltenbach)	1 – 2	11	<i>Betula</i> sp.	Ede, 28.IX.1980
<i>Synydobius oblongus</i> (von Heyden)	2 – 3	9	<i>Betula</i> sp.	Wageningen, 19.V.1980
<i>Euceraphis punctipennis</i> (Zetterstedt)	3	3	<i>Betula</i> sp.	Wageningen, 11.IX.1980
<i>Calaphis flava</i> Mordvilko	3	5	<i>Betula</i> sp.	Wageningen, 19.V.1980
<i>Betulaphis brevipilosa</i> Börner	4	3	<i>Betula</i> sp.	Wageningen, 29.VII.1979
<i>Callipterinella tuberculata</i> (von Heyden)	4	5	<i>Betula</i> sp.	Wageningen, 20.V.1980
<i>Callipterinella calliptera</i> (Hartig)	5	4	<i>Betula</i> sp.	Ede, 12.VIII.1979
<i>Callipterinella calliptera</i> (Hartig)	5 – 6	4	<i>Betula</i> sp.	Ax les Thermes, France, 27.VII.1980
Drepanosiphinae				
<i>Drepanosiphum platanoidis</i> (Schrank)	5	4	<i>Acer pseudoplatanus</i>	Wageningen, 16.V.1980
<i>Drepanosiphum acerium</i> (Walker)	6	4	<i>Acer pseudoplatanus</i>	Bennekom, 1.VIII.1980
<i>Drepanosiphum aceris</i> Koch	6 – 7	6	<i>Acer campestre</i>	Wageningen, 28.VIII.1980
<i>Drepanaphis</i> sp.	7	2	<i>Acer saccharinum</i>	Long Beach, Florida, U.S.A., 14.VI.1981
Phyllaphidinae				
<i>Phyllaphis fagi</i> (Linnaeus)	1 – 2	5	<i>Fagus sylvatica</i>	Wageningen, 14.V.1980
<i>Stegophylla</i> sp.	7	2	<i>Quercus alba</i>	Glen Dale, Florida, U.S.A., 24.VI.1981

Table 14 List of species of the tribe Myzocallidini and those of the subfamily Saltusaphidinae, their host plant, and locality data. These species are characterized by 1) a stomach which lies either left or right in the ventral region of the body cavity and 2) a midgut with two filtersystems: a concentric filtersystem in which the stomach is encapsulated by the caecal intestine and a parallel filtersystem in which the anterior region of the crenated intestine is fused with the posterior region of the descending intestine (Figure 22; Ponsen, 1979). The mycetome consists of mycetocytes harbouring irregularly shaped (like a ginger-root) symbionts which multiply by a budding process (Figures 36F and 37B).

Aphid	Host plant	Locality, data
Myzocallidinae – Myzocallidini		
<i>Chromaphis juglandicola</i> (Kaltenbach)	<i>Juglans regia</i>	Wageningen, 9.VI.1980
<i>Ctenocallis setosus</i> (Kaltenbach)	<i>Sarothamnus</i> sp.	Ax les Thermes, Pyrenees, France, VII.1980
<i>Dasyaphis rhusae</i> (Shinji)	<i>Juglans mandshurica</i>	Yamagata Pref., Japan, 24.VII.1998
<i>Eucalopteris tiliae</i> (Linnaeus)	<i>Tilia</i> sp.	Wageningen, 23.IX.1979
<i>Hoplocallis pictus</i> (Ferrari)		Lisbon, Portugal, 11.VI.1981
<i>Mexicallis analitiae</i> Remaudière	<i>Quercus</i> sp.	Mexico, 17.X.1994
<i>Mexicallis areolata</i> Remaudière	<i>Quercus</i> sp.	Mexico, 17.X.1994
<i>Monellia caryella</i> (Fitch)		Florida, U.S.A., 1981
<i>Monelliopsis nigropunctata</i> (Granovsky)		Florida, U.S.A., 1981
<i>Myzocallis carpini</i> (Koch)	<i>Carpinus</i> sp.	Wageningen, 19.V.1980
<i>Myzocallis coryli</i> (Goeze)	<i>Corylus</i> sp.	Wageningen, 15.IV.1980
<i>Myzocallis castanicola</i> Baker	<i>Castanea sativa</i>	Leersum, VII.1980
<i>Myzocallis myricae</i> (Kaltenbach)	<i>Myrica gale</i>	Wageningen, 3.VIII.1980
<i>Myzocallis walshii</i> (Monell)	<i>Quercus rubra</i>	Wageningen, 23.VI.2000
<i>Neocranaphis arundinariae</i> (Takahashi)	<i>Bambusa</i> sp.	Taiwan, Republic of China, VI.1999
<i>Neosymydobius albasiphus</i> (Davies)	<i>Quercus stellata</i>	Silver Spring, Florida, U.S.A., 28.VII.1981
<i>Panaphis juglandis</i> (Goeze)	<i>Juglans regia</i>	Gerendal, Limburg, 13.VI.1980
<i>Pterocallis alni</i> (de Geer)	<i>Alnus</i> sp.	Wageningen, 15.IV.1980
<i>Pterocallis maculatus</i> (von Heyden)	<i>Alnus</i> sp.	Bennekom, 8.VI.1980
<i>Shivaphis celti</i> B. Das	<i>Celtis</i> sp.	Gainesville, Florida, U.S.A., 10.X.1997
<i>Takecallis arundicolens</i> (Clarke)	<i>Pseudosasa japonica</i>	Wageningen, 8.V.1999
<i>Takecallis arundinariae</i> (Essig)	<i>Phyllostachys</i> sp.	Atrium I.B.N., Wageningen, 7.V.1999
<i>Therioaphis trifolii</i> (Monell)	<i>Melilotus indica</i>	Faisalabad, Pakistan, 11.III.1980
<i>Tinocallis caryaefoliae</i> (Davies)		Florida, U.S.A., 1981
<i>Tinocallis platani</i> (Kaltenbach)	<i>Ulmus</i> sp.	Wageningen, 26.VI.1980
<i>Tinocallis saltans</i> (Nevsky)	<i>Ulmus</i> sp.	Wageningen, 29.VIII.1980
<i>Tuberculatulus querceus</i> (Kaltenbach)	<i>Quercus robur</i>	Wageningen, 7.VII.1980
<i>Tuberculatulus annulatus</i> (Hartig)	<i>Quercus robur</i>	Wageningen, 15.V.1980
Saltusaphidinae		
<i>Iziphya bufo</i> (Walker)	<i>Carex arenaria</i>	Wekerom, Gelderland, 22.IX.1981
<i>Saltusaphis scirpus</i> Theobald	<i>Cyperus</i> sp.	Faisalabad, Pakistan, 10.III.1980
<i>Subsaltusaphis ornata</i> (Theobald)	<i>Carex riparia</i>	Culture Inst. Phytopathological Res., Wageningen, 1977
<i>Subsaltusaphis picta</i> (Hille Ris Lambers)	<i>Carex</i> sp.	Opheusden, Gelderland, 22.IX.1982
<i>Subsaltusaphis rossneri</i> (Börner)	<i>Carex remota</i>	Bennekom, Gelderland, 23.IX.1981 (ex culture HRL)
<i>Thripsaphis cyperi</i> (Walker)	<i>Carex rostrata</i>	Wageningen, 18.IX.1981
<i>Thripsaphis producta</i> Gillette	<i>Carex nigra</i>	Wageningen, 14.VII.1982

Table 15 Total number of pharyngeal muscles and structure of the midgut of species of the Phylloxeridae, Adelgidae, and Aphididae. The subdivision of the Aphididae in subfamilies, tribes, and subtribes is according to Remaudière and Remaudière (1997). + = present, - = absent; ± individuals with or without a filtersystem. In parentheses 1 or 2 filtersystems. The diagrams illustrating the existing forms of the digestive system are given in Figure 22.

Family	Subfamily	Tribe	Aphids	Total number of pharyngeal muscles	Stomach	Total number of loops and/or coils of crenated intestine	Caecal intestine	Descending intestine	Filter-system
Phylloxeridae			Table 3 in Ponsen, 1997	14	ventral	0	+	-	-
Adelgidae			Table 2	14	ventral	0	-	+	-
Aphididae									
	Lizeriinae (Table 24)		<i>Lizerius tuberculatus</i> (Blanchard)	14	ventral	1	-	+	-
			<i>Lizerocallis flavus</i>	31	ventral	1	-	+	-
			Sousa-Silva & Ilharco						
			<i>Paoliella terminaliae</i> (Hall)	31	ventral	2 - 4	+	+	-
	Parachaitophorinae		Table 13	31	ventral	7	-	+	-
	Taiwanaphidinae		Table 13	31	ventral	1	-	+	-
	Myzocallidinae	Calaphidini	Table 13	31	ventral	1 - 11	-	+	-
	Drepanosiphinae		Table 13	31	ventral	2 - 6	-	+	-
	Phyllaphidinae		Table 13	31	ventral	2 - 5	-	+	-
	Myzocallidinae	Myzocallidini	Table 14	31	ventral		+	+	+
	Saltusaphidinae		Table 14	31	ventral		+	+	+
	Thelaxinae		Table 23	31	dorsal	1	-	+	+
	Chaitophorinae		Table 23	31	dorsal	1 - 3	-	+	-
	Neophyllaphidinae		<i>Neophyllaphis grobleri</i> Eastop	31	dorsal	1 - 3	-	+	-
	Israelaphidinae		Table 1 in Ponsen, 1990a	31	dorsal	1 - 3	-	+	-
	Greenideinae	Greenideini	Table 1 in Ponsen, 1990a	31	dorsal	1	-	+	-
	Greenideinae	Schoutedenini	<i>Schoutedenia ralumensis</i> Ruhsaamen	31	dorsal	1	-	+	-
	Neuenaphidinae		<i>Neuenaphis sensoria</i>	31	dorsal		-	+	-
			Hille Ris Lambers						
	Anocciinae		Table 1 in Ponsen, 1987a	31	dorsal	2 - 3	-	+	-
	Mindariniae		Table 21	31	central		-	+	-
	Phloeomyzinae		Ponsen (1982c)	31	central	6	+	-	-
	Lachninae		Ponsen (1981)				+	-	+
	Aphidinae		Table 11 in Ponsen, 1991	31	dorsal	4 - 6	+	-	+
			<i>Acaudinum centaureae</i> (Koch)	31	dorsal		+	-	+
			<i>Capitophorus elaeagni</i> (del Guercio)	31	dorsal		+	-	+
			<i>Cryptomyzus ribis</i> (Linnaeus)	31	dorsal		+	-	+
			<i>Cryptomyzus galeopsidis</i> (Kaltenbach)	31	dorsal		+	-	+
			<i>Coloradoa tanacetina</i> (Walker)	31	dorsal	4 - 6	+	-	±
			<i>Hyalopterus</i> sp.	31	dorsal	4 - 6	+	-	±
			TABLE 1 in Deacon, 1990a	31	dorsal	1 - 4	-	+	-

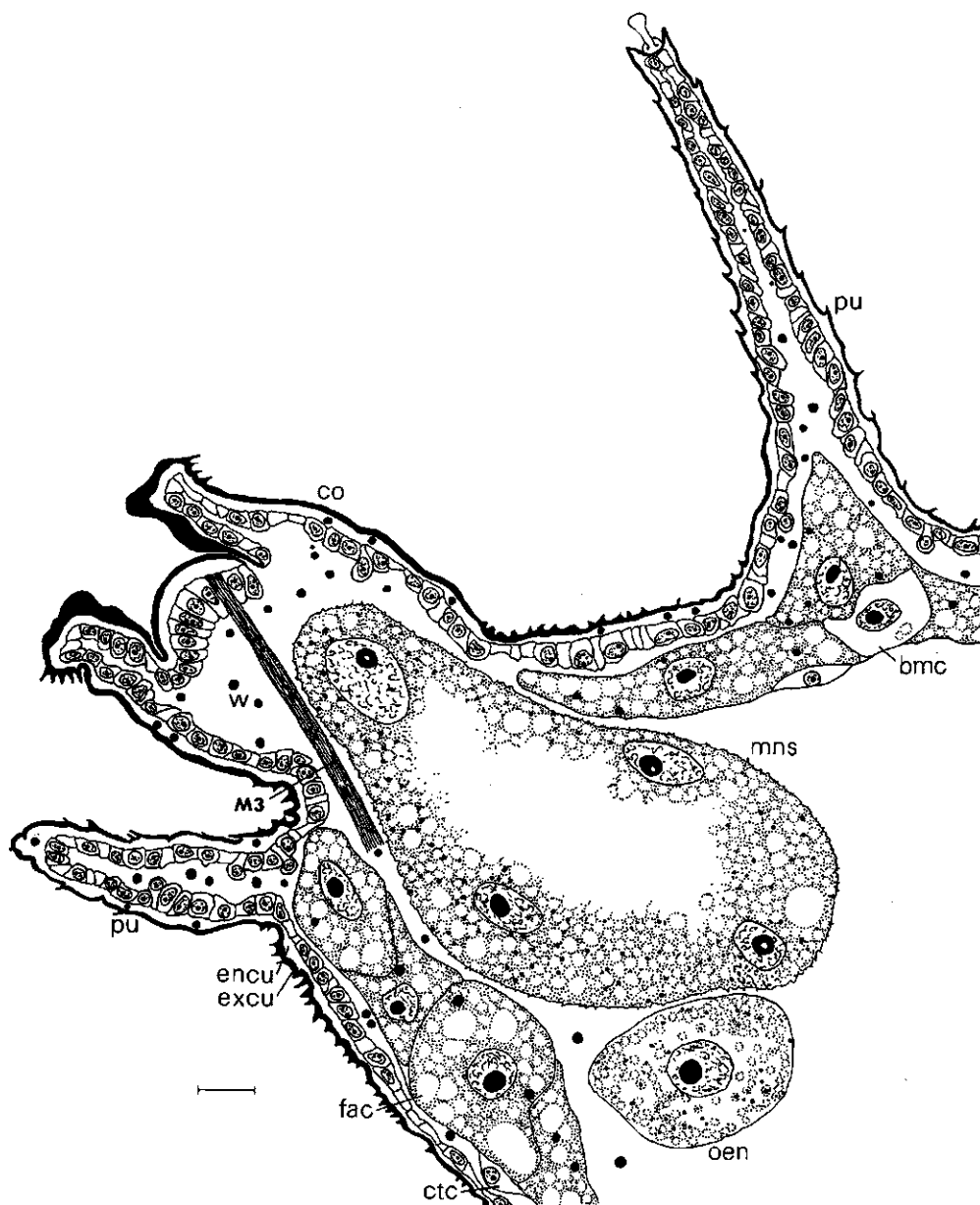


Figure 32 Transverse section of a left siphunculus (cornicle) on sixth abdominal tergite of a winged viviparous larva of *Neuquenaphis sensoriata* Hille Ris Lambers showing the multinucleated structure and the two processes. The siphunculi are in open connection with the body cavity and are closed at their top with a valve-like flap. The flap is opened by contraction of a muscle (M3) which runs throughout the length of the siphunculi to the posterior edge of the seventh abdominal sternite. The processes of *Neuquenaphis sensoriata* are similar to those of *Israelaphis* (Figure 34), *Ctenocallis setosus* (Kaltenbach), and *Paoliella terminaliae* (Hall). Bar represents 10 µm. For list of abbreviations see page 102.

families possess 10 pairs of pharyngeal pump muscles (Figure 9) to suck up sap from these cells. Species of the Adelgidae defecate and those of the Phylloxeridae do not do that. The most plausible explanation for this phenomenon is the absence of the anal dorsal muscles of the anal opening in the Phylloxeridae (Figures 14 and 16 in Ponsen, 1997) so that they cannot excrete any honeydew. By contrast these muscles are present both in the Adelgidae (Figure 18) and in the Aphididae (Figure 14D in Ponsen, 1997) to open the anal opening for excretion of honeydew.

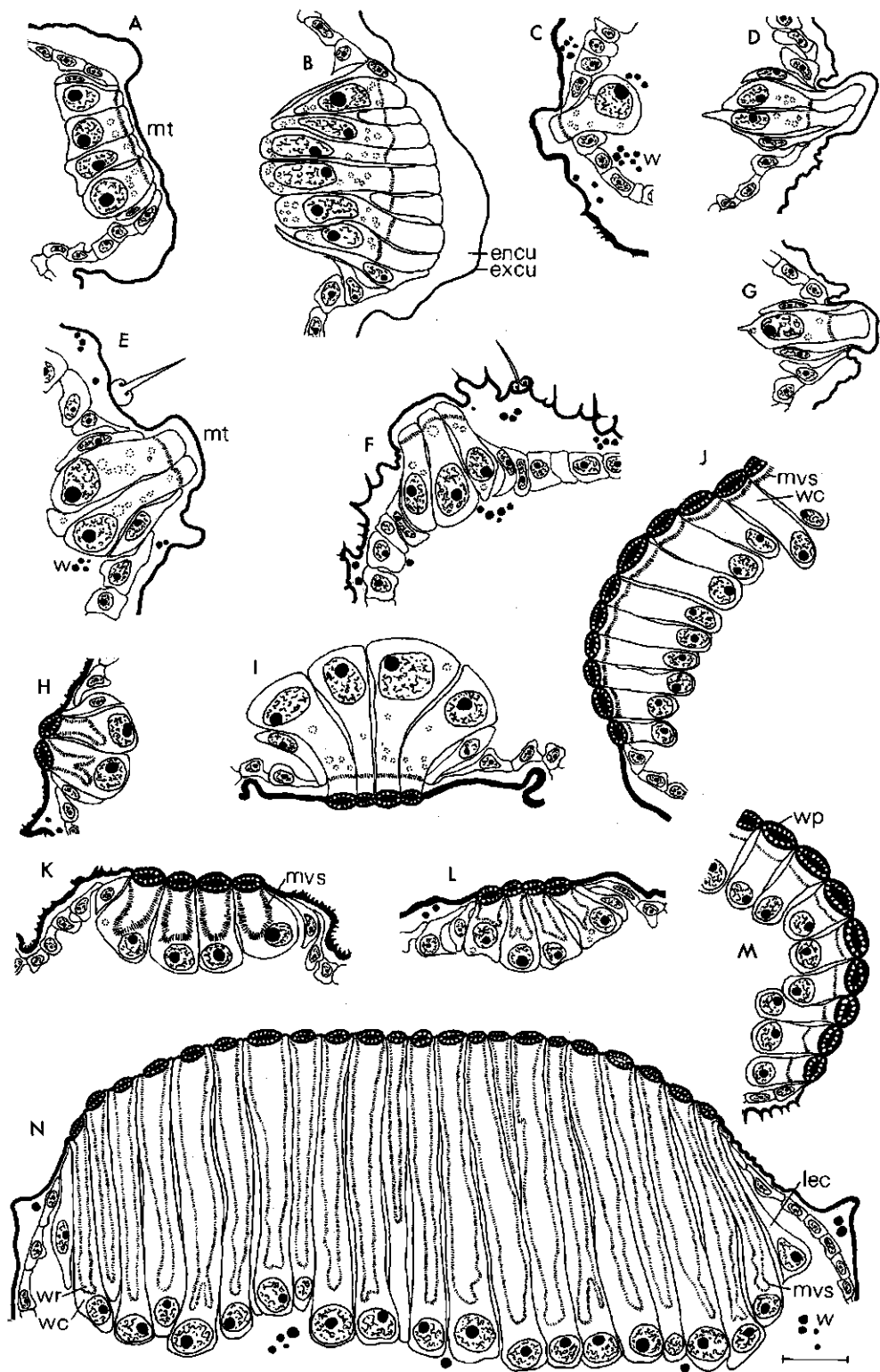
According to the authors cited in Table 11, the wingless dwarfish sexuales of the Adelgidae possess well-developed mouthparts (Figures 1A, 4, 6D, and 8A). They are able to insert their stylets into the needles of their host plant and subsequently excrete honeydew. However, the sexuales of *Adelges cooleyi* and *Adelges laricis* (Table 2) which hatch and moult under the spread wings of their mother, do not excrete any honeydew. Their salivary glands are degenerated showing empty nuclei in a spongy tissue. This implies that they cannot produce any saliva to dissolve the contents of the parenchyma cells necessary for sucking up the food. Moreover, the cells of the midgut are also degenerated (Figures 8A-E, 19A, and 25F). These phenomena apply to the males (exules) of *Mindarus* (Figure 23C-E), and probably also to the males (exules) of *Forda formicaria* von Heyden (Figure 24C-E).

The posterior end of the descending intestine, rectum, and anterior region of the epidermal invagination of *Forda formicaria* and *Forda marginata* Koch are surrounded by a ring of polygonal cells forming a rectal organ (Figure 24A; Ponsen, 1991). The cells are interconnected by a cytoplasmic bulge which locks in a membrane invagination of the neighbouring cell like pieces of a jigsaw puzzle (Figure 25A-D). This construction allows the haemolymph to circulate freely among the cells of the rectal organ. Moreover, this organ can expand synchronously with the vigorous peristaltic movements of the descending intestine. Histologically, these polygonal cells resemble the basophilic mesodermal cells which are individually dispersed among the fat cells but without the jigsaw puzzle structure (Figures 17-19, 28C-D, 29B, and 30-32). Probably this rectal organ is important for the function of the digestive system since it is absent in the exules of *Forda formicaria* (Figure 24B).

Within the Pemphiginae there still are four species with a rectal organ, viz. *Geoica setulosa*, *Geoica utricularia*, *Smynthuroides betae* Westwood, and *Tetraneura ulmi* (Linnaeus). The structure of these rectal organs differs considerably (Figure 15 in Ponsen, 1991) from that of *Forda formicaria* and *Forda marginata* (Figure 25A-D).

All aphid species of the Phylloxeridae (Ponsen, 1997) and those of the several sub-families of the Aphididae (Tables 16 and 17) possess oenocytes. The majority of them occur as single cells but sometimes also in groups of 2-3 oenocytes in intimate contact with each other in the lateral and occasionally in the dorsal side of the body cavity between the

Figure 33 Transverse sections of tubercles on pronotum of a wingless oviparous larva of *Anoecia* sp. (A) and a winged viviparous larva of *Aphis sambuci* Linnaeus (B); on first abdominal tergite of a wingless viviparous *Thelaxes dryophila* (Schrank) (C), a winged viviparous *Aphis idaei* van der Goot (D), *Rhopalosiphum padi* (Linnaeus) (E), and *Anuraphis farfarae* (Koch) (F); on fifth abdominal tergite of a winged viviparous *Aphis pomi* de Geer (G). Transverse sections of wax glands on pronotum of a wingless oviparous larva of *Mindarus abietinus* Koch (H), on fourth abdominal sternite of a wingless viviparous *Tetraneura ulmi* (Linnaeus) (I), on seventh abdominal tergite of a wingless viviparous larva of *Phyllaphis fagi* (Linnaeus) (J), on metanotum of a sexuparous larva of *Adelges viridana* (K), on first abdominal tergite of a wingless viviparous larva of *Aploneura lentisci* (Passerini) (L), on eighth abdominal tergite of a winged viviparous adult of *Shivaphis celti* B. Das (M), and on the left half of the seventh abdominal tergite of a wingless viviparous larva of *Phloeomyzus passerinii* (Signoret) (N). Bar represents 10 µm. For list of abbreviations see page 102.



mesodermal tissue and internal organs of the thorax and the first eight abdominal segments (Figures 10A-B, 23B, 24A-B, 26A, 27, 28A, and 29A). In other species the oenocytes are closely connected with the mycetome, viz. *Stomaphis quercus*, *Subsaltusaphis ornata* (Theobald) (Figure 37B), and *Tetraneura ulmi*. The total number of oenocytes varies from three for *Smynthuroides betae* to 286 for *Stomaphis quercus*; the size of the oenocytes varies from very small for *Pemphigus passeki* Börner to very big for *Pseudoregma bambucicola* (Takahashi). In winged viviparae of *Forda formicaria* oenocytes occur but they are lacking in wingless viviparae (Table 17).

However, in some adelgid species and their asexual morphs the oenocytes are lacking (Table 12). In these species there are granulated mesodermal cells which are individually distributed among the fat cells (Figures 18D and 28C-D). The granules in the cytoplasm of the oenocytes originate from the nuclei and those of the granulated mesodermal cells from the cytoplasm. In the latter cells the nuclei remain intact during larval life and those of the oenocytes gradually disappear (Figures 31, 32, and 34-37). Within the Pemphiginae (Table 17) there are species that have neither oenocytes nor granulated mesodermal cells. The total number of oenocytes seems to vary both between the several subfamilies (Table 16), genera, and species (Table 17), but not within one species as shown for *Myzus persicae* (Ponsen, 1972) and *Adelges cooleyi* (Table 12).

The haemolymph of all species of the Aphididae investigated is characterized by the absence of circulating cells (Table 15). However, Gouli et al. (2000) reports the presence of six types of haemocytes in haemolymph smear preparations after removal of one metathoracic leg of *Adelges tsugae* sistens, viz. plasmatocytes, adipohaemocytes, oenocytoides, vermiform cells, prohaemocytes, and formative cells. In fact, these cells are not haemocytes: the first two cell types are fat cells and the oenocytoides are the basophilic mesodermal cells (Figures 17, 18A-D, 19A-C, 28C-D, 29B, 30-32, and 34), whereas the vermiform cells are the symbionts (Figure 35C). The last two cell types have never been observed in paraplast sections. These results show that 1) the vermiform cells or symbionts freely occurring in the haemolymph result from dissolution of the cell membrane of the mycetocytes in the last larval stage (Ponsen, 1972), and 2) during larval life the mesodermal tissue (fat body) loses its structure and their cells are released into the haemolymph. Moreover, it appears that the granulated mesodermal cells are lacking in the sistens of *Adelges tsugae*, as well as in the sistens of *Adelges cooleyi* and *Aphrastasia pectinatae* (Table 12).

In species of some subfamilies of the Aphididae (Table 18) a multinucleated structure has been observed in the body cavity on each lateral side of the mycetome (Figures 27 and 29 A). These structures have already been reported by Hottes (1928) for *Monellia caryella* (Fitch), *Myzocallis bellus* (Walsh), and *Symydobius americanus* Baker. They are located in the fourth and fifth abdominal segment of species of which the siphunculi are situated dorsolaterally on the fifth abdominal tergite; in species with siphunculi on the sixth abdominal tergite these structures are located in the fifth and sixth abdominal segment. In old larvae and adults these structures terminate on the base of the siphunculi or extend somewhat into the cavity of the siphunculi (Figure 32). They are not connected by a duct with one of the several organs or with the distal end of the siphunculi. The siphunculi are in open connection with the body cavity (Figure 27 in Ponsen, 1972; Figures 31 and 32). These multinucleated structures may be endocrine glands although their function is unknown. The total number of nuclei in these structures varies from six for *Chaitophorus populeti* (Panzer) to ten for *Monaphis antennata*.

In young embryos these structures are observed as a somewhat spherical body consisting of cells with indistinct lateral cell membranes. The basal cell membranes show

minute evaginations (Figure 29B-C). The apical part of these cells contains big vacuoles which gradually coalesce to one big vacuole (Figure 29D-F). This body is surrounded by a basophilic mesodermal cell, an oenocyte, a mycetocyte, and fat cells (Figure 29B). During embryonic and larval development the cells gradually increase in size as do the nuclei and nucleoli. The basal part of the cells start to produce small vacuoles forming a network of vacuoles which subsequently coalesce with the big vacuole. In other species the small vacuoles coalesce to big ones which in turn coalesce with the very big one (Figure 29G). This process continues during larval life (Figure 29H) and in the adult stage the majority of the network of vacuoles is partly or completely dissolved. The nuclei start to degenerate by vacuolization and granulation of the chromatine (Figures 29I and 32). After amputation of a siphunculus of *Takecallis arundicolens* (Clarke) larvae (Table 14) the multinucleated structures show a relatively big, opaque compact body.

In species of the Drepanosiphinae, Mindarinae, Aphidinae, and the *Aphis*-group (Table 18) degenerating fat cells occur in the vicinity of the siphunculi and also within them (Figures 30B-C and 31). Similar cells have previously been observed by Hottes (1928) in *Drepanaphis acerifoliae* (Thomas) and described as hollow and partially hollow spheres, each containing a single nucleus. The degeneration process of the fat cells has been described in detail for *Myzus persicae* (Ponsen, 1972).

At the base of the siphunculi of *Anoecia* larvae there are cells of which the cytoplasmic structure is quite different from that of the fat cells (Figure 30A). Both the above-mentioned structures and the siphunculi are absent in the asexual morphs of species of the Phylloxeridae and those of the Adelgidae (Table 18).

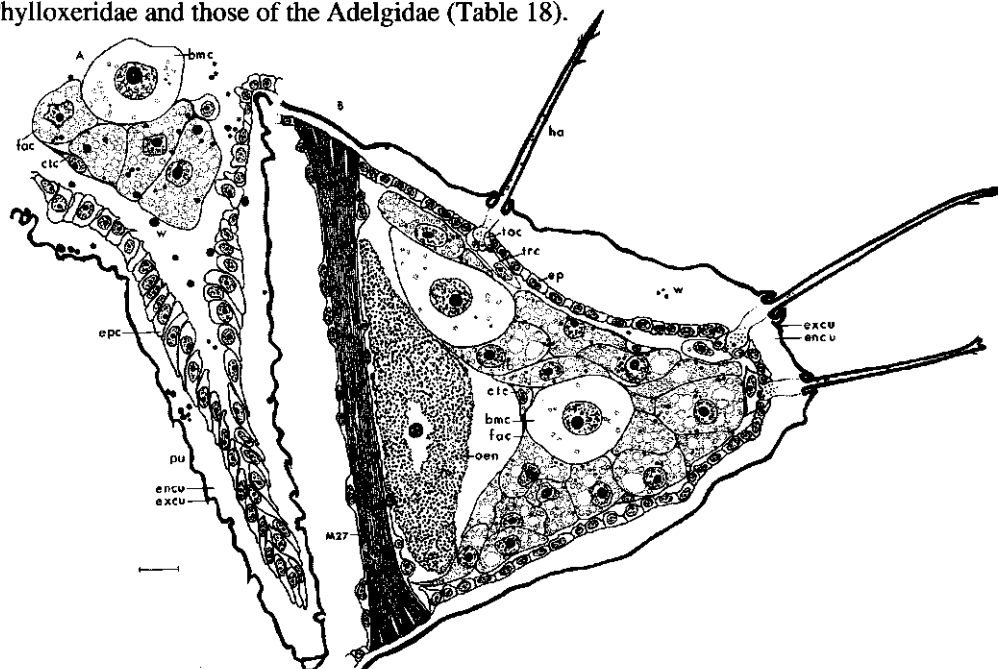


Figure 34 A. Sagittal section of a process, a hollow outgrowth of the eighth abdominal tergite of a wingless oviparous *Israelaphis carmini* Essig. The cuticle, epidermis, and basement membrane of the process is a continuation of those of the body wall. B. Transverse section of the larval part of the fourth abdominal segment of a wingless viviparous *Greenidea formosana* (Maki) showing three long hairs with its cells and a granulated oenocyte of which the nucleus has completely disappeared leaving a nucleolus in an amorphous mass. Bar represents 10 μ m. For list of abbreviations see page 102.

Table 16 Total number of oenocytes and their position in the body cavity of one individual of one species of each subfamily, tribe, or subtribe of the Aphididae, their morph and host plant. I-III refer to thoracic segments; 1-9 refer to abdominal segments.

Subfamily – Tribe – Subtribe	Aphid	Morph	Host plant	Oenocytes start in	Oenocytes end in	Total number of oenocytes
Anoeciinae	<i>Anoecia</i> sp.	wingless oviparous	<i>Cornus</i> sp.	I	6	7
Aphidinae – Aphidini – Aphidina	<i>Aphis violae</i> Schouteden	wingless viviparous	<i>Viola tricolor</i>	II	6	31
Aphidinae – Aphidini – Rhopalostiphina	<i>Hyalopterus</i> sp.	wingless viviparous	<i>Phragmites australis</i>	I	7	42
Aphidinae – Macrosiphini	<i>Macrosiphum albifrons</i> Essig	winged viviparous	<i>Lupinus arboreus</i>	II	7	56
Chaitophorinae – Atheroidini	<i>Siphia glyceriae</i> (Kaltenbach)	wingless viviparous	<i>Agrostis tenuis</i>	III	6	27
Chaitophorinae – Chaitophorini	<i>Chaitophorus populeti</i> (Panzer)	winged viviparous	<i>Populus alba</i>	III	7	21
Drepanosiphinae	<i>Drepanosiphum platanoidis</i> (Schrank)	winged viviparous	<i>Acer pseudoplatanus</i>	III	6	19
Greenideinae – Greenideini	<i>Greenidea eugeniae</i> Takahashi	winged male	<i>Eugenia jambalana</i>	I	5	16
Greenideinae – Schoutedenini	<i>Schoutedenia ralumensis</i> Rübsaamen	wingless viviparous		II	7	31
Israelaphidinae	<i>Israelaphis carmini</i> Essig	wingless oviparous	<i>Anisantha rigida</i>	I	6	23
Lachninae – Cinarini	<i>Eulachnus brevipilosus</i> Börner	winged viviparous	<i>Pinus montana</i>	I	6	22
Lachninae – Lachnini	<i>Stomaphis quercus</i> (Linnaeus)	wingless viviparous	<i>Quercus robur</i>	III	7	286
Lachninae – Tramini	<i>Trama rara</i> Mordvilko	wingless viviparous	<i>Hypochoeris radicata</i>	3	7	74
Lizeriinae	<i>Lizerius tuberculatus</i> (Blanchard)	winged viviparous	<i>Nectandra megapotamica</i>	II	7	45
	<i>Lizerocallis flavus</i> Sousa-Silva & Ilharco	wingless viviparous	<i>Tibouchina granulosa</i>	III	5	9
Mindarinae	<i>Paoliella terminaliae</i> (Hall)	winged viviparous	<i>Terminalia sericæ</i>	III	6	15
Myzocallidinae – Calaphidini	<i>Mindarus abietinus</i> Koch	wingless oviparous	<i>Abies homolepis</i>	2	5	8
Myzocallidinae – Myzocallidini	<i>Betulaphis brevipilosa</i> Börner	wingless viviparous	<i>Betula</i> sp.	III	5	20
Neophyllaphidinae	<i>Myzocallis walsbyi</i> (Monell)	wingless viviparous	<i>Quercus rubra</i>	I	5	10
Neuquenaphidinae	<i>Neophyllaphis grobleri</i> Eastop	winged viviparous	<i>Podocarpus</i> sp.	III	6	7
	<i>Neuquenaphis sensoriata</i> Hille Ris Lambers	winged viviparous	<i>Nothofagus obliqua</i>	III	6	18
Parachaitophorinae	<i>Parachaitophorus spiraeae</i> (Takahashi)	wingless oviparous	<i>Spiraea thunbergii</i>	II	6	34
Phloeomyzinae	<i>Phloeomyzus passerinii</i> (Signoret)	wingless viviparous	<i>Populus</i> sp.	2	4	4
Phyllaphidinae	<i>Phyllaphis fagi</i> (Linnaeus)	wingless viviparous	<i>Fagus sylvatica</i>	3	6	8
Pterocommatinae	<i>Pterocomma populeum</i> (Kaltenbach)	wingless viviparous	<i>Populus nigra</i>	II	7	36
Saltusaphidinae	<i>Subsaltusaphis ornata</i> (Theobald)	wingless viviparous	<i>Carex riparia</i>	2	4	9
Taiwanaphidinae	<i>Sensoriaphis nothofagi</i> Cottier	winged viviparous	<i>Nothofagus</i> sp.	II	5	19
Thalassinae	<i>Thalassaphis drunghila</i> (Schrank)	wingless viviparous	<i>Quercus robur</i>	III	4	5

Table 17 Total number of oenocytes and their position in the body cavity of one individual of each species of the Pemphiginae and Hormaphidinae, their host plant and locality data. All species are winged or wingless viviparous individuals. + = present, - = absent. I-III refer to thoracic segments; 1-9 refer to abdominal segments.

Subfamily - Tribe	Viviparae	Host plant	Oenocytes start in	Oenocytes end in	Total number of oenocytes	Locality, data
Aphid						
Pemphiginae - Eriosomatini						
<i>Eriosoma lanigerum</i> (Hausmann)	winged	<i>Pyraecanthus coccinea</i>	II	4	11	Wageningen, 30.VI.1992
<i>Eriosoma lanuginosum</i> (Hartig)	winged	<i>Ulmus</i> sp.	III	7	15	Herveld, Betuwe, 29.VI.1984
<i>Eriosoma patchiae</i> (Börner & Blunck)	winged	<i>Ulmus</i> sp.	III	7	16	Heudicourt, Champagne, France, 22.VII.1987
<i>Eriosoma pyricola</i> Baker & Davidson	wingless	<i>Pyrus communis</i>	II	5	10	Buñ, Metropolitana, Chile, 23.III.1993
<i>Eriosoma ulmi</i> (Linnaeus)	winged	<i>Ulmus campestris</i>	III	6	14	Wageningen, 18.VI.1977
<i>Tetraneura ulmi</i> (Linnaeus)	wingless	<i>Lolium multiflorum</i>	2	5	9	Wageningen, 12.VII.1982
Pemphiginae - Fordini						
<i>Aploneura lentisci</i> (Passerini)	wingless	<i>Festuca ovina</i>	-	-	-	Wageningen, Culture Dept. Ent. 1982
<i>Baizongia pistaciae</i> (Linnaeus)	wingless	<i>Pistacia palaestina</i>	-	-	-	Botanical Garden Tel Aviv, Israel, 15.X.1993
<i>Forda formicaria</i> von Heyden	wingless	<i>Deschampsia flexuosa</i>	-	-	-	Ede, 21.IX.1982
<i>Forda formicaria</i> von Heyden	winged	<i>Deschampsia flexuosa</i>	3	6	7	Ede, 21.IX.1982
<i>Forda formicaria</i> von Heyden	winged	<i>Pistacia palaestina</i>	1	2	5	Canada park, Israel, 12.X.1993
<i>Forda marginata</i> Koch	wingless	<i>Deschampsia flexuosa</i>	1	4	9	Ede, 21.IX.1982
<i>Geocica setulosa</i> (Passerini)	wingless	<i>Agrostis canina</i>	-	-	-	Bennekom, 26.VIII.1982
<i>Geocica utricularia</i> (Passerini)	wingless	<i>Agrostis canina</i>	-	-	-	Bennekom, 26.VIII.1982
<i>Geocica utricularia</i> (Passerini)	winged	<i>Pistacia palaestina</i>	-	-	-	Canada park, Israel, 24.IX.1993
<i>Paracletus cimiciformis</i> von Heyden	winged	<i>Pistacia palaestina</i>	-	-	-	Canada park, Israel, 12.X.1993
<i>Smynturodes betae</i> Westwood	wingless	<i>Cardamine flexuosa</i>	1	4	3	Bennekom, 21.IX.1982
Pemphiginae - Pemphigini						
<i>Pemphigus bursarius</i> (Linnaeus)	winged	<i>Populus nigra</i>	2	6	9	Wageningen, 19.VI.1984
<i>Pemphigus passeti</i> Börner	wingless	<i>Carum carvi</i>	2	5	8	Wageningen, 4.XI.1985 (ex culture)
<i>Pemphigus populinigrae</i> (Schränk)	wingless	<i>Gnaphalium uliginosum</i>	II	6	19	Wageningen, 29.VII.1986
<i>Pemphigus spyrothecae</i> Passerini	winged	<i>Populus nigra</i>	III	7	31	Wageningen, 18.VI.1984
<i>Prociphilus oriens</i> Mordvilko	winged	<i>Abies sachalinensis</i>	III	6	16	Sapporo, Japan, 24.IX.1993
Hormaphidinae - Cerataphidini						
<i>Cerataphis palmarum</i> Ghesquière	wingless	Palm	I	8	34	Funchal, Madeira, 13.X.1981
<i>Pseudoregma bambucicola</i> (Takahashi)	winged	Bamboo	II	6	56	Baturraden, Java, Indonesia, 18.VII.1988

Table 18 The presence (+) or absence (-) of the multinucleated structure, lateral epidermal gland, and degenerating fat cells in the vicinity of the siphunculi of species of the Phylloxeridae, Adelgidae, and Aphididae.

Family	Subfamily – Tribe	Aphids	Siphunculi on tergite	Multinucleated structure	Lateral epidermal gland	Degenerating fat cells
Phylloxeridae		Table 3 in Ponsen, 1997	-	-	-	-
Adelgidae		Table 2	-	-	-	-
Aphididae						
	Lizerinae (Table 24)	<i>Lizerius tuberculatus</i> (Blanchard)	6	-	+	-
		<i>Lizerocallis flavus</i> Sousa-Silva & Ilharco	6	-	+	-
		<i>Paoliella terminaliae</i> (Hall)	6	-	+	-
	Drepanosiphinae	Table 13	6	-	-	+
	Myzocallidinae – Calaptidini	Table 13	6	+	-	-
	Parachaitophorinae	Table 13	6	+	-	-
	Phyllaphidinae	Table 13	6	+	-	-
	Taiwanaphidinae	Table 13	6	+	-	-
	Myzocallidinae – Myzocallidini	Table 14	6	+	-	-
	Salusaphidinae	Table 14	6	+	-	-
	Thelaxinae	Table 23	6	+	-	-
	Chaitophorinae	Table 23	5 or 6	+	-	-
	Neophyllaphidinae	<i>Neophyllaphis grobleri</i> Eastop	6	+	-	-
	Neuquenaphidinae	<i>Neuquenaphis sensoriata</i> Hille Ris Lambers	6	+	-	-
	Israelaphidinae	Table 1 in Ponsen, 1990a	6	+	-	-
	Greenideinae – Greenideini	Table 1 in Ponsen, 1990a	6	+	-	-
	Greenideinae – Schoutedenini	<i>Schoutedenia ralumensis</i> Rübsaamen	6	-	-	-
	Phloeomyzinae	Ponsen, 1982c	6	-	-	-
	Anoeciinae	Table 1 in Ponsen, 1987	6	-	-	-
	Mindarinae	Table 21	6	-	-	+
	Aphidinae	Table 11 in Ponsen, 1991	6	-	-	+
	Aphis-group	Table 1 in Ponsen, 1990b	6	-	-	+

Table 19 The presence (+) or absence (-) of several organs in the sexuales of the Phylloxeridae and Adelgidae, and in the males of the Mindarinae, *Stomaphis quercus* (Linnaeus) (Lachninae), *Forda formicaria* von Heyden (Pemphiginae), and *Anoecia* sp. (Anoeciinae). The sexuales of the Phylloxeridae have a rectum and anal opening except *Aphanostigma ulmifoliae* (Aoki) and *Phylloxera devastatrix* Pergande of which the stomach ends blindly (Table 5 in Ponsen, 1997). The protein crystals occur both in the fat cells and in the haemolymph (Figures 8 and 19).

	Phylloxeridae female sexuales and males	Adelgidae female sexuales and males (Table 2)	Mindarinae males (Table 21)	<i>Forda formicaria</i> embryonic males	<i>Stomaphis quercus</i> males (Table 21)	Anoeciinae <i>Anoecia</i> sp. males (Table 20)
Retort-shaped organs	-	+	+	+	-	+
Stylets	-	+	+	+	-	+
Pharyngeal duct	-	+	+	+	-	+
Pharyngeal valve	-	+	+	+	-	+
Pharyngeal pump	+	+	+	+	+	+
Gustatory organs	-	+	+	+	-	+
Salivary glands	-	degenerated	degenerated	+	-	+
Salivary pump	-	+	+	+	-	+
Midgut	degenerated	degenerated	degenerated	primitive	degenerated	primitive
Rectum	+	+	+	+	+	+
Anal opening	+	+	+	+	+	+
Anal dorsal muscles	-	+	+	?	-	+
Anal lateral muscles	+	+	+	?	+	+
Mycetome	-	reduced	-	reduced	-	+
Oenocytes	-	-	-	+	-	+
Basophilic mesodermal cells	+	+	+	+	+	+
Protein crystals	+	+	-	-	-	-
Siphunculi	-	-	-	-	-	-

Table 20 The only males of all species investigated of the Aphididae by the author since 1972. The digestive system, mycetome including the symbionts, and oenocytes are identical to those of the viviparae and oviparae within each species. Only the males of *Anoecia* sp. have a primitive but not degenerated digestive system (Table 19). I-III refer to thoracic segments; 1-9 refer to abdominal segments.

Aphid	Number of males / total number of aphids sectioned	Males	Host plant	Mycetome starts in	Mycetome ends in	Symbionts (Table 22)
<i>Greenidea eugeniae</i> Takahashi	5/14	winged	<i>Engenia jambalana</i>	I-2	4-5	thin rod- and irregularly-shaped
<i>Greenidea formosana</i> (Maki)	5/9	winged	<i>Psidium guajava</i>	I-2	4-5	thin rod- and irregularly-shaped
<i>Greenidea</i> sp.	9/13	winged	<i>Eugenia jambalana</i>	I-2	5	thin rod- and irregularly-shaped
<i>Eucallipterus tiliae</i> (Linnaeus)	5/10	winged	<i>Tilia</i> sp.	III	4-5	irregularly-shaped
<i>Iziphya bufo</i> (Walker)	4/5	wingless	<i>Carex arenaria</i>	III	6	irregularly-shaped
<i>Monaphis antennata</i> (Kaltenbach)	5/10	winged	<i>Betula</i> sp.	III	5-6	irregularly-shaped
<i>Anoecia</i> sp. (Table 19)	4/8	wingless	<i>Cornus</i> sp.	I	6	irregularly-shaped and granules in nucleated sheath
<i>Aphis epilobiaria</i> Theobald	1/8	winged	<i>Epilobium hirsutum</i>	III	5	big spherical
<i>Aphis farinosa</i> Gmelin	16/47	wingless	<i>Salix</i> sp.	III-1	5-6	big spherical
<i>Aphis tripolii</i> Laing	6/20	winged	<i>Aster tripolium</i>	III	5-6	big spherical
<i>Coloradoa tanacetina</i> (Walker)	7/19	wingless	<i>Tanacetum vulgare</i>	III	5-6	big spherical
<i>Hyalopteris</i> sp.	26/112	winged	<i>Phragmites australis</i>	III-1	6-7	big spherical
<i>Plocamaphis amerinae</i> (Hartig) (Table 24)	4/12	wingless	<i>Salix</i> sp.	III	6-7	big spherical

Table 21 Species of *Mindarus* and *Stomaphis quercus* (Linnaeus) of which the males have a degenerated digestive system and consequently no mycetome and oenocytes (Table 19). All species investigated of the Lachninae (Ponsen, 1981) possess a complicated filtersystem in their midgut but this system is absent in the males of *S. quercus*.

Aphid	Number of males / total number of aphids sectioned	Males	Host plant	Locality, data
<i>Mindarus abietinus</i> Koch	1/8	wingless	<i>Abies homolepis</i>	Wageningen, 11.VI.1983
<i>Mindarus abietinus</i> Koch	2/16	wingless	<i>Abies pinsapo</i>	Wageningen, 4.VI.1997
<i>Mindarus japonicus</i> Takahashi	8/25	wingless	<i>Abies firma</i>	Kurayama, Japan, V.2001
<i>Mindarus obliquus</i> (Cholodkovsky)	2/11	wingless	<i>Picea pungens</i>	Wageningen, 4.VI.1997
<i>Mindarus obliquus</i> (Cholodkovsky)	2/18	wingless	<i>Picea glauca</i>	Wageningen, 5.VI.1997
<i>Stomaphis quercus</i> (Linnaeus)	6/11	wingless	<i>Quercus robur</i>	Wageningen, IX.1992

Both the sexuales of the Adelgidae (Table 11) and those of the Mindarinae (Nüsslin, 1910b; Sorin, 1966; Heie, 1980) are wingless dwarfish individuals. They have well-developed mouthparts similar to those of the asexual morphs of the Adelgidae (Figures 1-4, 6, and 8) and the viviparae and oviparae of the Mindarinae (Figure 21). The mycetome of the adelgid sexuales is a very small compact structure consisting of mycetocytes with empty nuclei (Figures 10C and F and 35D-E).

On the other hand, both the wingless dwarfish sexuales of the Phylloxeridae and the males of *Stomaphis quercus* are characterized by the absence of mouthparts (Table 19). Consequently the retort-shaped organs, stylets, pharyngeal duct, pharyngeal valve, gustatory organs, salivary glands, and salivary pump are lacking (Ponsen, 1997). The complicated filtersystem which is present in all species investigated of the Lachninae (Ponsen, 1981) is lacking in the degenerated midgut of the males of *Stomaphis quercus* as well as the mycetome (Table 19; Figure 25F).

The wingless dwarfish sexuales of the Pemphiginae have no rostrum (Haracsi, 1938; Heie, 1980; Remaudière, pers. com.) which agrees with the absence of salivary glands in the sexuales of *Pemphigus spyrothecae* (Toth, 1938, 1939). Moreover, in the female sexuales of *Pemphigus bursarius* and *Pemphigus spyrothecae* the mycetome consists of some mycetocytes whereas in the males it is absent (Lampel, 1959).

The digestive system of the sexuales of the Phylloxeridae consists of one straight tube without any loop or coil (Ponsen, 1997). Similar structures are also observed in the males of *Mindarus abietinus* and *Mindarus obliquus* (Nüsslin, 1910b) (Figure 23A). In all phylloxerid and adelgid sexuales and males of the Mindarinae the midgut and salivary glands have a degenerated structure showing pycnotic or empty nuclei (Figures 8, 19A, and 23C-E). Moreover, the mycetome and oenocytes are lacking in the males of the Mindarinae (Figure 23A; Tables 19 and 21).

The six wingless embryonic males (exules) in one winged viviparous fourth stage larva of *Forda formicaria* (Pemphiginae, Table 17) possess well-developed mouthparts and retort-shaped organs which produce the stylets. The digestive system is one straight tube without any loop or coil in contrast with that of the viviparae having 2-3 loops (Figure 24A-B). Moreover, the rectal gland present in the viviparae is lacking in the males (Figures 24A-B and 25A-D). The straight tube of the exules is similar to that of the sexuales of the Phylloxeridae. The mycetome of the embryonic exules of *Forda formicaria* consists of very small mycetocytes in contrast with the well-developed mycetome of the embryonic viviparae.

The straight tube of the digestive system, the absence of the rectal gland, and the reduced mycetome (small mycetocytes) indicate that the midgut of the exules of *Forda formicaria* will be also degenerated. However, the nuclei of the salivary glands and those of the midgut of the embryonic exules contain chromatin material and a nucleolus (Figure 24C-E) similar to those of the embryonic viviparae (Figure 25D). From this it can be concluded that the degenerating process of the above-mentioned organs starts after birth of the sexuales and the exules of *Forda formicaria*.

The sexuales of the Anoeciinae are wingless dwarfish individuals with a rostrum (Zwölfer, 1957; Heie, 1980). The slender wingless males (exules) have also well-developed mouthparts similar to those of the viviparae and oviparae (Figure 26B). They have a primitive, not degenerated digestive system (Figure 26A). The crenated intestine of the oviparae possesses one and that of the viviparae two additional loops (Ponsen, 1987). Both the males and the viviparae and oviparae have a well-developed mycetome including the mycetocytes harbouring irregularly-shaped symbionts (Figure 37A; Table 19 and 22).

Table 23 List of species and their endosymbionts of the subfamilies Thelaxinae, Neophyllaphidinae, and Chaitophorinae (Ponsen, 1982b, 1983, and 1990a).
+ = present, - = absent (Figure 36).

Subfamily	Tribe	Aphid	Endosymbionts		Siphunculi on abdominal tergite
			Small spherical ($\pm 1.3 \mu\text{m}$)	Irregularly-shaped	
Thelaxinae		<i>Glyphina betulae</i> (Linnaeus)	+	+	6
		<i>Glyphina jacutensis</i> Mordvilko	+	+	6
		<i>Thelaxes dryophila</i> (Schrank)	+	+	6
		<i>Thelaxes suberi</i> (del Guercio)	+	+	6
		<i>Neophyllaphis grobleri</i> Eastop	+	-	6
Neophyllaphidinae	Atheroidini	<i>Caricosipha paniculatae</i> Börner	+	-	6
		<i>Atheroides serrulatus</i> Haliday	+	+	5
		<i>Laingia psammae</i> Theobald	+	+	6
		<i>Sipha elegans</i> del Guercio	+	+	5
		<i>Sipha glyceriae</i> (Kaltenbach)	+	+	5
Chaitophorinae	Chaitophorini	<i>Periphyllus acericola</i> (Walker)	+	+	5
		<i>Periphyllus obscurus</i> Mamontova	+	+	5
		<i>Periphyllus testudinaceus</i> (Fermie)	+	+	6
		<i>Chaitophorus capreae</i> (Mosley)	-	+	6
		<i>Chaitophorus horii</i> Takahashi	-	+	6
		<i>Chaitophorus leucomelas</i> Koch	-	+	6
		<i>Chaitophorus niger</i> Mordvilko	-	+	6
		<i>Chaitophorus populeti</i> (Panzer)	-	+	5
		<i>Chaitophorus populialbae</i> (Boyer de Fonscolombe)	-	+	6
		<i>Chaitophorus saliceti</i> (Schrank)	-	+	6
		<i>Chaitophorus truncatus</i> (Hausmann)	-	+	6
		<i>Chaitophorus vitellinae</i> (Schrank)	-	+	6

Table 24 List of species of the subfamilies Lizeriinae and Pterocommatinae, their host plant, and relevant locality data.

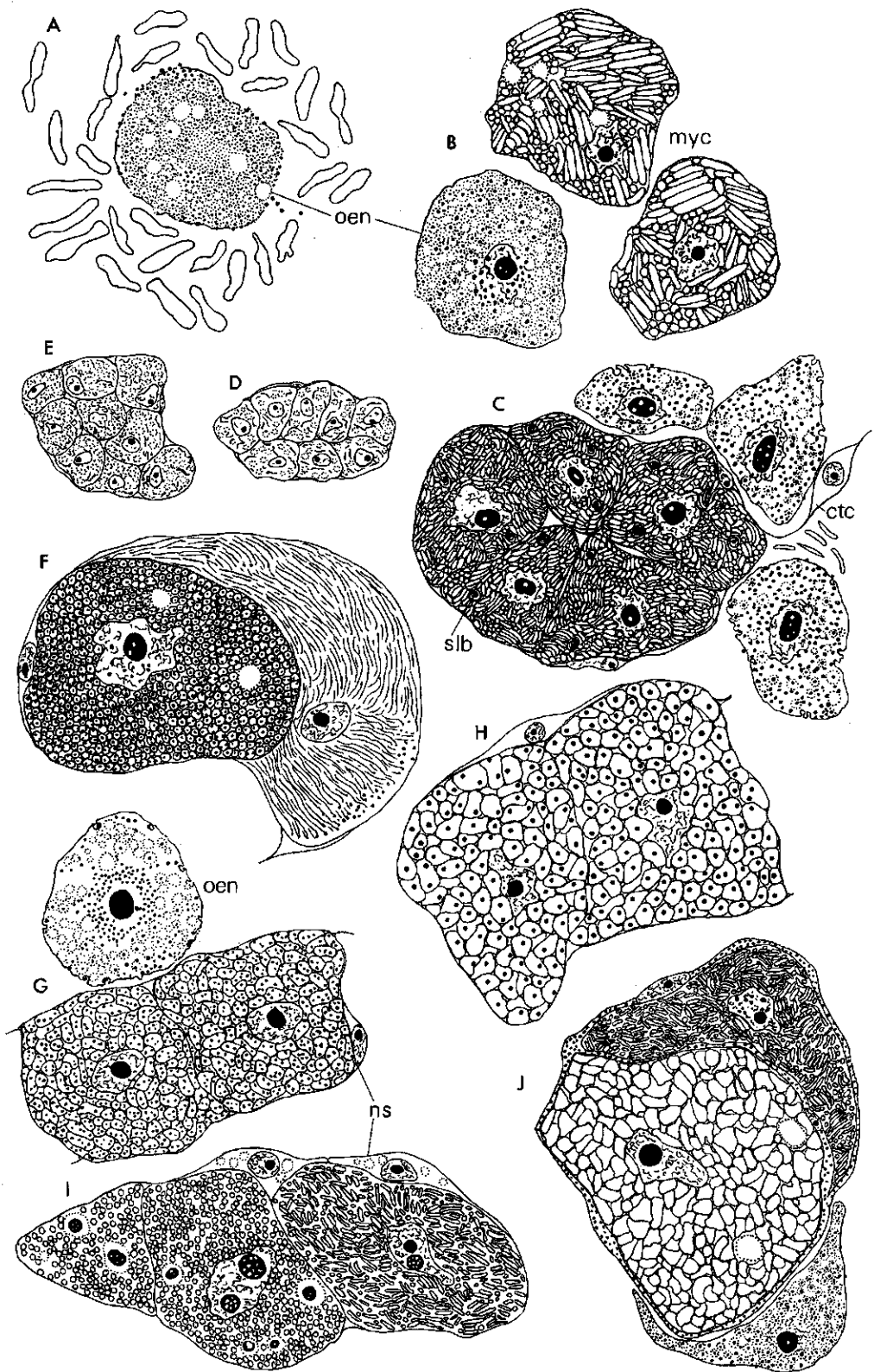
Subfamily Aphid	Host plant	Locality data
Lizeriinae		
<i>Lizerius tuberculatus</i> (Blanchard)	<i>Nectandra megapotamica</i>	São Carlos SP, Brazil, 26.XI.1999
<i>Lizerocallis flavus</i> Sousa-Silva & Ilharco	<i>Tibouchina granulosa</i>	Brazil, 24.XII.1999
<i>Paoliella terminaliae</i> (Hall)	<i>Terminalia sericea</i>	Sonstraal, Cape Province, South Africa, 23.III.1983
Pterocommatinae		
<i>Placamaphis amerinae</i> (Hartig)	<i>Salix</i> sp.	Wageningen, 23.VII.1982
<i>Pterocomma jacksoni</i> Theobald	<i>Salix</i> sp.	Wageningen, 7.VII.1981
<i>Pterocomma populeum</i> (Kaltenbach)	<i>Populus nigra</i>	Bennekom, 8.VI.1982
<i>Pterocomma pilosum</i> Buckton	<i>Salix</i> sp.	Wageningen, 3.VII.1982
<i>Pterocomma salicis</i> (Linnaeus)	<i>Salix</i> sp.	Wageningen, 7.X.1977

As summarized in Table 20, the males of aphid species of the Aphididae have both a well-developed digestive system and mycetome including symbionts which are identical to those of the viviparae and oviparae. It appears that a degenerated midgut 1) correlates with either a reduced (degenerated) mycetome or the absence of a mycetome (Table 19), and 2) is not able to digest food so that symbionts are lacking. Consequently the symbionts play an important role in the metabolism of aphids to supplement the protein-poor diet from the phloem.

The asexual morphs of the Phylloxeridae have a well-developed alimentary tract but there are no symbionts housing in a mycetome or loosely scattered in the haemolymph (Ponsen, 1997). They feed on a protein-rich diet ingested from non-vascular tissue cells (Harrewijn et al., 1998). However, the asexual morphs of the Adelgidae which also take their nourishment from the parenchyma tissues (Table 4), have both a well-developed alimentary tract (Figures 10A-B, 11, and 12) and a mycetome with thin rod-shaped symbionts (Figure 35C; Table 22).

According to Remaudière and Remaudière (1997) the two species, viz. *Cerataphis palmae* Ghesquière and *Pseudoregma bambucicola* belong to the tribe Cerataphidini, a subfamily of the Hormaphidinae (Table 17). In *Cerataphis palmae* the mycetome is lacking and the amoeboid-like symbionts (Figure 35A) live free in the haemolymph (Profft, 1937; Buchner, 1953). On the other hand, *Pseudoregma bambucicola* possesses a mycetome of which the majority of the mycetocytes harbour granulated spherical

Figure 35 Transverse sections of loosely scattered symbionts in the body cavity of a wingless viviparous *Cerataphis palmae* Ghesquière (A) and loosely scattered mycetocytes in the body cavity of a winged first larval stage viviparous *Lizerius tuberculatus* (Blanchard) (B; see Figure 28). Transverse sections of a part of a mycetome showing some mycetocytes of a progredien larva of *Adelges nordmannianae* (C), a female sexuales of *Adelges cooleyi* (D), a male of *Adelges laricis* (E), a winged viviparous *Pseudoregma bambucicola* (Takahashi) (F), a wingless viviparous *Lizerocallis flavus* Sousa-Silva & Ilharco (G), a winged viviparous *Paoliella terminaliae* (Hall) (H), a winged viviparous *Neuquenaphis sensoriata* Hille Ris Lambers (I), and a winged male of *Greenidea formosana* (Maki) (J). Note the vacuolization of the degenerating mycetocytes of the adelgid sexuales (D and E). Bar represents 10 µm. For list of abbreviations see page 102.



symbionts and in some mycetocytes thread-like symbionts (Figure 35F; Table 22). Probably each of these two species belongs to a separate tribe.

The subfamily Lizeriinae (Table 24) comprises three species viz. *Lizerius tuberculatus* (Blanchard), *Lizerocallis flavus* Sousa-Silva & Ilharco, and *Paoliella terminaliae* (Quednau, 1974; Remaudière and Remaudière, 1997; Sousa-Silva and Ilharco, 2003) which are completely different with respect to the alimentary tract and the symbionts (Tables 15 and 22). All aphid species of the Aphididae have 31 or more pairs of muscles to control the pharyngeal valve and pump, except *Lizerius tuberculatus*. This species has 14 pairs of muscles even as many as the species of the Phylloxeridae and those of the Adelgidae (Figures 9 and 21A) which take their nourishment from the parenchyma tissue.

The digestive system of both *Lizerius tuberculatus* (Figure 28A) and *Lizerocallis flavus* is similar to that of both *Latgerina orizabaensis* Remaudière and *Sensoriaphis nothofagi* Cottier (Table 13; Figure 29A). The digestive system of *Paoliella terminaliae* has two intestines which pass into the rectum, viz. a blindly starting intestine or caecal intestine and a descending intestine (Figure 7 in Ponsen, 1990). These two intestines form no filtersystem in contrast with species of the Myzocallidini and those of the Saltusaphidinae which have two filtersystems, viz. a concentric and a parallel one (Figure 22; Table 14).

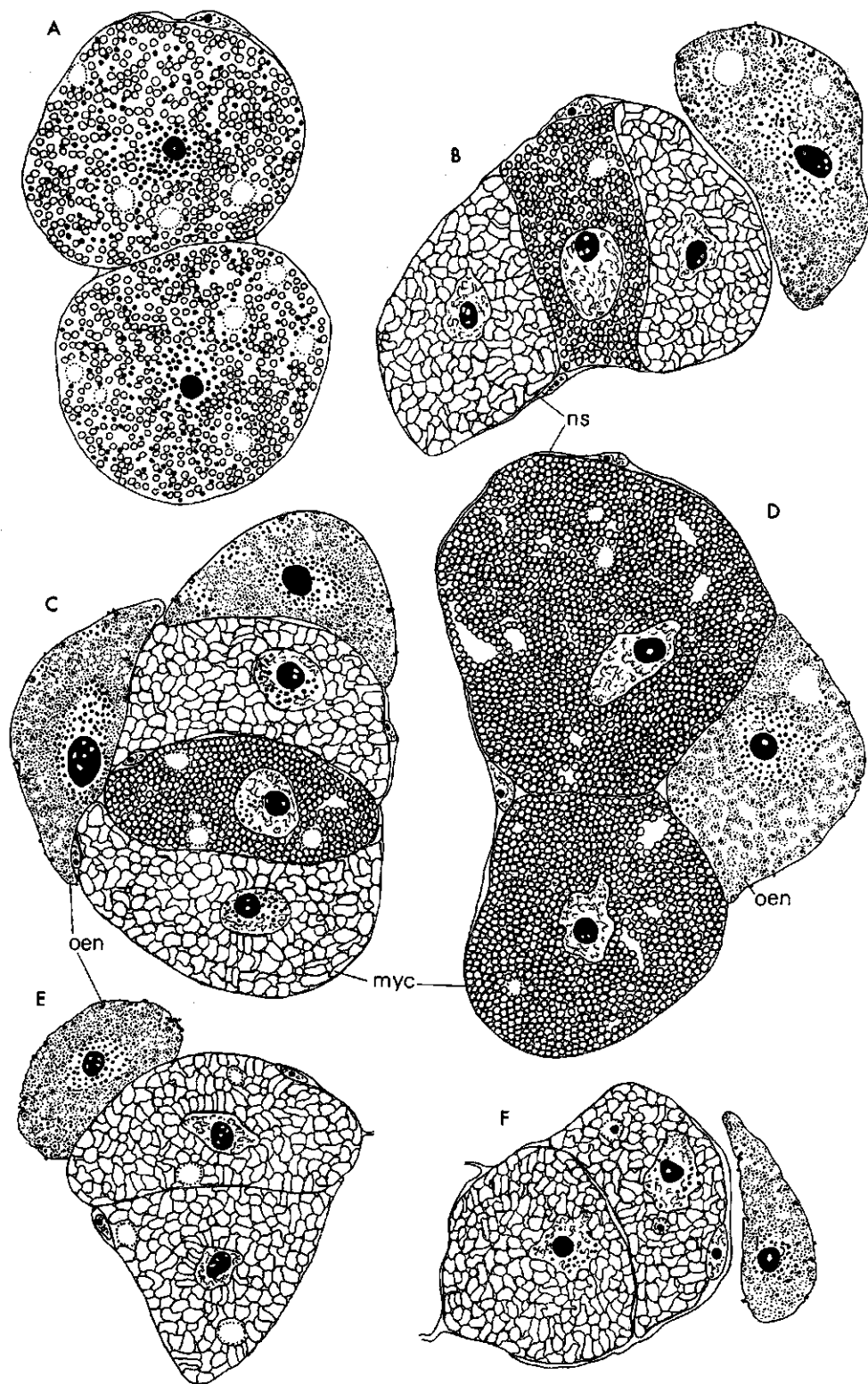
The mycetome of *Latgerina orizabaensis* and *Sensoriaphis nothofagi* consists of mycetocytes harbouring irregularly-shaped symbionts (like ginger roots) which multiply by a budding process (Figures 35-37; Table 22). These symbionts are similar to those of the species summarized in Tables 13 and 14. *Lizerius tuberculatus* did not have a mycetome; the mycetocytes are scattered throughout the body cavity and they harbour thick rod-shaped symbionts (Figures 28B and 35B). In *Lizerocallis flavus* the mycetocytes with granulated irregularly-shaped symbionts (Figure 35G) form a mycetome surrounded by a nucleated sheath. *Paoliella terminaliae* has a mycetome of which the mycetocytes harbour irregularly-shaped symbionts with a "nucleus" (Figure 35H).

However, all three species (Table 18) are characterized by the presence of a lateral epidermal gland in the fifth abdominal segment (Figures 27F and 28A). In embryos each gland consists of two cells but in larvae they are fused to one cell forming a pear-shaped structure (Figure 26C). The apical part of each gland has a chitinous plate with pores and the two nuclei are situated on the basal part of the gland. The cytoplasm contains numerous vacuoles, fine granular material, and granules which increase in number during larval life. They excrete no wax filaments but a fluid of unidentified material as observed in paraplast sections of three specimens. The structure of these glands is not similar to that of both the tubercles and wax glands (Figure 33).

On the basis of total number of pharyngeal muscles, the structure of the digestive system, and the symbionts these three species do not belong to one subfamily but each of them should be placed in a separate subfamily or tribe.

Based on morphological characteristics, Remaudière and Remaudière (1997) divided the subfamily Chaitophorinae into two tribes, viz. Atheroidini and Chaitophorini (Table 23). All species of both tribes have exactly the same digestive system (Ponsen, 1983).

Figure 36 Transverse sections of a part of a mycetome showing some mycetocytes of a wingless viviparous *Schoutedenia ralumensis* Rübsaamen (A), a winged viviparous *Glyphina betulae* (Linnaeus) (B), a wingless viviparous *Periphyllus testudinaceus* (Fernie) (C), a wingless oviparous *Caricosipha paniculatae* Börner (D), a winged viviparous *Chaitophorus populiabae* (Boyer de Fonscolombe) (E), and a wingless oviparous *Parachaitophorus spiraeae* (Takahashi) (F). Bar represents 10 µm. For list of abbreviations see page 102.



However, the mycetome of the species of the Atheroidini and that of the three *Periphyllus* species consists mainly of mycetocytes harbouring irregularly-shaped symbionts and some mycetocytes with small spherical symbionts (Figure 36C). Such a mycetome with two types of symbionts is similar to that of species of the Thelaxinae (Figure 36B; Table 23). All mycetocytes of the species of *Chaitophorus* have only irregularly-shaped symbionts (Figures 36E) similar to those of the species summarized in Tables 13 and 14 (Figures 36F and 37B). In *Caricosipha paniculatae* Börner all mycetocytes harbour small spherical symbionts (Figure 36D). From this it can be concluded that the genera *Periphyllus* belongs to the Atheroidini whereas *Caricosipha paniculatae* should be placed in the Neophyllaphidinae or in a separate tribe.

Morphologically the genera *Israelaphis* (Israelaphidinae) and *Greenidea* (Greenideinae), and the species *Neuquenaphis sensoriata* Hille Ris Lambers (Neuquenaphidinae) and *Schoutedenia lutea* van der Goot (= *S. ralumensis* Rübsaamen; Greenideinae Schoutedenini) have exactly the same alimentary tract (Table 15). The most characteristic feature of the digestive system is the stomach. This somewhat dilated organ lies centrally in the dorsal part of the aphid and bends half-way either to the right or to the left ventral part of the aphid before joining the crenated intestine (Figure 22).

The mycetome of the first three species is a compact structure between the metathorax and sixth abdominal segment. However, the mycetocytes of *Israelaphis* harbour spherical symbionts with a diameter of 2.7 μm similar to those of the Aphidinae, *Aphis*-group, and Pterocommatinae (Tables 22 and 24; Figures 37C-E).

The mycetome of the Greenideini has two types of symbionts: mycetocytes with thin rod-shaped symbionts and mycetocytes with irregularly-shaped symbionts (Figure 35J). The latter are similar to those of species summarized in Tables 13 and 14 (Figures 36F and 37B). The mycetocytes of the compact mycetome are surrounded by a nucleated sheath of which the cytoplasm contains granular material. This material looks like that of the oenocytes. In the mycetome of embryos these granules are absent. *Neuquenaphis sensoriata* has two types of symbionts viz. mycetocytes with thin rod-shaped symbionts and mycetocytes with small spherical symbionts (Figure 35I; Table 22). The mycetome of *Schoutedenia ralumensis* consists of two longitudinal masses of mycetocytes which subsequently join together forming a y-shaped structure. All mycetocytes harbour both small spherical symbionts and brown granules (Figure 36A). The latter do not occur in the embryonal mycetocytes. They are probably degenerated symbionts or granulated nuclear material which are released into the mycetocytes. Consequently *Schoutedenia ralumensis* belongs to a separate subfamily. Moreover, this species has rectal gland cells in the dorsal region of the rectum (Figure 15B in Ponsen, 1991) and no multinucleated structure as in species of *Israelaphis*, *Greenidea*, and *Neuquenaphis sensoriata* (Table 18).

The mycetome including the irregularly-shaped symbionts of the males of *Anoecia* sp. (Table 22) is similar to that of the viviparae and oviparae. Granular material is present in the nucleated sheath of the mycetome (Figure 37A). It is more numerous in the males than in the viviparae and oviparae, but is lacking in embryos. These granules look like those of the oenocytes and those present in fat cells.

Within the subfamily Aphidinae, except the *Aphis*-group (Table 15) all individuals of the first four species possess a complicated filtersystem (Ponsen, 1977) and those of the last two species with or without a primitive filtersystem. The remaining species of the Aphidinae have had a filtersystem as evidenced by the presence of filterchamber cells (Tables 10 and 11 in Ponsen, 1991). All these species and all species of the Lachninae with a filtersystem, and those mentioned in Table 14 have a caecal intestine (Figure 22).

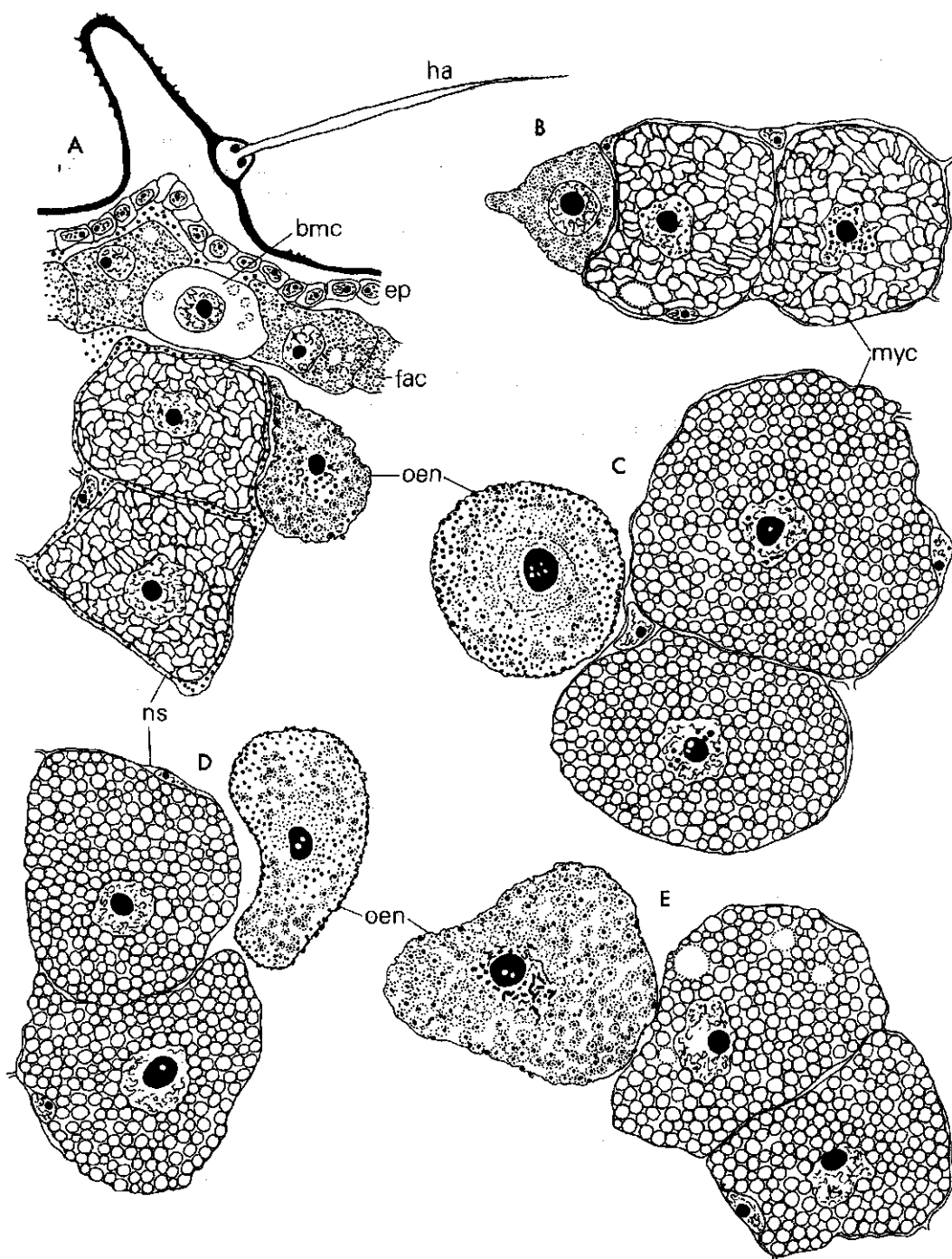


Figure 37 Transverse sections of a part of a mycetome showing some mycetocytes of a wingless male of *Anoecia* sp. (A), a wingless viviparous *Subsaltusaphis ornata* (Theobald) (B), a wingless oviparous *Cryptosiphum artemisiae* Buckton (C), a wingless male of *Aphis farinosa* Gmelin (D), and a wingless oviparous *Israelaphis alistana* Mier Durante (E). Bar represents 10 μ m. For list of abbreviations see page 102.

On the other hand, species of the *Aphis*-group (Table 1 in Ponsen, 1990b) have a crenated intestine which morphologically is quite different from that of the Aphidinae. Probably this group which also possesses a descending intestine (Figure 22) belongs to a separate subfamily of the Aphididae.

Both in species of the Aphidinae and those of the *Aphis*-group the mycetome consists of mycetocytes harbouring big spherical symbionts with a diameter of 2.7 μm (Figure 37C-D; Table 22). Identical symbionts are also present in mycetocytes of species of the Pterocommatinae (Tables 20 and 24). They multiply by binary fission.

Summarized in Table 22 it appears that species of the Phylloxeridae have no endosymbionts and the adelgids a well-developed mycetome consisting of mycetocytes with thin rod-shaped symbionts. Within the Aphididae there are morphologically ten different types of endosymbionts; each subfamily has its own type of endosymbiont although all species of the Aphididae are phloem suckers. Species of two subfamilies, viz. Neuquenaphidinae and Greenideinae Greenideini, have thin rod-shaped endosymbionts similar to those of species of the Adelgidae (Figures 35-37).

Figure 38 A. Electron micrograph of an area of a mycetocyte harbouring ellipsoid-shaped symbionts of a first stage gallicolous larva of *Adelges nordmannianae* (see Figure 35C). B. Scattered among the symbionts there occur spiral-like bodies (s l b) which show a filamentous structure at high magnification. Bar represents 1 μm . For list of abbreviations see page 102.



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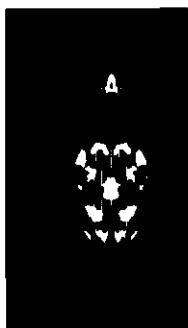
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Abbreviations used in figures

a d m	anal dorsal muscles	g m c	granulated mesodermal cell
a l m	anal lateral muscles	g o	gonopore
a o	anal opening	h a	hair
a s d	afferent salivary duct	h p	hypopharynx
b m c	basophilic mesodermal cell	h p g o	hypopharyngeal gustatory organ
b s c	bottle-shaped cell	h p l	hypopharynx lip
c a	corpus allatum	i s	intraalvular space
c e	compound eye	i s s	irregularly-shaped symbiont
c e i	common epidermal invagination	l	lumen
c f	chitinous fibrils	l a	labium (rostrum)
c i	caecal intestine	l b	labrum
c l	clypeus	l c	labial clamp
c l b	clypeo-labrum	l e c	lateral epidermal cell
c o	cornicle (siphunculus)	l e g	lateral epidermal gland
c o v	cornicle valve	l e i	lateral epidermal invagination
c p b	cytoplasmic bulge	l g	labial groove
c r	crumena	l s	labyrinthine system
c r i	crenated intestine	m d	mandibular stylet
c s d	common salivary duct	m d c	mandibular canal
c t c	connective tissue cell	m d r	mandibular retort-shaped organ
d e	dendrite	m l	mandibular lever
d f a c	degenerating fat cell	m n s	multinucleated structure
d i	descending intestine	m o d	median oviduct
d v	dorsal vessel	m t	marginal tubercle
e	epipharynx	m v s	microvillar system
e c u	embryonic cuticle	m x	maxillary stylet
e g o	epipharyngeal gustatory organ	m x r	maxillary retort-shaped organ
e i	epidermal invagination	m x s	maxillary sclerite
e m	extracellular microtubules	m y	mycetome
e n c u	endocuticle	m y c	mycetocyte
e p	epidermis	M2	circular muscle fibres
e p c u	epicuticle	M3	cornicle valve retractor muscle
e p i	epicranium	M4	divaricator muscle
e s d	efferent salivary duct	M6	elevator muscle of tentorial bar
e x c u	exocuticle	M7	lateral muscle of clypeus
e x c u n	exocuticle new	M8	lateral muscle of mandibular stylet
e x c u o	exocuticle old	M9	lateral muscle of maxillary stylet
f	foregut	M10	lateral pharyngeal valve muscle
f a c	fat cell		
f a g	female accessory gland		
f c	food canal		
f e	foregut epithelium		
f i s	filtersystem		
f m	fibrous mass		

M11	longitudinal muscle fibres	p h p	pharyngeal pump
M13	protractor muscle of mandibular stylet	p h p r	pharynx protuberance
M14	protractor muscle of maxillary stylet	p h v	pharyngeal valve
M15	retractor muscle of mandibular stylet	p l	plaque
M16	retractor muscle of maxillary stylet	p r c	protein crystal
M17	retractor muscle of salivary pump piston	p s	pump system
M19	retractor muscle of salivary pump wall	p t	piston
M20	retractor muscle of afferent salivary duct	p u	processus
M21	ventral pharyngeal pump muscle	r	rectum
M23	mandibular muscle to pharyngeal pump floor	r e b	rectal bladder
M24	maxillary muscle to pharyngeal pump floor	r o	rectal organ
M25	lateral pharyngeal pump muscle	s	symbiont
M26	transverse labial muscles	s b	stylet bundle
M27	lateral dorsoventral muscle	s c	salivary canal
n	nucleus	s e p	sensillary pore
n s	nucleated sheath	s j	septate junction
n u	nucleolus	s l	stylet
N13	medial dorsal nerve	s l b	spiral-like body
o	ostium	s p	salivary pump
o c	ocellus	s t	stomach
o e n	oenocyte	t b	tentorial bar
o p	ovipositor	t e	tendon
o v	oesophageal valve	t g	thoracic ganglion
p	protocerebrum	t o	triommatidion
p c	pumpcylinder	t o c	tormogen cell
p c c	pericardial cell	t p c	triplet cells
p c h	pumpchamber	t r	trachea
p h d	pharyngeal duct	t r c	trichogen cell
p h e	pharyngeal epithelium	t s	testis
		u c e	undeveloped compound eye
		u c o	undeveloped cornicle
		v g	vagina
		v m	visceral muscles
		v r	ventral rod
		w	waxy droplet
		w c	wax cell
		w g	wax gland
		w p	wax plate with pores
		w r	wax reservoir
		z a	zonula adherens