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The histology of the labial glands of some Delphacidae (Hemiptera : Homoptera)

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The histology of the labial glands of some Delphacidae (Hemiptera: Homoptera)

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With 14 Text-figures

Synopsis

The histological characteristics and staining reactions of the salivary glands of six species of Delphacidae are described and discussed in relation to their possible functional differentiation.

I. Introduction

In their early work on the structure and histology of the salivary glands of the Hemiptera, Bugnion & Popoff (1908–10) devoted more attention to the Heteroptera than to the Homoptera. This emphasis has tended to persist in subsequent work: the heteropteran glands have now been investigated in a wide variety of groups (*e.g.* Baptist (1941) and Southwood (1955)), and some species have been described in considerable histological detail (*e.g.* by Barth (1955) and Miles (1967, and earlier papers)). In the Homoptera, despite careful study of the Coccoidea by Pesson (1944) and of representative Aphidoidea by Fortin (1956) and Moericke & Wohlfarth-Botterman (1960*a*, 1960*b*), less seems to be known of the histology and functional differentiations of the salivary glands. It is, however, clear from the work of Dobroscky (1931*a*, 1931*b*), Willis (1949), Nuorteva (1954, 1956) and Berlin & Hibbs (1963) that the salivary glands of the Cicadellidae differ from those of the Heteroptera and the Sternorrhynchan groups, and that they comprise several histologically distinct lobes. In the Fulgoroidea the only available information seems to be a brief account of conditions in *Fulgora maculata* Olivier by Bugnion & Popoff (1910) and a fuller description of the histology and histochemistry of the glands of *Lycorma deliculata* White by Sun (1964). Preliminary observations on serial sections of *Stenocranus minutus* (F.) showed that the salivary glands of this species are well-developed, highly differentiated organs, which would provide favourable material for investigating the diversity of secretory cells in the Delphacidae. In the present paper, therefore, the histology of the labial glands in six species of Delphacidae is described and some functional aspects of their division into several lobes are briefly discussed. The information presented shows the need for further histochemical work on salivary secretion in the Auchenorrhynchan Homoptera and illustrates the suitability of the Delphacidae for such a study.

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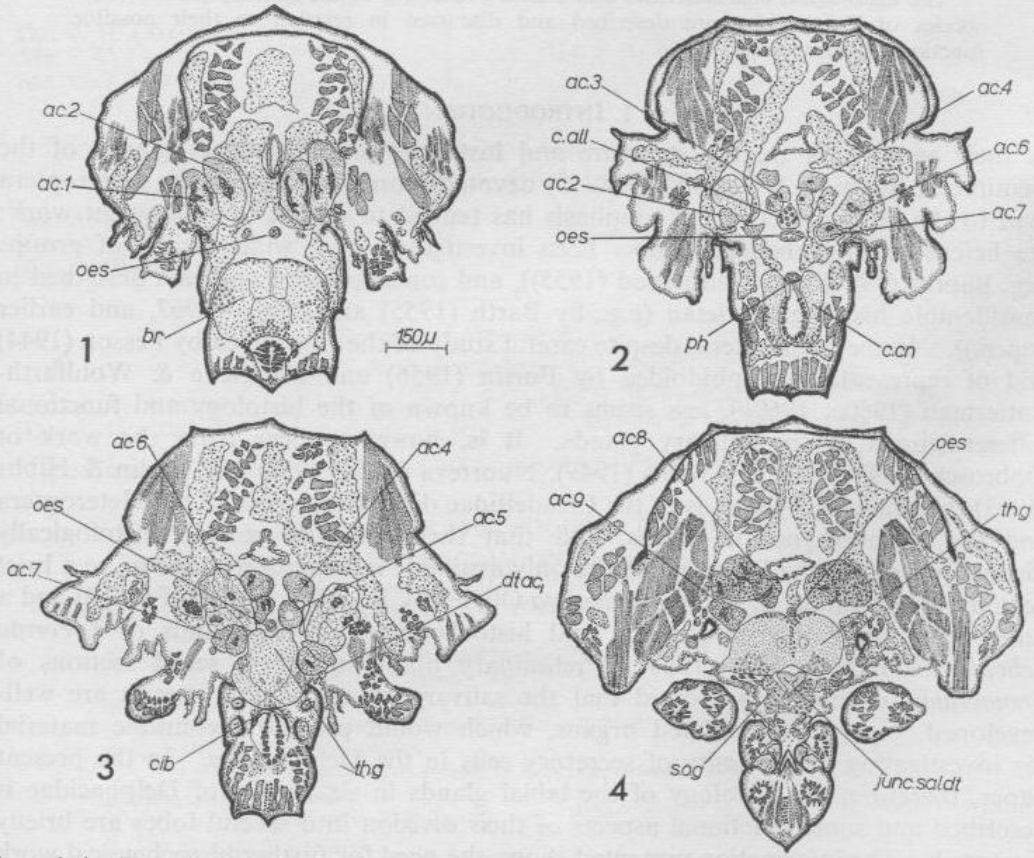
II. Materials and Methods

Specimens of the following Delphacids were collected in the field: *Stenocranus minutus* (F.), *Conomelus anceps* (Germar), *Ditropis pteridis* (Spinola), *Criomorphus albomarginatus* Curtis, *Dicranotropis hamata* (Boheman) and *Javesella pellucida* (F.). Freshly killed insects were fixed in Bouin for *c.* 18 hours after removal of the legs, wings and abdomen. They were then dehydrated in three changes of anhydrous dioxan (diethylene dioxide), embedded in paraffin wax and sectioned serially at 5 μ. Sections were stained with some or all of the following: Mallory's phosphotungstic acid haematoxylin (Drury & Wallington, 1967), paraldehyde-function with Light Green/ Orange G counterstain (Halmi, 1952), Alcian Blue with Phloxin counterstain (Delphin, 1963) and Heidenhain's Azan (Pantin, 1946). The most complete observations were made on *Stenocranus minutus* and *Conomelus anceps*. Measurements of the size of the various histological structures were made with eyepiece graticules, volumes being determined by calculation from areas in successive sections of known thickness. Quantitative data are based on serial sections of four specimens of *Stenocranus* and *Conomelus*, three of *Dicranotropis*, two of *Javesella* and *Ditropis* and one only of *Criomorphus*.

III. Histology of Acini

The labial glands are quite highly differentiated organs, lying in the dorsal part of the prothorax above the level of the brain and composed of a total of 18 acini arranged slightly asymmetrically with nine acini on each side of the oesophagus.



FIGS. 1–4.—Transverse sections through successively posterior regions of head and thorax of *Stenocranus minutus*, showing position and relations of salivary glands. ac_1 to ac_9, first to ninth acini; *br*, brain; *c. all*, corpus allatum; *c. cn*, circumoesophageal connective; *cib*, cibarium; *dt.* ac_1, duct of first acinus; *junc. sal. d*, junction of common salivary ducts; *oes*, oesophagus; *ph*, pharynx; *s.o.g*, suboesophageal ganglion; *th. g*, thoracic ganglion.

The acini of each side are provided with an acinar duct system, which finally gives rise to a common duct. This eventually joins its fellow of the opposite side to form a median duct entering the salivary pump. There is no salivary reservoir. Figures 1–4 show the positions and relations of the acini in serial sections through *Stenocranus*.

The nine acini found in each gland of all investigated species differ in two ways. Firstly, within a species there are well-defined differences in staining reactions and histological appearance between most of the acini. Secondly, although the same nine directly comparable acini can be recognised in four of the species (*Stenocranus*, *Criomorphus*, *Dicranotropis* and *Javesella*), the other two species (*Conomelus* and *Ditropis*) lack one of the acinar forms, and each has in its place a different kind of acinus. The simplest way to proceed, therefore, is to number similarly the acini that correspond in their histological characteristics. In what follows they are denoted as acini I to IX in *Stenocranus*, *Criomorphus*, *Dicranotropis* and *Javesella*; *Conomelus* and *Ditropis* both lack acinus VI and have in its place what are denoted respectively as X and XI. All acinar cells are binucleate, but the number of cells per acinus varies as indicated in Table I. Within any one species, each type of acinus has a characteristic and apparently constant number of cells. Corresponding acini differ somewhat from one species to another, although in several acinar types there is almost complete constancy of cell number in all six species studied. Further quantitative information on the dimensions of the acini and their nuclei are given in Tables I to III, and the histological characteristics of the various types may be summarised as follows:

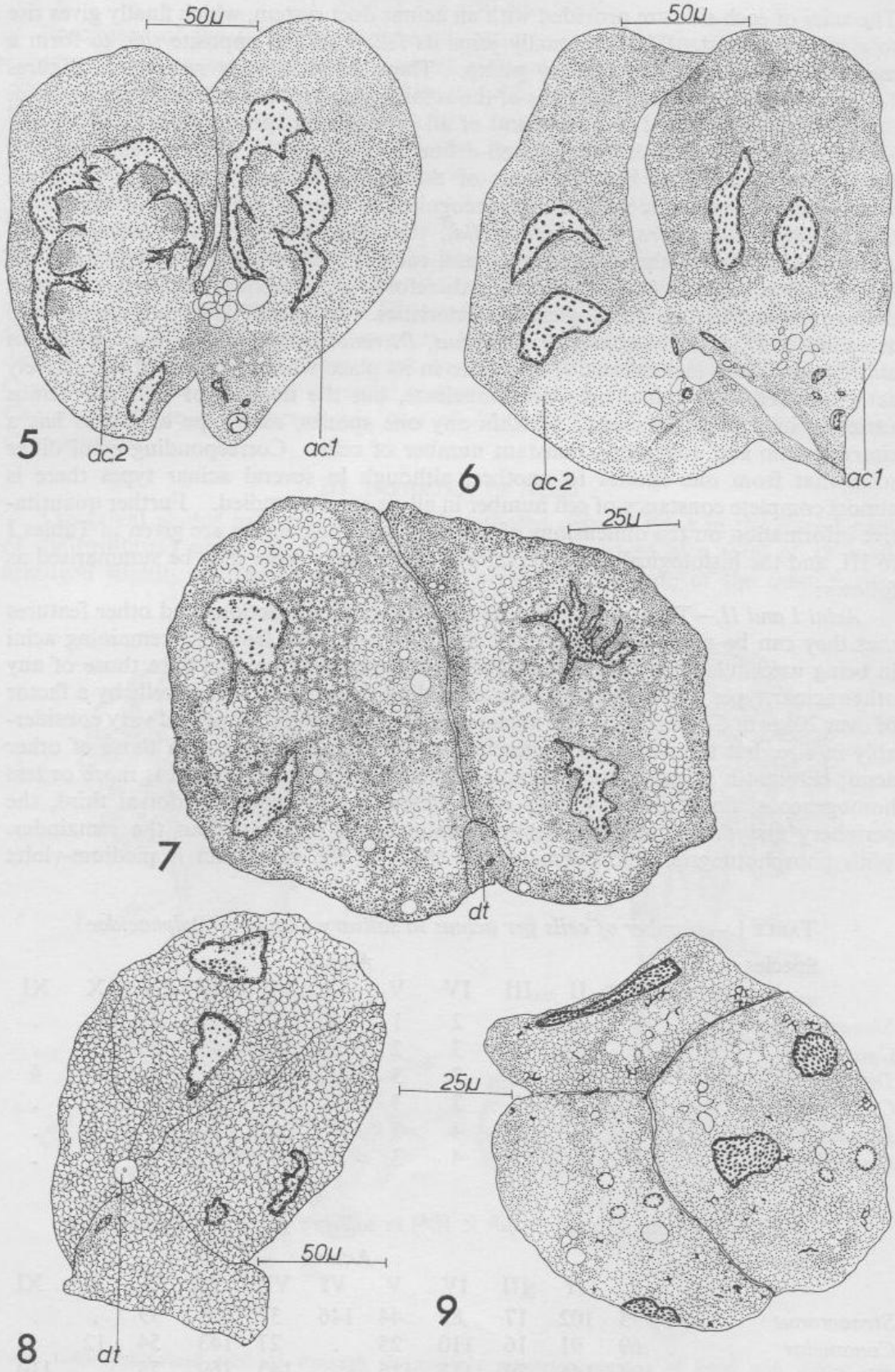
Acini I and II.—These are so similar in their staining reactions and other features that they can be treated together (figs. 5, 6). They differ from the remaining acini in being unicellular, the cells being appreciably greater in volume than those of any other acinar types and sometimes even exceeding the smallest acinar cells by a factor of over 20, as in *Conomelus*. The nuclei are of very irregular shape and vary considerably in size, but their maximum dimensions are always greater than those of other acini; chromatin granules are moderately abundant. The cytoplasm is more or less homogeneous, finely granular, and stains rather lightly, with the dorsal third, the periphery and the perinuclear region staining more strongly than the remainder. With phosphotungstic acid haematoxylin (PTAH) the cytoplasm is medium-violet

TABLE I.—*Number of cells per acinus in salivary glands of Delphacidae*

Species	Acinus										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Stenocranus	1	1	2	2	1	4	3	7	4	.	.
Conomelus	1	1	2	3	2	.	6	4	4	3	.
Ditropis	1	1	2	3	3	.	6	6	4	.	4
Criomorphus	1	1	2	2	3	5	6	7	5	.	.
Dicranotropis	1	1	2	4	3	6	6	6	5	.	.
Javesella	1	1	2	4	3	6	6	9	4	.	.

TABLE II.—*Volume of acini (in* $\mu^3 \times 10^4$*) in salivary glands of Delphacidae*

Species	Acinus										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Stenocranus	95	102	17	82	44	146	37	261	99	.	.
Conomelus	69	91	16	110	25	.	27	143	54	12	.
Ditropis	124	146	29	112	116	.	143	169	75	.	110
Criomorphus	59	60	19	34	46	71	28	122	39	.	.
Dicranotropis	62	69	17	84	60	167	67	200	63	.	.
Javesella	40	42	59	64	54	44	21	243	42	.	.



FIGS. 5–9.—Transverse sections through acini: (5) first and second acini of *Stenocranus minutus*; (6) first and second acini of *Ditropis pteridis*; (7, 8 and 9) fourth, sixth and seventh acini of *Stenocranus minutus*. ac_1, ac_2, first and second acini; *dt*, parts of duct system.

in colour, with paraldehyde-fuchsin and counterstain (PF) it stains a characteristically light bluish-green and with Alcian Blue/Phloxin (ABP) the more heavily staining zones are blue and the less dense regions slightly phloxinophil. In Azan-stained sections of *Conomelus*, acini I and II are blue. The cytoplasm is bounded by a very thin cell membrane, less than 0·5 μ thick; as in all the acini, no further layers intervene between this outer basement membrane and the haemocoel.

Acinus III.—This lies just lateral to the corpus allatum and medial to acini I and II. It is usually the smallest acinus in the system and consists of two binucleate cells. The nuclei themselves are small and compact but somewhat lobate with few chromatin granules; the cytoplasm is homogeneous and finely granular, with a few vacuoles about 4–7 μ in diameter. With PTAH the cytoplasm stains a very light violet and with ABP and Azan (*Conomelus* only) it stains light blue. The clearest distinction between this acinus and acini I, II and V, however, depends on its fuchsinophil reaction, the cytoplasm being coloured reddish-purple in PF, a shade similar to that of acinus IX.

Acinus IV.—Acinus IV lies close to acini V and VIII, although its exact relations to these differ in the different species. It comprises two to four cells, the number apparently varying little if at all within the species examined (fig. 7). The acinus is moderately large, and the nuclei are irregularly shaped and full of chromatin granules; in *Conomelus* an occasional cell had one or more than two nuclei. Unlike the previously described acini, this one has heterogeneous and highly vacuolated cytoplasm, the vacuoles tending to cluster towards the centre of each cell (which therefore appears more lightly staining), with a narrow granular peripheral zone. The vacuoles vary in diameter from less than one to over 12 μ and have no contents in Bouin-fixed material; the cytoplasmic granules are much smaller than those of acini VII and IX. The cytoplasm is rather more basiphil than in acini I–III, staining dark violet with PTAH in the more granular zones. PF-stained preparations are dark lavender in colour, whereas in ABP the cytoplasm is various shades of blue, dark in the granular regions. In *Conomelus* the cells stain red in Azan. The whole acinus is enclosed in a relatively conspicuous basement membrane 1–2 μ thick.

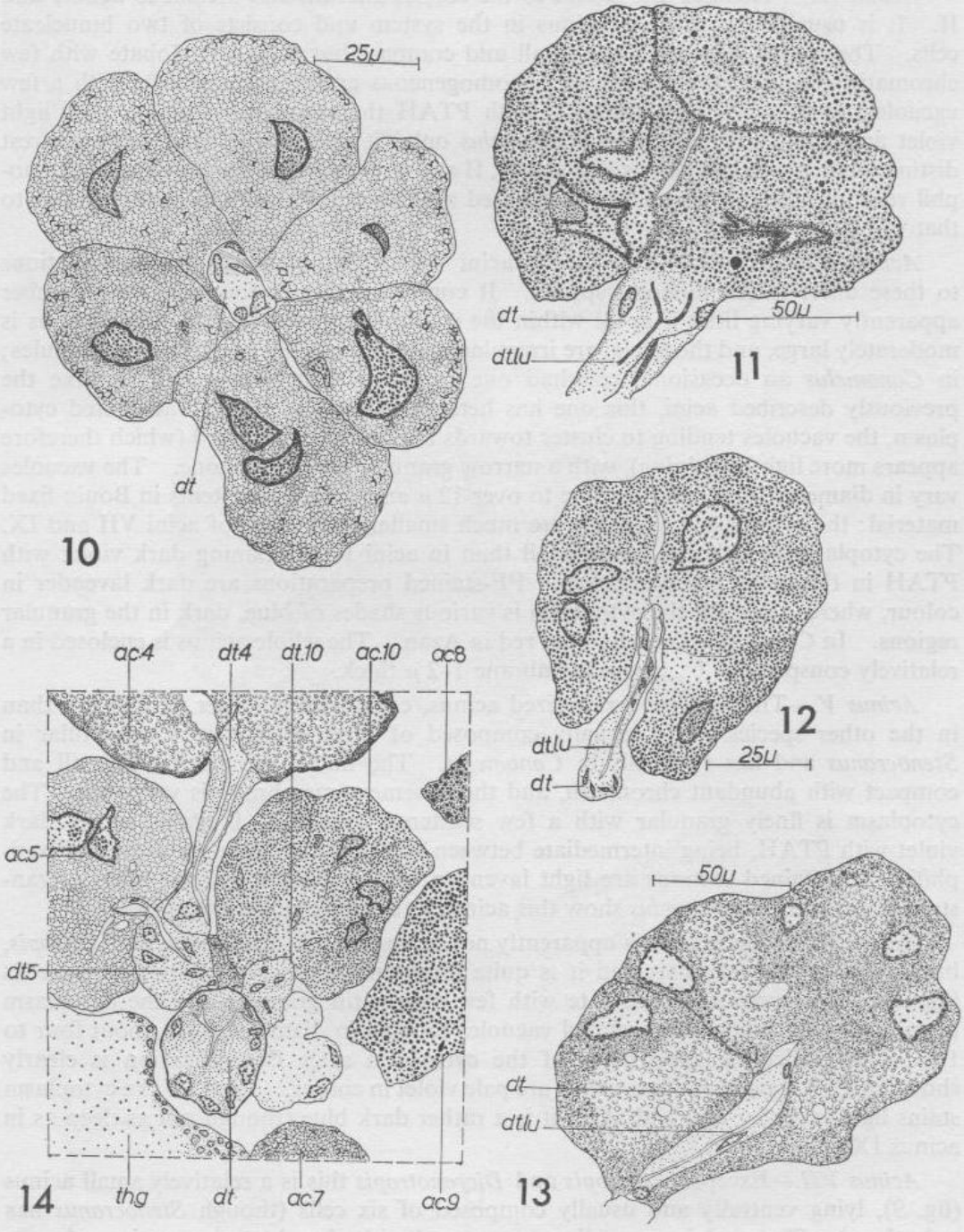
Acinus V.—This is a moderate-sized acinus, considerably larger in *Ditropis* than in the other species. It is usually composed of three cells, but is unicellular in *Stenocranus* and has two cells in *Conomelus*. The nuclei are relatively small and compact with abundant chromatin, and the basement membrane is very thin. The cytoplasm is finely granular with a few scattered vacuoles. It stains rather dark violet with PTAH, being intermediate between acini III and IV in its degree of basiphilia. PF-stained sections are light lavender, and in ABP it is light blue. Azan-stained sections of *Conomelus* show this acinus as a light orange structure.

Acinus VI.—This acinus is apparently not represented in *Conomelus* and *Ditropis*, but in the other species studied it is quite large and composed of four to six cells (fig. 8). The nuclei are vesiculate with few chromatin granules and the cytoplasm is uniformly reticulate with isolated vacuoles ranging in diameter from about four to 18 μ. The reticulate appearance of the cytoplasm after Bouin-fixation is clearly shown in PTAH preparations, which are pale violet in colour. With PF the cytoplasm stains light lavender and with ABP it is a rather dark blue (though not as deep as in acinus IX).

Acinus VII.—Except in *Ditropis* and *Dicranotropis* this is a relatively small acinus (fig. 9), lying ventrally and usually composed of six cells (though *Stenocranus* has only three). The nuclei are small, compact and with abundant chromatin and seem to lie consistently one above the other. The acinus is enclosed in a well-defined basement membrane about 1 μ or so thick. Its reticulate cytoplasm contains a few granules and is more strongly basiphil than in any other acinus, staining dark violet in PTAH. Preparations stained with PF show a red and blue streaked appearance,

and in ABP the cytoplasm takes up the blue stain to a considerable extent but also shows phloxinophil elements. In *Conomelus* it stains orange in Azan (fig. 10).

Acinus VIII.—This is the largest acinus (fig. 11), although the individual cells composing it are always exceeded in volume by those of I and II and often also by IV and V. The nuclei are irregular in shape and contain moderate amounts of chromatin. The most distinctive feature of this acinus, however, is its strongly



FIGS. 10–14.—Transverse sections through acini and ducts: (10) seventh acinus of *Conomelus anceps*; (11) eighth acinus and duct of *Stenocranus minutus*; (12) tenth acinus and duct of *Conomelus anceps*; (13) eleventh acinus and duct of *Ditropis pteridis*; (14) junction of ducts to form common salivary duct of *Conomelus anceps*. ac_4 to ac_9, fourth to ninth acini; *dt*, parts of duct system; *dt. lu*, duct lumen; *th. g*, thoracic ganglion.

basiphil appearance, due to the presence of very numerous granules that range in size from about 0·7 to 5 μ (average about 2 μ) and are distributed in a more homogeneous matrix. The granules stain very dark violet in PTAH, against the lighter, dull violet matrix. In PF they vary from reddish-purple to reddish-orange against a blue matrix. In ABP they are purple or blue, and in Azan-stained sections of *Conomelus* they are orange.

Acinus IX.—This last generally distributed type of acinus is much smaller than acinus VIII, which it resembles in its highly granular cytoplasm. The nuclei, however, are vesiculate structures, variable in shape, and the staining reactions are somewhat different. The granules are less strongly basiphil and rather smaller (0·5 to 4 μ in diameter), staining bluish-purple in PF and clear blue in ABP. In Azan preparations of *Conomelus* the cells of acinus IX are orange. In all species studied, acinus IX is apparently bilobed; the anterior lobe consists of two larger cells, the posterior one of two smaller cells. A small duct connects the lobes.

Acinus X.—This type has been found only in *Conomelus anceps*, in which it is the smallest acinus and occupies a position similar to that of acinus VI in other species (fig. 12). It differs from VI, however, in the abundant chromatin of the nucleus and the highly granular appearance of the non-vacuolate cytoplasm. The granules vary from about 0·5 to 2·5 μ in diameter and the cells are strongly basiphil, appearing dark bluish-violet in PTAH, dark lavender in PF and dark blue in ABP and in Azan.

Acinus XI.—This type occurs only in *Ditropis pteridis* (fig. 13), in which it occupies the position otherwise taken by VI. It differs sufficiently from VI and from acinus X of *Conomelus* to justify a separate description. The cytoplasm is basically reticulate with scattered aggregates of vacuoles (ranging in diameter from about one to 18 μ) and with granules of about 1·5 to 4 μ in the non-vacuolar regions. These granules stain a lavender colour in PF and light blue in ABP.

IV. Salivary Duct System

Associated with each acinus is part of a system of ducts, which lead finally to the median duct entering the salivary pump. The cells comprising the ducts are much smaller than the acinar cells and quite different in histological appearance. Near their origin the ducts are closely associated with the acinar cells, although their detailed relations with the latter are often difficult to make out. It appears, however, that secretion collects in the acinar cells in temporary intracellular secretory channels before passing into the very narrow intercellular lumen of the duct system. All ducts have compact oval nuclei, which are generally much smaller than the acinar cell nuclei and are more uniform in dimensions. Those of *Conomelus*, for example, vary from about 5 $\times$ 4 μ to about 15 $\times$ 13 μ, and of *Ditropis* from about 6 $\times$ 3 μ to about 18 $\times$ 9 μ. The cytoplasm of the ducts does not show the diversity of staining reactions exhibited by the acini, and the lumen of all parts of the duct system is very narrow (about 2 μ in diameter).

The ducts present and the way in which they communicate seem to be as follows, judging from a detailed study in *Stenocranus* and *Conomelus*:—Acini I and II are joined by a short duct, from which arises another very long one that runs back and eventually communicates with the common salivary duct. Similarly acini III and V are linked by a duct in connection with another long one that arises near V and also runs to the common salivary duct. Acinus IV communicates with the duct from III and V in *Stenocranus* but has its own long connection with the common salivary duct in *Conomelus*. Acini VI to XI send their own relatively short ducts to join the common duct. The common ducts run one each side of the thoracic ganglion and meet near the junction between the suboesophageal and thoracic ganglia (fig. 4). The median salivary duct thus formed is only about 10 μ long and enters the salivary pump.

V. Discussion

A distinction between the labial and maxillary glands of the Hemiptera was made long ago by Bordas (1905). Although much less is known of the maxillary glands, they have been reported from aquatic and terrestrial groups of Heteroptera and may well be of general occurrence in that suborder (Parsons, 1958; Linder, 1956; Slater & Carayon, 1963). Bugnion & Popoff (1908–10) reported maxillary glands in *Fulgora maculata*, but they do not otherwise seem to have been described in the Homoptera and are not discussed further here. The labial glands of the Heteroptera have already been widely described (*e.g.* Baptist, 1941; Southwood, 1955). They comprise an accessory gland—which may be tubular or vesicular—and a principal gland divided into two or more lobes or digitations; as many as nine such divisions have been reported in *Syromastes marginatus* (L.) (Nuorteva, 1956*b*). The secretory cells of the principal gland are arranged in an epithelial layer around a large central secretion-filled cavity (Barth, 1954; Sudershan, 1964). In the Homoptera, conditions are apparently more variable, as the following notes show, but in all instances there seems to be a basic distinction between the two suborders in that the principal glands of the Homoptera are not vesicular, but are compactly cellular, enclosing relatively small intracellular channels and an intercellular duct system of much smaller cells. Even in the Peloridiidae, the glands of which are considered by Pendergrast (1962) to resemble those of the Heteroptera, their histological structure is much more like that of other Homoptera. In the Auchenorrhyncha, the principal gland is divided into a number of lobes or acini. These number only two in the Peloridiidae, three in *Typhlocyba* (Willis, 1949) and four in *Empoasca flavescens* (F.) (Nuorteva, 1954) and *E. fabae* (Harris) (Berlin & Hibbs, 1963), but rather more lobes occur in other species of Cicadelloidea (Miles, 1964; Nuorteva, 1956*a*; Saxena, 1954), and *Cicadula sexnotata* (Fallén) has 21 lobules or acini, all unicellular (Dobroscky, 1931*a*). The two Cercopids studied by Nuorteva (1956*a*) resemble the Cicadelloids, but the Cicadoidea apparently have a rather different system with two clusters of tubular lobules in each principal gland (Gadd, 1909; Bugnion & Popoff, 1908–10). Nuorteva (1956*a*), who realised the possible taxonomic interest of the various conditions, defined the fulgoromorph type of principal salivary gland as bilobed, with the posterior lobe very voluminous and extending to the caudal part of the abdomen, but the few Fulgoroids examined seem to be more variable than his definition suggests. *Fulgora maculata* has a small principal gland and a very long abdominal gland (described as an accessory gland by Bugnion & Popoff, 1908–10), whereas *Lycorma deliculata* has one enormous major principal gland and one smaller four-lobed minor principal gland on each side (Sun, 1964). *Siphanta acuta* Walk. (Flatidae), on the other hand, has a principal gland of 10 more or less ovoidal lobes resembling that of the Cicadelloids (Miles, 1964), and the Delphacids described above are evidently also very much like *Siphanta*. In many accounts of the Homoptera there is also reference to an accessory salivary gland, which is linked to the principal gland by a relatively long duct. In the Delphacidae acini I and II are so linked and might be spoken of as the accessory gland, although it is difficult to see any histological grounds for separating these acini from the remaining ones. The Sternorrhyncha also show considerable variation in salivary gland structure, the principal glands of *Macrosiphum solanifolii* Ashmead, for example, consisting of a single large lobe containing five types of cells (Fortin, 1956), whereas in the Coccoidea (Pesson, 1944) the different cell types are segregated in eight separate lobes. It seems likely that further information on the highly differentiated salivary glands of the Homoptera will help in defining the major taxonomic divisions of the group.

One of the remarkable features of the salivary glands of the Delphacidae, and of other Homoptera described in the literature, is the very large size of some of the cells. Data on the subject of cell-size in insects is not readily accessible, and Table III indicates the average size of the acinar cells and their nuclei in the six species studied. The

wide range of variation from one acinus to another is striking, but there is a general tendency for the cells of a given acinar type to vary much less from one species to another. One might imagine that nuclear and cell dimensions would tend to vary together, and an attempt was made to assess this statistically. The individual measurements are not reproduced here, but there is in fact a very highly significant correlation between cell-volume and nuclear volume ($r = +0{\cdot}83$, $P < 0{\cdot}001$) for all species and acini considered together and an almost exactly similar correlation ($r = +0{\cdot}86$, $P < 0{\cdot}001$) between cell-volume and nuclear surface area. It should, however, be noted that the volume of lobate or irregular nuclei is difficult to measure; in this work all nuclei were treated as ellipsoidal, and the volumes and surface areas calculated from measurements of the maximum and minimum diameters.

TABLE III.—*Volume of acinar cells and nuclei* ($\mu^3 \times 10^4$) *in salivary glands of Delphacidae*

Acinus	*Stenocranus*	*Conomelus*	*Ditropis*	*Criomorphus*	*Dicranotropis*	*Javesella*
I	95	69	124	59	62	40
	1·99	2·69	4·20	0·10	1·02	0·42
II	102	91	146	60	69	42
	0·61	1·92	2·51	0·10	0·69	0·59
III	8	8	14	10	9	29
	0·10	0·12	0·20	0·06	0·19	0·07
IV	41	37	37	17	21	16
	0·35	0·30	0·66	0·03	0·24	0·20
V	44	13	39	15	20	18
	0·17	0·19	0·48	0·16	0·22	0·24
VI	36	.	.	14	28	7
	0·42	.	.	0·09	0·48	0·10
VII	12	5	24	5	11	4
	0·11	0·10	0·39	0·03	0·23	0·03
VIII	37	36	28	18	34	27
	1·34	0·24	0·52	0·11	0·40	0·45
IX	25	14	19	8	13	10
	0·47	0·20	0·20	0·05	0·24	0·13
X	.	4	.	.	.	.
	.	0·06	.	.	.	.
XI	.	.	27	.	.	.
	.	.	0·19	.	.	.

The binucleate condition of the acinar cells is an interesting feature, the significance of which is not known, especially as published accounts of the salivary glands of other Hemiptera do not agree on this subject. There is, for example, no mention of binucleate cells in the histological descriptions of *Empoasca fabae* (Berlin & Hibbs, 1963) and *Macrosiphum solanifolii* (Fortin, 1956), and the salivary gland cells are also apparently mononucleate in *Drosicha stebbingi* (Gr.) (Latif & Alam, 1960), *Dysdercus koenigii* (F.) (Sudershan, 1964), *Hemidoecus veitchii* Hacker and *Xenophyes cascus* Bergroth (Pendergrast, 1962) and *Lycorma deliculata* (Sun, 1964). On the other hand, all secretory cells of the salivary glands are binucleate in *Cicadula sexnotata* and *Euscelis striatulus* (Fallén) (Dobroscky, 1931*a*, 1931*b*) as well as in *Triatoma infestans* (Klug) (Barth, 1954) and in the principal salivary glands of *Typhlocyba ulmi* (L.) (Willis, 1949). It is perhaps interesting that Kershaw (1913) found in *Flata* and some

other Fulgoroids that the young cells of the mid-gut epithelium have a single nucleus, whereas older cells are mostly binucleate, and that Yanai (1952) found the binucleate condition in 10–100 per cent. of the mid-gut epithelial cells of several species of gymnocerate Heteroptera, although they were absent from other species and absent or rare in the Cryptocerata examined. The fat-body cells of *Rhodnius* may also become binucleate after starvation and as a preliminary to nuclear fusion (Wigglesworth, 1967). It seems unlikely, however, that the binucleate cells of the salivary glands of Delphacidae are due to senescence or starvation, as they occur consistently in young specimens collected on their natural hosts. And in *Cicadula sexnotata* Dobroscky (1931*a*) noted no differences in salivary gland structure between fed and starved insects. More probably the presence of two nuclei per cell is a widespread natural condition in the salivary glands of the Hemiptera, perhaps associated with the very large size of the cells; it should be sought again more carefully in those species in which it has not previously been noted.

In *Typhlocyba ulmi*, Willis (1949) was unable to find any great differences in histological structure between the three lobes of the principal glands, but other Homoptera seem to show clear histological differentiation. Even in *Hemidoecus* and *Xenophyes*, in which the principal gland is very simple in structure, its two lobes differ in staining reactions and in the appearance of the cytoplasmic inclusions (Pendergrast, 1962). In *Empoasca fabae* each of the four lobules of the principal gland is histologically distinct and has its characteristic staining reaction with toluidine blue (Berlin & Hibbs, 1963), and in *Euscelis striatulus* and *Cicadula sexnotata* the five types of acini differ in the degree of vacuolation of cytoplasm, the appearance of secretory globules and in staining reactions (Dobroscky, 1931*a*, 1931*b*). In Aphidoidea and Coccoidea, too, there are several histologically distinct types of cells (Fortin, 1956; Pesson, 1944) and in *Myzus persicae* (Sulz) many ultrastructural differences between the principal and accessory glands have been noted (Moericke & Wohlfarth-Botterman, 1960*a*; Wohlfarth-Botterman & Moericke, 1960). The differences described above in the acini of the Delphacidae are therefore part of a general histological diversity found in the salivary glands of the Homoptera (and, for that matter, of the Heteroptera, although the observations on the latter are not discussed here). It is less clear how far the described variations are permanent and represent functionally distinct cell types or how far they might be due to fluctuations in secretory activity. The fact that the same acini can be recognised in Delphacids collected at different times in the season suggests that they are distinct cell types, and in *Stenocranus* the constancy over almost the whole year (including the overwintering period) is very striking. Dobroscky (1931*a*) showed, however, that although the four types of "mucous cells" were unaffected by starvation in *Cicadula sexnotata*, the "serous cells" altered under these conditions. And, of course, very marked histological alterations have been noted during the secretory cycle of the zymogenic cells of the salivary glands of other insects, notably *Periplaneta* (Day, 1951). Further observations on this subject are clearly needed.

The histochemistry of salivary secretion in insects and its relation to the histological and cytological characteristics of the gland cells is much less well understood than in the vertebrates (*cf.* Jakowska, 1963), and only in recent years has evidence become available to show that different materials are produced in different regions of the gland. The most detailed work on this subject in the Hemiptera has been done on *Oncopeltus fasciatus* (Dallas): Miles (1967, and earlier papers) has shown that the anterior lobe contributes a sulphydryl-rich protein sheath precursor, gelling by the formation of disulphide linkages, the lateral lobe contributes a different protein sheath precursor that gels by hydrogen bonding, the posterior lobe secretes most of the enzymes of the saliva (invertase, amylase, protease and an esterase) and the accessory lobe secretes a polyphenolase (*see also* Bronskill *et al.*, 1958; Salkeld, 1960). How far a comparable division of labour exists in the Homoptera remains to be seen, but there is appreciable

evidence of some functional differentiation within the gland there. Phenolase activity is restricted to one of the 10 lobes of the principal gland in *Siphanta acuta* (Miles, 1964), four different salivary components have been identified by electron microscopy in *Myzus persicae* and their origins traced in each of four different cell types (Moericke, 1961) and in other aphid species a phenolase is produced in certain cells only and sulphydryl-rich material is concentrated in other sites (Miles, 1965). In *Lycorma deliculata*, cytoplasmic RNA is very abundant in the mucous cells but scantily distributed in the zymogenic cells, where mucopolysaccharides, mucoproteins and lipoprotein materials have been identified (Sun, 1964). The diverse staining reactions of the glands in Delphacids indicate that comparable functional differentiation occurs there. Although no specific histochemical tests have been made, some of the staining reactions are suggestive in the light of the findings reviewed above. The heavily basiphil character of acini VII, VIII, IX and X, for example, might be associated with a high content of RNA and more intense protein synthesis. Again, the positive reaction to Alcian Blue and to paraldehyde-fuchsin after permanganate oxidation suggests the presence of sulphydryl groups (Pearse, 1960; Sloper, 1957), although it is worth mentioning that Hinks (1968) has found an association between PF-positive granules and glycoproteins in the neurosecretory cells of various Lepidoptera.

Finally it remains to point out that some Delphacidae—including *Javesella pellucida*—are vectors of plant virus diseases (Slykhuis & Watson, 1958; Watson & Sinha, 1959), and it seems reasonable to suppose that transmission occurs via the salivary glands. Sukhov (1940) even went so far as to claim that the fuchsinophil X-bodies which he found "in huge masses" in Mallory-stained sections of the salivary glands of *Delphax striatella* Fallén (a vector of "zakuklivanie") represented the virus protein. This seems improbable, and certainly nothing like the X-bodies has been noted in any of the Delphacids studied here. What appear to be plant-pathogenic viruses have been detected in the insect vector *Nephotettix cincticeps* (Uhl.) by electron microscopy, but only in the haemocytes, gut and Malpighian tubules (Fukushi *et al.*, 1960). Serjeant (1967), who was unable to find virus particles in electron micrographs of the salivary glands of infective *Javesella pellucida*, did however show that extracts of the thorax were infective on injection into virus-free insects, a fact consistent with the presence of the virus in the salivary glands.

VI. Summary

The histology of the salivary glands has been studied in six species of Delphacidae, all of which have nine acini in each gland. In almost all instances the same acinar types are recognisable in all species. Acini I and II differ from the others in being unicellular and have longer ducts; they may be regarded as the accessory salivary gland. The staining reactions and histological characteristics suggest well-defined functional differences between the acini, possibly related to differences in the content of RNA, sulphydryl-rich materials or glycoproteins.

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