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MORPHOLOGY AND ULTRASTRUCTURE OF INTEGUMENTARY GLANDS OF *SEMIADALIA UNDECIMNOTATA* SCHN. (COLEOPTERA : COCCINELLIDAE)

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Abstract—The ultrastructure of integumentary glands of the adult ladybird, *Semiadalia undecimnotata* (Coleoptera : Coccinellidae) is described. Two types of glands can be found distributed over the head, thorax, and abdomen: glands without ducts and glands with secretory ducts. Glands without ducts consist of a single cell and a secretory apparatus located within the thickness of the cuticle and equipped with a cuticular cribriform plate; this cribriform plate separates 2 superimposed cavities, and epicuticular filaments fill the lower cavity. Glands without ducts are thought to release volatile pheromones. Glands with a duct appear to be made of 2 kinds of cells: one cell forms the receiving duct and later synthesizes the secretory products, one (or more) cell makes the evacuating duct. Their secretions are abundant and released on the surface of the cuticle in the shape of tortuous cylinders, which are resistant to acetone treatment. Glands without ducts and glands with secretory ducts correspond, respectively, to classes 1 and 3 gland cells according to the nomenclature of Noirot and Quennedey (1974, *Annu. Rev. Entomol.* **19:** 61–80).

Index descriptors (in addition to those in title): Sex pheromone, aphidophagous.

INTRODUCTION

THE USE of ladybirds in the biological control of insect pests in agriculture, has led to extensive research into their biology. Work on aphidophagous species of ladybirds has been done mainly on the search strategy and capture of prey (Ferran and Larroque, 1984; Nakamuta, 1985; Honek, 1985a, b), the migration and aggregation of adults at diapause sites (summer until the end of winter) (Iperti and Hodek, 1976; Brun, 1980; Iperti *et al.*, 1983; Iperti, 1986) and on their reproduction (Obata, 1987). However, chemical messages, which are involved in these behaviours, have remained totally unknown, either between species involved (predator–prey relationships) or at the intraspecific level (migration and aggregation on sites of diapause) or between sexes (reproductive behaviour). Little research has so far been done on sensory receptors and glands in Coccinellidae, which receive or release chemical signals.

Chemoreceptors of maxillary palps in *Semiadalia undecimnotata* were studied first because they were thought to be primarily involved in predator–prey relationships

(Barbier *et al.*, 1989). The sensory system of antennae was studied next, and showed a sexual dimorphism characterized by the presence of specific chemoreceptors on the male antenna (unpublished results). This paper reports on the distribution and ultrastructure of integumentary glands in male and female *S. undecimnotata*.

MATERIALS AND METHODS

S. undecimnotata was reared under standardized conditions, which do not induce a diapause of adults, 27°C, and 60–70% R. H. with a photoperiod of 16 hr light. Newly emerged ladybirds were fed on a population of aphids (consisting mainly of apterous parthenogenetic females). The aphid *Acyrtosiphon pisum* was reared on young shoots of *Pisum sativum* (pea) 2–3 cm high. Rearing was done in a temperature-controlled cage at 12°C with a photoperiod of 12 hr light. Under these conditions, the aphid population reproduced by thelygenic parthogenesis only.

Scanning electron microscopy

The head capsule, thorax, abdomen, elytra and tarsi of the ladybird, were dehydrated first in ethanol and then in acetone. They were either air or critical-point dried, gold coated, and examined with a JEOL J.S.M. 35C scanning electron microscope (SEM).

Transmission electron microscopy

Samples were fixed in 2.5% glutaraldehyde, followed by treatment in 2% osmium tetroxide in 0.2 M sodium phosphate buffer, pH 7.4. They were then embedded in Epon. Ultrathin sections were contrasted with uranyl acetate and lead citrate. A JEOL CX 100 microscope was used.

RESULTS

Numerous gland openings are seen under SEM over the entire body and appendages of adult males and females of *S. undecimnotata*. Two types of gland openings can be distinguished by their different diameters, which correspond to 2 distinct types of glands. Generally, both types of glands are found grouped together, but there are small areas where only one type of gland is present or predominant.

I. *Structure of the 2 Types of Glands*

A. *Glands without ducts*

Glands without ducts communicate with pores with a large diameter (1.5–2 μm). Each gland consists of a single cell localized within the epidermis. The cell was found to go through at least 2 successive stages: a morphogenetic stage during which the cuticle of the secretory apparatus is synthesized, followed by a secretory stage during which secretion products are produced.

1. *Morphology of the secretory apparatus*. The secretory apparatus is laid within the entire thickness of the cuticle located above the gland. Below the external opening visible on the surface of the cuticle, the secretory apparatus consists of 2 superimposed cavities originating from a complete modification of the cuticular structure. *The upper cavity*, cylindrical in shape, results from a depression in the superficial cuticle so that the base of the cavity corresponds to the epicuticle. The epicuticle has become thicker, deeply scarred and modified into a cuticular cribriform plate featuring about 40 pores, each with a diameter approximately 0.1 μm (Figs 1, 2E, F, G, 3A, D). The depth of the upper cavity reaches 3 μm for glands of maxillary palps, but it can be smaller for glands

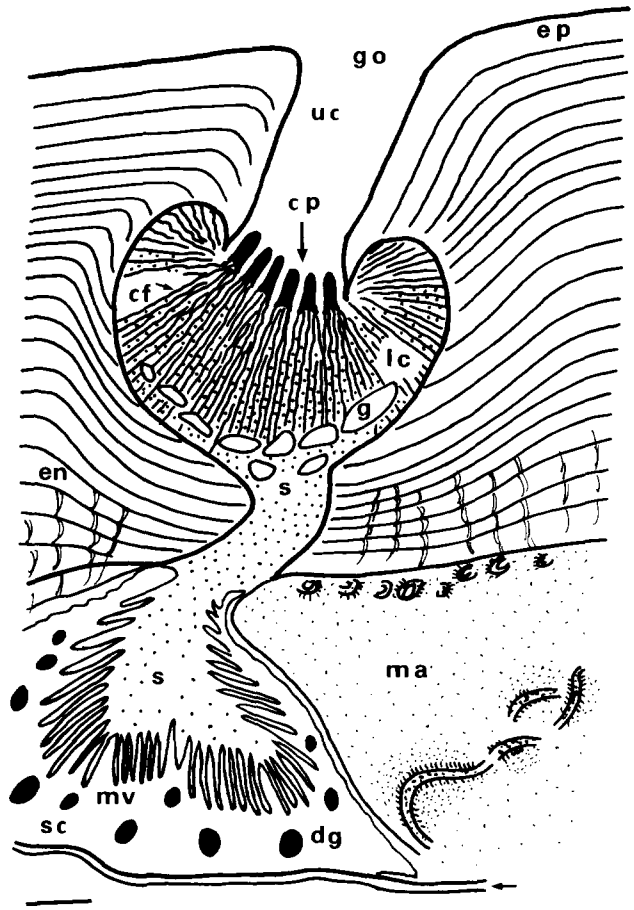

FIG. 1. Diagram of an integumentary gland without duct in *S. undecimnotata*, female, maxillary palp. cf = cuticular filaments; cp = cuticular cribriform plate; dg = dense secretory granule; en = endocuticule; ep = epicuticule; g = gaps; go = gland opening; lc = lower cavity of cuticular secretory apparatus; ma = muscle attachment; mv = microvilli lining apical cavity of glandular cell; s = secretory products; sc = secretory cell; uc = upper cavity of cuticular secretory apparatus. Scale bar = 1 μm.

of the elytra. *The lower cavity* is located under the cuticular cribriform plate. It is nearly spherical in shape and larger than the upper cavity, its diameter reaching 4–5 μm (Figs 1, 2G, 3A, D, E). It results from a modification of the endocuticle, located above the glandular cell, which consists of numerous cuticular filaments. These are packed very closely but remain separate; their structure is tubular having a diameter of about 0.02 μm. They fill the lower cavity almost completely, except at the base where a layer of electron-clear gaps can be seen (Figs 1, 2G, 3A, E). All cuticular filaments end within the epicuticle and this makes up the pores of the cribriform plate (Fig. 3D, E). The glandular cell gives rise to the structure and orientation of cuticular filaments during cuticulogenesis. During the same period, neighbouring epidermal cells have made the

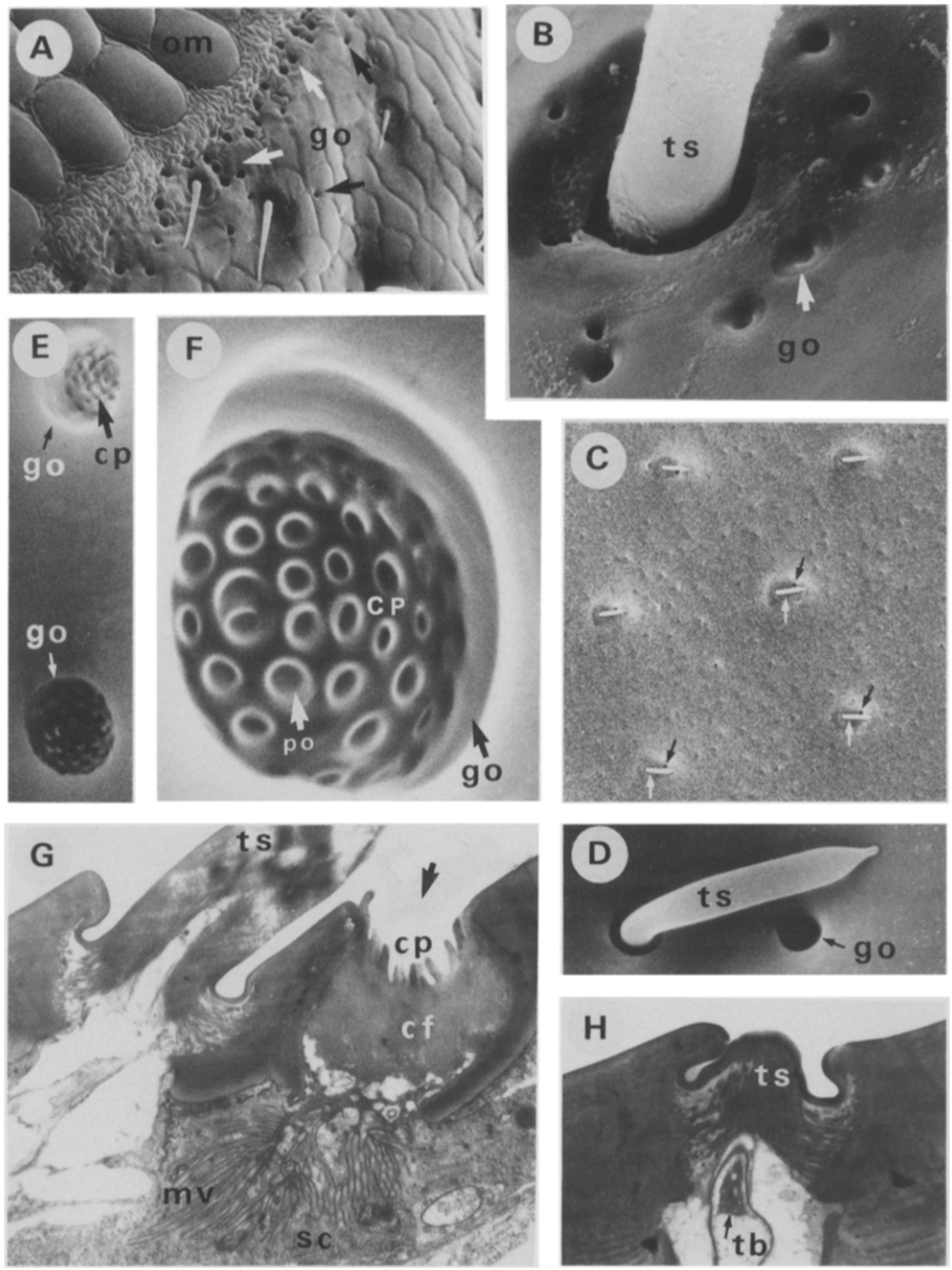

FIG. 2. Integumentary glands without ducts in *S. undecimnotata*, female. (A) cephalic capsule: gland openings (go) are located near ommatidia (om), (SEM) × 500. (B) External face of labrum: numerous gland openings (go) are distributed around a trichoid sensillum (ts), (SEM) × 4000. (C) External face of elytron has a regular pattern of gland openings (black arrows), each with a curved trichoid sensillum (white arrows), (SEM) × 400. (D) Detail of gland opening (go) associated

true endocuticle with its fibrous, helicoidal structure, which limits the cavity. Finally, the opening of the lower cavity, through which secretions are to flow, is the result of a lack in cuticle formation due to involution of the apical membrane of the glandular cell.

2. *Secretory stage of the glandular cell.* The secretory stage follows the morphogenesis of the secretory apparatus. The cell modifies by creating an extracellular apical cavity, which fits the opening of the lower cavity of each secretory apparatus (Figs 1, 2G, 3A, B). The apical cavity of each secretory cell lies next to a muscle attachment, which crosses the epidermis and inserts into the cuticle (Fig. 3A). Within the cell cytoplasm, the secretion is seen as electron-dense granules with well-defined outlines (Fig. 3C), but in the apical cavity of the cell, it has a very fine granular structure (Fig. 3B, C). When the secretion penetrates the lower cavity of the secretory apparatus, it has the appearance of fine granules, which are initially clustered together between electron-clear gaps (Figs 1, 3A). Granules then travel upwards between cuticular filaments and continue through the cribriform plate (Fig. 3A). However, we have never detected the secretion in the upper cavity, i.e. above the cribriform plate, nor at the surface of the cuticle above the gland opening.

B. *Glands with secretory ducts*

Glands with secretory ducts communicate with openings of small diameter (0.5 μm) observed on the cuticle. Unlike glands without ducts, they consist of at least 2 cells: the glandular cell, which forms the short receiving duct and synthesizes secretory products, and at least one cell of the evacuating duct, which is involved in its cuticulogenesis (Figs 4, 5A, B).

The receiving duct is included within the extracellular cavity surrounded by the microvilli of the glandular cell. It has a wall made of porous, granular mass which lacks an external epicuticle (Figs 4, 5D). Initially, the secretion has the aspect of electron-dense granules when it is present in the cytoplasm of the glandular cell (Fig. 5E). It then acquires a homogeneous structure with very fine granules, as soon as it goes through the extracellular cavity, and then it crosses the wall of the receiving duct where it accumulates prior to secretion.

The evacuating duct is rectilinear with a constant diameter equal to that of the opening (0.5 μm). It connects the receiving duct to the surface of the cuticle (Figs 4, 5A, B). The wall of the evacuating duct is made of an external epicuticle (cuticulin) and an internal epicuticle (dense protein layer). During morphogenesis of the duct, numerous filaments extend the wall of the duct to the microvilli of the duct cell (Figs 4, 5B). When evacuating ducts reach the integumentary cuticle, they cross it very obliquely and their outlet is always turned towards the end of the abdomen. Thus, during extrusion, the secretion comes out at a tangent on the surface of the cuticle and the tortuous cylinders produced

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with its curved trichoid sensillum (ts), (SEM) × 4500. (E) Two gland openings (go) and a cuticular cribriform plate (cp), (SEM) × 8000. (F) High magnification of a gland opening (go) showing numerous pores (po) of cuticular cribriform plate (cp), (SEM) × 30,000. (G) Section passing through a gland opening (arrow), cribriform plate (cp), cuticular filaments (cf), microvilli (mv) of secretory cell (sc) and through basal part of curved trichoid sensillum (ts), (TEM) × 8000. (H) Section passing through basal part of curved trichoid sensillum (ts) showing tubular body (tb) of mechanoreceptor nerve ending, (TEM) × 7000.

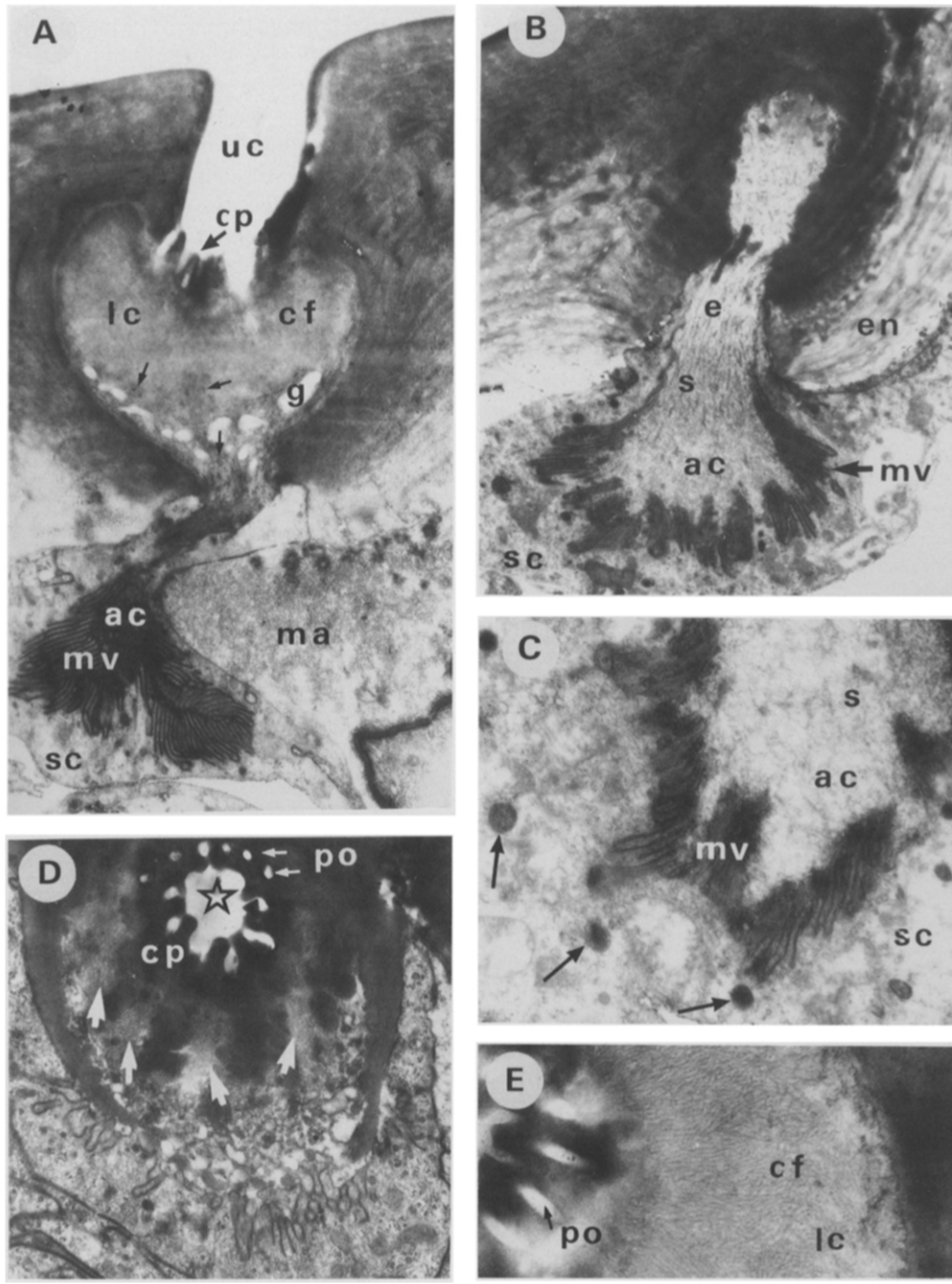

FIG. 3. Integumentary glands without duct (TEM) in *S. undecimnotata*, female, maxillary palp. (A) Apical cavity (ac) of secretory cell (sc) is lined with microvilli (mv) and located near a muscle attachment (ma). Upper cavity (uc) of secretory apparatus is separated from lower cavity (lc) by cuticular cribriform plate (cp). Fine secretory granules (black arrows) move up between cuticular filaments which fill lower cavity almost entirely. Electron-clear gaps (g) are present in lower cavity,

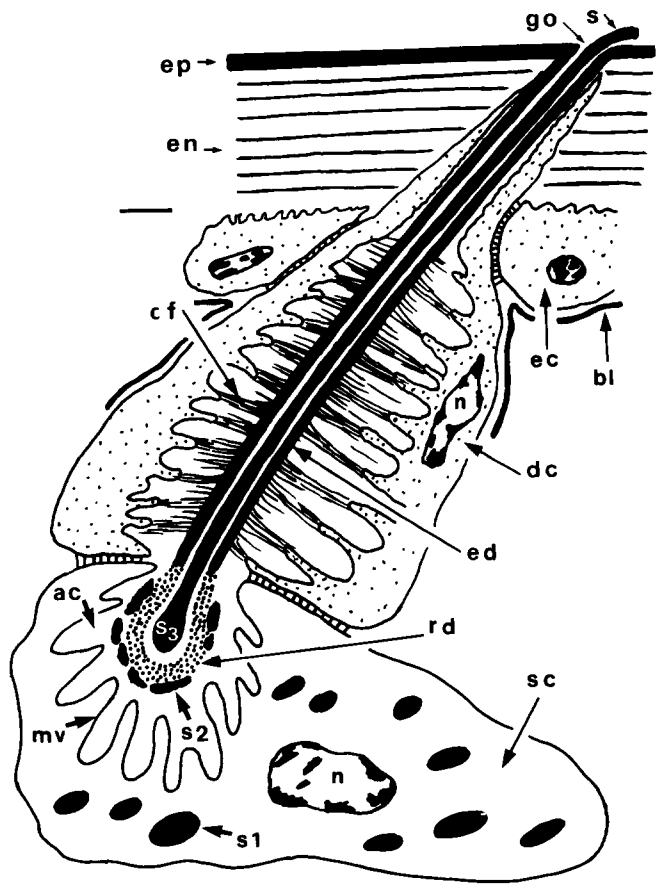

FIG. 4. Diagram of an integumentary gland with a duct in *S. undecimnotata*, female, labium. ac = apical cavity; cf = cuticular filaments; dc = duct cell; ec = epidermal cell; ed = evacuating duct; en = endocuticle; ep = epicuticle; go = gland opening; mv = microvilli; n = nucleus; rd = receiving duct; s = secretion; sc = secretory cell; S1 = secretion located in secretory cell; S2 = secretion located in apical cavity of secretory cell; S3 = secretion located in receiving duct. Scale bar = 1 μm.

are pushed towards the end of the insect. Each cylinder of secretion then tends to break up but keeps sticking to the cuticle. Secretion products are not solvable in either ethanol or acetone and are resistant to ultrasonic cleaning.

(TEM) × 10,000. (B) Apical cavity (ac) of secretory cell (sc) is limited by microvilli (mv) and is connected to lower cavity (lc) of secretory apparatus allowing secretions (s) to pass through endocuticle (en), (TEM) × 6600. (C) Secretions are seen as dense granules (black arrows) just below microvilli (mv) and as fine granules (s) within apical cavity (ac) above microvilli, (TEM) × 13,200. (D) Tangential section of cribriform plate showing cuticular filaments (white large arrows) and cuticle of cribriform plate (cp) and pores (po). White area (star) corresponds to middle of cribriform plate excluded from plane of section, (TEM) × 13,000. (E) Cuticular filaments (cf) in lower cavity (lc) of secretory apparatus finish in cuticular walls of pores (po) of cribriform plate, (TEM) × 23,000.

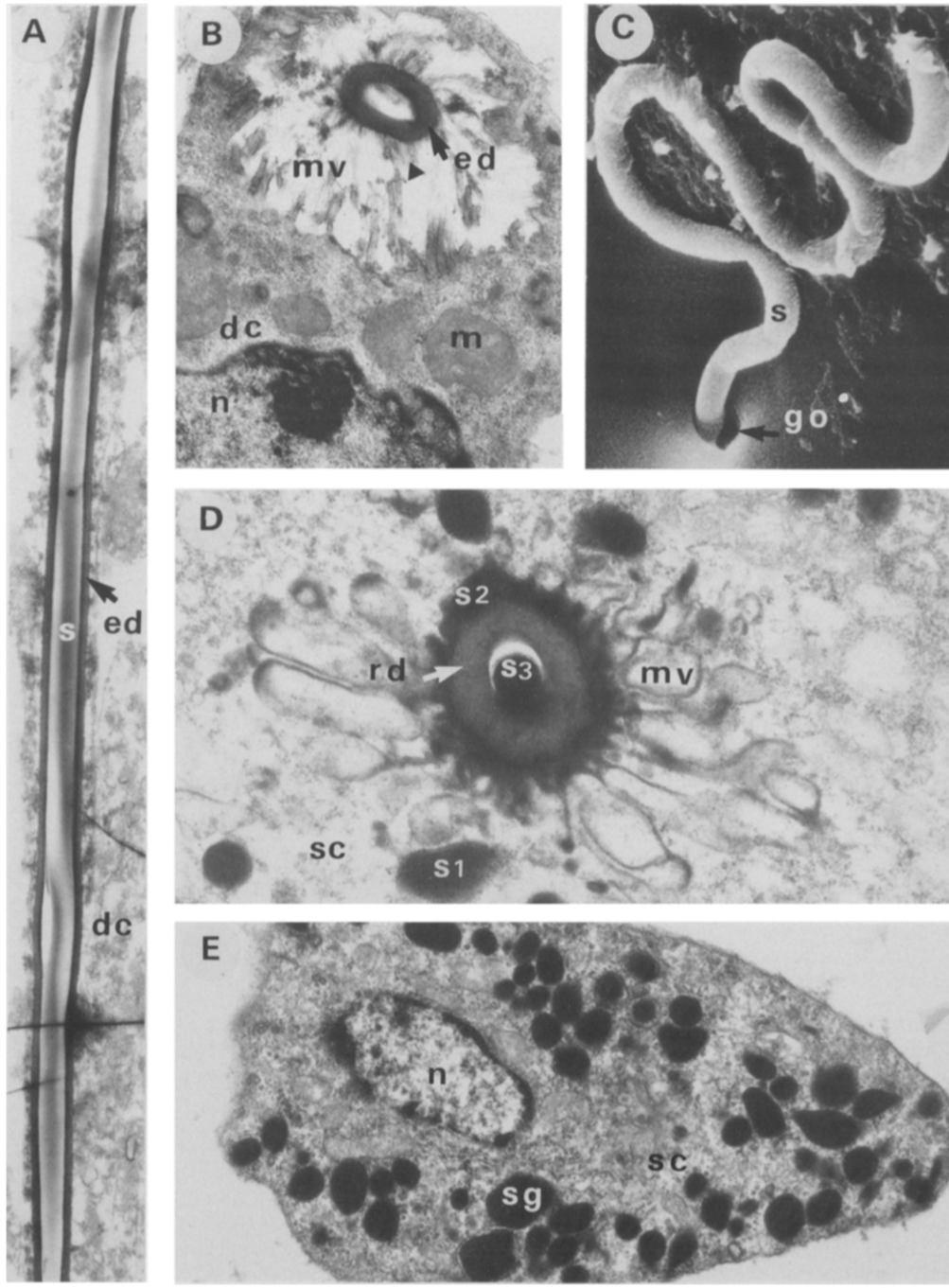

FIG. 5. Integumentary glands with secretory ducts in *S. undecimnotata*, female, labium. (A) Longitudinal section. Within duct cell (dc), epicuticular evacuating duct (ed) contains secretions (s), (TEM) × 9000. (B) Cross-section of duct cell (dc) during end of cuticulogenesis showing nucleus (n), mitochondria (m), and microvilli (mv) surrounding epicuticular evacuating duct (ed) and cuticular filaments (black arrowhead), (TEM) × 13,200. (C) Secretion (s) on external face of cuticle. A tortuous cylinder escapes through a gland opening (go), (SEM) × 10,000. (D) Section through distended microvilli (mv) of apical cavity of a secretory cell (sc) and through receiving duct (rd). Secretion is present within secretory cell (S1), apical cavity (S2) and receiving duct (S3), (TEM) ×20,700. (E) Secretory cell (sc) showing nucleus (n) and numerous secretion granules (sg), (TEM) × 13,200.

II. *Distribution and Localization of Glands*

A. *General distribution*

The 2 types of integumentary glands are found on the head capsule as well as on the antennae and mouthparts of adult males and females. They are also present on the thoracic and abdominal segments and on the legs, but they appear to be more numerous on the tergites and sternites of the last 2 segments. With the exception of a few specific localizations, the openings of the 2 types of glands are distributed in a random fashion, and there is no apparent difference between the 2 sexes.

B. *Specific localizations*

We have observed a few areas where only one type of gland is found or is predominant. Several glands without ducts cluster in groups under the lateral parts of the vertex precisely on the internal edge of the compound eyes (about 20,000/mm^2) (Fig. 2A). On the upper side of the labrum, several openings of glands without ducts are arranged in a circle around some of the trichoid sensilla (Fig. 2B).

The cuticle of the labium shows numerous openings of glands with secretory ducts (about 4000/mm^2). The distal surface of the last segment of maxillary palps has, in between gustative chemoreceptors, numerous openings of glands with secretory ducts whilst the lateral sides of this segment shows glands without ducts. On the legs, the glands without ducts are also very numerous (about 10,000/mm^2 on the tarsus). Some areas of the elytra have glands without ducts regularly spaced (about 500/mm^2), and each gland is coupled to a curved sensillum, which is always turned towards the end of the insect. The external element of the sensillum covers the gland opening or is located next to it (Fig. 2C, D, G). Sections reveal the presence of a tubular body indicating that the sensillum has at least one mechanoreceptor neuron (Fig. 2H).

DISCUSSION AND CONCLUSION

The aphidophagous ladybird, *S. undecimnotata* has 2 types of integumentary glands: one type without a duct, the other with a secretory duct. Their localizations on the cuticle have been determined by measuring the diameter of gland openings, glands without ducts having the largest diameter. These glands are distributed over the entire body of the ladybird and on all its appendages in males and females.

The structure of the glands without ducts in *S. undecimnotata*, suggests that they correspond to class 1 gland type according to the nomenclature of Noirot and Quennedey (1974). The secretory apparatus is differentiated within the thickness of the cuticle located just above the glandular cell. It has a cuticular cribriform plate similar to those found in several Coleoptera including the coccidophagous ladybird *Rhyzobius boucardi* and the tenebrionids, *Palorus subdepressus* and *Tenebrio molitor* (Faustini and Halstead, 1982). However, in *S. undecimnotata*, the cribriform plate is located at the base of a cuticular pit or upper cavity, whereas in *R. boucardi* and in the 2 tenebrionid beetles, it is located in the centre of a slight depression in the cuticle. This pattern is also found in the ladybird, *Chilocorus schioltei*, which is a coccidophagous species (personal observation). The secretory apparatus of glands of *S. undecimnotata* has, in addition, a lower cavity located between the cribriform plate and the apex of the gland, and its originality lies in the presence of a high density of cuticular filaments. Tubular structure and diameter of

these filaments are indicative of epicuticular filaments. According to the diagrams published by Faustini and Halstead, glands of tenebrionides, *P. subdepressus* and *T. molitor* do not have a lower cavity or cuticular filaments. The gland without a duct in *S. undecimnotata*, consists of a single secretory cell, which does not penetrate through the lower cavity, whereas the gland of the 2 tenebrionides is made of several cells extending to the cuticular cribriform plate. Aphidophagous ladybirds used in our experiments were newly emerged adults. This might explain the absence of secretion in the upper cavity and the lack of exudate above the gland opening, on the cuticle. However, we cannot exclude the possibility that the acetone treatment of samples has not removed the exudates in some glands especially if they contain lipidic substances like those in gland exudates of the flour beetle, *Tribolium castaneum* (Faustini, 1981).

Glands without ducts can be divided into at least 3 groups. On the peri-ocular cuticle of the vertex, they are very close to each other and separated by neighbouring sensilla. Over some areas of the elytra, they are regularly spaced and each one is associated with a sensillum equipped with at least one mechanoreceptor neuron. This distribution is similar to that of glands of abdominal sternites in the adult mealworm, *Tenebrio molitor* L. (Faustini and Halstead, 1982). Lastly, glands are commonly distributed among the numerous sensilla of the cuticle. The structure and presence of glands without ducts in both males and females of *S. undecimnotata*, suggests that they could play a role in mutual attraction of both sexes as in some Coleoptera, such as the hide beetle, *Dermestes maculatus* (Levinson *et al.*, 1978; Levinson *et al.*, 1980; Francke *et al.*, 1979) and *T. castaneum* (Faustini *et al.*, 1981, 1982). A study of how the quantity of secretory granules changes with time from emergence to sexual maturity of adults, should help confirm this hypothesis. There is already some evidence for the presence of specific chemoreceptors on the male antenna (unpublished results). Their response to extracts from various gland areas of the females in electrophysiological tests should reveal whether sex pheromones or aphrodisiacs are being released. Finally, the production of an aggregation pheromone cannot be excluded; it could have a role at a later stage, during and/or just after migration, and would assist in the regrouping of individuals on sites of diapause. Another possibility is that defensive pheromones are also involved.

Glands with ducts of *S. undecimnotata* correspond to class 3 gland type in the nomenclature of Noirot and Quennedey (1974). Their morphogenesis and renewal of the secretory apparatus during moulting are known (Barbier, 1974, 1975, 1982; Berry and Johnson, 1975; Sreng and Quennedey, 1976; Cassier, 1977; Quennedey, 1991). Their structure has been described more frequently than glands without ducts and they have been reported in all insect groups from Apterygota (Bitsch, 1989) to Hymenoptera (Billen, 1987) and Coleoptera (Plutot-Sigwalt, 1988; Biémont *et al.*, 1990). Nevertheless, this is the first description of such glands in Coccinellidae. The secretory apparatus of glands in this ladybird consists of the 2 usual fundamental elements: first, within the extracellular cavity of the secretory cell, the short receiving duct or end apparatus is composed of a wall lacking an external epicuticule, which will allow secretory products go through at a later stage; second, enclosed by the duct cell, the long evacuating duct, having epicuticular walls, joins the gland to the opening on the insect cuticle. Its rectilinear shape is in contrast to the one described in other insects such as in the cockroach, *Leucophaea maderae* (Porcheron, 1975). Filaments that cover the external surface of the evacuating duct distinguish it from the receiving duct. These filaments characterize the end of its cuticulogenesis. They do not correspond to cuticular filaments

of hemipteran, *Harpobittacus australis* (Crossley and Waterhouse, 1969) and of the Coleoptera, *Acanthoscelides obtectus* (Biémont *et al.*, 1990) where they are found only around the receiving duct. The very wide distribution of glands with secretory ducts and particularly the copious production of secretions on the surface of the cuticle of *S. undecimnotata*, could contribute to the strong smell of this insect. Biochemical analyses and behavioural studies will establish with certainty the role(s) of this 2nd type of gland.

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