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The fine structure of sternal pheromone glands in the two caddisfly species from the Rhyacophilidae and Limnephilidae families (Insecta: Trichoptera)

Тонкое строение стернальных феромонных желёз двух видов ручейников из семейств Rhyacophilidae и Limnephilidae (Insecta: Trichoptera)

Stanislav I. Melnitsky[1] & Roman V. Deev[2]
С. И. Мельницкий[1], Р.В. Деев[2]

[1] Department of Entomology, St. Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg 199034, Russia. E-mail: simelnitsky@hotbox.ru.

[2] Department of Histology, S.M. Kirov Military Medical Academy, Akademika Lebedeva St., 6. St. Petersburg 194175, Russia.

[1] Кафедра энтомологии, Санкт-Петербургский государственный университет, Университетская наб. 7/9, С-Петербург 199034, Россия.

[2] Кафедра гистологии, Военно-медицинская академия им. С.М.Кирова, ул. Академика Лебедева 6, С-Петербург 194175, Россия.

KEY WORDS: Trichoptera, caddisflies, sternal pheromone glands, fine structure, *Rhyacophila obliterata*, *Chaetopteryx villosa*, chemical communication, secretory cells, canal cells, end apparatus, ultrastructure.

КЛЮЧЕВЫЕ СЛОВА: Trichoptera, ручейники, стернальные феромонные железы, тонкое строение, *Rhyacophila obliterata*, *Chaetopteryx villosa*, химическая коммуникация, секреторные клетки, канальцевые клетки, концевой аппарат, ультраструктура.

ABSTRACT. To study the ultrastructure of cells forming sternite pheromone glands of the 5th abdominal segment of caddisflies *Rhyacophila obliterata* (Rhyacophilidae) and *Chaetopteryx villosa* (Limnephilidae) transmission electron microscopy was used. The glands have been shown to be formed by cells of three types: secretory, canal and hypodermal cells. A combination of secretory and canal cells form a unit where secretory cells produce their secret, canal cells form receiving and conducting cuticular canals which take part in releasing the secret into a cavity of the gland cuticular reservoir.

РЕЗЮМЕ. С помощью трансмиссионной электронной микроскопии исследована ультраструктура клеток, входящих в состав стернальных феромонных желёз V сегмента брюшка ручейников *Rhyacophila obliterata* (Rhyacophilidae) и *Chaetopteryx villosa* (Limnephilidae). Показано, что железы образованы клетками трёх типов: секреторными, канальцевыми и гиподермальными. Совокупность секреторных и канальцевых клеток образует единый комплекс, в котором секреторные клетки продуцируют секрет, а канальцевые — формируют собирательный и выводящий кутикулярные канальцы, участвующие в выведении секрета в полость кутикулярного резервуара железы.

Introduction

Caddisflies (Trichoptera) comprise a relatively small (about 13000 species) insect order with a distinct cycle of development, related to the Lepidoptera order. Together the two orders comprise the superorder Amphiesmenoptera, which in turn belongs to Mecopteroidea orders. The modern representatives of Trichoptera order are subdivided into two suborders: Hydropsychina and Phryganeina.

Sex pheromones of caddisflies and primitive Lepidoptera are produced by special organs — sternal pheromone glands. Sternal glands whose ducts are open on an anterior part of the 5th abdominal segment were described in the first half of the last century in archaic Amphiesmenoptera for the first time [Philpott, 1925; Eltringham, 1931]. Some investigators considered these glands to have a defense function [Philpott, 1925; Duffield et al., 1977; Ansteeg & Dettner, 1991]. However, behavior and physiological studies of the last decades have showed these glands to synthesize and excrete sex pheromones [Resh & Wood, 1985; Solem, 1985; Löfstedt et al., 1994; Bjostad et al., 1996; Ivanov et al., 2000, 2008; Syrnikov et al., 2005]. At present the morphology of pheromone glands and associated cuticular structures of the 5th sternites of the abdomen in representatives of 48 families of fossil and recent caddisflies have been

studied in detail, with four morphological types of sternal glands being identified [Ivanov & Melnitsky, 1999; Melnitsky, 2004]. While sternal glands are located on the 5th segment in representatives of 27 recent families of all 9 superfamilies of the Trichoptera and in 5 primitive families of the Lepidoptera [Ivanov & Melnitsky, 1999, 2002; Melnitsky, 2004], terminal pheromone glands are on the end of the abdomen in higher lepidopterans [Löfstedt & Kozlov, 1996].

The histological structure of pheromone glands have been described in more than 20 caddisfly species from 12 families [Melnitsky, 2001, 2007; Ivanov & Melnitsky 2002]. It has been revealed that cells of four types may constitute pheromone glands in different representatives of the caddisfly order; they are hypodermal, secretory, canal and muscle cells [Melnitsky, 2007]. However, the cellular ultrastructure of pheromone glands and cytophysiological aspects of pheromone glands functioning in the Trichoptera order have not been studied yet.

Secretory cells of insect epidermal pheromone glands developed from hypodermal cells during ontogenesis. Differentiated secretory cells are various in size and shape, with their structure being similar in many cases [Noirot & Quenneedey, 1974, 1991]. Two main types of insect secretory cells are described [Noirot & Quenneedey, 1974]. Secretory cells of the first type are directly connected with a cuticular part of the gland by microvilli located on the apical or lateral surface of a cell, through which the secret is being excreted out or into a reservoir. The second type cells excrete their secret through receiving and conducting canals, formed by special canal cells. According to the existing classification of insect epidermal glands the glands excreting their secret through special cuticular canals of canal cells are referred to a N3 type, while the glands excreting synthesized substances directly are of a C1 type [Noirot & Quenedey, 1991]. To name a complex system consisting of secretory cells of several types and excreting a secret of cuticular canals a special term — *end apparatus* — was proposed [Mercer & Brunet, 1959]. Later this term was used to define a combination of cuticular receiving canals and microvilli of secretory cells [Noirot & Quenedey, 1991].

At present the ultrastructure of pheromone glands of the Amphiesmenoptera has been studied in some representatives of higher lepidopterans, having terminal glands. However, fine structure of sternal pheromone glands of caddisflies and primitive lepidopterans has not been described yet. Therefore, this investigation was aimed to carry out a comparative morphological study of ultrastructure of pheromone glands in representatives of different caddisfly suborders, as well as to propose a scheme of phylogenesis of Amphiesmenoptera using the data received.

Material and methods

Male and female sternal pheromone glands of two species — *Rhyacophila obliterata* McLachlan, 1863 of the Rhyacophilidae family (suborder Hydropsychina) and *Chaetopteryx villosa* (Fabricius, 1798) of the Limnephilidae family (suborder Phryganeina) were studied. Rhyacophilidae and Limnephilidae belong to different evolution branches of the caddisfly order. They differ in a precopulation signal system and a chemical composition of pheromone volatilies. There are also differences in the morphology of pheromone glands and associated sternal structures. The search of morpho-functional peculiarities underlying the difference of sexual communication in these families determined the selection of investigation subjects. The caddisflies were collected in the Leningrad region in headwaters of the river Ruditsa in the vicinity of the village Novaya Burya.

Pheromone glands containing the V sternite area were dissected while preparing alive insects. The glands were fixed in 2.5% glutaraldehyde for 24 hours. Later the fixation of samples was completed in a 2% solution of osmium tetroxide. Electron microscopic samples were prepared according to the standard scheme. Semifine sections were made and stained with toluidine blue. The sections were studied under light microscope. When oriented the sample, a region containing the gland was cut out and ultrathin sections were made. Double contrasting was used: firstly with uranyl nitrate, then with lead citrate. An electron microscope JEM–100C was applied to study the samples with different magnification.

Results and Discussion

The ultrastructure of pheromone glands of *Rhyacophila obliterata*

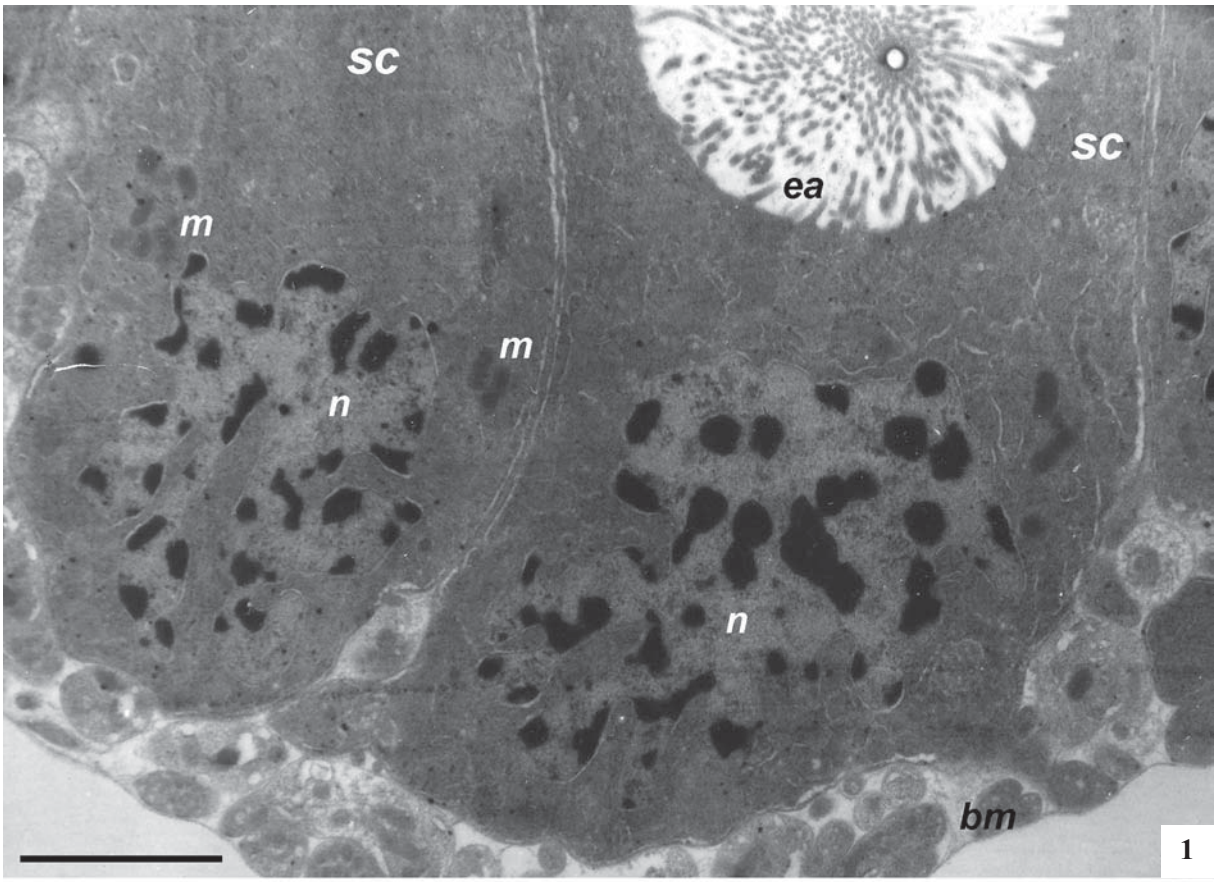
An organ represents a simple alveolar gland with a reservoir and efferent duct. A gland wall is made of several aisles of cells which can be subdivided into three types according to their morphological and functional characteristics. A gland body is formed by large secretory cells located directly on a basal membrane, there being bodies of canal cells between them close to the apical region. Secretory cell apical parts contact with small hypodermal cells underlying a reservoir cuticular lining which they synthesize.

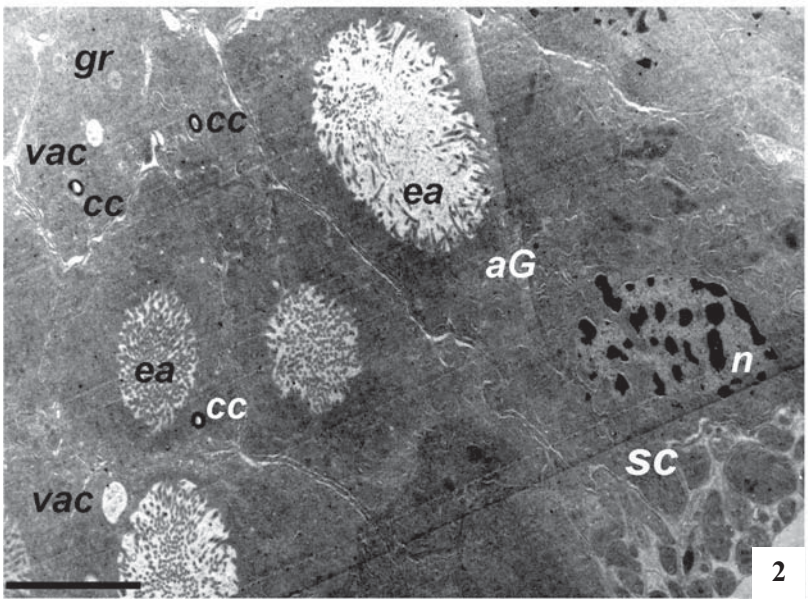
Secretory cells are columnar in form narrowing in the apical part. The basal membrane is smooth without projections (Figs 1, 6, 9). Female secretory cells are slightly larger than those of males. Within pheromone gland secretory cell cytoplasm there are all the proper organelles: a nucleus, mitochondria, membrane endoplasmic reticulum, ribosomes, a Golgi apparatus, as well as electron-dense inclusions, glycogen and granules. Cell cytoplasm is predominantly electron-dense, however there are cells (or cell parts) with a decrease in density of cytoplasmatic matrix.

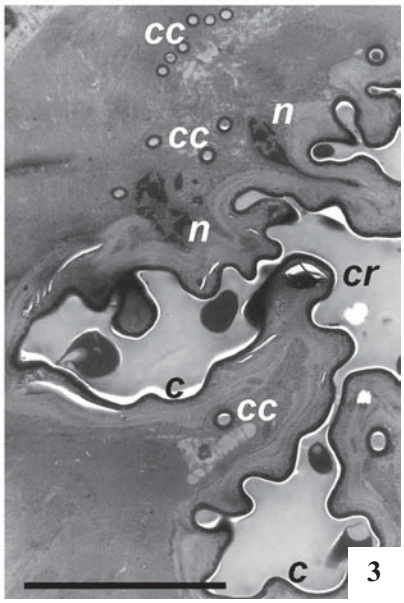
Within the basal part there is an irregular nucleus, that is more common in female secretory cells (Figs 1–2). Chromatin is well visualized in cell nuclei that is organized as multiple electro-dense deposits, located along the nucleus (Figs 1–2). There is one irregular

nucleolus or rarely two ones with electron-tenuous regions within their central parts (Fig. 9).

The Golgi apparatus is mainly located nearby the nucleus — within the cell basal region (Figs 2, 8). Within secretory cell cytoplasm rough endoplasmic reticulum (rER) is well developed. Within some cells rough ER occupies a lot of cytoplasm space along the basal membrane (Figs 10–11). Smooth endoplasmic

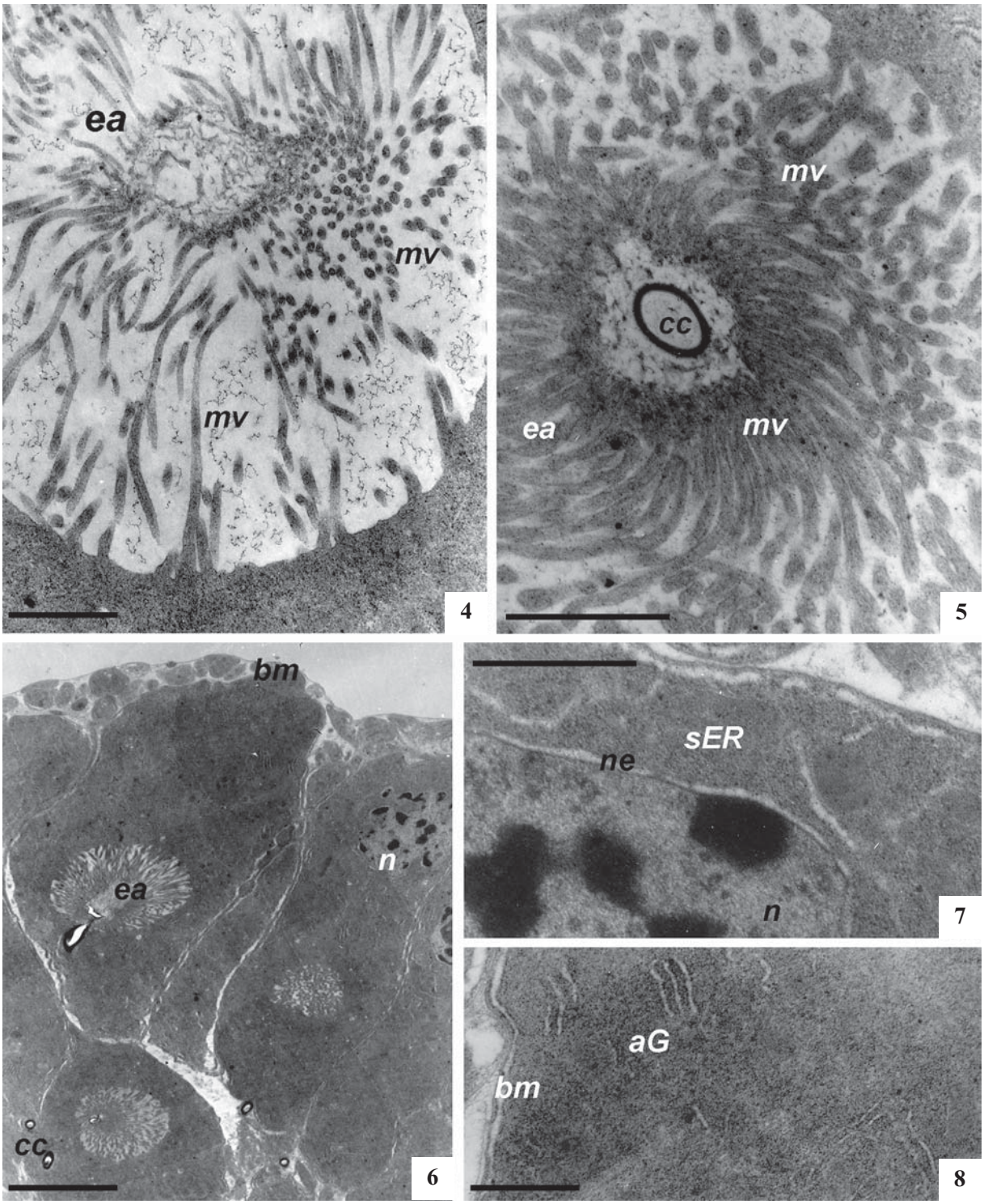






Figs 1–3. The ultrastructure of a sternal pheromone gland of a *Rhyacophila obliterata*, female: 1 — a basal region of secretory cells, ×6000; 2 — end apparatus within secretory cells, ×4000; 3 — a cuticular reservoir and hypodermal cell nuclei, ×6000; scale bar — 5 μm; TEM.

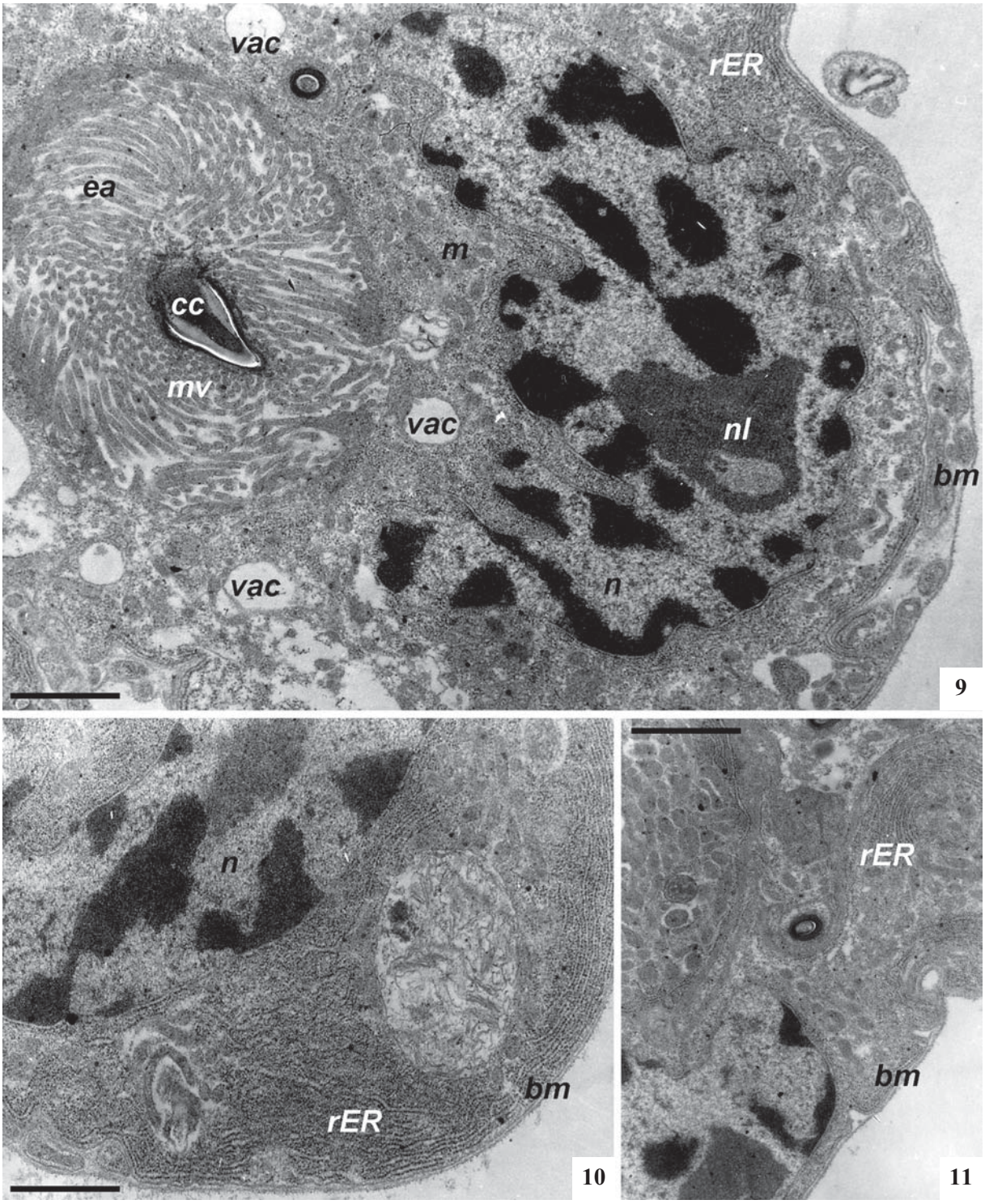
Рис. 1–3. Ультраструктура стернальной феромонной железы *Rhyacophila obliterata*, самка: 1 — базальный отдел секреторных клеток, ×6000; 2 — концевые аппараты в секреторных клетках, ×4000; 3 — кутикулярный резервуар и ядра гиподермальных клеток, ×6000; масштаб — 5 μm; ТЭМ.



Figs 4–8. The ultrastructure of a sternal pheromone gland of a *Rhyacophila obliterata*, female: 4 — an end apparatus within secretory cells, ×20000; 5 — an end apparatus within secretory cells, ×30000; 6 — secretory cells within the basal membrane, ×4000; 7 — smooth endoplasmic reticulum in the basal region of a secretory cell, ×30000; 8 — Golgi apparatus in the basal region of a cell, ×20000; scale bars — 1 μm for 4–5, 7–8; 5 μm for 6; TEM.

Рис. 4–8. Ультраструктура стернальной феромонной железы *Rhyacophila obliterata*, самка: 4 — концевой аппарат в секреторных клетках, ×20000; 5 — концевой аппарат в секреторных клетках, ×30000; 6 — секреторные клетки в области базальной мембраны, ×4000; 7 — гладкая эндоплазматическая сеть в базальном отделе секреторной клетки, ×30000; 8 — аппарат Гольджи в базальном отделе клетки, ×20000; масштаб — 1 μm на рис. 4–5, 7–8; 5 μm на рис. 6; ТЭМ.

reticulum (sER) is homogeneous within the cytoplasm, as a rule. Sometimes a net of tubular and vesicular structures of smooth ER is localized within the cell basal part nearby the nucleus (Fig. 7). Mitochondria are few in number, they are large and located mainly within the cell basal part, however, they can be found within



Figs 9–11. The ultrastructure of pheromone gland secretory cells of a *Rhyacophila obliterata*, male: 9 — a secretory cell of the pheromone gland, ×10000; 10 — a basal region of a secretory cell, ×20000; 11 — a basal region of a secretory cell, ×20000; scale bars — 1 μm for 10–11, 7–8, 2 μm for 9; TEM.

Рис. 9–11. Ультраструктура секреторных клеток феромонной железы *Rhyacophila obliterata*, самец: 9 — секреторная клетка феромонной железы, ×10000; 10 — базальная область секреторной клетки, ×20000; 11 — базальная область секреторной клетки, ×20000; масштаб — 1 μm на рис. 10–11, 2 μm на рис. 9; ТЭМ.

the apical region (Fig. 1). Along all the cytoplasm there are inclusions, seemingly of glycogen as well as vacuoles and granules (Figs 2, 9); separate lysosomes are also revealed.

Within the apical part of secretory cells specific structures are also located, that can be seen in light microscope — end apparatus which are a combination of a receiving canal of a canal cell and associated microvilli of a secretory cell (Figs 1–2, 4–6, 9). An end apparatus in pheromone gland secretory cells of a *R. obliterata* female is a little bit larger than that of male (7.5×5 ìm and 4.5×4.5, respectively). The length of a microvillus in an end apparatus can achieve 3 ìm. The diameter of a receiving canal is 0.25 ìm.

Cells of the hypoderm located between secretory cells and the cuticular lining of a gland reservoir are smaller than secretory cells. Nuclei of hypodermal cells are of approximately the same size in a male and female (2.2×5 ìm) (Fig. 3).

The cuticle of a pheromone gland reservoir forms multiple folds (Fig. 3). Epicuticle is thick, equally wide along the reservoir perimeter. Within the space between the cuticular reservoir and secretory cells multiple cross-cut conducting canals of canal cells are seen (Fig. 3). Every secretory cell is associated with the only canal cell that demonstrates manifold curvatures of conducting canals of canal cells, especially their apical regions.

The ultrastructure of pheromone gland cells of *Chaetopteryx villosa*

Pheromone glands of a representative of the Phryganeina suborder — *C. villosa* have in general the same architecture, their wall formed by the same types of cells. The secretory cells are larger than those of the foregoing species. Their length in female can achieve 27 ìm, the width — 19 ìm. Nuclei within cells can occupy significant space. The size of male secretory cell nuclei is less than that of females. It must be noticed, that the nuclei of secretory cells in the species given are less polymorphic, have a more regular shape and are characterized by the less number of projections (Fig. 12). Within the secretory cell nuclei of *C. villosa* females two nucleoli with the diameter of 1.5–2.5 ìm are well visualized.

Cell cytoplasm in both sexes is less electron-dense. Rough ER is located nearby the basal membrane of secretory cells as in the foregoing species. Within the cytoplasm there are multiple electron-dense inclusions, glycogen and granules (Fig. 12). An end apparatus is also located within the apical part of secretory cells. Its diameter achieves 3.75 ìm in females and 1 ìm in males. The diameter of cuticular conducting canals is approximately 0.37 ìm in female cells, and 0.2 ìm in male ones.

Apical parts of canal cells and multiple cross-cut sections of these cell conducting canals can be seen within the cuticular reservoir folds. As in the foregoing species hypoderm cells are significantly smaller than secretory ones and are located between secretory cells and the cuticle (Figs 13–14). The hypodermal cell bodies are of various shape. At the same time nuclei with the size of 5×2.5 ìm in females and 4×2.5 ìm in males occupy a larger space. Heterochromatin is organized as large deposits, located along the nucleus periphery. The epicuticle thickness is 1.5 ìm (Figs 13–14). Within the epicuticle superficial layer pores are well visualized (Fig. 14).

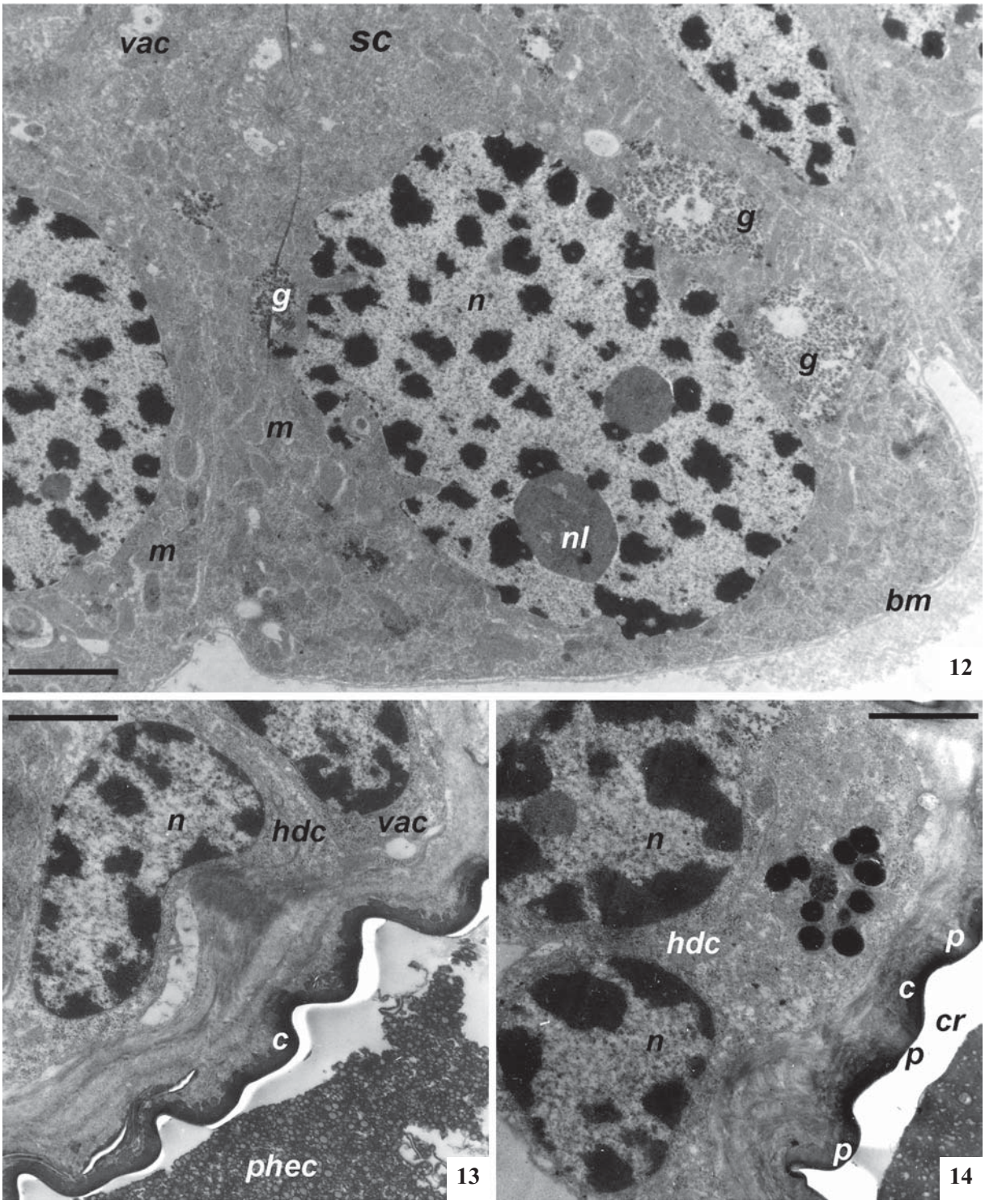
Thus, the analysis of the data received suggests caddisfly pheromone glands having the same architecture as epidermal glands of other insects. A sternal pheromone gland of caddisflies of the species studied (*R. obliterata* and *C. villosa)* consists of a cuticular reservoir and cells of three types: secretory, canal and hypodermal ones.

The presence of a well-developed nucleus, endoplasmatic reticulum (ER), granules and ribosomes within secretory cells, revealed by electron microscopic studies proves these cells to be functionally active. The ultrastructure of pheromone gland secretory cells indicates more functional activity of these cells in females compared with that in males. It is proved by the presence of more polymorphic nuclei with projections in female secretory cells of the species studied, as well as a more developed synthesis cell apparatus compared with a male one, that might be evident of more intensive chemical synthesis in female pheromone glands in comparison with that of a male. The degree of intensity of pheromone synthesis might not be due to the size of a gland as in some species the male sternal glands have more linear size than those of females [Ivanov & Melnitsky, 2002].

Despite some investigators considering the possibility of defensive functions in sternal pheromone glands in Amphiesmenoptera [Duffield et al., 1977; Ansteeg & Dettner, 1991], the behavioral data suggest sternal glands playing the leading role in pheromone communication and in synthesis of attractive chemical stimuli. In most cases both sexes of Trichoptera have pheromone glands, however it is the females that are communicatively attractive which produce and release sex pheromones attracting males of their species.

In most caddisfly species studied the substances which are pheromones belong to alcohols or ketones [Lofstedt et al., 1994; Bjostad et al., 1996; Bergmann, 2002]. Sometimes in secreted pheromone compositions there may be organic acids and some other classes of organic compounds but in trace quantities as a rule. In most cases organic acids might be precursors of attractive substances (alcohols and ketones) or by-products of their synthesis. Chemical analysis of male pheromone glands extracts of *R. obliterata* revealed the presence of a mixture of organic acids as pheromone compounds. In the female extracts heptane–2–ol and heptane–2–one were identified in the ratio of 7:10 [Bergmann, 2002]. In male pheromone compositions of *C. villosa* 4–methylhexane–3–one and 4–methylheptane–3–one were revealed, while 4–methylhexane–3–one, 4–methylheptane–3–one, (3S,4S)–4–methylhexane–3–ol and (3R,4S)–4–methylheptane–3–ol identified in females [Bergmann, 2002]. The physiological role of these substances and their compositions requires additional in-

vestigation, however behavioral experiments on the Limnephilidae family have shown methylated compounds of pheromone compositions to act as attractive substances in intraspecific communication [Syrnikov et al., 2005; Ivanov et al., 2008]. Thus, a complex process of simultaneous synthesis of several final and interme-



Figs 12–14. The ultrastructure of pheromone gland secretory cells of *Chaetopteryx villosa*: 12 — secretory cells of a female pheromone gland, ×4000; 13 — hypodermal cells and a cuticular reservoir in a female gland, ×10000; 14 — hypodermal cells and a cuticular reservoir in a male gland, ×10000; scale bars — 2 μm for 13–14; 5 μm for 12; TEM.

Рис. 12–14. Ультраструктура секреторных клеток феромонной железы *Chaetopteryx villosa.* 12 — секреторные клетки феромонной железы самки, ×4000; 13 — гиподермальные клетки и кутикулярный резервуар в железе самки, ×10000; 14 — гиподермальные клетки и кутикулярный резервуар в железе самца, ×10000; масштаб — 2 μm на рис. 13–14; 5 μm на рис. 12; ТЭМ.

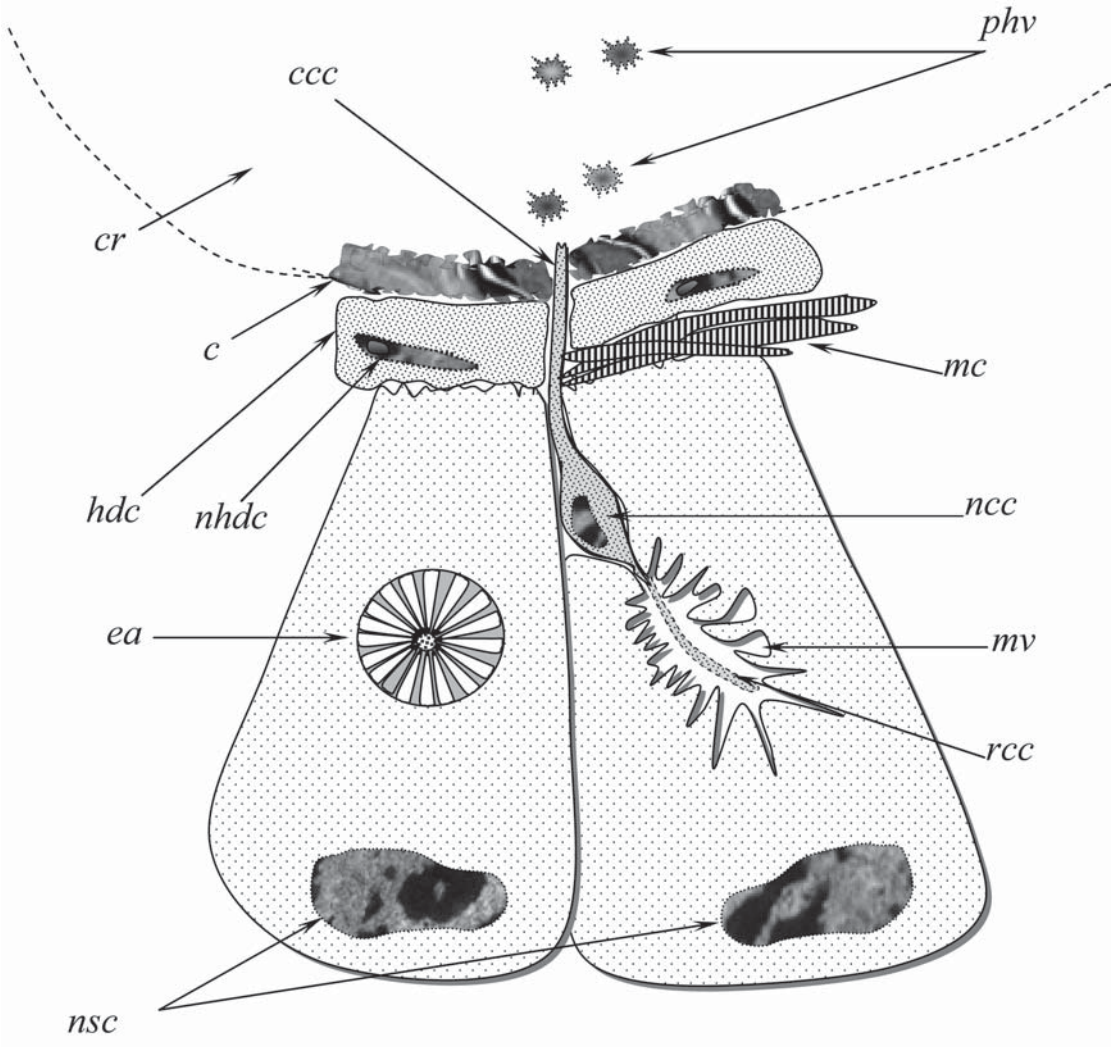


Fig. 15. A scheme of a cellular structure of sternal pheromone glands of Trichoptera.
Рис. 15. Схема клеточного строения стернальных феромонных желез Trichoptera.

diate components of a pheromone composition notably in a particular proportion has to take place in pheromone gland cells.

A special investigation of the ultrastructure of pheromone glands of primitive Lepidoptera has never been done, however, their sternal pheromone glands are known to be organized as that of caddisflies in the C3 type, i.e. there is a complex cellular combination including secretory and canal cells [Kristensen, 1984; Nielsen & Kristensen, 1996]. Canal cells, located between secretory cell bodies as a rule, form two types of cuticular canals: receiving and conducting ones. A receiving canal has a perforated cuticle with pores and drifts into a secretory cell where forms an end apparatus together with microvilli of secretory cell apical and lateral regions. An conducting canal begins in the outlet of a receiving canal from the cavity of a secretory cell, opens into a cavity of the gland cuticular reservoir and is characterized by a dense cuticle without pores [Noirot & Quennedey, 1991].

Terminal glands of higher lepidopterans are organized differently: they have no cuticular canals and canal cells, their secretory cells contact with the cuticle directly by microvilli in the apical region. The cuticle is penetrated by tubular structures associated with pores [Percy, 1974, 1979]. Parallel to cellular reorganization, in higher lepidopterans the chemical substances acting as pheromones undergo alteration, the total amount of pheromones produced decrease manifold. In their pheromone communication low-toxic acetates of fatty acids are used as a rule unlike pheromones of Trichoptera and primitive Lepidoptera [Arn et al., 1992].

In the present state of investigation the question about the site of synthesis of a final pheromone composition has not been solved yet. Alcohols and their derivatives cannot be synthesized in a cell directly. Secretory cells do not appear to produce the alcohols themselves but their low-toxic and non-volatile precursors, that enter conducting canals from terminal cells, then pass into a gland cuticular reservoir where final processing

of pheromones takes place. That there are traces of enzymes and lipid components within gland cuticular reservoirs and in the lumen of cuticular canals of canal cells confirms this hypothesis. It is the high toxicity of final components of a pheromone composition for cellular structures that may explain the presence of a complex C3-cellular combination in pheromone glands of caddisflies and other insects employing such toxic substances for communication.

A structure and functioning of canal cells have to be studied. Their bodies with nuclei are localized amidst hypoderm cells or between secretory cell bodies. The light microscopy findings give evidence that stained nuclei are very often detected within lateral surfaces of secretory cells [Melnitsky, 2007]. It is impossible to exclude a probability that cuticular canals were formed during the late pupa stage and by the beginning of gland functioning canal cells producing them degenerated partially or completely.

There is no doubt that glands originated from ectoderm. It is supported by the presence of hypodermal cells and a cuticular lining within a pheromone gland which might have been formed by invagination of epidermal cells during an early ontogenesis. The findings of transmission electron microscopy support our suggestion that every secretory cell is associated with one canal cell. As a general view a scheme of a structure of a pheromone gland wall part has been reconstructed and is given in Fig. 15.

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Abbreviations:

aG — Golgi apparatus;
bm — basal membrane;
c — cuticle;
cc — cuticular canal;
ccc — a conducting cuticular canal of a canal cell;
cr — a cuticular reservoir of a gland;
ea — an end apparatus;
g — glycogen;
gr — granules;
hdc — a hypodermal cell;
m — mitochondrium;
mc — muscle cells (only in representatives of Phryganeidae);
mv — microvilli;
n — nucleus;
ncc — nuclei of a canal cell,
ne — nuclear envelope;
nhdc — a nucleus of a hypodermal cell,
nl — nucleolus;
nsc — nuclei of secretory cells;
p — pores within a cuticle;
phec — pheromone-enzyme composition;
phv — pheromone volatilies;
rcc — a receiving cuticular canal of a canal cell;
rER — rough endoplasmic reticulum;
sc — secretory cell;
sER — smooth endoplasmic reticulum;
vac — vacuole.

Обозначения:

aG — аппарат Гольджи;
bm — базальная мембрана;
c — кутикула;
cc — кутикулярный каналец;
ccc — выводящий кутикулярный каналец канальцевой клетки;
cr — кутикулярный резервуар железы;
ea — концевой аппарат;
g — гликоген;
gr — гранулы;
hdc — гиподермальная клетка;
m — митохондрия;
mc — мышечные клетки (только у представителей Phryganeidae);
mv — микроворсинки;
n — ядро;
ncc — ядро канальцевой клетки;
ne — ядерная оболочка;
nhdc — ядро гиподермальной клетки;
nl — ядрышко;
nsc — ядра секреторных клеток;
p — поры в кутикуле;
phec — феромонно-ферментативная смесь;
phv — компоненты феромонной смеси;
rcc — собирательный кутикулярный каналец канальцевой клетки;
rER — шероховатая эндоплазматическая сеть;
sc — секреторная клетка;
sER — гладкая эндоплазматическая сеть.
vac — вакуоль.