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Morphology of the reproductive system of female cockroaches (Blattodea)

Морфология половой системы самок тараканов (Blattodea)

S.R. Shakirov, E.S. Grinuk, M.E. Mkrtchyan, P.S. Voznesenskaya
С.Р. Шакиров, Е.С. Гринюк, М.Э. Мкртчян, П.С. Вознесенская

Saint Petersburg State University of Veterinary Medicine, Chernigovskaya Str. 5, Saint Petersburg 196084 Russia. E-mail: cerafimshakir14@mail.ru; katyagrinyk4@mail.ru; laulilitik@yandex.ru; p.s.voznesenska@gmail.com.

ФГБОУ ВО Санкт-Петербургский государственный университет ветеринарной медицины, ул. Черниговская 5, Санкт-Петербург 196084 Россия.

Key words: Cockroaches, *Gromphadorhina portentosa, Lucihormetica verrucosa*, reproductive system, morphology.

Ключевые слова: тараканы, *Gromphadorhina portentosa*, *Lucihormetica verrucosa*, половая система, морфология.

Abstract. The reproductive system of insects is of great scientific interest due to its significant variability in morphological structure. The study of the reproductive system of cockroaches provides insights that can be applied in various scientific fields, beyond biological aspects. Our aim was to provide a morphological description of the different organs within the female reproductive system of cockroaches (*Blattodea*, Brunner von Wattenwyl, 1882). The study material included viviparous cockroaches of two species: *Gromphadorhina portentosa* (Schaum, 1853) and *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865). An adapted classical method of preparing histological sections was chosen to obtain informative histological samples. The results highlighted specific structural features of the female reproductive system of cockroaches, exemplified by the lateral oviducts, the main part of the principal oviduct, the genital chamber, the copulatory organ, and more.

Резюме. Половая система насекомых представляет большой интерес для науки в связи с тем, что она обладает большой вариабельностью с точки зрения морфологического строения. Приводится морфологическое описание различных органов половой системы самок тараканов (Blattodea Brunner von Wattenwyl, 1882). В качестве материала для исследования использовались живородящие тараканы 2 видов: *Gromphadorhina portentosa* (Schaum, 1853) и *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865). Выделены особенности строения половой системы самок тараканов, на примере латеральных яйцеводов, основной части главного яйцевода, генитальной камеры, копулятивного органа.

Introduction

The reproductive system of insects is of great scientific interest due to its high variability in morphological structure [Lavanchy et al., 2024]. The study of the reproductive system of cockroaches provides insights that can be applied in various scientific fields, not limited to biological aspects. For example, a detailed examination of the reproductive processes in cockroaches can contribute to the development of new engineering solutions, as has been demonstrated with other design innovations [Adams, Tariq, 2024]. The reproductive system of cockroaches has evolved over millions of years, optimizing its morphology for specific tasks. The degree of adaptation to perform a specific function is reflected not only in macroscopic structures but also in tissue architecture, which more accurately represents the specificity and narrow specialization of the organs [Sathiyaseelan et al., 2024]. The female reproductive system of cockroaches includes paired ovaries and lateral oviducts, a single spermatheca, as well as a main oviduct with an expansion (the genital chamber), which in viviparous species functions as a uterus similar to that of vertebrate animals, opening externally via a copulatory aperture. The female reproductive system is also equipped with a spermathecal gland and an accessory gland [Dey Roy, Taher, 2024].

The morphological description of the different organs of the female reproductive system of cockroaches (Blattodea Brunner von Wattenwyl, 1882) is the main objective of the research.

Materials and methods

The research was conducted in the histological laboratory of the Department of Biology, Ecology, and Histology at Saint Petersburg State University of Veterinary Medicine. The material for the study consisted of viviparous cockroaches of two species, *Gromphadorhina portentosa* (Schaum, 1853) and *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865) [Greven et al., 2013; Monahan et al., 2023]. Six adult specimens of each species were selected for the study. Dissection was carried out using fine ophthalmic scissors and tweezers.

An adapted classical method for preparing histological sections was used to obtain informative samples [Shakirov, 2023]. The adaptation involved double fixation. Initially, fixation in 10 % buffered formalin was performed on the dissected insect carcasses before the internal organs were removed from the integumentary

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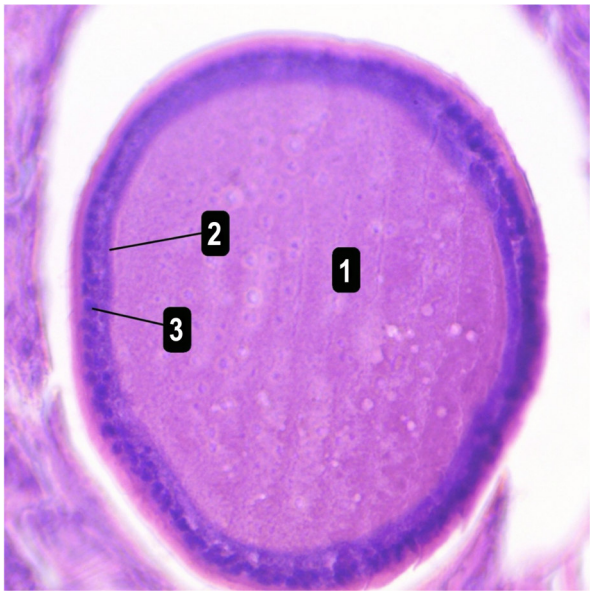

Fig. 1. Fragment of the follicle of *L. verrucosa*. Designations: 1 — centrolecithal yolk, 2 — chorion, vitelline membrane, and oolemma, 3 — follicular cells. H&E staining; magnification ×400.

Рис. 1. Фрагмент фолликула *L. verrucosa*. Обозначения: 1 — центролецитально расположенный желток, 2 — хорион, вителлиновая мембрана и оолема, 3 — фолликулярные клетки. Окраска ГЭ; увеличение ×400.

framework. The surface methylene cross-links formed between proteins in internal structures enhanced the resistance of soft tissues to deformation, facilitating further dissection. Subsequently, the extracted organs were isolated in histological cassettes and underwent secondary, more prolonged fixation. The adaptation of the classical histological preparation method also included shortened exposure to alcohol (up to 15 minutes) during dehydration and the omission of absolute alcohol in the processing (alcohol battery) to prevent sample over-drying. This caused challenges during the embedding stage, as the organs floated due to the presence of fat bodies, which retained minimal lipids, and the tracheal system, which contained residual air. To address this issue, the organs were pressed to the bottom of the embedding mold until the lower layers of paraffin solidified [Lavanchy et al., 2024].

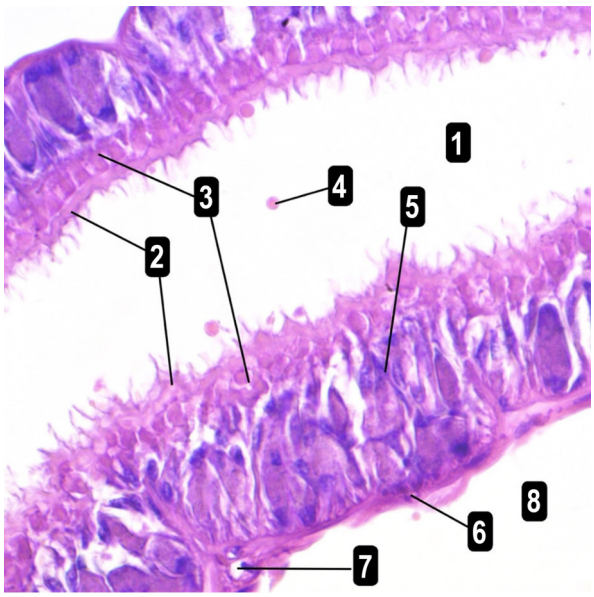

Fig. 2. Fragment of the lateral oviduct of *L. verrucosa*. Designations: 1 — organ lumen, 2 — exocuticle, 3 — endocuticle, 4 — secretory granule, 5 — epithelial layer, 6 — serous membrane, 7 — tracheal lumen, 8 — insect body cavity. H&E staining; magnification ×400.

Рис. 2. Фрагмент латерального яйцевода *L. verrucosa*. Обозначения: 1 — просвет органа, 2 — экзокутикула, 3 — эндокутикула, 4 — секреторная гранула, 5 — эпителиальный слой, 6 — серозная оболочка, 7 — просвет трахеи, 8 — полость насекомого Окраска ГЭ; увеличение ×400.

Sections 3.5 µm thick were prepared using a ROTMIK-2M rotary microtome. The histological sections were stained with hematoxylin and eosin (H&E).

Microscopy was performed using a Mikmed-5 light microscope at magnifications of ×40 and ×400 µm. Photodocumentation was conducted with a Lomo MC-3 digital camera (serial No. XC 1272).

The present work is registered in ZooBank (www.zoobank.org) under urn:lsid:zoobank.org:pub:170C4878-48E9-40AA-B4D2-84DBF4E40941

Research results and discussion

The gonads of *L. verrucosa* females (ovaries) consist of individual panoistic ovarioles (egg tubes) grouped into clusters. Ovarioles are classified as panoistic due to the absence of trophocytes, which provide additional nutrition to oocytes. In the specimens examined, the wall of the ovariole consists of follicular epithelium, surrounded externally by an outer sheath composed of various cells differing in origin and function, and internally adjacent to developing gametes by a basal membrane. Two regions of the ovariole were identified: the germarium and the vitellarium. The germarium serves as the area for gamete development, where oogonia multiply, oocytes differentiate, and follicle formation begins (Fig. 1).

The follicular wall in *L. verrucosa* consists of oocyte cytoplasm (oolemma), covered by a vitelline membrane, with the largest layer being the chorion, produced by follicular cells. Cockroach oocytes are characterized by an even distribution of yolk (centrolecithal configuration). Additionally, terminal filaments extend from the germarium of ovarioles within a single ovary, merging into a single bundle. This bundle is essential for anchoring the gonads within the insect's body cavity, suspending the ovaries from the dorsal diaphragm and nearby fat bodies. In the vitellarium, follicles fully develop, and eggshells form.

Lateral oviducts extend from the vitellarium of the ovarioles, one from each ovary. The macroscopic structure of this organ in the female reproductive system of cockroaches exhibits minimal structural variability: it has a typical tubular organization. Histological analysis of *L. verrucosa* specimens revealed that the lateral oviducts are lined with a cuticular layer, indicating their ectodermal origin (Fig. 2).

Based on the degree of chitinization and affinity to histological stains, it can be inferred that the oviducts consist primarily of procuticle. The epicuticle is absent, as it could impede the necessary expansion during the

passage of embryos and their accompanying membranes through the oviduct, which must significantly widen its lumen. The procuticle, in turn, is divided into exocuticle and endocuticle. In the prepared specimens, the cuticle displays a heterogeneous structure: the outermost layer, the exocuticle, directed toward the oviduct lumen, is a single layer with numerous chaotic projections that may participate in the formation of egg membranes. Below the exocuticle lies the endocuticle, which in the lateral oviducts exhibits a distinct transverse-circular orientation. This layer of the cuticle also contains secretory granules more frequently than the exocuticle.

The primary thickness of the lateral oviduct walls is formed by a single-layered pseudostratified columnar epithelium with a well-developed pool of secretory cells (including goblet and cuticle-forming cells). In some specimens, cells exhibiting alterations, such as damaged membranes and karyopyknosis, were observed. The basal membrane and connective tissue occasionally invaginate into the epithelial layer, increasing the contact surface area and enhancing the nutrition of adjacent regions. These areas are accompanied by tracheae. Cambial clusters of epithelial cells are located in this region. According to literature, the muscular layer of the ovary extends into the lateral oviduct and covers it throughout its length, eventually merging with the muscular layer of the main oviduct [Chaika, 2017]. However, in the specimens prepared for this study, the muscular layer in the lateral oviducts could not be differentiated.

Examination of both species revealed that the lateral oviducts are short and merge to form the main oviduct, which exhibits a more diverse structure and is divided into the primary segment (the actual main oviduct) and an ampullary expansion — the genital chamber. According to the results obtained from dissecting the cockroaches studied, the length of the primary segment in most individuals of the examined species is 3–4 times that of the lateral oviducts, while its width is approximately twice as large. The histological structure of the main oviduct in *L. verrucosa* includes a mucous membrane with a submucosal base and a muscular layer (Fig. 3).

Beneath the muscular layer, the connective tissue component of the hollow organ is poorly developed, which is typical for most insects. The serous membrane is weakly expressed.

The entire mucous membrane is folded into numerous folds. It was hypothesized that these folds could unfold as the walls of the main oviduct stretch, as indicated by the heterogeneous structure of the cuticle. The boundary between the exocuticle and endocuticle is not visible, and the entire procuticular layer varies in its degree of chitinization. At the apex of the fold, chitin impregnation in the cuticle is minimal, resulting in a more acidophilic staining compared to the lateral surfaces, where more chitin is present, giving a stronger yellow hue. This unique arrangement of regions with varying degrees of chitinization allows the organ to undergo significant stretching due to the flexible and deformation-resistant fold apexes without losing strength. This strength is ensured by a framework of highly chitinized

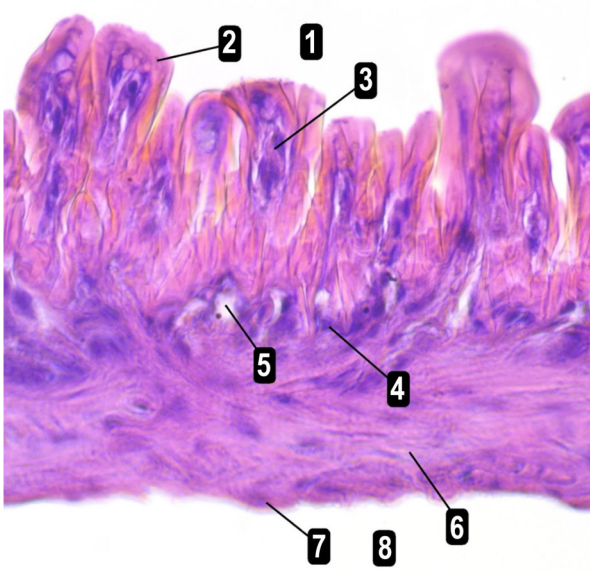

Fig. 3. Fragment of the main oviduct of *L. verrucosa*. Designations: 1 — organ lumen, 2 — cuticle, 3 — epithelial layer, 4 — submucosal base, 5 — tracheal lumen, 6 — muscular layer, 7 — serous membrane, 8 — body cavity. H&E staining; magnification ×400.

Рис. 3. Фрагмент основной части главного яйцевода *L. verrucosa*. Обозначения: 1 — просвет органа, 2 — кутикула, 3 — эпителиальный слой, 4 — подслизистая основа, 5 — просвет трахеи, 6 — мышечная оболочка, 7 — серозная оболочка, 8 — полость тела. Окраска ГЭ; увеличение ×400.

lateral surfaces that resist tearing while also maintaining a reduced volume in a collapsed state. The epithelium is single-layered and composed of polymorphic cells, making it difficult to determine its row arrangement.

The submucosal base has a typical structure. The muscular layer is well-developed, characteristic of an organ with active motility, and consists of cross-striated myosymplasts with multidirectional orientation. A network of numerous tracheae is present within its thickness.

The lateral oviducts of *G. portentosa* exhibit the following structural features: a lower degree of chitinization in the cuticle, both at the apex and on the lateral surfaces of the folds; a thinner muscular layer, but the overall wall thickness is comparable to that of *L. verrucosa* due to taller folds; the tracheal system extends outside the oviduct wall into the body cavity and has a greater degree of branching (Fig. 4).

Following the main part of the oviduct is the genital chamber. Examination revealed that this chamber has a larger diameter at an equal length compared to the main part of the oviduct. This organ functions as the site for carrying offspring in viviparous species. Macroscopically, the wall of the genital chamber forms large spreading folds.

Microscopy of histological sections of the genital chamber in *L. verrucosa* revealed that the surfaces of the large folds have secondary folds formed by the mucous membrane (Fig. 5).

The cuticle is more developed than in previous organs. The procuticle has a multilayered structure. The

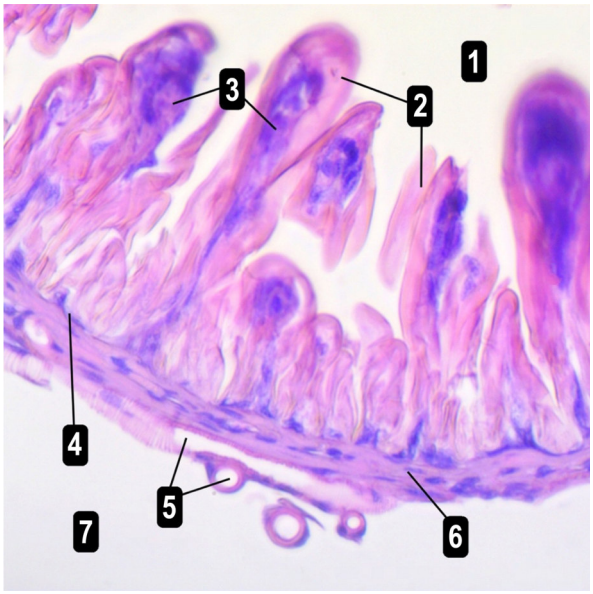

Fig. 4. Fragment of the main oviduct of *G. portentosa*. Designations: 1 — organ lumen, 2 — cuticle, 3 — epithelial layer, 4 — submucosal base, 5 — tracheal lumen, 6 — muscular layer, 7 — body cavity. H&E staining; magnification ×400.

Рис. 4. Фрагмент основной части главного яйцевода *G. portentosa*. Обозначения: 1 — просвет органа, 2 — кутикула, 3 — эпителиальный слой, 4 — подслизистая основа, 5 — просвет трахеи, 6 — мышечная оболочка, 7 — полость тела. Окраска ГЭ; увеличение ×400.

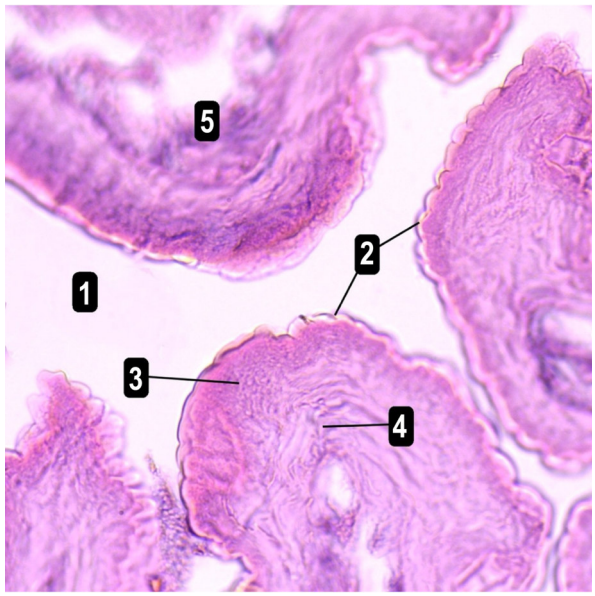

Fig. 5. Fragment of the genital chamber of *L. verrucosa*. Designations: 1 — organ lumen, 2 — «fringe» of the exocuticle, 3 — exocuticle, 4 — endocuticle, 5 — epithelial layer. H&E staining; magnification ×400.

Рис. 5. Фрагмент генитальной камеры *L. verrucosa*. Обозначения: 1 — просвет органа, 2 — «бахрома» экзокутикулы, 3 — экзокутикула, 4 — эндокутикула, 5 — эпителиальный слой. Окраска ГЭ; увеличение ×400.

exocuticle, with a granular nonuniformity, is distinguishable from the endocuticle, which contains fibers. At the distal parts of the genital chamber, areas covered by an epicuticle can be observed, forming a continuous layer in the copulatory organ. The surface of the exocuticle is adorned with «fringes» of numerous projections, the function of which remains unclear. It is presumed that these projections aid in embryo protection by cushioning movements of the insect, as females of most species maintain mobility during gestation. The muscular layer has a structure like that of the main part of the oviduct, with a slight increase in the number of myosymplasts.

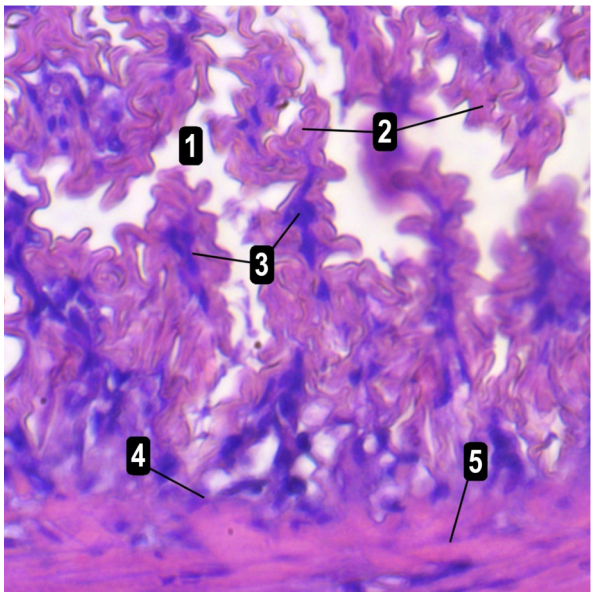

Fig. 6. Fragment of the genital chamber of *G. portentosa*. Designations: 1 — organ lumen, 2 — cuticle, 3 — epithelial layer, 4 — submucosal base, 5 — muscular layer H&E staining; magnification ×400.

Рис. 6. Фрагмент генитальной камеры *G. portentosa*. Обозначения: 1 — просвет органа, 2 — кутикула, 3 — эпителиальный слой, 4 — подслизистая основа, 5 — мышечная оболочка. Окраска ГЭ; увеличение ×400.

In contrast to *L. verrucosa*, the cuticular layers in *G. portentosa* are less pronounced; the exocuticle is difficult to differentiate from the endocuticle, and the mucous membrane is arranged into numerous complex folds with secondary projections of the cuticle (Fig. 6).

The copulatory organ, a significant part of the female reproductive system in insects, follows the main oviduct. Its structure is diverse, but certain general patterns can be identified. A portion of the wall of the copulatory organ is a continuation of the wall of the genital chamber, and thus shares a similar structure (Fig. 7).

However, the fringe on the surface of the exocuticle is less pronounced, mirroring the mucosal folds. Another part of the wall resembles the external integument in structure and contains all cuticular layers, including the epicuticle. It is distinguished from the exoskeleton by the absence of spines. In *G. portentosa*, complex outgrowths of the genital chamber and a well-developed muscular layer transition into a short, thin-walled copulatory organ (Fig. 8).

The region resembling the external integument in structure lacks distinctive features that could indicate species-specific differences with *L. verrucosa*. The wall, which is a direct continuation of the genital chamber, has

Fig. 7. Fragment of the copulatory organ of *L. verrucosa*. Designations: 1 — organ lumen, 2 — epicuticle, 3 — exocuticle, 4 — endocuticle, 5 — epithelial layer, 6 — cross-striated myosymplasts of the muscular layer, 7 — mucous secretion. H&E staining; magnification ×400.

Рис. 7. Фрагмент копулятивного органа *L. verrucosa*. Обозначения: 1 — просвет органа, 2 — эпикутикула, 3 — экзокутикула, 4 — эндокутикула, 5 — эпителиальный слой, 6 — поперечнополосатые миосимпласты мышечной оболочки, 7 — слизистый секрет. Окраска ГЭ; увеличение ×400.

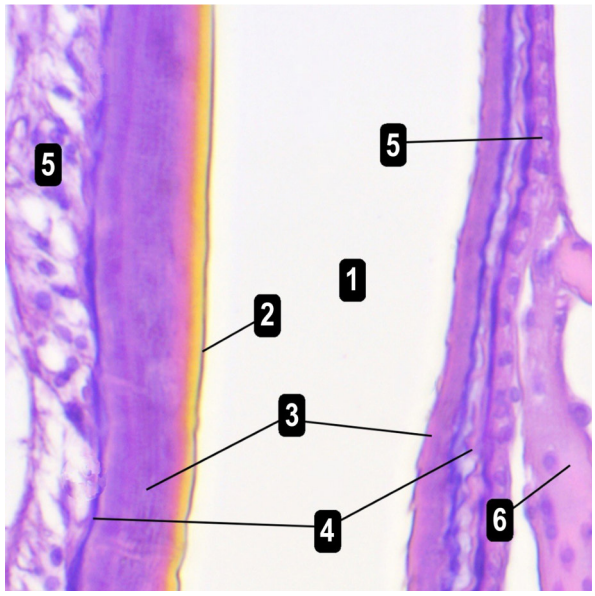

Fig. 8. Fragment of the copulatory organ of *G. portentosa*. Designations: 1 — organ lumen, 2 — epicuticle, 3 — exocuticle, 4 — endocuticle, 5 — epithelial layer, 6 — ligament suspending the copulatory organ in the insect body cavity. H&E staining; magnification ×400.

Рис. 8. Фрагмент копулятивного органа *G. portentosa*. Обозначения: 1 — просвет органа, 2 — эпикутикула, 3 — экзокутикула, 4 — эндокутикула, 5 — эпителиальный слой, 6 — связка, подвешивающая копулятивный орган в полости тела насекомого. Окраска ГЭ; увеличение ×400.

a multilayered cuticle structure with clearly distinguishable boundaries. The exocuticle on the external surface bears weakly pronounced tubercles.

Spermatheca (syn. sperm receptacle) — a specialized organ in the female reproductive system that stores the male ejaculate and maintains the sperm's viability over a prolonged period before activation. The spermatheca in cockroaches is relatively small compared to other reproductive organs, and its variable location within the body cavity complicates material collection and histological preparation. The cuticle of the *G. portentosa* spermatheca lacks an epicuticle; however, spines are present on the surface of the exocuticle (Fig. 9).

According to Chaika S.Yu., the spermatheca may contain cuticular innervated setae, but the spines observed in our study differ significantly from the described structures. Mechanoreceptive sensilla (setae) typically have a tubular body at their base. The spines observed in *G. portentosa* lack innervation, tubular bodies, and any connection to the epithelial layer. Structurally, they resemble the bristle apparatus of cockroach pharynxes but exhibit a lower degree of chitinization. We hypothesize that functionally these spines may serve to mix the viscous ejaculate with the secretions of the spermathecal glands, facilitate penetration, and evenly distribute the sperm-preserving secretory substances throughout the ejaculatory mass. This hypothesis is supported by the well-developed muscular layer of the spermatheca. The mucous membrane is arranged into folds, while the submucosa and muscular layers are penetrated by a

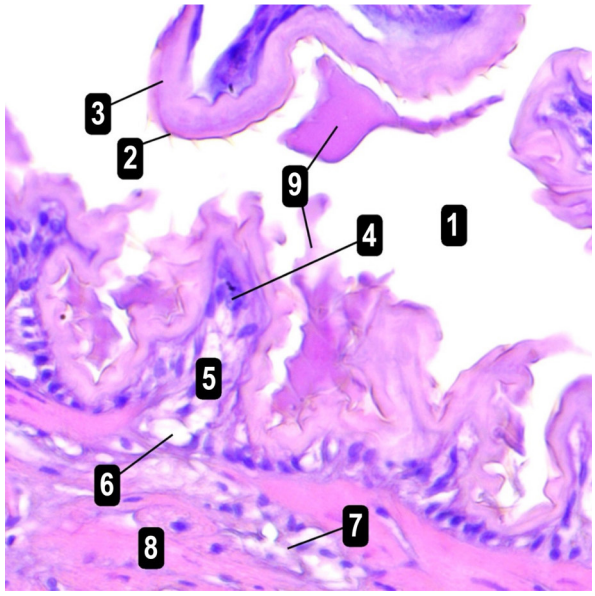

Fig. 9. Fragment of the spermatheca of *G. portentosa*. Designations: 1 — organ lumen, 2 — exocuticle with spines, 3 — endocuticle, 4 — epithelial layer, 5 — submucosal base, 6 — tracheal lumen, 7 — intramural glandular epithelium, 8 — muscular layer, 9 — organ secretions. H&E staining; magnification ×400.

Рис. 9. Фрагмент сперматеки *G. portentosa*. Обозначения: 1 — просвет органа, 2 — экзокутикула, несущая на себе шипы, 3 — эндокутикула, 4 — эпителиальный слой, 5 — подслизистая основа, 6 — просвет трахеи, 7 — интрамуральный железистый эпителий, 8 — мышечная оболочка, 9 — секреторные выделения органа. Окраска ГЭ; увеличение × 400.

tracheal network. Intramural clusters of glandular cells with ducts directed toward the organ's lumen are also present in the spermatheca walls.

Conclusion

We have described the reproductive organs of female *G. portentosa* and *L. verrucosa* and proposed hypotheses about their functions, which require further investigation. Most of our hypotheses are associated with the organization of the cuticle, as the most variable structure. Its morphology differs significantly in comparative anatomy between different cockroach species (*G. portentosa* and *L. verrucosa*) and within a single species across different organs or regions of organs (e.g., the main oviduct). The folds of the mucous membrane in the main oviduct are of particular interest, combining regions with varying degrees of chitinization and a uniquely structured cuticle. The unique multilayered cuticle of the lateral oviducts and the copulatory organ with layered structures were not previously described in the available literature, but also warrants mention. The combination of various organs with sharply differing morphologies makes the reproductive system of female insects unique.

Further research in this area could have a positive impact on the development of entomology.

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