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Anatomy of the springtail *Hypogastrura serrata* (Collembola: Hypogastruridae)

Анатомия ногохвостки *Hypogastrura serrata* (Collembola: Hypogastruridae)

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КЛЮЧЕВЫЕ СЛОВА: коллемболы, анатомия, морфология, почвенная фауна, миниатюризация.

ABSTRACT. While the existing data on springtail (Collembola) anatomy are extensive, they remain fragmentary in scope. To date, only one comprehensive anatomical study has documented all organ systems in a mature individual of an extremely miniature species [Panina *et al.*, 2019]. Here, we present the first integrative anatomical analysis of the medium-sized basal poduromorph *Hypogastrura serrata* (Ågren, 1904) using confocal microscopy and 3D computational modeling. The medium-sized (body length 1 mm) *H. serrata* possesses digestive, excretory, nervous, reproductive, and muscular systems comparable to those of larger springtails. The respiratory system is absent, although other springtails have tracheae (for instance, Sminthuridae). The circulatory system of *H. serrata* is reduced, whereas for large collembolans, without mentioning specific genera, the presence of a heart with 2–6 pairs of ostia has been described. The digestive system of *H. serrata* is clearly differentiated into sections, the presence of salivary glands is shown. The excretory system consists of labial nephridia. The nervous system comprises a brain, suboesophageal ganglion, three thoracic ganglia, and fused abdominal-thoracic ganglion. Reproductive organs include paired ovaries. The muscular system contains 37 head muscles, 63 pairs of thoracic muscles, and 82 pairs of abdominal muscles. By contrast, the miniature *Mesaphorura sylvatica* has one reduced ovary, no salivary glands or digestive system specialization, and has muscles penetrating the brain. This comprehensive description of the medium-sized *H. serrata* anatomy provides a reference for studying springtail morphology, particularly the effects of miniaturization.

РЕЗЮМЕ. Данные по анатомии коллембол достаточно обширны, но отрывочны: до сих пор опубликована лишь одна работа с анатомическим исследованием всех систем органов половозрелой особи одного крайне миниатюрного вида. В настоящей работе впервые, с помощью конфокальной микроскопии и трехмерного компьютерного моделирования, исследована анатомия одного из базальных видов подуроморфных коллембол средних размеров *Hypogastrura serrata* (Ågren, 1904). У среднеразмерной *H. serrata* (длина тела 1 мм), как и у крупноразмерных коллембол, присутствуют пищеварительная, выделительная, нервная, половая и мышечная системы органов. Дыхательная система отсутствует, хотя у других коллембол трахеи встречаются (в частности, у Sminthuridae). Кровеносная система у *H. serrata* редуцирована, тогда как для крупных коллембол, без упоминания конкретных родов, описано наличие сердца с 2–6 парами остий. Пищеварительная система *H. serrata* чётко дифференцируется на отделы, показано наличие слюнных желез. Выделительная система представлена лабиальными нефридиями. Нервная система: мозг, подглоточный ганглий, три грудных ганглия, брюшные ганглии слиты с третьим грудным. Половая система представлена двумя яичниками. В мышечной системе *H. serrata* описано 37 мышц головы, 63 пары мышц груди, 82 пары мышц брюшка. В свою очередь у миниатюрной *Mesaphorura sylvatica* редуцирован один из яичников, отсутствуют слюнные железы, не выражены отделы пищеварительной системы, мозг насквозь пронизывают мышцы. Комплексное опи-

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сание анатомии коллемболы среднего размера может стать референсом для дальнейшего изучения строения коллембол, в том числе и с точки зрения миниатюризации.

Introduction

Collembola, or springtails, are among the most diverse and abundant groups of small soil arthropods, distributed globally. Body size in this group varies remarkably, with the smallest species measuring approximately 0.2 mm in length and the largest representatives exceeding 17 mm [Christiansen *et al.*, 2009]. Soil-dwelling collembolans exhibit pronounced miniaturization due to habitat constraints, particularly the spatial limitations of soil pores and moisture requirements. Many collembolan genera include species under 0.5 mm long, whose anatomical study could advance understanding of a widespread evolutionary phenomenon — miniaturization. However, detailed anatomical investigations of medium-sized collembolans remain scarce, hindering comparative analyses of size-related anatomical adaptations. Earlier studies predominantly focused on large species and demonstrated a lack of comprehensive coverage of all organ systems.

Seminal contributions to collembolan anatomy were made by G. Bretfeld, A.D. Imms, J. Lubbock, and H. Wolter, whose foundational works describe organ systems across diverse genera and orders [Lubbock, 1871; Bretfeld, 1963; Wolter, 1963; Imms, 1977]. Anatomical and physiological studies of collembolan organ systems span multiple taxonomic groups [Lubbock, 1871; Denis, 1928; Bretfeld, 1963; Schaller, 1970; Manton, 1972; Hopkin, 1997], notably including the digestive system [Cassagnau *et al.*, 1968; Adams, Salmon, 1972; Altner, Thies, 1976], excretory system [Lubbock, 1871; Bretfeld, 1963; Wolter, 1963; Schaller, 1970; Berridge, Oschman, 1972; Manton, 1972; Imms, 1977; Verhoef *et al.*, 1979; Bitsch, Bitsch, 2002], and nervous system [Altner, Thies, 1976; Kollmann *et al.*, 2011]. Musculature has been documented in various body regions of different specimens [Lubbock, 1871; Bretfeld, 1963; Schaller, 1970; Manton, 1972; Imms, 1977; Bitsch, Bitsch, 2002], including the thorax and abdomen [Lubbock, 1871; Bretfeld, 1963; Schaller, 1970; Manton, 1972; Imms, 1977], head and antennae [Manton, 1972; Imms, 1977; Blanke, Machida, 2016], legs [Manton, 1972], abdomen and abdominal appendages [Prowázek, 1900; Oliveira, 2022; Rillich, Oliveira, 2023]. Subsequent studies expanded this field, including investigations into the musculature of the abdominal appendages in Entomobryomorpha and globular springtails [Oliveira, 2022; Oliveira, Smith, 2024], as well as analyses of neural organization [Kollmann *et al.*, 2011]. Nevertheless, only one study provides a holistic anatomical description of an extremely miniaturized species, *Mesaphorura sylvatica* [Panina *et al.*, 2019].

Collembolan anatomy is important for elucidating evolutionary trends within Hexapoda, particularly as springtails represent a basal hexapod lineage [Bellini *et al.*, 2023]. Miniaturization is a widespread evolutionary trend that drives profound changes in organismal and evolutionary biology [Hanken, Wake, 1993]. For a comparative anatomical study of springtails — particularly to investigate trends linked to miniaturization — objects are required that are comprehensively described across all their organ systems. Such frameworks rely on model organisms whose organ systems are fully characterized. Medium-sized species with comprehensive anatomical data would allow researchers to identify structural reductions, oligomerizations, and other adaptations associated with miniaturization.

This study aims to provide a comprehensive anatomical analysis of *Hypogastrura serrata* (Ågren, 1904), a medium-sized basal collembolan species, to establish a reference for evolutionary studies of miniaturization in springtails.

Materials and methods:

Specimens of *Hypogastrura serrata* (Ågren, 1904) were collected in 2019 in Moscow region, Russia and fixed in FAA (formalin, acetic acid, alcohol).

External morphology was studied using a Jeol JSM-6380LA scanning electron microscope (SEM) following critical point drying (Hitachi HCP-2) and sputter coating of samples with gold (Giko IB-3).

Internal morphology was studied using an Olympus FV-10i confocal laser scanning microscopy (CLSM). Specimens were fixed overnight in paraformaldehyde solution, depigmented using a DMSO/EtOH/H_2O_2 mixture (dimethyl sulfoxide, ethanol, hydrogen peroxide, 1:3:1), hydrated through a graded ethanol series (70%, 50%, 30%), and washed in PBST (0.1 M phosphate-buffered saline with 0.5% Triton X-100). For staining, Sytox and Rhodamin were used. Specimens were dehydrated in ethanol series and mounted between two cover glasses in a drop of BABB (benzyl alcohol-benzyl benzoate). The samples were imaged from both sides and subsequently merged into a single stack.

Three-dimensional modeling was performed using Bitplane Imaris 9.5.1 software with manual segmentation. Organ and body volumes were calculated via the software's standard statistical module, as described earlier [Polilov, Makarova, 2017]. Post-processing of 3D models was conducted in Blender 2.93.6.

The muscles were named following classical works on the thorax and abdomen [Bretfeld, 1963], head and antennae [Imms, 1923; Blanke, Machida, 2016], legs [Manton, 1972], and abdominal appendages, namely the furca and ventral tube [Rillich, Oliveira, 2023].

The nomenclature was based on earlier studies of the digestive system [Altner, 1968; Cassagnau *et al.*, 1968; Adams, Salmon, 1972], the excretory system [Wolter, 1963; Berridge, Oschman, 1972; Verhoef *et al.*, 1979], and the nervous system [Altner, Thies, 1976; Kollmann *et al.*, 2011].

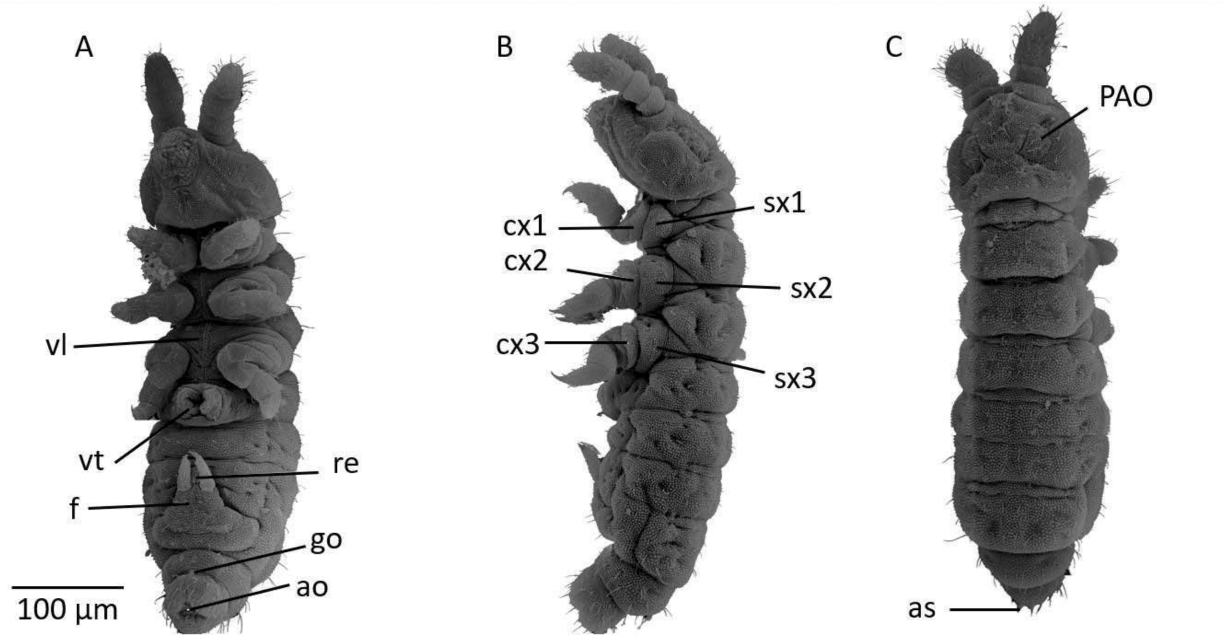

Fig. 1. Habitus of *Hypogastrura serrata*, SEM. A — ventral view, B — lateral view, C — dorsal view; vl — ventral line, vt — ventral tube, f — furca, re — retinaculum, go — genital opening, ao — anal opening, cx1–cx3 — pro-, meso-, and metacoxae, sx1–sx3 — pro-, meso-, meta-subcoxae, PAO — postantennal organ, as — anal spine.

Рис. 1. Габитус ногохвостки *Hypogastrura serrata*, СЭМ. А — вентрально, В — латерально, С — дорсально; vl — вентральная линия, vt — вентральная трубка, f — фурка, re — зацепка, go — генитальное отверстие, ao — анальное отверстие, cx1–cx3 — тазики ног, sx1–sx3 — субкоксы ног, PAO — постантеннальный орган, as — анальные шипы.

Results

General anatomy

The body length is 0.6–1.33 mm (M = 0,7, n = 5). The first segment of the abdomen has a ventral tube, the last has small straight anal spines (Fig. 1). The tergites are well developed. The head has a postantennal organ, consisting of 4–5 lobes and twice the size of the ocellus.

The internal organs are arranged as follows: the brain and suboesophageal ganglion collectively occupy a substantial portion of the head capsule (Fig. 2). The thoracic region houses the thoracic musculature, ganglia, foregut, midgut, and the anterior part of the reproductive system. The abdominal region contains the abdominal muscles, midgut and hindgut, and ovaries. The posterior thoracic ganglion of the nervous system extends partially into the abdominal region, where it merges with the fused abdominal ganglia. Total body volume measures 11.7 nL.

Skeleton

Tagmosis is remarkably similar to the one seen in Insecta. The body is divided into a head, thorax (3 segments) and abdomen (6 segments). The head has six fused segments: the labral, the antennal, the postantennal (fused with antennal), the mandibular, the maxillary, and the labial. The thorax has well developed tergites; sternites and pleurites are barely distinguishable. Each leg is made up of a subcoxa, coxa, trochanter, femur, tibiotarsus, pretarsus with a claw, and empodial appendage. The first segment of abdomen bears a ventral tube, the third bears the retinaculum, the fourth bears a furca, and the fifth bears a genital opening. The cuticle thickness is 0.5–4.8 µm (M = 1.58, n = 80).

The endoskeleton is represented by the pseudotentorium of the head, endosternites, endotergites, endopleurites, antecostas and furcae of the thorax, and apodemes of the abdomen.

The pseudotentorium consists of a base — the body, and processes extending from it.

The volume of the skeletal structures is 0.28 nL (2.38% of the total body volume).

Digestive and excretory systems

The digestive system comprises a straight, unbranched tract divided into the foregut, midgut, and hindgut, lined with a peritrophic membrane (Fig. 3). The foregut originates at the oral cavity and transitions into a pharynx, into which the paired salivary glands duct empty. The salivary glands open into the pharynx. A pair of salivary glands is located in the head; their ducts open into the oral cavity posterior to the maxillae, and the glands terminate in the middle region of the head. The pharynx connects to an oesophagus (diameter: 5.44 µm), which traverses the thorax to reach the first thoracic segment. At this level, a cardiac valve demarcates the transition to the midgut, which exhibits an oval cross-section (height: 38.4 μm) and dorsoventral flattening. The midgut-hindgut junction occurs at the fourth abdominal segment (pyloric region), marked by a prominent ring of circular musculature. The intestinal lumen narrows progressively from 36.7 μm at the pyloric junction to 8.87 μm in the hindgut. The rectum, situated in the fifth abdominal segment, has a diameter of 29.2 μm, with the digestive tract terminating at the anus in the sixth abdominal segment.

The excretory system consists of paired labial nephridia located in the posterior cephalic region. Each nephridium comprises a dorsally situated reservoir connected to a convoluted tubule, which transitions into a straight nephridial duct that empties into the oral cavity. Notably, the canal lacks secondary looping or branching.

The digestive system occupies 0.11 nL (0.91% of total body volume), while the excretory system accounts for 0.03 nL (0.29%).

Nervous system

The nervous system consists of a supraoesophageal ganglion (brain), suboesophageal ganglion, and three thoracic ganglia (Fig. 4). The brain originates at the antennal bases, extending posteriorly but terminating anterior to the cephalothoracic junction. The suboesophageal ganglion is located in the ventral cephalic region, spanning from the mid-head to the cephalothoracic boundary. The thoracic ganglia are interconnected by elongated connectives traversing the intersegmental regions (one per thoracic segment). Abdominal ganglia are fused with the third thoracic ganglion.

The nervous system occupies 0.33 nL (2.8% of total body volume), with the brain accounting for 0.12 nL (1.04%).

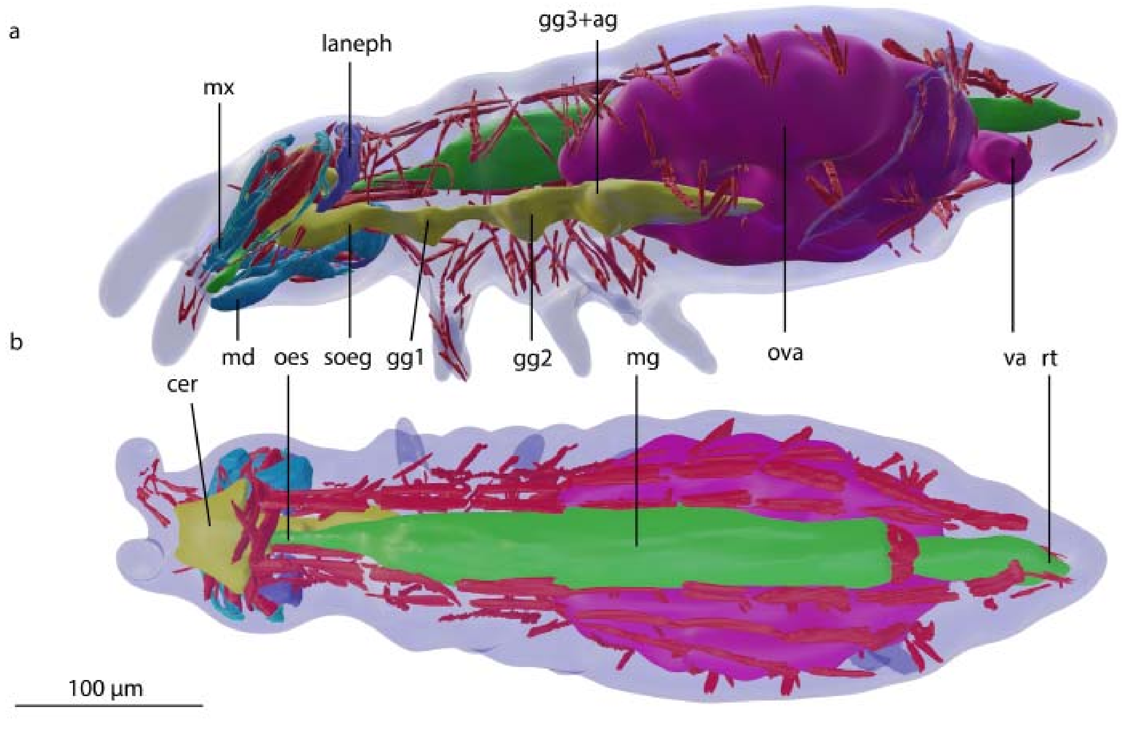

Fig. 2. General anatomy of *Hypogastrura serrata*, 3D. Colors: blue — mouthparts, light blue — pseudotentorium, green — digestive system, yellow — central nervous system, red — musculature, pink — reproductive system, violet — excretory system. A — lateral internal view; b — dorsal view; cer — brain; gg1, 2, 3 + ag — pro-, meso-, and metathoracic + abdominal ganglia; laneph — labial nephridia; mg — midgut; md — mandible; mx — maxilla; oes — oesophagus; ov — ovaries; rt — rectum; soeg — suboesophageal ganglion; va — vagina. Antennal muscles are shown on the right side only; leg muscles are shown in the left foreleg only.

Рис. 2. Общая анатомия *Hypogastrura serrata*, 3D. Цвета: синий — ротовые части, голубой — псевдотенториум, зеленый — пищеварительная система, желтый — центральная нервная система, красный — мускулатура, розовый — половая система, фиолетовый — выделительная система. A — внутреннее строение, латерально; b — дорсально; cer — мозг; gg1, 2, 3 + ag — передне-, средне- и заднегрудной + брюшной ганглии; laneph — лабиальный нефридий; mg — средняя кишка; md — мандибула; mx — максилла; oes — пищевод; ov — яичники; rt — ректум; soeg — подглоточный ганглий; va — влагалище. Антеннальная мускулатура показана только на правой стороне тела; мышцы ног показаны только на левой передней ноге.

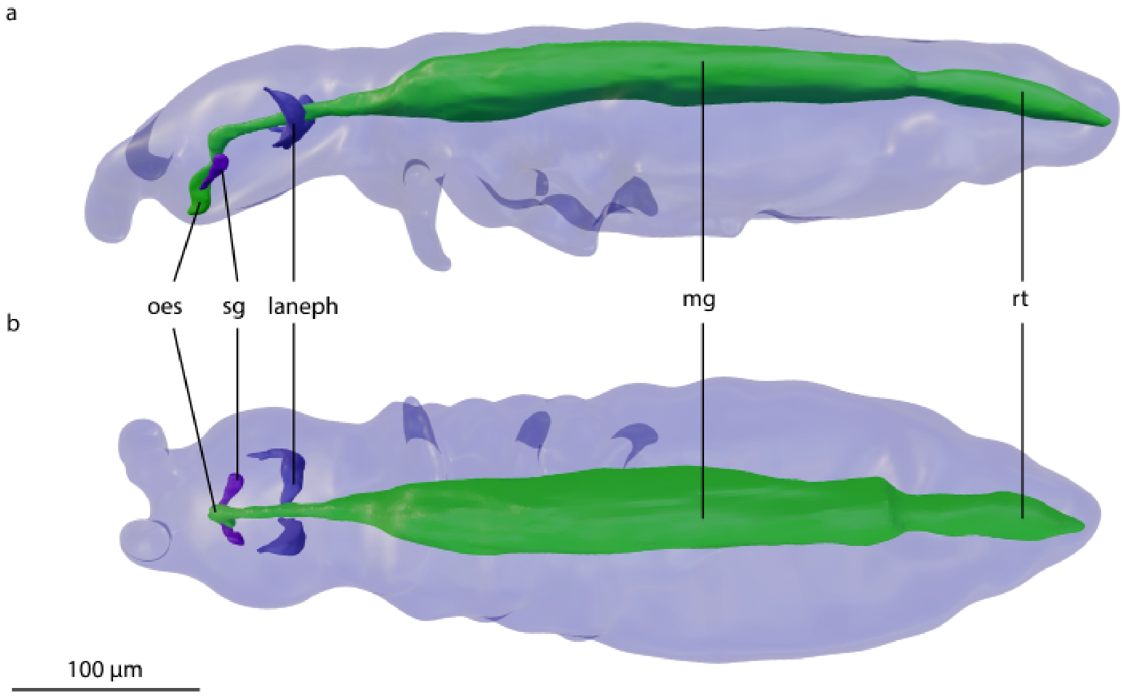

Fig. 3. Digestive and excretory systems of *Hypogastrura serrata*, 3D. A — lateral internal view; b — dorsal view. Oes — oesophagus; sg — salivary glands; laneph — labial nephridia, mg — midgut, rt — rectum.
Рис. 3. Пищеварительная и выделительная системы *Hypogastrura serrata*, 3D. A — внутреннее строение, латерально; b — дорсально. Oes — пищевод; sg — слюнные железы; laneph — лабиальные нефридии, mg — средняя кишка, rt — ректум.

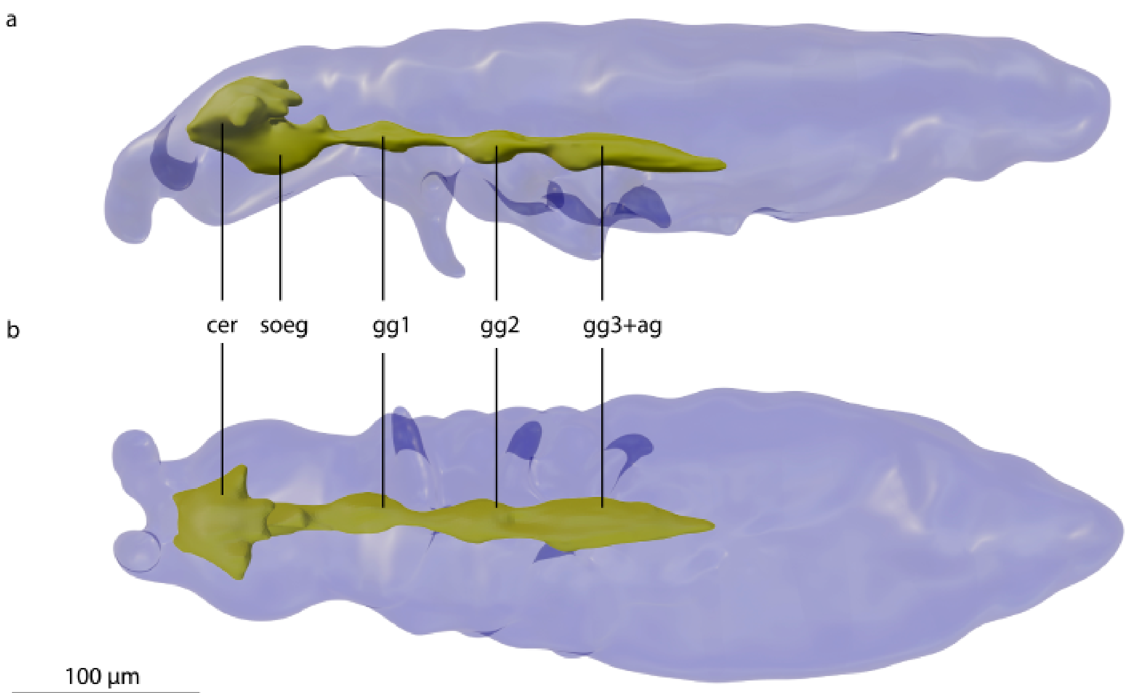

Fig. 4. Nervous system of *Hypogastrura serrata*, 3D. A — lateral internal view; b — dorsal view. Cer — brain; soeg — suboesophageal ganglion; gg1, 2, 3 + ag — pro-, meso-, and metathoracic + abdominal ganglia.
Рис. 4. Нервная система *Hypogastrura serrata*, 3D. A — внутреннее строение, латерально; b — дорсально. Cer — мозг; soeg — подглоточный ганглий; gg1, 2, 3 + ag — передне-, средне- и заднегрудной + брюшной ганглии.

Muscular system

The cephalic musculature comprises mandibular, pharyngeal, pseudotentorial, and antennal muscle groups (Fig. 5, table 1).

Table 1. Head muscle origins and insertions.
Таблица 1. Отхождение и прикрепление мышц головы.

Abbrev.	Origin	Insertion
Mn1	Cuticle of the anterior third of the head capsule (anterioventral part)	Mandible, dorsal to Mn2
Mn2	Cuticle of the anterior third of the head capsule (anterioventral part)	Mandible, ventral to Mn1
Mn3	Pseudotentorium	Mandible, at the insertion site of Mn2
Mn4.chm	Posterior surface of the frons, crossing the median plane	Ventroposterior area, outer angle of the large triangular opening of the mandible
Mn5	Head endoskeleton, frons area	Base of the pseudotentorium
Mn6	Head endoskeleton, occipital region	Posterior surface of the mandible, proximal to the molar plate
Mn7	Head endoskeleton, occipital region	Posterior surface of the mandible, proximal to Mn6
Mn8	Head endoskeleton, occipital region, proximal to Mn7	Medial part of the mandible, proximal to Mn7
Mn9	Lateral to the midpoint of the dorsal surface of the head	Inner side of the basal ring of the mandible
Mn10	Projection of the endoskeleton on the dorsal side of the head capsule, medial upper chitinous process near the base of the head, lateral to Mn7	Posteroventral edge of the mandible
Mn11	Head endoskeleton in the occipital region	Base of the mandible
Lb1	Pseudotentorium, Folsom arms	Outer side of the labium, distally
Lb2	Head endoskeleton, occipital region, distal to Mn8	Proximal edge of the labium
Lb3	Base of the pseudotentorium in the middle of the head	Medial part of the labium, dorsally
Lb4	Base of the pseudotentorium in the middle of the head	Medial part of the labium, dorsally, distal to Lb3
Mx1–3	Cuticle of the head capsule at the neck transition, occipital region	Middle part of the maxilla
Mx4	Pseudotentorium	Stipes of the maxilla
Mx5.chm	Concave part of the cardo	Head endoskeleton in the frons area
Mx6	Dorsal part of the head	Basal part of the mandible
Mx7	Dorsal part of the head	Basal part of the mandible
Mx8	Dorsal part of the head	Base of the maxilla
Mx9	Posterodorsolateral part of the head, anterior to Mx10	Outer edge of the maxilla, anterior to Mx10
Mx10	Posterodorsolateral part of the head, posterior to Mx9	Outer edge of the maxilla, posterior to Mx9
Mx11	Head capsule, cheek region	Medial part of the maxilla
Dlm.1	Occiput, anterior to Dlm.1	Medial surface of the frons, anterior to Dlm.1
Dlm.2	Occiput, medial to Dlm.2	Medial surface of the frons, medial to Dlm.2
Hy1	Anteroventral part of the head capsule	Hypopharynx
Fl	Base of the scapus, dorsal to L.fl.	Base of the pseudotentorium, in the center of the head, just below the supraesophageal ganglion
L.fl.	Base of the scapus, deeper than dp	Base of the pseudotentorium, in the center of the head, just below the supraesophageal ganglion
Ph1	Medial surface of the anterior head margin	Esophagus
Pst.1	Medial surface of the posterior head margin, anterior to Pst.2	Body of the pseudotentorium, anterior to Pst.2
Pst.2	Medial surface of the posterior head margin, posterior to Pst.2	Body of the pseudotentorium, posterior to Pst.2
Pst.3	Head capsule in the vertex region	Lateral projections of the pseudotentorium, from above
Pst.4	Cuticle of the head capsule	Base of the tentorium, in the upper third of the head
Pst.5	Medial surface of the anterior head margin	Body of the pseudotentorium

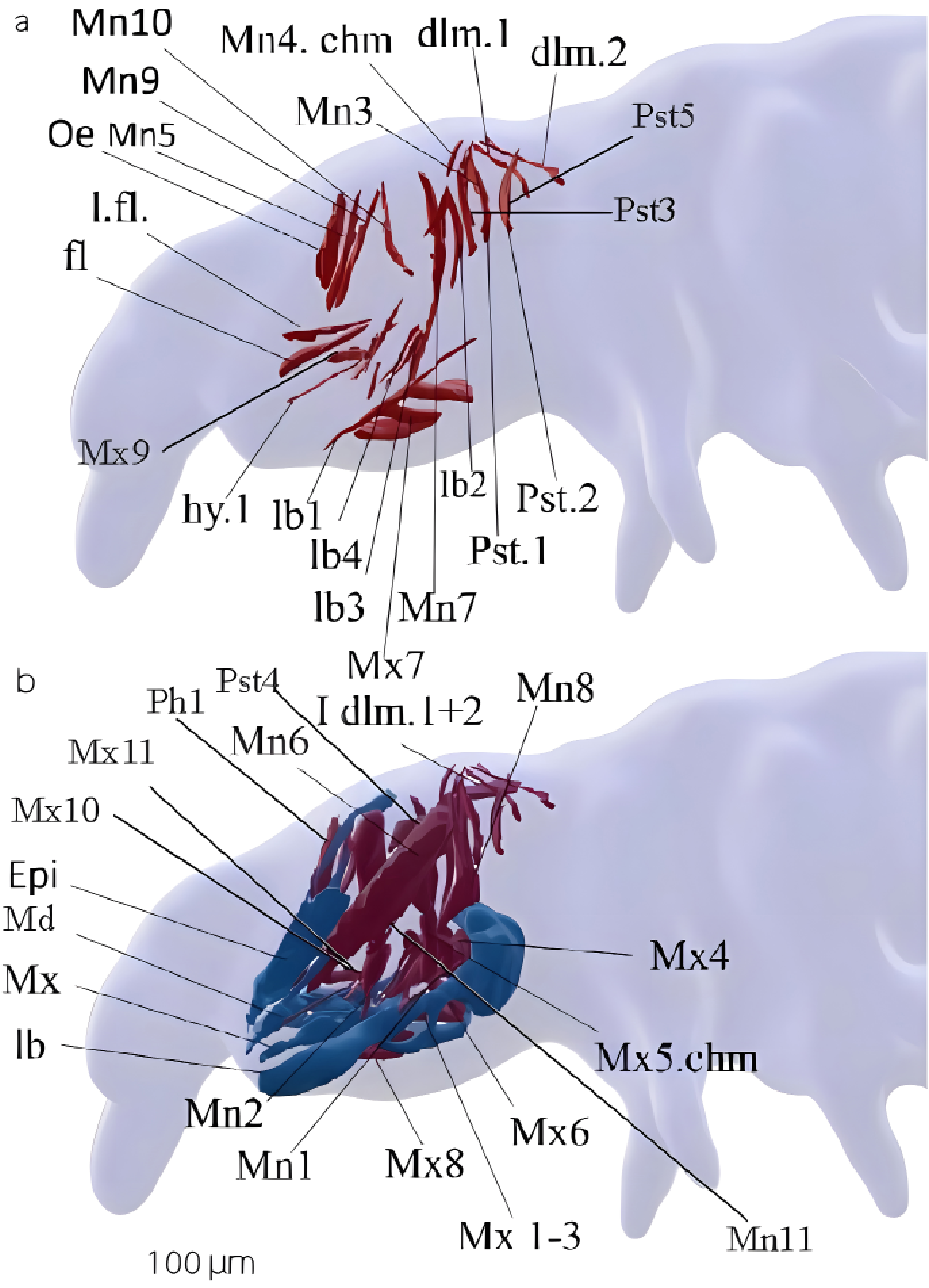

Fig. 5. Musculature of head in *Hypogastrura serrata*, 3D. A — lateral internal view; b — lateral internal view with mouthparts. Md — mandibula; mx — maxilla; epi — epipharynx, lb — labium.

Рис. 5. Мускулатура головы *Hypogastrura serrata*, 3D. A — внутреннее строение, латерально; b — внутреннее строение, латерально, с ротовыми частями. Md — мандибула; mx — максилла; epi — эпифаринкс, lb — нижняя губа.

Antennal musculature is represented by ten distinct muscles (Fig.6, table 2): four extrinsic muscles (lv, ex.1, ex.2, ex.3) and six intrinsic muscles (lv.4, dp.4, ex.4, lv.3, dp., l.fl.2).

Table 2. Antennal muscle origins and insertions.
Таблица 2. Отхождение и прикрепление антеннальных мышц.

Abbrev.	Origin	Insertion
lv	Body of the pseudotentorium	Dorsal edge of the first antennal segment, slightly closer to the outer margin
lv.3	Base of the second antennal segment	Base of the third antennal segment
lv.4	Dorsal side of segment III, approximately one-quarter length from its apex	Base of the fourth segment
dp.1	Base of the scape	Base of the first segment
dp.4	Laterally from the base of the third segment	Ventrally to the base of the fourth segment
l.fl.2	Base of the third antennal segment	Base of the first segment
ex.1	Base of the basal antennal segment	Inner side of the first antennal segment
ex.2	Base of the first antennal segment	Inner side of the second antennal segment
ex.3	Posterior region of the head capsule floor	Inner side of the basal antennal segment
ex.4	Base of the second antennal segment	Base of the third antennal segment

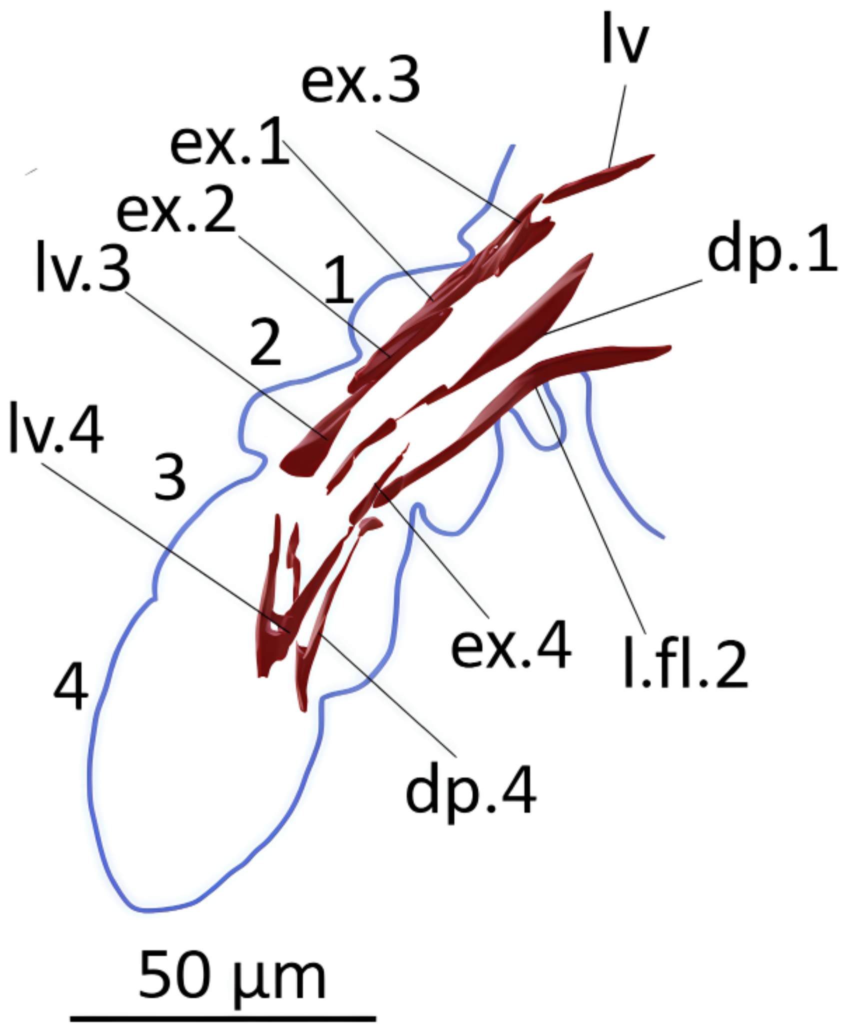

Fig. 6. Musculature of antenna in *Hypogastrura serrata*, 3D.
Рис. 6. Мускулатура антенн *Hypogastrura serrata*, 3D.

The thorax contains 21 paired prothoracic muscles, 20 paired mesothoracic muscles, and 22 paired metathoracic muscles (Fig.7, table 3).

Table 3. Thorax muscle origins and insertions.
Таблица 3. Отхождение и прикрепление грудных мышц.

Abbrev.	Origin	Insertion
I dlm.1	Inner edge of the postocciput, medially to dlm.2.neck	Antecosta I (of the first thoracic segment), medially to dlm.2.neck
I dlm.2	Inner edge of the postocciput, laterally to dlm.2.neck	Antecosta I (of the first thoracic segment), laterally to dlm.2.neck
Lb vlm.2	Lateral surface of the foreleg coxa	Anterior surface of the furca-like structure, together with I.vlm.5
I vlm.1	Posterior arms of the pseudotentorium	Endosternite between the pro- and mesothorax
I vlm.2	Posterior arms of the pseudotentorium, laterally to I vlm.4	Anterior surface of the foreleg coxa, laterally to I vlm.4
I vlm.3	Posterior arms of the pseudotentorium, medially to I.vlm.2	Endosternite between the pro- and mesothorax, medially to I.vlm.2
I vlm.4	Posterior part of the pseudotentorium, lateral to I vlm.5	Endosternite of the prothorax, lateral to I vlm.5
I vlm.5	Posterior part of the pseudotentorium, medial to I vlm.4	Endosternite of the prothorax, medial to I vlm.4
I ism.1	Antecosta I	Posterior arms of the pseudotentorium, together with I.ldvm.2
I ism.2	Edge of the postocciput	Posterior arms of the pseudotentorium
I dvm.1	Antecosta I	Anterolateral edge of the foreleg coxa
I dvm.2	Posterior arms of the pseudotentorium	Edge of the postocciput, together with ism.5
I ldvm.1	Edge of the postocciput, together with I ism.5, I dvm.2	Posterior arms of the pseudotentorium (posterior to Lb.dvm.1)
I ldvm.2	Anterolateral foreleg coxa	Posterior arms of the pseudotentorium, together with I ldvm.1
I ldvm.3	Anterolateral foreleg coxa, medial to I ldvm.2	Posterior arms of the pseudotentorium, medial to I ldvm.2
Lb dvm.1	Edge of the postocciput, together with I ism.5, I dvm.2, I ldvm.1, lateral to Lb dvm.2	Posterior arms of the pseudotentorium, upper edge, lateral to Lb dvm.2
Lb dvm.2	Edge of the postocciput, together with I ism.5, I dvm.2, I ldvm.1, medial to Lb dvm.1	Posterior arms of the pseudotentorium, upper edge, medial to Lb dvm.1
I scm.1	Posterior edge of the furca-like structure, medial to I scm.4	Lateral part of the foreleg coxa, medial to I scm.4
I scm.2	Posterior edge of the furca-like structure, medial to I scm.1, I scm.4	Lateral part of the foreleg coxa, medial to I scm.1, I scm.4
I scm.3	Posterior edge of the furca-like structure, medial to I scm.1, I scm.4, I scm.2	Lateral part of the foreleg coxa, medial to I scm.1, I scm.4, I scm.2
I scm.4	Posterior edge of the furca-like structure, lateral to I scm.1	Lateral part of the foreleg coxa, lateral to I scm.1
II dlm.1	Antecosta I, lateral to I dlm.2	Antecosta II, lateral to I dlm.2
II dlm.2	Antecosta I, medial to I dlm.2	Antecosta II, medial to I dlm.2
II vlm.1	Endosternite of the prothorax	Endosternite of the mesothorax
II vlm.2	Endosternite of the prothorax, below II vlm.1	Endosternite of the mesothorax, below II vlm.1
II ldvm.1	Antecosta III	Endosternite of the mesothorax, anterior to II dvm.5.1.-5.2
II ldvm.2	Endopleurite between the pro- and mesothorax, anterior to II ldvm.3	Anterolateral part of the midleg coxa
II ldvm.3	Endopleurite between the pro- and mesothorax, posterior to II ldvm.2	Posterolateral part of the midleg coxa
II ldvm.4	Midpart of the lateral section of the mesothoracic endosternite	Anterolateral part of the midleg coxa
II scm.1	Posterior part of the furca-like structure	Anterolateral part of the midleg coxa
II scm.2	Anterior part of the furca-like structure	Posterolateral part of the midleg coxa, lateral to II ldvm.3
II scm.3	Anterior part of the furca-like structure, lateral to II scm.2	Posterolateral part of the midleg coxa, lateral to II scm.2
II scm.4	Anterior part of the furca-like structure, medial to II scm.2	Posterolateral part of the midleg coxa, medial to II scm.2
II scm.5	Endopleurite between the pro- and mesothorax, anterior to II ldvm.2	Anterolateral part of the midleg coxa
II scm.6	Endopleurite between the pro- and mesothorax, medial to II scm.5.1-5.2	Anterolateral part of the midleg coxa, anterior to II scm.5.1-5.2
II ism.2	Anterior edge of the mesonotum, together with II ism.3	Posterolateral edge of the midleg coxa, together with II ism.3
II ism.3	Anterior edge of the mesonotum, together with II ism.2	Posterolateral edge of the midleg coxa, together with II ism.2
II ism.4	Midpart of the lateral section of the mesonotum	Posterior edge of the midleg coxa
II dvm.4	Endopleurite of the mesothorax, lateral to II dvm.5	Posterolateral surface of the midleg coxa, lateral to II dvm.5
II dvm.5	Endopleurite of the mesothorax, medial to I dvm.4	Posterolateral surface of the midleg coxa, medial to II dvm.4
II dvm.6	Endopleurite between the pro- and mesothorax	Posterolateral surface of the furca-like structure
III dvm.4	Anterolateral part of the metanotum	Upper edge of the subcoxa, anterior to III dvm.3
III dvm.5	Endosternite of the mesothorax, medial to III vlm.1	Posterolateral part of the hindleg coxa, lateral to III scm.5
III ldvm.2	Endopleurite between the meso- and metathorax, together with II dvm.4	Anterolateral part of the hindleg coxa
III ldvm.3	Endosternite of the mesothorax, anterior to III dvm.5	Anterolateral part of the hindleg coxa, together with III scm.3
III scm.1	Endopleurite between the metathorax and abdomen, lateral to III scm.2	Posterolateral part of the hindleg coxa, together with III scm.2
III scm.2	Endopleurite between the metathorax and abdomen, medial to III scm.2	Anterolateral part of the hindleg coxa, together with III scm.3

Table 3 (*continued*).
Таблица 3 (*окончание*).

Abbrev.	Origin	Insertion
III scm.3	Endopleurite between the meso- and metathorax, together with III ldvm.2, medial to III scm.4	Posterolateral part of the hindleg coxa, together with III scm.1
III scm.4	Endopleurite between the meso- and metathorax, together with III ldvm.2, lateral to III scm.3	Anterior part of the hindleg coxa, together with III scm.5
III scm.5	Anterolateral part of the metathoracic endopleurite	Upper edge of the subcoxa, anterior to III dvm.5
III dlm.1	Antecosta II, lateral to III dlm.2	Antecosta III, lateral to III dlm.2
III dlm.2	Antecosta II, medial to III dlm.2	Antecosta III, medial to III dlm.2
III ism.1	Antecosta III	Endosternite of the metathorax
III ism.2	Antecosta III, medial to III ism.1	Endosternite of the metathorax, medial to III ism.1
III ism.3	Posterolateral part of the furca-like structure, posterior to III dvm.4	Endopleurite between the meso- and metathorax, posterior to III dvm.4
III dvm.1	Midpart of the lateral section of the mesonotum, anterior to III dvm.2	Anterolateral part of the furca-like structure, anterior to III dvm.2
III dvm.2	Midpart of the lateral section of the mesonotum, posterior to III dvm.2	Anterolateral part of the furca-like structure, posterior to III dvm.2
III dvm.6	Midpart of the metathoracic endosternite, anterior to III dvm.7	Midpart of the metathoracic endopleurite, anterior to III dvm.7
III dvm.7	Midpart of the metathoracic endosternite, posterior to III dvm.7	Midpart of the metathoracic endopleurite, posterior to III dvm.7
III dvm.4	Posterolateral part of the furca-like structure, anterior to III ism.3	Endopleurite between the meso- and metathorax, anterior to III ism.3
III dvm.5	Midpart of the lateral section of the mesonotum, posterior to II dvm.2	Endosternite of the metathorax, posterior to III ism.2
III vlm.1	Endosternite of the mesothorax, lateral to III vlm.2	Endosternite of the metathorax, lateral to III vlm.2
III vlm.2	Endosternite of the mesothorax, medial to III vlm.1	Endosternite of the metathorax, medial to III vlm.1

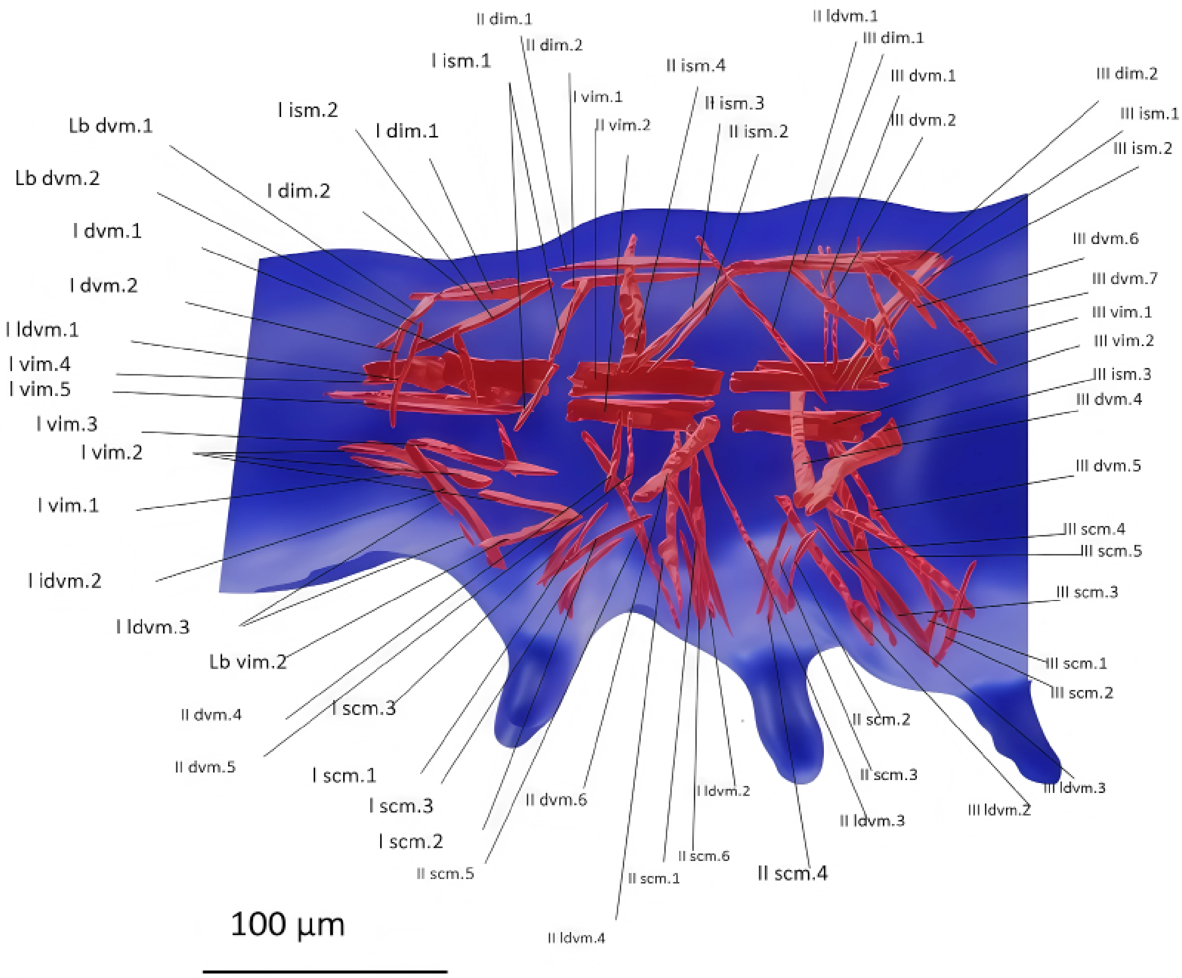

Fig. 7. Musculature of thorax in *Hypogastrura serrat*a, 3D.
Рис. 7. Мускулатура груди *Hypogastrura serrata*, 3D.

Leg musculature is organized into eight muscles spanning five functional categories: extensors, flexors, adductors, depressors, and retractors (Fig. 8, table 4).

Table 4. Leg muscle origins and insertions.
Таблица 4. Отхождение и прикрепление мышц ног.

Abbrev.	Origin	Insertion
Ex	Tendon of the coxa	Anterolateral part of the femur, anterior to dp.1
Lev.1	Tendon of the coxa, posterior to ex.	Tendon of the trochanter
Red	Tendon of the coxa	Tendon of the femur
Fl	Tendon of the femur	Tendon of the tibiotarsus
Dp.1	Tendon of the trochanter	Base of the pretarsus, anterior to dp.2
Dp.2	Tendon of the tibiotarsus	Base of the pretarsus, posterior to dp.2

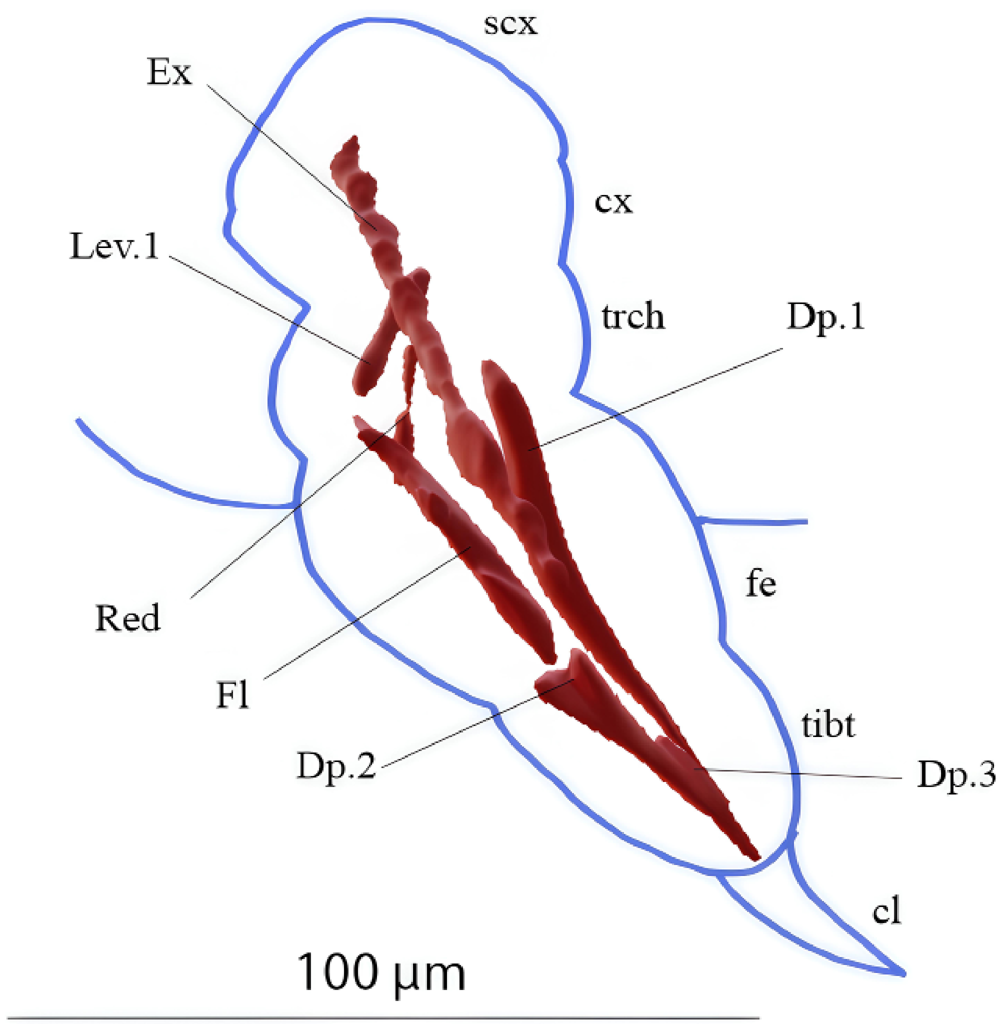

Fig. 8. Musculature of leg in *Hypogastrura serrata*, 3D. Ex — extensors, lev — levators, red — reductors, dp — depressors, fl — flexors. Sections of the leg: scx — subcoxae, cx — coxae, trch — trochanter, fe — femur, tibt — tibiotarsus, cl — claws.
Рис. 8. Мускулатура ног *Hypogastrura serrata*, 3D. Ex — мышцы разгибатели, lev — приводящие мышцы, red — мышцы редукторы, dp — опускающие мышцы, fl — мышцы сгибатели. Отделы ноги: scx — предтазик, cx — тазик, trch — вертлуг, fe — бедро, tibt — голенелапка, cl — коготок.

The abdomen harbors 88 pairs of muscles, with specialized subsets comprising 20 ventral tube muscles and 25 furca (jumping apparatus) muscles (Fig. 9, table 5).

Table 5. Abdomen muscle origins and insertions.
Таблица 5. Отхождение и прикрепление брюшных мышц.

Abbrev.	Origin	Insertion
AI dlm.1	Antecosta III, lateral to AI dlm.2	Antecosta IV, lateral to AI dlm.2
AI dlm.2	Antecosta III, medial to AI dlm.2	Antecosta IV, medial to AI dlm.2
AI ism.1	Antecosta IV, anterior to AI ism.2	Posterolateral part of the furca-like structure, anterior to AI ism.2
AI ism.2	Antecosta IV, posterior to AI ism.1	Posterolateral part of the furca-like structure, posterior to AI ism.1
AI dvm.1	Middle part of the first abdominal segment, anterior to AI dvm.2	Lateral part of the furca-like structure, anterior to AI dvm.2
AI dvm.2	Middle part of the first abdominal segment, posterior to AI dvm.1	Lateral part of the furca-like structure, posterior to AI dvm.1
AI dvm.3	Antecosta III, together with III dlm.1, III dlm.2	Upper margin of the subcoxa, posterior to III dvm.4
AI dvm.4	Middle part of the first abdominal segment, posterior to AI dvm.2	Tendon, together with AI dvm.5
AI dvm.5	Antecosta IV, lateral to AI dvm.3	Tendon, together with AI dvm.4
AI dvm.6	Posterolateral part of the furca-like structure, posterior to III dvm.1	Endopleurite between the metathorax and abdomen, posterior to III dvm.1
AI dvm.VT	Endosternite	Lateral surface of the ventral tube, anterior to AI lm.1
AI dm.1	Furca-like structure, together with AI dm.3	Anterior surface of the ventral tube, together with AI dm.3
AI dm.2	Endosternite	Posterior surface of the ventral tube
AI dm.3	Furca-like structure, together with AI dm.1	Anterior surface of the ventral tube, together with AI dm.1
AI dm.4	Endosternite, medial to AI dm.6	Posterolateral surface of the ventral tube, medial to AI dm.6
AI dm.5	Endosternite	Posterior surface of the ventral tube
AI dm.6	Endosternite, lateral to AI dm.4	Posterolateral surface of the ventral tube, lateral to AI dm.4
AI lm.1	Tendon	Lateral surface of the ventral tube, posterior to AI dvm.VT
AI vlm.1	Endosternite	Intersegmental area between segments 2 and 3
AI vlm.2	Posterolateral part of the furca-like structure of the first abdominal segment, lateral to III vlm.2	Anterolateral part of the furca of the second abdominal segment, lateral to III vlm.2
AI vlm.3	Endosternite of the mesothorax, lateral to III vlm.3	Upper margin of the subcoxa of the hind leg
AI vlm.4	Endosternite of the mesothorax of the first abdominal segment, medial to III vlm.2	Endosternite of the metathorax of the second abdominal segment
AI vlm.5	Endosternite of the mesothorax of the first abdominal segment, lateral to III vlm.1	Endosternite of the metathorax of the second abdominal segment, lateral to III vlm.1
AI ldvm.1	Midpart of the endosternite of the metathorax, anterior to III dvm.4	Endopleurite between the metathorax and abdomen, together with III dvm.1
AII dlm.1	Antecosta IV, medial to AII dlm.2	Antecosta V, medial to AII dlm.2
AII dlm.2	Antecosta IV, lateral to AII dlm.2	Antecosta V, lateral to AII dlm.2
AII ism.1	Midpart of the sternite of the second abdominal segment, anterior to AII ism.2	Tendon, anterior to AII ism.2
AII ism.2	Midpart of the sternite of the second abdominal segment, posterior to AII ism.1	Tendon, posterior to AII ism.1
AII dvm.1	Antecosta IV, posterior to AII dvm.2	Tendon, posterior to AII dvm.2
AII dvm.2	Antecosta IV, anterior to AII dvm.1	Tendon, posterior to AII dvm.1
AII dvm.3	Midpart of the lateral surface of the segment	Midpart of the sternite
AII vlm.1	Endosternite	Intersegmental area between the sternites of segments 2 and 3 of the abdomen
AII vlm.2	Endosternite, below AII vlm.3	Intersegmental area between the sternites of segments 2 and 3 of the abdomen, below AII vlm.3
AII vlm.3	Endosternite, below AII vlm.1	Intersegmental area between the sternites of segments 2 and 3 of the abdomen, below AII vlm.1
AII vlm.4	Endosternite, above AII vlm.1	Intersegmental area between the sternites of segments 2 and 3 of the abdomen, above AII vlm.1
AII vlm.6	Endosternite, together with AII vlm.7, AII vlm.8	Intersegmental area between segments 2 and 3
AII vlm.7	Endosternite, together with AII vlm.6, AII vlm.8	Intersegmental area between segments 2 and 3

Table 5 (*continued*).
Таблица 5 (*продолжение*).

Abbrev.	Origin	Insertion
AII vlm.8	Endosternite, together with AII vlm.6, AII vlm.7	Intersegmental area between segments 2 and 3
AII dvm.4	Posterior part of the segment	Intersegmental area, together with AII dvm.5-7
AII dvm.5	Posterior part of the segment	Intersegmental area, together with AII dvm.4, AII dvm.6, AII dvm.7
AII dvm.6	Midpart of the segment, anterior to AII dvm.7	Intersegmental area, together with AII dvm.4, AII dvm.5, AII dvm.7
AII dvm.7	Midpart of the segment, posterior to AII dvm.6	Intersegmental area, together with AII dvm.4-6
AIII dlm.1	Antecosta V, medial to AII dlm.2	Antecosta VI, medial to AII dlm.2
AIII dlm.2	Antecosta V, lateral to AII dlm.2	Antecosta VI, lateral to AII dlm.2
AIII ism.1	Midpart of the sternite of the third abdominal segment, anterior to AIII ism.2	Tendon, anterior to AIII ism.2, AIII dvm.1-2
AIII ism.2	Midpart of the sternite of the third abdominal segment, posterior to AIII ism.1	Tendon, posterior to AIII ism.1, together with AIII dvm.1-2
AIII dvm.1	Midpart of the segment, anterior to AIII dvm.2	Tendon, together with AIII ism.1-2, AIII dvm.2
AIII dvm.2	Midpart of the segment, posterior to AIII dvm.1	Tendon, together with AIII ism.1-2, AIII dvm.1
AIII dvm.3	Midpart of the segment, posterior to AIII dvm.5	Intersegmental area, together with AIII dvm.4-6
AIII dvm.4	Midpart of the segment, anterior to AIII dvm.5	Intersegmental area, together with AIII dvm.3, AIII dvm.5-6
AIII dvm.5	Midpart of the segment, posterior to AIII dvm.4	Intersegmental area, together with AIII dvm.3-4, AIII dvm.6
AIII dvm.6	Midpart of the segment, anterior to AIII dvm.5	Intersegmental area, together with AIII dvm.3-5
AIII dvm.7	Midpart of the lateral surface of the segment	Midpart of the sternite
AIII vlm.8	Endosternite, together with AIII vlm.9-10	Intersegmental area between segments 3 and 4, together with AIII vlm.9-10
AIII vlm.9	Endosternite, together with AIII vlm.8, AIII vlm.10	Intersegmental area between segments 3 and 4, together with AIII vlm.8, AIII vlm.10
AIII vlm.10	Endosternite, together with AIII vlm.8-9	Intersegmental area between segments 3 and 4, together with AIII vlm.8-9
AIII vlm.11	Endosternite, together with AIII vlm.12-13	Intersegmental area between segments 3 and 4, together with AIII vlm.12-13
AIII vlm.12	Endosternite, together with AIII vlm.11, AIII vlm.13	Intersegmental area between segments 3 and 4, together with AIII vlm.11, AIII vlm.13
AIII vlm.13	Endosternite, together with AIII vlm.11-12	Intersegmental area between segments 3 and 4, together with AIII vlm.11-12
AIII vlm.14	Endosternite, together with AIII vlm.15	Intersegmental area between segments 3 and 4, together with AIII vlm.15
AIII vlm.15	Endosternite, together with AIII vlm.14	Intersegmental area between segments 3 and 4, together with AIII vlm.14
AIV dlm.1	Antecosta VI, lateral to AIV dlm.2	Antecosta VII, lateral to AIV dlm.2
AIV dlm.2	Antecosta VI, medial to AIV dlm.1	Antecosta VII, medial to AIV dlm.1
AIV dvm.1	Midpart of the segment, anterior to AIV dvm.2	Intersegmental area, together with AIV dvm.2
AIV dvm.2	Midpart of the segment, posterior to AIV dvm.1	Intersegmental area, together with AIV dvm.1
AIV dvm.3	Midpart of the segment, posterior to AIV dvm.2	Intersegmental area
AIV ldvm.1	Upper anterior margin of the segment, anterior to AIV ldvm.2	Anterolateral margin of the ventral surface of the segment, anterior to AIV ldvm.2
AIV ldvm.2	Upper anterior margin of the segment, posterior to AIV ldvm.1	Anterolateral margin of the ventral surface of the segment, posterior to AIV ldvm.1
AIV ldvm.3	Upper anterior margin of the segment, anterior to AIV ldvm.2	Anterolateral margin of the ventral surface of the segment, anterior to AIV ldvm.2
AIV ldvm.4	Anterolateral margin of the segment, posterior to AIV ldvm.5	Anterolateral margin of the ventral surface of the segment, posterior to AIV ldvm.5
AIV ldvm.5	Anterolateral margin of the segment, anterior to AIV ldvm.4	Anterolateral margin of the ventral surface of the segment, anterior to AIV ldvm.4
AIV vlm.1	Endosternite, together with AIV vlm.2	Intersegmental area between segments 4 and 5, together with AIV vlm.2
AIV vlm.2	Endosternite, together with AIV vlm.1	Intersegmental area between segments 4 and 5, together with AIV vlm.1
AIV vlm.3	Endosternite, together with AIV vlm.5-6	Intersegmental area between segments 4 and 5, together with AIV vlm.5-6

Table 5 (*continued*).
Таблица 5 (*окончание*).

Abbrev.	Origin	Insertion
AIV vlm.4	Endosternite, together with AIV vlm.7	Intersegmental area between segments 4 and 5, together with AIV vlm.7
AIV vlm.5	Endosternite, together with AIV vlm.3, AIV vlm.6	Intersegmental area between segments 4 and 5, together with AIV vlm.3, AIV vlm.6
AIV vlm.6	Endosternite, together with AIV vlm.3, with AIV vlm.5	Intersegmental area between segments 4 and 5, together with AIV vlm.3, with AIV vlm.5
AIV vlm.7	Endosternite, together with AIV vlm.4	Intersegmental area between segments 4 and 5, together with AIV vlm.4
AV dlm.1	Antecosta VII, medial to AII dlm.2	Antecosta VIII, medial to AII dlm.2
AV dlm.2	Antecosta VII, medial to AII dlm.1	Antecosta VIII, medial to AII dlm.1
AV ism.1	Midpart of the upper margin of the segment	Intersegmental area, its lateral part
AV ldvm.1	Endosternite, together with AV vlm.1	Intersegmental area, together with AV vlm.1
AV vlm.1	Endosternite, together with AV ldvm.1	Intersegmental area, together with AV ldvm.1
AVI dvm.1	Upper posterior margin of the segment, together with AVI dvm.2-3	Rectum
AVI dvm.2	Upper posterior margin of the segment, together with AVI dvm.1, AVI dvm.3	Rectum
AVI sm.1	Sternum, posterior to AVI sm.2	Rectum, posterior to AVI sm.2
AVI sm.2	Sternum, anterior to AVI sm.1	Rectum, anterior to AVI sm.1
AVI vlm.1	Lower lateral margin of the segment	Rectum, below AVI sm.1

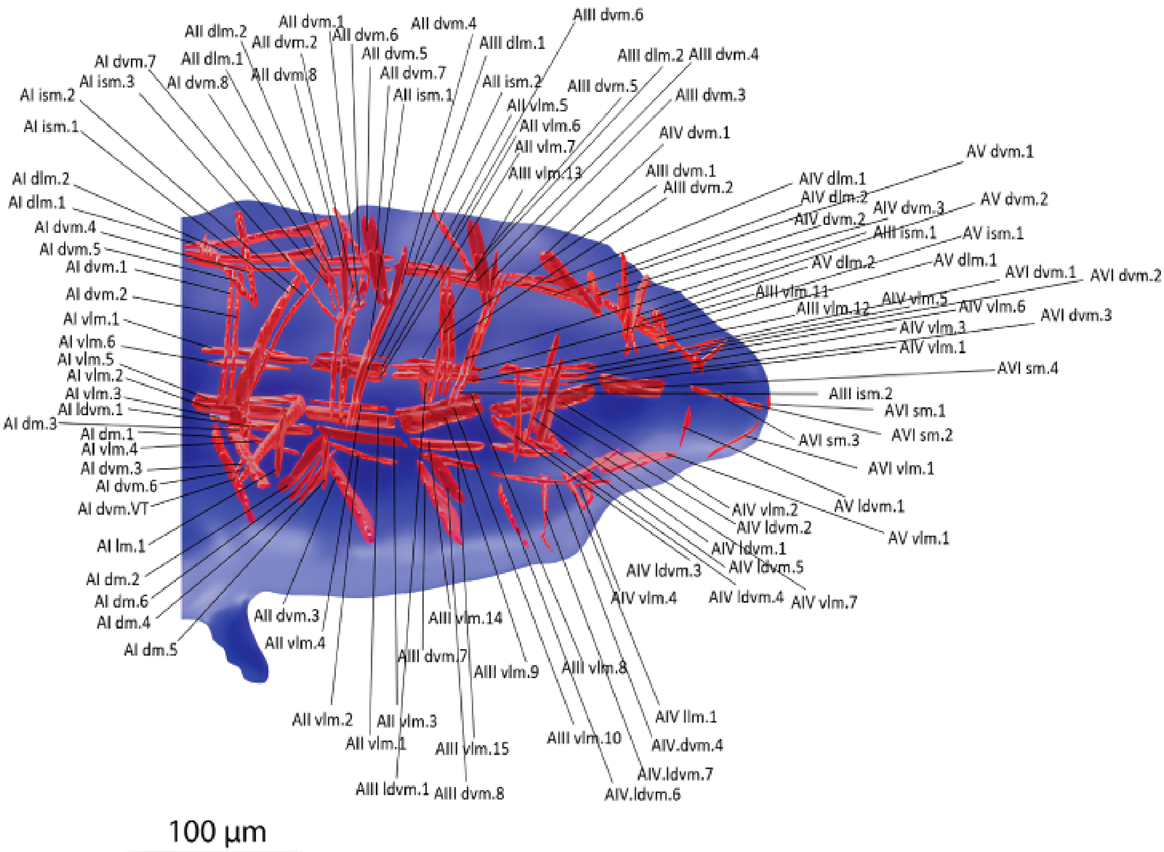

Fig. 9. Musculature of abdomen in *Hypogastrura serrat*a, 3D.
Рис. 9. Мускулатура брюшка *Hypogastrura serrata*, 3D.

The muscular system occupies 0.629 nL, representing 5.38% of the total body volume.

Reproductive system

The female reproductive system comprises paired, sac-shaped ovaries lacking discrete ovarioles (Fig. 10). Each ovary is differentiated into a germarium, containing linear clusters of germ cells, and a vitellarium, where a single central cell within each cluster differentiates into an oocyte, receiving nutrients via follicular cells. Paired oviducts originate in the fourth abdominal segment, converging into a single vagina that terminates at a genital opening on the fifth abdominal segment.

The reproductive system occupies 1.95 nL, constituting 16.67% of the total body volume.

Circulatory system and fat body

The organs of the circulatory system (heart, blood vessels) are absent.

Respiratory system

The respiratory system (trachea) is absent.

Discussion

Comparison of *H. serrata* and large-sized springtails

The digestive, nervous, reproductive, and excretory systems of *Hypogastrura serrata* have a structure typical of large springtails and contain all the sections identified by researchers [Lubbock, 1871; Adams, Salmon, 1972; Imms, 1977; Hopkin, 1997]. The muscular system of *H. serrata* contains some differences from the previously described springtails. The muscles of the antennae of entomobryomorph springtails were described earlier [Denis, 1928; Imms, 1977], whereas *H. serrata* is poduromorphic. Therefore, the differences in the number of muscles can be associated with the differences in the morphology of these orders: poduromorph springtails have cylindrical, shorter antennae, while entomobryomorph springtails have longer, thinner, and often more mobile antennae [Bellini *et al.*, 2023]. In *H. serrata* 10 antennal muscles have been described, as well as the musculature of the antennae of *Orchesella villosa* (14 muscles), *Isotomurus palustris* (8 muscles) [Imms, 1977]. Other authors focused earlier on the description of the mandibular and maxillary muscles, so we provide a comparison of the mandibular and maxillary muscles of *H. serrata* with the results of previous works. *H. serrata* has 10 mandibular and 9 maxillary muscles, while *Anurida maritima* described by Walter has 6 mandibular and 10 maxillary muscles [Wolter, 1963]. The genera *Hypogastrura* and *Anurida* have been shown to lack mandibular rotator muscles, so they are not able to rotate the mandibles, but only perform translational movements in one plane (forward and backward relative to the edge of the oral cone). *Anurida maritima* was chosen as the object of comparison in this work due to the similarity of the structure of its oral cone with *H. serrata*. Differences in the number of pairs of chest muscles are shown: 63 in *H. serrata*, 58 in the previously described *Orchesella cincta* (Entomobryomorpha: Entomobryidae)

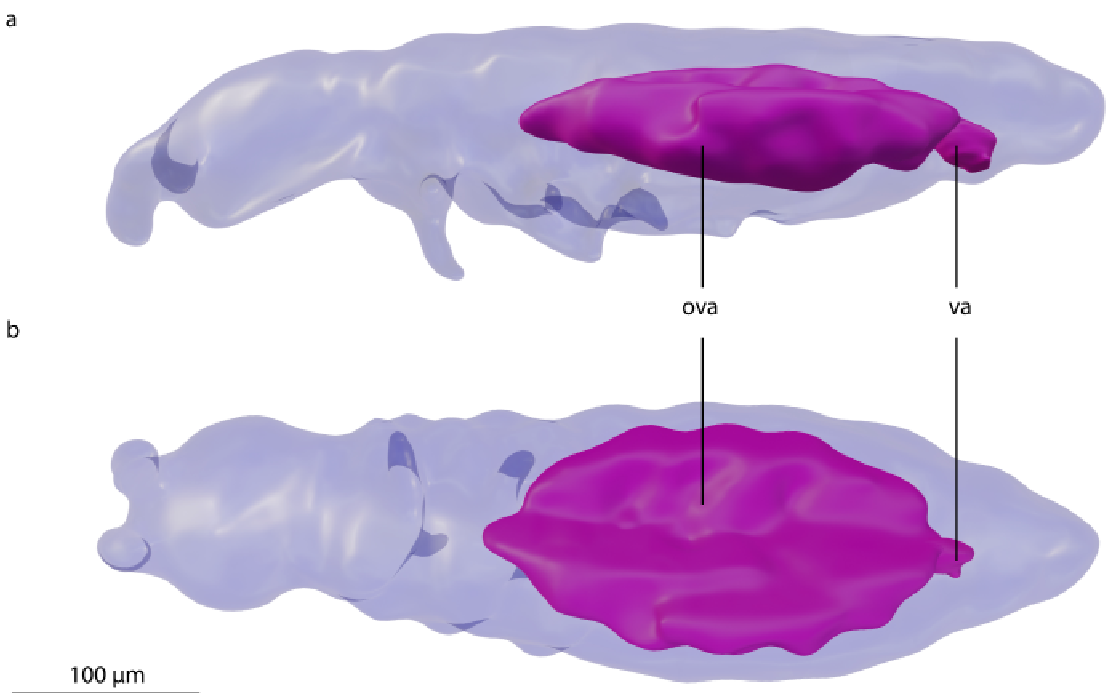

Fig. 10. Reproductive system of *Hypogastrura serrata*, 3D. A — lateral internal view; b — dorsal view. Ova — ovaries; va — vagina.
Рис. 10. Половая система *Hypogastrura serrata*, 3D. A — внутреннее строение, латерально; b — дорсально. Ova — яичники; va — влагалище.

and 67 in *Neanura muscorum* (Poduromorpha: Neanuridae) [Bretfeld, 1963]. It can be assumed that such differences are explained by two factors: 1) Bretfeld's description of the muscular system of the chest of springtails is incomplete and does not include muscles related to the appendages, whereas in this work some muscles not described by Bretfeld are included in the group of "pectoral" and "abdominal", respectively; 2) the greatest discrepancy is noted with *Orchesella cincta*, a representative of another order, and also the owner of a reduced prothorax, in connection with which it has significant reductions in the set of muscles. Also, Bretfeld described the abdominal musculature of *Orchesella cincta*: 84 pairs of muscles [Bretfeld, 1963]. In *H. serrata*, 86 pairs of muscles are described.

The number of muscles is a species-specific feature. In *Hypogastrura serrata*, the circulatory and respiratory systems were not found.

The circulatory system of large springtails is represented by the heart with 2–6 pairs of ostia and the cephalic aorta extending forward from the heart [Schaller, 1970; Imms, 1977]. The respiratory system is represented by the tracheal system in the genus *Sminthurus* [Imms, 1977] and the remains of the tracheal system in *Dicyrtoma fusca* [Lubbock, 1871; Schaller, 1970; Hopkin, 1997]. Davies and Lubbock write that the branches of the trachea diverge into the head, legs and abdominal cavity, but no anostomoses are observed between parts of the opposite body parts [Lubbock, 1871; Davies, 1927]. In springtails of the genus *Sminthurus*, a well-developed tracheal system is described, and in the species *Dicyrtoma fusca*, remnants of the tracheal system are found [Lubbock, 1871; Schaller, 1970; Imms, 1977; Hopkin, 1997].

Comparison of *H. serrata* and the miniature *Mesaphorura sylvatica*

In the nervous system, unlike those of medium- and large-sized collembolans, muscles pass through the brain in *M. sylvatica* [Panina *et al*., 2019]. This is due to the limitation imposed by the nervous system on reducing the size, due to its conservative morphology and the existence of lower limits on the size of neurons and the diameter of axons [Makarova, Polilov, 2013].

The digestive system of medium-sized *H. serrata* differs from that of the miniature *M. sylvatica* in more clearly defined sections (for instance, the rectum, which is a section of the hindgut) [Panina *et al*., 2019].

In the reproductive system of *H. serrata* and other medium and large springtails, the ovaries are usually paired, while in *M. sylvatica* there is a reduction associated with a decrease in its size - the miniature springtail has only one ovary [Panina et al, 2019].

The muscular system of the medium-sized *H. serrata* is characterized by a more complete set of muscles, while in the miniature springtail there are various reductions associated with its critical sizes [Panina *et al.*, 2019].

The obtained results are summarized in Table 6.

Table 6. Comparison of the internal structure of springtails of different size classes.
Таблица 6. Сравнение внутреннего строения ногохвосток из разных размерных классов.

Organ system	**Large-sized springtails** [Lubbock, 1871; Bretfeld, 1963; Wolter, 1963; Imms, 1977; Hopkin, 1997]	**Medium-sized *H. serrata***	**Miniature *M. sylvatica*** [Panina *et al*., 2019]
Digestive	Foregut, midgut and hindgut, salivary glands, acinary glands	Foregut, midgut and hindgut, salivary glands	The intestinal sections are less pronounced, the salivary glands are not detected
Excretory	Labial nephridia	Labial nephridia	Labial nephridia
Nervous	Brain, suboesophageal and three thoracic ganglia	Brain, suboesophageal and three thoracic ganglia	Brain, suboesophageal and three thoracic ganglia, muscles pass through the brain, the ganglia are displaced by one segment
Reproductive	Paired ovaries	Paired ovaries	Reduction of one ovary
Circulatory	Heart with 2–6 pairs of ostia, the cephalic aorta extends forward	Absent	Absent
Respiratory	*Sminthurus*: well-developed tracheal system; *Dicyrtoma fusca*: remnants of the tracheal system	Absent	Absent
Muscular			
head (number of muscles)	*Anurida maritima* ?: 6 mandibular, 10 maxillar	54: 10 mandibular, 9 maxillar	48: 9 mandibular, 6 maxillar
thorax (pairs of muscles, in brackets sequentially: pro-, meso-, metathorax)	*Orchesella cincta*: (15+32+11)=58; *Neanura muscorum*: (24+21+22)=67	(21+20+22)=63	(14+19+18)=51
abdomen (pair of muscles)	*Orchesella cincta*: 84	88	61

Legend: ? — no data

Comparison of relative organ volumes of *H. serrata*, *M. sylvatica* and insects

The relative volume of the skeletal structures of *H. serrata* (2.38%) is smaller than that of the miniature springtail *M. sylvatica*. The volume of its skeletal structures relative to the body is 5.8% [Panina *et al.*, 2019]. In insects of the same size class (about 1 mm), for instance, in adult Coleoptera, it varies from 10 to 20%, and in Paraneoptera adults it is 6% [Polilov, Makarova, 2017].

The relative volume of the muscles of *H. serrata* (5.4%) is smaller than that of the miniature springtail, in which it is 5.2% [Panina *et al.*, 2019]. It is also smaller than that of Paraneoptera adults (about 6%) and Coleoptera adults (10.5–12%) [Polilov, Makarova, 2017]. Such differences may be due to the high specialization of the muscular system in springtails.

The relative volume of the digestive and excretory systems of *H. serrata* (1.2%) is smaller than that of *M. sylvatica* (8.6%) [Panina *et al.*, 2019], Coleoptera (about 9–10% digestive and 0.3–2% excretory) and Paraneoptera (about 21% digestive and excretory about 1%) [Polilov, Makarova, 2017].

The relative volume of internal tissues in *H. serrata* (73%) is greater than that in *M. sylvatica* (52.2%) [Panina *et al.*, 2019]**,** Coleoptera (30–60%) and Paraneoptera adults (56%) [Polilov, Makarova, 2017]. The fat body serves as an accumulation of metabolic products [Hopkin, 1997], which can explain such a discrepancy.

The relative volume of the reproductive system in *H. serrata* (16.67%) is comparable to that in *M. sylvatica* (18.9%) [Panina *et al.*, 2019]. In Coleoptera adults, the volume of the reproductive system is about 20-30%, and in Paraneoptera adults it is about 15% [Polilov, Makarova, 2017].

Conclusion

This study of the anatomy of the medium-sized springtail *Hypogastrura serrata* allowed us to identify key features of its internal structure and compare them with data on miniature and larger springtails. The results confirm that medium (1–3 mm) and large (3–10 mm) springtails can be considered in the same size class, since their internal structure shows no fundamental differences. However, *H. serrata* lacks the organs of the tracheal and circulatory systems that were previously discovered in some larger springtails.

Our results demonstrate that the obtained morphological data significantly refine the interpretation of miniaturization effects in springtails. In particular, the presence of reductions and oligomerizations in the organ systems of the miniature *M. sylvatica* is confirmed. The results can serve as a basis for further studies of evolutionary trends and their impact on the morphology of springtails. Thus, this work makes a significant contribution to the understanding of the anatomy of springtails and provides important comparative data for the study of miniaturization in this group.

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References

Adams E.C.G., Salmon J.T. 1972. The mouth-parts and feeding methods of Brachystomella parvula (Schaeffer) (Collembola: Brachystomellidae) // Transactions of the Royal Entomological Society of London. Vol.124. No.3. P.269–286.

Altner H. 1968. Die ultrastruktur der labialnephridien von *Onychiurus quadriocellatus* (Collembola) // Journal of Ultrastructure Research. Vol.24. No.5. P.349–366.

Altner H., Thies G. 1976. The postantennal organ: A specialized unicellular sensory input to the protocerebrum in apterygotan insects (Collembola) // Cell and Tissue Research. Vol.167. No.1. P.97–110.

Bellini B.C., Weiner W.M., Winck B.R. 2023. Systematics, Ecology and Taxonomy of Collembola: Introduction to the Special Issue // Diversity. Vol.15. No.2. P.1–221.

Berridge M.J., Oschman J.L. 1972. Transporting epithelia. New York: Academic Press. 91 pp.

Bitsch C., Bitsch J. 2002. The endoskeletal structures in arthropods: cytology, morphology and evolution // Arthropod Structure & Development. Vol.30. No.3. P.159–177.

Blanke A., Machida R. 2016. The homology of cephalic muscles and endoskeletal elements between Diplura and Ectognatha (Insecta) // Organisms Diversity & Evolution. Vol.16. No.1. P.241–257.

Bretfeld G. 1963. Zur Anatomie und Embryologie der Rumpfmuskulatur und der abdominalen Anhänge der Collembolen // Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere. Bd.80. No.3. S.309–468.

Cassagnau P., Juberthie C., Raynal G. 1968. Structures nerveuses, neurosécrétion et organes endocrins chez les Collemboles // General and Comparative Endocrinology. Vol.10. No.1. P.61–69.

Christiansen K.A., Bellinger P., Janssens F. 2009. Chapter 55 – Collembola: (Springtails, Snow Fleas) // Encyclopedia of Insects (Second Edition) / ed. by V.H. Resh, R.T. Cardé. San Diego: Academic Press. P.206–210.

Davies W.M. 1927. On the Tracheal System of Collembola, with special reference to that of Sminthurus viridis, Lubb // Journal of Cell Science. Vol.s2-71. No.281. P.15–30.

Denis J.R. 1928. Etudes sur l'anatomie de la tete de quelques Collemboles, suivies de considerations sur la morphologie de la tete des insects // Archives de Zoologie Expérimentale et Générale. Vol.68. P.1–291.

Hanken J., Wake D.B. 1993. Miniaturization of Body Size: Organismal Consequences and Evolutionary Significance // Annual Review of Ecology and Systematics. Vol.24. P.501–519.

Hopkin S.P. 1997. Biology of the Springtails—Insecta: Collembola. Oxford University Press. 330 pp.

Imms A.D. 1977. IMMS' General Textbook of Entomology: Volume I: Structure, Physiology and Development. Dordrecht: Chapman and Hall. 418 pp.

Kerkut G.A., Gilbert L.I. 1985. Comprehensive Insect Physiology, Biochemistry and Pharmacology. Oxford, N.Y., Toronto, Sydney, Paris, Frankfurt: Pergamon Press. 656 pp.

Kollmann M., Huetteroth W., Schachtner J. 2011. Brain organization in Collembola (springtails) // Arthropod Structure & Development. Vol.40. No.4. P.304–316.

Makarova A.A., Polilov A.A. 2013. Peculiarities of the brain organization and fine structure in small insects related to miniaturization. 2. The smallest Hymenoptera (Mymaridae, Trichogrammatidae) // Entomological Review. Vol.93. No.6. P.714–724.

Manton S.M. 1972. The evolution of arthropodan locomotory mechanisms: Part 10. Locomotory habits, morphology and evolution of the hexapod classes // Zoological Journal of the Linnean Society. Vol.51. No.3–4. P.203–400.

Oliveira F.G.D.L. 2022. On springtails (Hexapoda: Collembola): a morphofunctional study of the jumping apparatus // Frontiers in Zoology. Vol.19. No.21. P.1–22.

Oliveira F.G.L., Smith A.A. 2024. A morphofunctional study of the jumping apparatus in globular springtails // Arthropod Structure & Development. Vol.79. P.1–14.

Panina I.V., Potapov M.B., Polilov A.A. 2019. Effects of miniaturization in the anatomy of the minute springtail *Mesaphorura sylvatica* (Hexapoda: Collembola: Tullbergiidae) // PeerJ. Vol.7.e8037. P.1–28.

Polilov A.A., Makarova A.A. 2017. The scaling and allometry of organ size associated with miniaturization in insects: A case study for Coleoptera and Hymenoptera // Scientific Reports. Vol.7. No.43095. P.1–7.

Rillich B., Oliveira F.G.L. 2023. On latches in biological systems: a comparative morphological and functional study of the retinaculum and the dens lock in Collembola // Frontiers in Zoology. Vol.20. No.1. P.1–16.

Schaller F. 1970. Collembola (Springschwänze) // Handbuch der Zoologie. Bd.4. No.2. S.1–72.

Lubbock J. 1871. Monograph of the Collembola and Thysanura. London: the Ray Society. 276 pp.

Verhoef H.A., Bosman C.A.W., Bierenbroodspot A., Boer H.H. 1979. Ultrastructure and function of the labial nephridia and the rectum of *Orchesella cincta* (L.) (Collembola) // Cell and Tissue Research. Vol.198. No.2. P.237–246.

Wolter H. 1963. Vergleichende Untersuchungen zur Anatomie und Funktionsmorphologie der stechend-saugenden Mundwerkzeuge der Collembolen // Zoologische Jahrbücher. Bd.81. S.27–100.