

Larval description of *Nodynus leucofasciatus* Lewis, 1879
(Coleoptera: Staphylinidae: Apateticinae) with discussion of
Staphylinidae chaetotaxy

Описание личиночных стадий *Nodynus leucofasciatus* Lewis, 1879
(Coleoptera: Staphylinidae: Apateticinae) с обсуждением
хетотаксии Staphylinidae

Artejom A. Zaytsev¹, Alexandra S. Tokareva²
Артём А. Зайцев¹, Александра С. Токарева²

¹ Moscow State Pedagogical University, Institute of Biology and Chemistry, Department of Zoology and Ecology, Kibaltchicha str. 6, buld. 3, 129164 Moscow, Russia. E-mail: ztema@mail.ru

¹ Московский Педагогический Государственный Университет, институт биологии и химии, кафедра зоологии и экологии, ул. Кибальчича 6, корп. 3, 129164 Москва, Россия.

² Museum and Institute of Zoology, Laboratory of Systematics, Zoogeography and Ecology of Invertebrates, Wilcza str. 64, 00-679 Poland, Warsaw. E-mail: alexan4tok@gmail.com

KEY WORDS: Coleoptera, larva, chaetotaxy, Staphylinidae, Apateticinae.

КЛЮЧЕВЫЕ СЛОВА: жесткокрылые, личинка, хетотаксия, Staphylinidae, Apateticinae.

ABSTRACT. Larvae of instars I–III of *Nodynus leucofasciatus* are described, including data on chaetotaxy. The possibility of applying Bousquet and Goulet [1984] nomenclatural system for Staphylinidae is discussed. An attempt to establish homologous chaetome elements among Staphylinidae and Carabidae is performed. Taxonomic position of Apateticinae is briefly discussed.

РЕЗЮМЕ. Приводится описание личинок I–III возраста *Nodynus leucofasciatus*, включая данные об их хетотаксии. Обсуждается возможность применения номенклатурной системы Буске и Гуле [Bousquet, Goulet, 1984] для Staphylinidae. Произведена попытка выявления гомологичных элементов хетомы у Staphylinidae и Carabidae. Кратко обсуждается таксономическое положение Apateticinae.

Introduction

Apateticinae Fauvel, 1895 is a small subfamily of Staphylinidae, consisting of 2 genera: *Apatetica* Westwood, 1848 and *Nodynus* Waterhouse, 1876 with 19 and seven species accordingly [Newton, 2018], described mostly from South Palaearctic and Oriental regions. The single species, *Nodynus leucofasciatus*, known from Russian Far East [Shavrin, 2008]. The taxonomic position of this group has changed significantly over time. Both genera were originally described as members of Silphidae [Westwood, 1848; Waterhouse, 1876] due to the

superficial resemblance of adults, but later assigned to Staphylinidae by Fauvel [1895], who placed them in Piestini as section Apateticae. Subsequently, this group was moved to Oxytelinae [Bernhauer, Schubert, 1910], Piestinae [Kasule, 1966, Newton, 1982a] and finally considered as separate subfamily Apateticinae [Newton, Thayer, 1992]. Lawrence and Newton [1995] placed Apateticinae near Scaphidiinae in their Oxytelinae-group. Grebennikov and Newton [2012] noted that Apateticinae may not be as closely related to Oxytelinae as they thought to be and considered Apateticinae (together with Trigonurinae) as basal group of Staphylinidae. In the most comprehensive molecular phylogenetic study so far [McKenna et al, 2015] Apateticinae regarded as a sister-group of Scaphidiinae and this clade was found as one of the basal lineages of the family. Alternatively, some authors proposed to return *Apatetica* and *Nodynus* to Silphidae [Jansson, 1947; Madge, 1979] or even count them as separate family Apateticidae [Hansen, 1997], but these hypothesis were not widely approved. It should be noted, that in most studies, mentioned above, larval features of Apateticinae have not been discussed.

The knowledge of Apateticinae larvae is rather poor. Last instar of *Nodynus leucofasciatus* Lewis, 1879 was formally described by Fukuda [1959], but the description itself is very short and sketchy. Some larval characters of *Nodynus* were mentioned in papers of Kasule [1966] and Newton [1982a], mostly based on Fukuda's study. The larva of *Apatetica* sp. was described by

Grebennikov and Newton [2012], and some differences from *N. leucofasciatus* were pointed out (in this paper photos of last-instar larva of *N. leucofasciatus*, provided by the first author, were used). So the first goal of the present study is to provide the detailed description of all three larval instars of *N. leucofasciatus*, which could help in clarifying the taxonomic position of this group.

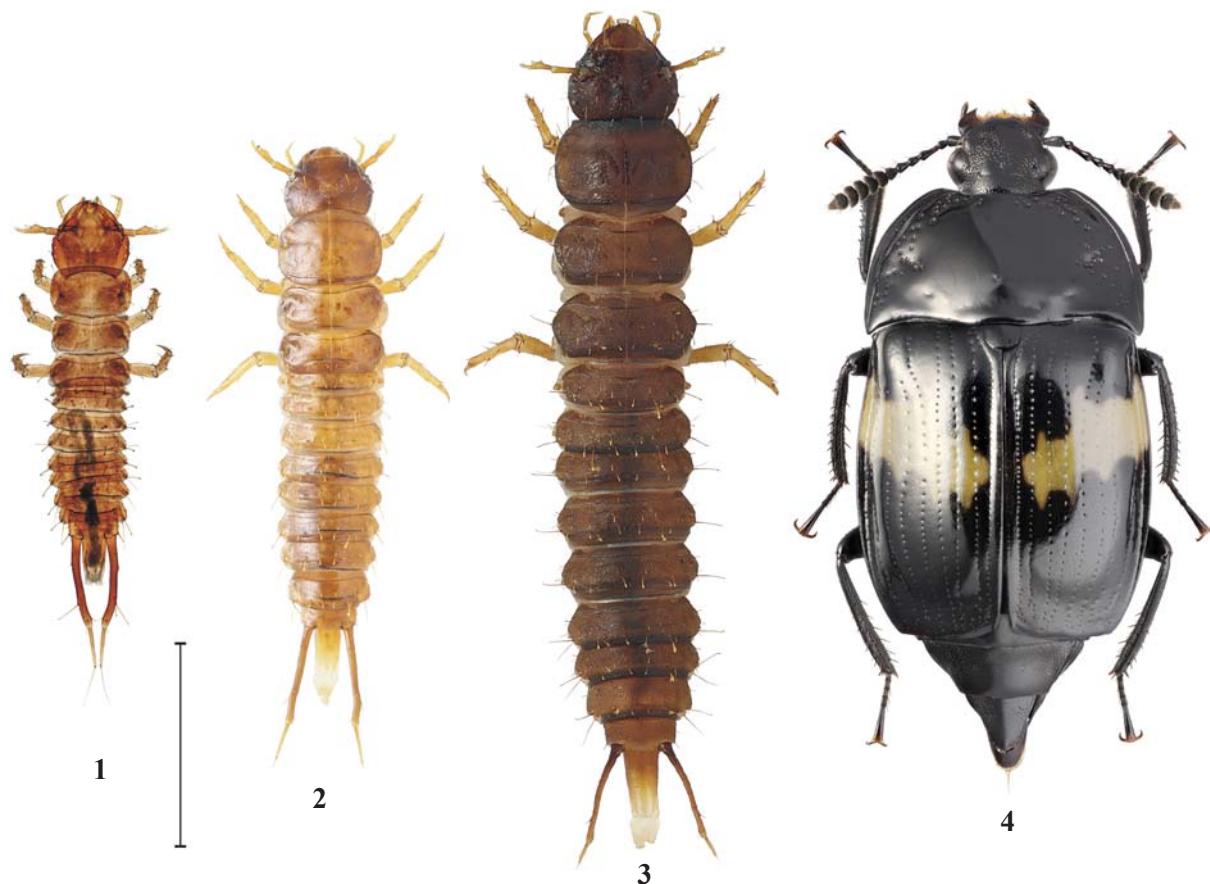
The second aim of our work is connected with larval chaetotaxy of Staphylinidae and Coleoptera in general. Traditionally, chaetotaxy pattern of staphylinid larvae is described using nomenclatural system proposed by Ashe and Watrous [1984] for Aleocharinae. However, although that system is strictly homology-based, this principle is not often followed in studies outside Aleocharinae, which leads to certain confusion [Solodovnikov, 2007, also see Discussion]. As a result, we made an attempt to apply the system by Bousquet and Goulet [1984], originally proposed for Carabidae, instead. For doing this, first of all it is necessary to establish homologies between carabid and staphylinid chaetome elements, what we try to perform in present study. One of the arguments supporting this approach can be the fact that certain degree of similarity between Staphylinidae and Carabidae larval chaetotaxy has already been pointed out [Kovarík, Passoa, 1993; Makarov, 1996].

Material and methods

Larvae of *N. leucofasciatus* were identified by the association with adults (Figs 1–4). Material examined: 1 first-instar, 2 second-instar and 2 third-instar larvae together with adults: Russia, South Kuril Islands, Kunashir Island, 44°16'31"N 145°56'29"E, on fermented *Betula* sap, 4.VII.2008, leg., det. K. Makarov (MSPU).

Habitus photographs were taken with a Canon EOS 40D camera with a MP-E 65 mm macro lens. Photos of slide mounts were taken with Canon EOS6D camera attached to a Carl Zeiss AXIO Scope.A1 microscope. All photos were processed using Helicon Focus 7.0 software. Line drawings were made in CorelDRAW 12. The specimens were preserved in 70% ethanol or on slides with Faure's Berlese media and are deposited in Moscow Pedagogical State University, Moscow, Russia (MSPU).

The measurements were taken with an ocular-micrometer mounted on a MBS1 (Lomo) stereo microscope. Sclerites nomenclature mostly follows Lawrence [1991]. The nomenclature of the primary setae and pores follows Bousquet and Goulet [1984] with modifications [Makarov, 1996] and compared with those of Ashe and Watrous [1984]. In some cases (e.g. abdominal segment IX and



Figs 1–4. *Nodynus leucofasciatus*, habitus, dorsal view: 1 — first-instar larva; 2 — second-instar larva; 3 — third-instar larva; 4 — adult male. Scale bar: 3 mm.

Рис. 1–4. *Nodynus leucofasciatus*, габитус, сверху: 1 — личинка первого возраста; 2 — личинка второго возраста; 3 — личинка третьего возраста; 4 — имаго, самец. Масштаб: 3 мм.

urogomphi), when setae have not been coded in the original publication, we use data from Thayer's work [2000]. When uncertain in establishing homologies, we use asterix (*) before supposed number. Setae and pores which we fail to homologize are not coded, but their topology is described. Additional setae, which appear in larval instars II–III and have constant quantity and position, are coded with Greek letters. Secondary setae in larval instars II–III with variable quantity and position are marked with *.

The following abbreviations were used:

1) body sclerites: EM — epimeron, EP — epipleurite, ES — episternum, EU — eusternum, FR — frontal sclerite, HY — hypopleurite, ME — mesonotum, MT — metanotum, PA — parietal sclerite, PR — pronotum, PS — prosternite, ST — sternite, TE — tergite;

2) thoracic apodemes: Aem2–3 — epimeral apodeme (numeric corresponds to segment, on which apodeme is developed), Aes2–3 — episternal apodeme, Ais1–3 — intersegmental apodeme, Apl1–3 — pleural apodeme, F1–3 — furca;

3) appendages and their parts: AN — antenna, Sa — sensorial appendage, LB — labrum, MN — mandible, Mnt — mentum, Pmnt — prementum, Smnt — submentum, Mxa — maxillary articulating area, Ma — mala, Dstcd — disticardo, Prxcd — proxicardo, Stp — stipes, Pf — palpifer, CO — coxa, TR — trochanter, FE — femur, TT — tibiotarsus, UN — uncus, Cx — coxal cavity;

4) various structures: Asp — atrophied spiracle, Atp — anterior tentorial pit, Eb — egg-bursters, Eg — epicranial gland, Es — epicranial suture, Mps — multiporose structure, Hyp.rod — hypopharyngeal rod, Hyp.ch. — hypopharyngeal chitization area, Hyp.br. — hypopharyngeal bracon, Pp — pleuropod, Ptg — pretergal gland, RI–RII — additional hypopharyngeal rods, Sa — sensorial appendage, Sp — spiracle, Tg — tergal gland.

Results and discussion

First-instar larva

Figs 1–32.

Body length (from anterior margin of labrum to the apex of abdominal segment X) 5.6 mm; head length 1.0 mm; head width 1.1 mm, urogomphi length 1.9 mm; maximum width of thorax 1.1 mm; maximum width of abdomen 1.0 mm. Head slightly narrower than prothorax; body elongate, semi-cylindrical; widest across prothorax, then tapering posterad; urogomphi well developed, 2-segmented (Fig. 1).

Head light brown; labrum, antennae and maxilla a bit lighter; mandibles dark brown. Condyle area on parietal sclerite dark brown. Parietal sclerite lighter ventrally, but heavily darkened near ventral epicranial ridge. Thoracic and abdominal tergites dark yellow, anterior carina brown; sternites and pleurites yellow; area of pleural apodemes heavily darkened. Thoracic sternites pigmented lighter; ventrites of abdominal segments VIII–IX pigmented heavier. Urogomphi brown; abdominal segment X brown at the base and yellow on apex. Legs dark yellow, trochanter and claw pigmented heavier. Coxal condyle almost black.

Dorsal surface of head and all body segments except X covered with larger apically frayed or bifurcated setae and smaller simple setae; ventral surfaces membranous, covered mostly with simple setae.

Head (Figs 5–14) prognathous, slightly wider than long. Epicranial suture rather long, about 0.3 as long as head capsule; frontal sutures v-shaped, reaching antennal insertions; their bases contiguous (Fig. 5). Frontoclypeal suture indistinct, slightly defined at lateral margins. Stemmata six on each side (Fig. 6), forming two rows with three stemmata each. Clypeolabral suture distinct; labrum trapezoidal, about 0.4 as long as basal wide; its anterior margin smooth, slightly rounded. Labrum (Fig. 7) with five well sclerotized portions separated by less sclerotized areas; with five setae (*FR₈₋₁₁ and one medial seta) and single pore (*FR_g) on each side. Frontal sclerites smooth with honeycomb pattern (Figs 5, 54); with eight setae (FR₁₋₆, *FR₇ and seta located between FR₂ and frontal suture) and two pores (FR_b, *FR_{c/e}) on each side. Parietal sclerites smooth with barely visible toothed microsculpture (Figs 5, 8, 57); with 18 setae (PA₁₋₇, PA₉₋₁₀, PA₁₂, PA₁₇, two dorsal setae located near PA₃ and PA₁₀, four lateral setae and one ventral), eight pores (PA_{a-b}, PA_d, *PA_{f-g}, *PA_i, *PA_n and lateral pore located near the base of antenna) and single epicranial gland (Eg) on each side.

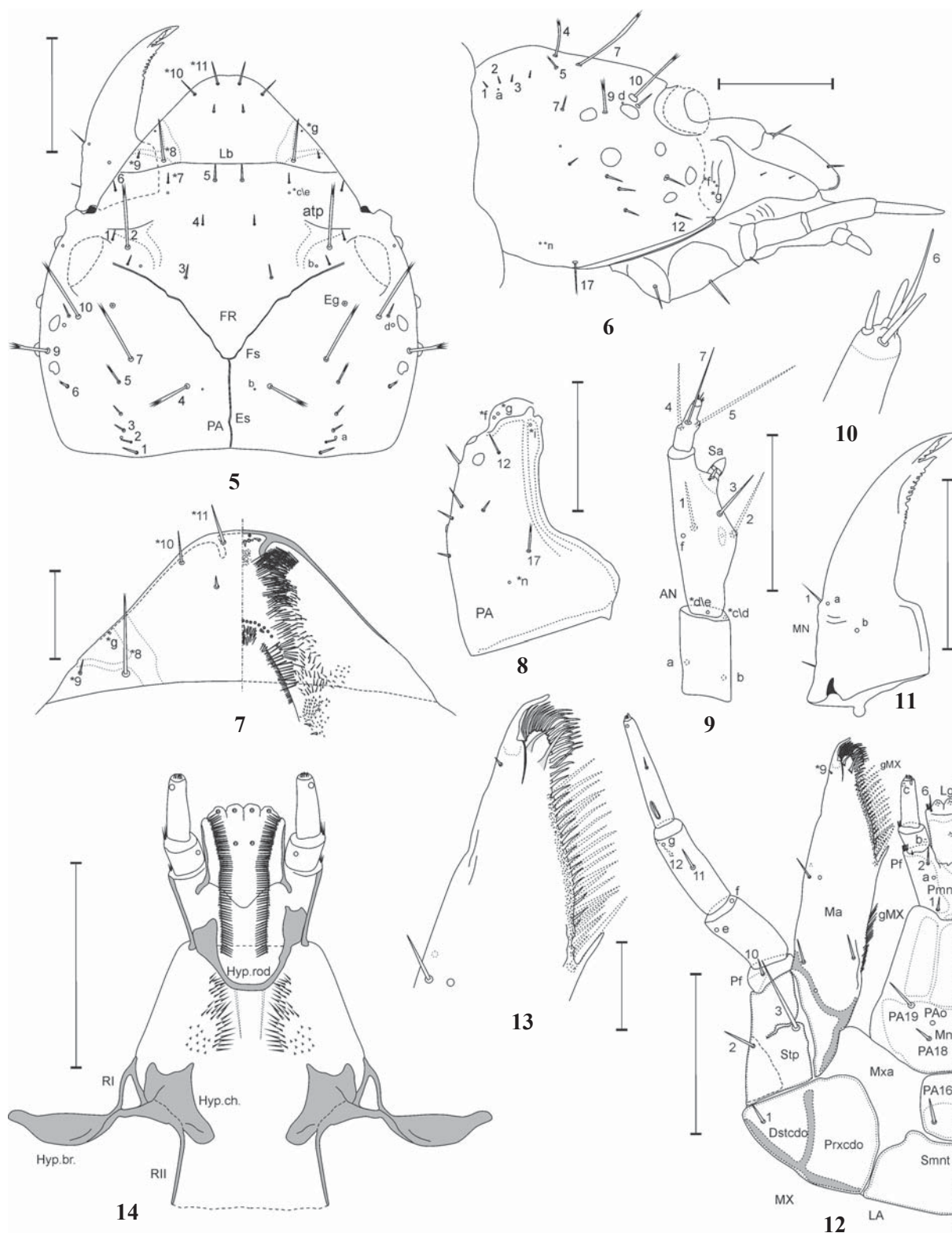
Antenna (Figs 9–10) with three antennomeres, 0.6 as long as head length. Antennomere I 1.8 as long as wide, dorsally with three pores (AN_{a-b}, *AN_{c/d}), ventrally with apical pore *AN_{d/c}. Antennomere II 1.9 as long as antennomere I and 2.9 as long as wide, with two dorsal (AN₁₋₂) and one ventral (AN₃) setae; also single ventral pore (FR_p) present. Its apical part with conical Sa which is 0.4 as long as antennomere III. Also, two smaller sensillae are present ventrally near the base of Sa. Antennomere III 0.35 as long as antennomere II and three as long as wide, with two dorsal (AN₄₋₅) and one ventral (AN₆) setae; its apical part with three elongated sensilla surrounding seta AN₆.

Epipharynx (Fig. 7) with numerous microtrichia of various length, each side with group of five apical sensillae, two sensillae located posterior, and a group of eight sensillae arranged in a arcuate row with adjacent multiporose structure (Figs 15–16). Posterior part of epipharynx with two sensillae on each side.

Mandibles (Fig. 11) almost symmetrical, slightly curved; each 2.1 as long as basal width, unidentate; incisor edge with serrate margin and single large subapical tooth. Prostheca and mola absent. Basal part with dorsal surface smooth, bearing two pores (MN_a–MN_b); outer edge with two lateral setae (MN_i and seta near the base).

Maxilla (Figs 12–13, see also Fig. 46 of instar III) with somewhat trapezoidal cardo, which is “divided” by the internal sclerotization into two unequal parts — larger proxicardo with smooth surface, and smaller disticardo bearing seta MX₁; maxillary articulating area membranous. Ventrally stipes partially divided by less sclerotized area; with two setae (MX₂₋₃). Dorsal side of stipes mostly membranous, except triangular sclerite near the outer margin.

Mala oblique truncate, its proximal part uniformly widened, with a group of microtrichia on inner margin (gMX) and seta located near it; outer margin with two setae and pores; also single pore located near the border of stipes and mala. Distal part gradually narrowed apically, with well developed conical tooth and about 20 lesser projections as well as group of about 25 lateroventral macrosetae (gMX) all along its inner margin (Fig. 13). Apex of mala narrowly longitudinally divided; inner (“lacinial”) lobe ventrally bears two mesal slightly curved unci; well developed brush of microtrichia present on its apex; outer (“galeal”) lobe with curved conical uncus and ventral seta *MX_g. Maxillary palps 3-jointed, palpifer with ventral seta MX₁₀ on its sclerotized part. Palpomere I 1.8 as long as wide, ventrally with two



Figs 5–14. *Nodynus leucofasciatus*, first-instar larva: 5–6 — head; 7 — parietale; 8 — antenna; 9 — apical joint of antenna; 10 — right mandible; 11 — labrum (left — dorsal view, right — ventral view); 12 — labio-maxillary complex; 13 — mala, apical part; 14 — labium; 5, 10, 14 — dorsal view; 6 — lateral view; 7–8, 12–13 — ventral view. Scale bars: 5–10, 12, 14 — 0.3 mm; 11, 13 — 0.1 mm.

Рис. 5–14. *Nodynus leucofasciatus*, личинка первого возраста: 5–6 — голова; 7 — парietальный склерит; 8 — антенна; 9 — апикальный членик антенны; 10 — правая мандибула; 11 — верхняя губа (слева — сверху, справа — снизу); 12 — лабио-максиллярный комплекс; 13 — вершинная часть мала; 14 — нижняя губа; 5, 10, 14 — сверху; 6 — сбоку; 7–8, 12–13 — снизу. Масштаб: 5–10, 12, 14 — 0,3 мм, 11, 13 — 0,1 мм.

apical pores (MX_{c-p}). Palpomere II 1.25 as long as palpomere I and 3.0 as long as wide, its ventral and dorsal side each with single seta (MX_{11-12}) and apical pore (MX_g and one with uncertain homology). Palpomere III 1.1 as long as palpomere II and 5.5 as long as wide, ventrally with digitiform sensillum near base, one mesal seta and apical pore. Apex of palpomere III with a group of three short conical sensillae.

Labium (Figs 12, 14, 17, 60). Ligula transverse, almost as long as wide, "tetra-lobed" [after Grebennikov, Newton, 2012], dorsally each apical lobe with single sensilla; ventrally with apical seta LA_6 located close to outer margin (Fig. 17). Each side of prementum ventrally with single seta LA_1 and pore LA_a ; palpifer with seta LA_2 , one apical seta and a group of microtrichia on outer apical edge. Labial palps 2-jointed. Palpomere I about as long as wide, dorsally with basal pore LA_b . Palpomere II 1.9 as long as palpomere I and 3.0 as long as wide, dorsally with subapical pore LA_c ; apex with a group of four short conical sensilla. Hypopharynx (Fig. 14) with two parallel rows of microtrichia originated from antero-lateral edges of ligula, numerous asperities of various length and single sensilla on each side. Hypopharyngeal sclerotisation well-defined and consists of several structures: 1) hypopharyngeal rod [after Dorsey, 1940], originated as paired structure near the base on both sides of prementum which are fusing forming arcuated structure; 2) hypopharyngeal chitinization — paired large sclerotized areas located at the level of latero-basal edges of mentum area; 3) hypopharyngeal bracon, which extends from hypopharyngeal chitinization reaching the point of ventral mandibular articulation on anterior part of the hypostomal ridge; 4) a pair of rods, both extending from sclerotized area, one supporting the outer margin of hypopharyngeal region, and other longitudinal, parallel and connected with oesophagus [after Böving, 1921]. Mentum (Figs 12, 60) distinct, trapezoidal, consists of four sclerites: single large posterior,

lacking asperities and bearing two setae (PA_{18-19}) and pore PA_6 on each side; three anterior sclerites without sensilla. Submentum divided into two parts, posterior entirely sclerotized, smooth and lacks setae; anterior partly membranous, its sclerotized part also smooth and bears seta PA_{16} on each side.

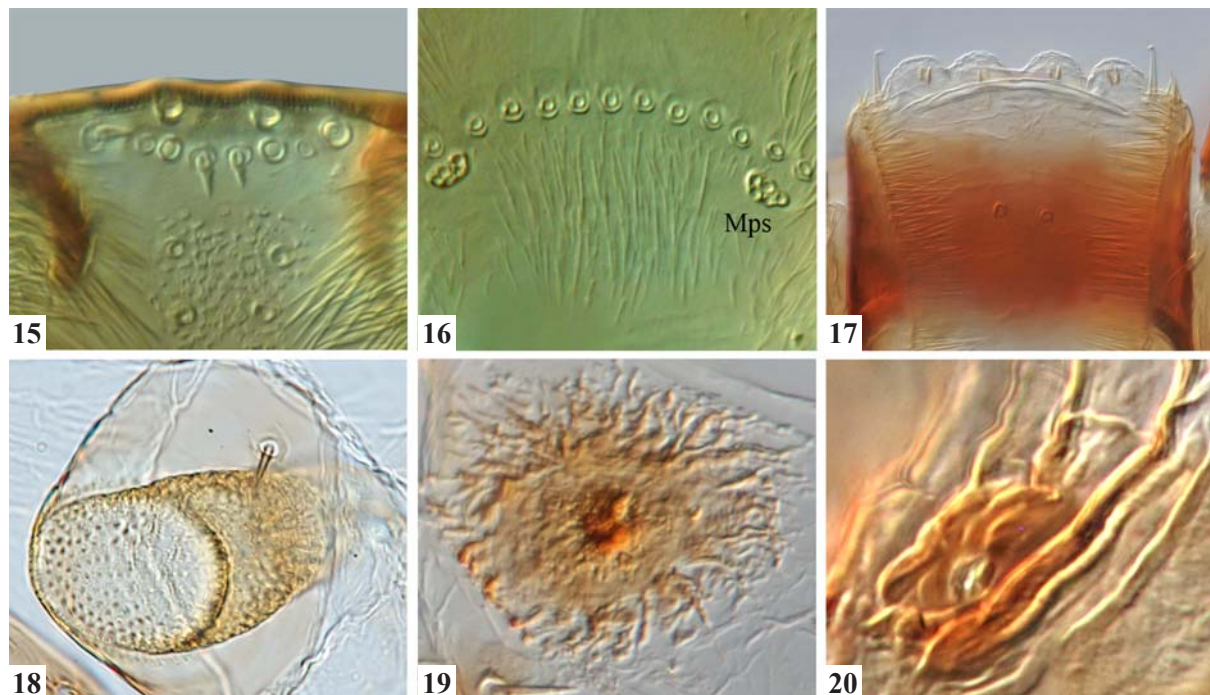
Thorax (Figs 21–23, 63, 66). Cervicosternum consists of paired presternum with two setae each and single eusternum with two setae on each side (all composing GPS).

Thorax about 0.3 as long as total body length, widest across prothorax. Prothorax is 0.6 as long as wide, 1.3 as long as mesothorax and 1.5 as long as metathorax.

Thoracic tergites with smooth surface (Figs 63, 66), meso- and metanotum differ in presence of anterior carina with group of medial asperities, possibly egg-bursters (Fig. 21). Ecdysial line well defined on all thoracic segments. Thoracic pleurites and sternites smooth, membranous areas covered in microtrichia. Mesothoracic spiracle annular (Figs 18, 24), metathoracic spiracle rudimentary (Figs 22–23).

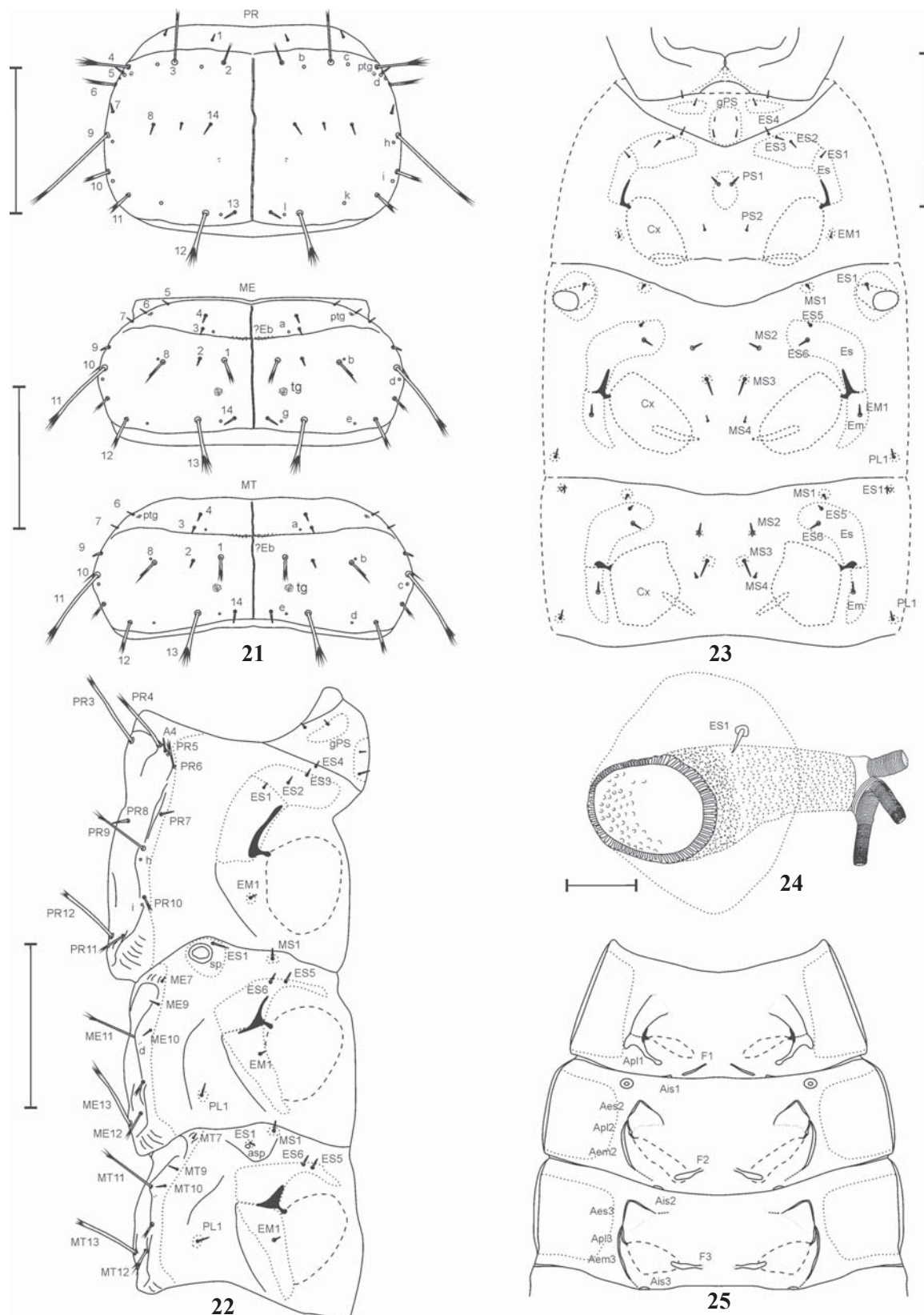
Chaetotaxy (Figs 21–23). Prothorax: each side of pronotum with 16 setae (PR_{1-14} , one seta on anterior margin, other one located between PA_8 and PA_{14}) and eight pores (PR_{b-c} , PR_{b-i} , PR_{k-l}), with well developed pretergal gland located near pore PR_d . Episternum with four setae (ES_{1-4}); epimeron with single seta EM_1 ; prosternite with two setae (PS_{1-2}).

Mesothorax: mesonotum with 15 setae (ME_{1-14} , seta located between ME_{11} and ME_{12}) and five pores (ME_{a-b} , ME_{d-e} , ME_g) on each side; pretergal gland located near seta ME_6 , also another glandular structure (Tg) present in the medial part of sclerite. Episternum divided into two sclerites: smaller anterior on which spiracle is located, with single seta ES_1 , and larger posterior one with two setae (ES_{5-6}). Epimeron with single seta EM_1 ; pleurite also with single seta PL_1 . Mesosternite with four setae on each side (MS_{1-4}). Chaetotaxy of metathorax is almost identical except the reduction of seta ME_5 .



Figs 15–20. *Nodynus leucofasciatus*, first-instar larva: 15–16 — epipharyngeal sensillae; 17 — ligula; 18 — mesothoracic spiracle; 19 — abdominal segment I, "pleuropodium"; 20 — abdominal segment IX, pretergal gland. Not to scale.

Рис. 15–20. *Nodynus leucofasciatus*, личинка первого возраста: 15–16 — сенсиллы эпифаринкса; 17 — лигула; 18 — среднегрудное дыхальце; 19 — I брюшной сегмент, "плеуроподий"; 20 — IX брюшной сегмент, железа на передней части тергита. Не в масштабе.



Figs 21–25. *Nodynus leucofasciatus*, first-instar larva, thorax: 21 — dorsal view, 22 — lateral view, 23 — ventral view; 24 — mesothoracic spiracle; 25 — thoracic endoskeleton. Scale bars: 21–23 — 0.5 mm; 24 — 0.05 mm.

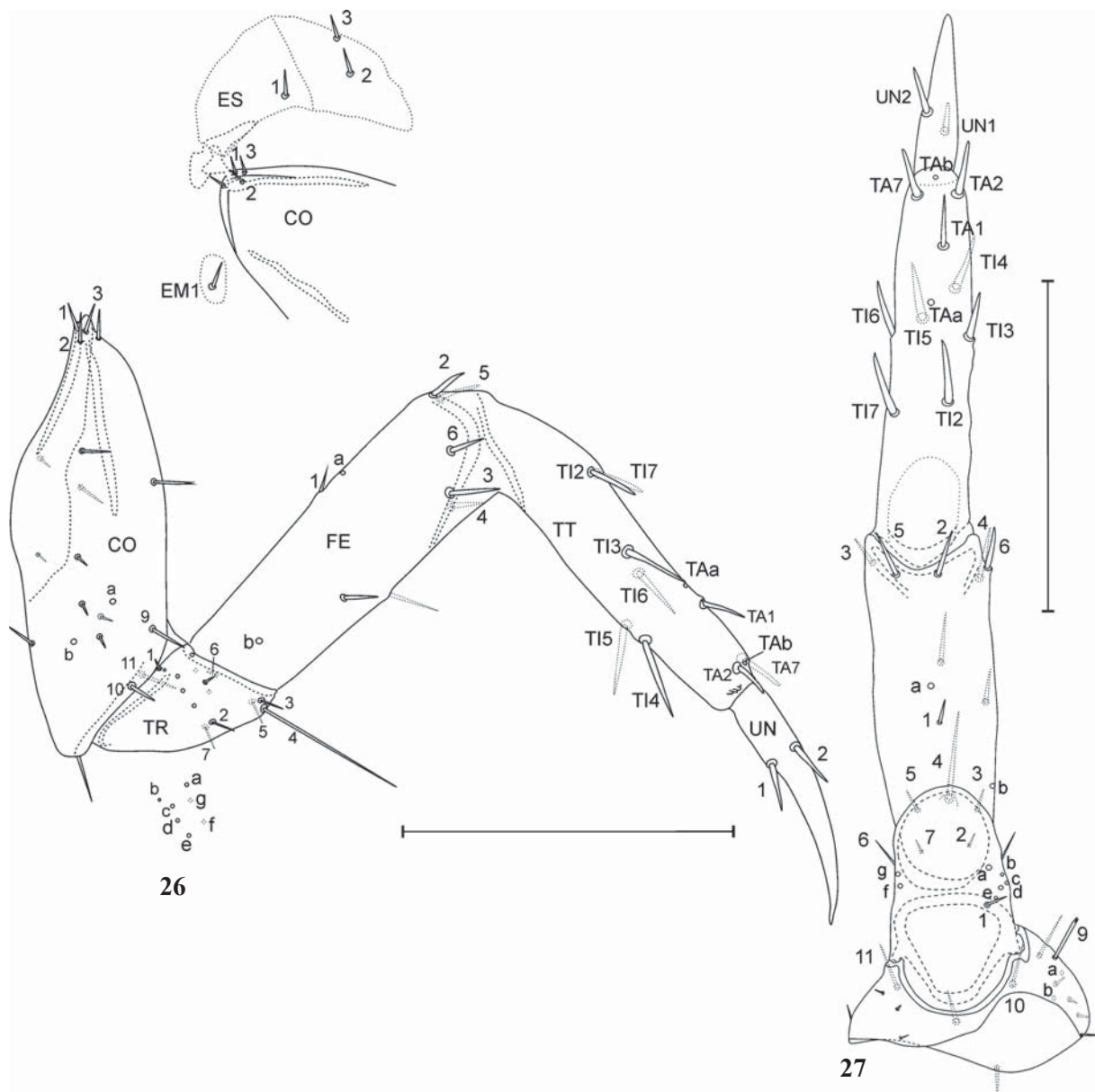
Рис. 21–25. *Nodynus leucofasciatus*, личинка первого возраста, грудной отдел: 21 — сверху, 22 — сбоку, 23 — снизу; 24 — среднегрудное дыхальце; 25 — эндоскелет груди. Масштаб: 21–23 — 0,5 мм; 24 — 0,05 мм.

Thoracic endoskeleton (Fig. 25). Prothorax: pleural apodemes rectangular, bifurcated, with long apical process; profurcae elongated, narrowed; intersegmental apodemes small, with broad base. Meso- and metathorax with well developed episternal and epimeral apodemes; pleural apodemes reduced; meso- and metafurcae distinctly wider than profurcae; intersegmental apodemes similar to those on prothorax.

Legs (Figs 26–27, 75) 5-jointed, its surface smooth, all three pairs similar in structure and chaetotaxy; length ratio of its joints to coxa is 0.5 : 1.25 : 1.25 : 0.8. Coxa with 18 setae (basal CO₁₋₃; anterior CO₉₋₁₀; posterior CO₁₁; eight anterior and four posterior setae of uncertain homology) and two pores (CO_{a-b}). Trochanter with eight setae (anterior TR₁₋₃; posterior TR₅₋₇; ventral TR₄; one anterior apical seta of uncertain homology) and seven pores (anterior TR_{a-c}; posterior TR_{f-g}). Femur with a group of anterior asperities near apex; with eight setae (anterior FE₂, FE₃, FE₆; posterior FE₄₋₅; dorsal FE₁; one anterior

or and posterior setae of uncertain homology) and two pores (FE_{a-b}). Tibiotarsus with nine setae (anterior TI₂₋₄, TA₁₋₂; posterior TI₅₋₇, TA₇) and two anterior pores (TA_{a-b}). Pretarsus with single long and sharp claw bearing two setae (UN₁₋₂).

Abdomen (Figs 28–32, 69, 72). About 0.4 as long as total body length, widest across abdominal segment V. Abdominal tergites (AT) I–IX with smooth surface, anterior carina present (Fig. 69); AT I–VIII with medial group of asperities located posterior from carina. Abdominal pleurites, sternites and membranous areas smooth (Fig. 72). Position and structure of pleural sclerites varies significantly (Fig. 31): abdominal segment I with epipleurite consisting of two small sclerites, and single small hypopleurite; abdominal segments II–III each with single fused epipleurite and much larger hypopleurite; abdominal segment IV with epipleurite fused with tergite and hypopleurite get closer to sternite; abdominal segments V–IX with both epipleurite and hypopleurite fused with



Figs 26–27. *Nodynus leucofasciatus*, first-instar larva, fore leg: 26 — anterior view; 27 — dorsal view. Scale bars: 0.5 mm.

Рис. 26–27. *Nodynus leucofasciatus*, личинка первого возраста, нога первой пары: 26 — спереди; 27 — сверху. Масштаб: 0,5 мм.

tergite and sternite respectively. Moreover, on each side of abdominal segment I, close to anterior epipleural sclerite, heavy sclerotized area with small medial projection located (Figs 18, 29). Most likely it appears to be the remains of so-called «pleuropodium» — the structure which is thought to facilitate the process of hatching [Kobayashi et al, 2003] and was observed earlier in larvae of various families of Coleoptera, but as far as we know never for Staphylinidae.

Abdominal spiracles annular (Fig. 31). Urogomphi (Figs 32, 78) 2-jointed, 0.3 as long as total body length; basal joint 2.1 as long and 2.5 as wide as apical one. Surface of urogomphi with rather weak scale-like sculpture. Pygopod (abdominal segment X) about 1.7 as long as abdominal segment IX; its apex with five membranous eversible lobes with numerous small hooks (Fig. 32); dorsal surface covered in numerous small asperities, ventral smooth.

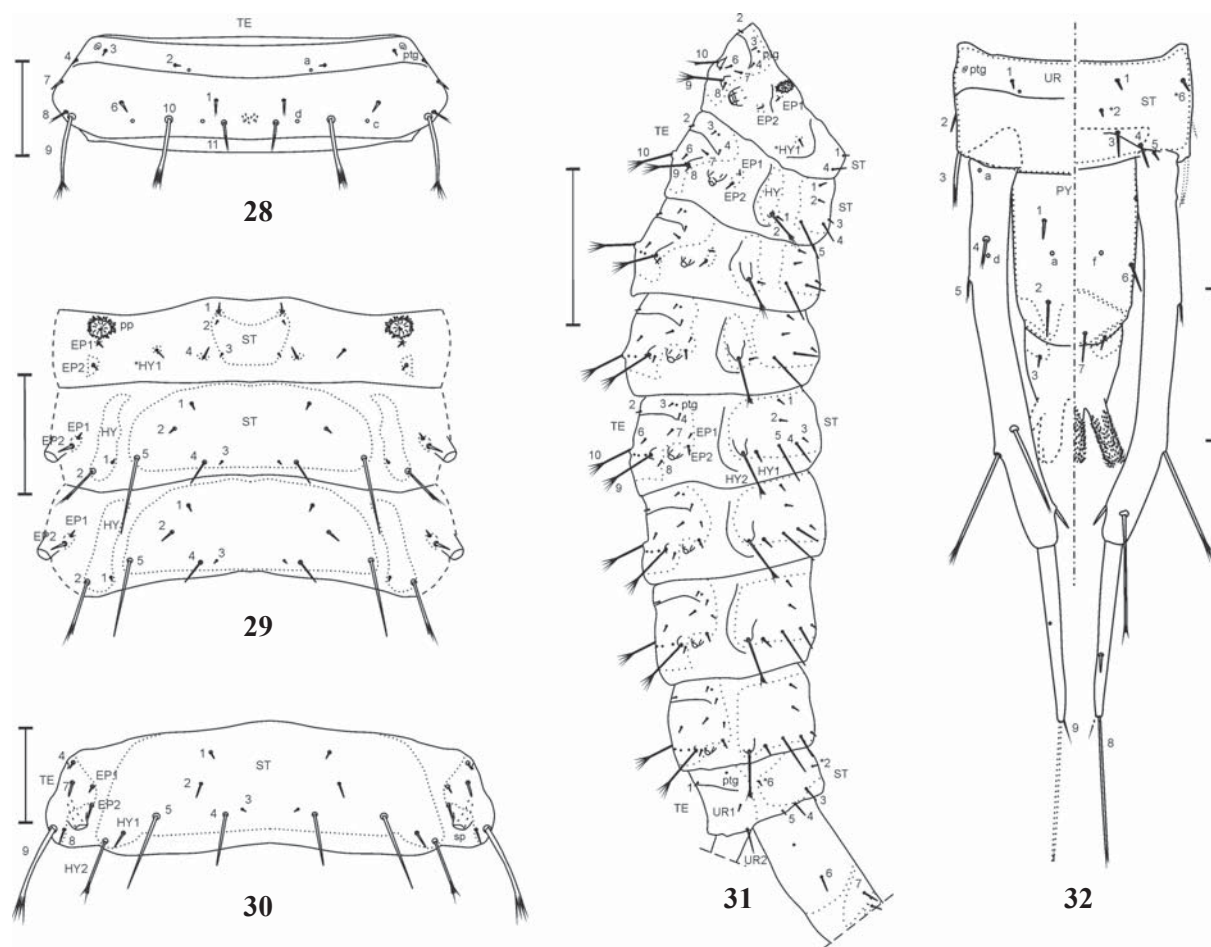
Chaetotaxy (Figs 28–32). Each side of AT I–III with 10 setae (TE_{1-4} , TE_{6-11}), three pores (TE_a , TE_{c-d}) and pretergal gland located close to TE_3 . AT IV–VIII have similar chaetotaxy but differ by presence of two setae (EP_{1-2}), as a result of fusion with epipleurite. AT IX with three setae (UR_{1-3}), one pore located near UR_1 and pretergal gland (Fig. 20). Basal joint of each urogomphi with six setae (UR_{4-5} ; one dorsal, two

lateral and one ventral setae) and two pores (UR_8 , UR_9); apical joint with three setae (UR_{8-9} and one ventral seta) and a single pore. Epipleurite of abdominal segments I–III with two setae (EP_{1-2}); hypopleurite of abdominal segment I with single seta $*HY_1$, on abdominal segments II–IV with two setae (HY_{1-2}). Abdominal sternite (AS) I consists of two pairs of small sclerites, each with single seta (ST_1 , ST_4), and single large sclerite with two setae (ST_{2-3}) on each side. AS II–IV consists of single large sclerite with 5 setae (ST_{1-5}) on each side; AS V–VIII with two extra setae (HY_{1-2}) as a result of fusion with hypopleurite. AS IX with 6 setae (ST_1 , ST_{3-5} , $*ST_2$, $*ST_6$). Pygopod dorsally with 3 setae (PY_{1-3}) and single pore PY_a , ventrally with three setae (PY_{6-7} and one apical seta) and two pores (PY_f and one lateral pore).

Second-instar larva

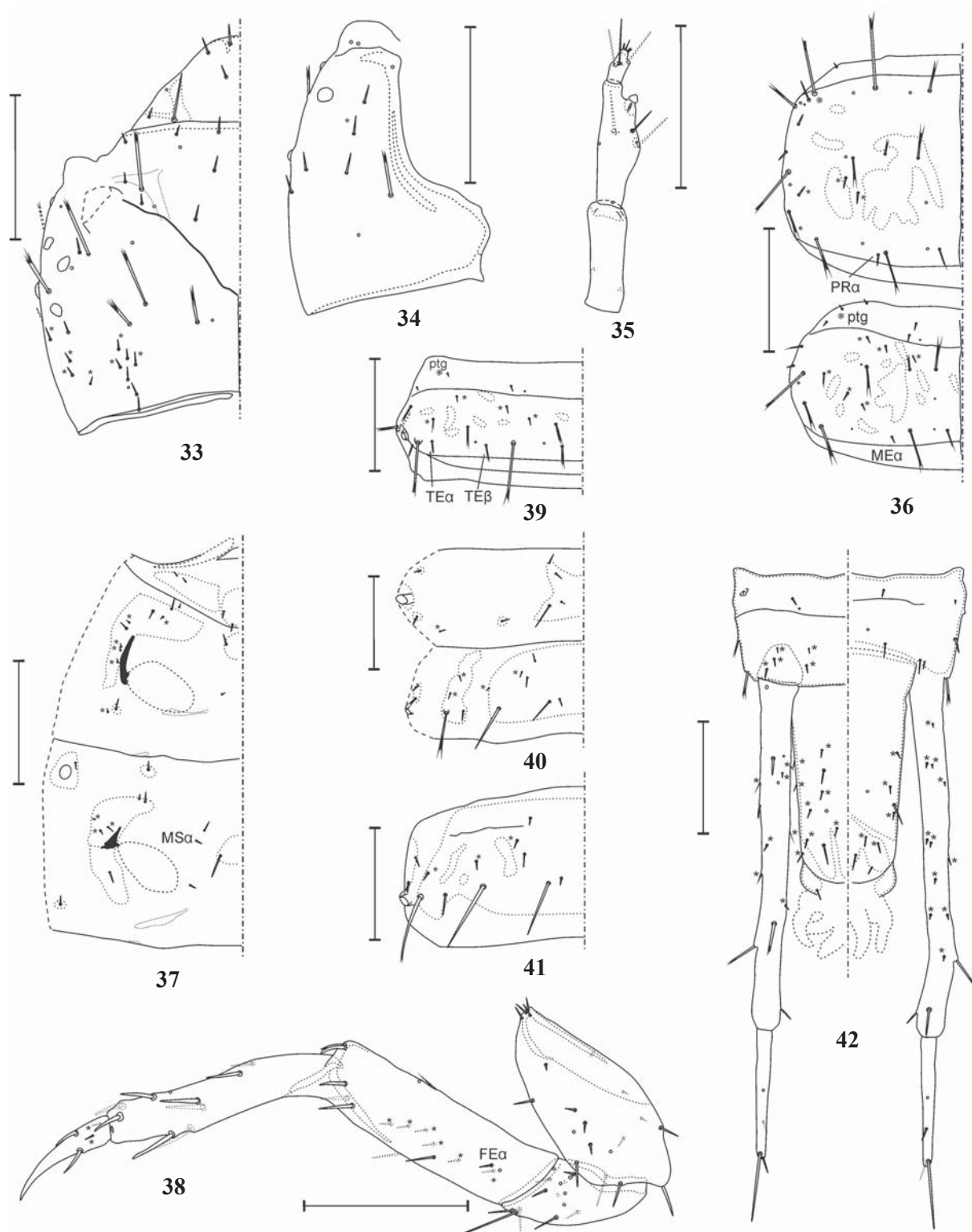
Figs 33–42.

Differences from the first instar are the following. Body length 8.2 mm; head length 1.3 mm; head width 1.5 mm, urogomphi length 2.2 mm; maximum width of thorax 1.8 mm; maximum width of abdomen 1.6 mm. Body widest across mesothorax (Fig. 2). Most setae increase in size in comparison with first instar.



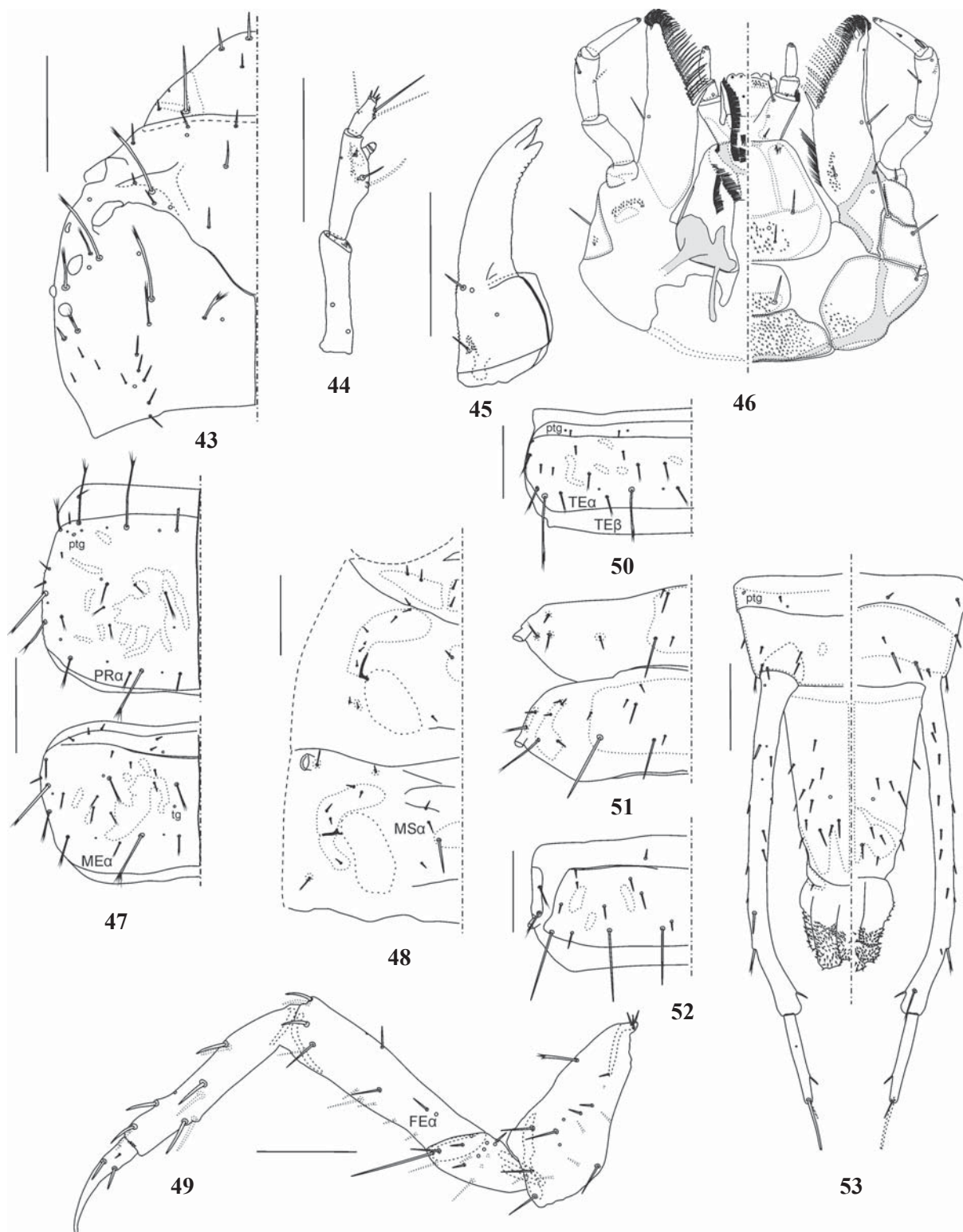
Figs 28–32. *Nodynus leucofasciatus*, first-instar larva. 28 — abdominal segment V; 29 — abdominal segments I–III; 30 — abdominal segment VI; 31 — abdominal segments I–X; 32 — abdominal segments IX–X (left — dorsal view, right — ventral view); 28 — dorsal; 29–30 — ventral; 31 — lateral. Scale bars: 28–30 — 0.3 mm; 31–32 — 0.5 mm.

Рис. 28–32. *Nodynus leucofasciatus*, личинка первого возраста. 28 — V брюшной сегмент; 29 — I–III брюшные сегменты; 30 — VI брюшной сегмент; 31 — I–X брюшные сегменты; 32 — IX–X брюшные сегменты (слева — сверху, справа — снизу); 28 — сверху; 29–30 — снизу; 31 — сбоку. Масштабные линейки: 28–30 — 0.3 мм; 31–32 — 0.5 мм.



Figs 33–42. *Nodynus leucofasciatus*, second-instar larva: 33 — head; 34 — parietale; 35 — antenna; 36 — pro- and mesothorax; 37 — pro- and mesothorax; 38 — fore leg; 39 — abdominal segment V; 40 — abdominal segments I–II; 41 — abdominal segment VI; 42 — abdominal segments IX–X (left — dorsal view, right — ventral view); 33, 36–37, 39 — dorsal view; 34–35, 40–41 — ventral view; 38 — anterior view. Scale bars: 0.5 mm. Secondary setae marked with *.

Рис. 33–42. *Nodynus leucofasciatus*, личинка второго возраста: 33 — голова; 34 — парietальный склерит; 35 — антенна; 36 — передне- и среднегрудь; 37 — передне- и среднегрудь; 38 — нога первой пары; 39 — V брюшной сегмент; 40 — I–II брюшные сегменты; 41 — VI брюшной сегмент; 42 — IX–X брюшные сегменты (слева — сверху, справа — снизу); 33, 36–37, 39 — сверху; 34–35, 40–41 — снизу; 38 — спереди. Масштаб: 0,5 мм. Вторичные хеты обозначены *.



Figs 43–53. *Nodynus leucofasciatus*, third-instar larva: 43 — head; 44 — antenna; 45 — right mandible; 46 — labio-maxillary complex (left — ventral view, right — dorsal view); 47 — pro- and mesothorax; 48 — pro- and mesothorax; 49 — fore leg; 50 — abdominal segment V; 51 — abdominal segments I–II; 52 — abdominal segment VI; 53 — abdominal segments IX–X (left — dorsal view, right — ventral view); 43, 45, 47, 50 — dorsal view; 44, 48, 51–52 — ventral view; 49 — anterior view. Scale bars: 0.5 mm.

Рис. 43–53. *Nodynus leucofasciatus*, личинка третьего возраста: 43 — голова; 44 — антенна; 45 — правая мандибула; 46 — лабио-максиллярный комплекс (слева — снизу, справа — сверху); 47 — передне- и среднегрудь; 48 — передне- и среднегрудь; 49 — нога первой пары; 50 — V брюшной сегмент; 51 — I–II, брюшные сегменты; 52 — VI брюшной сегмент; 53 — IX–X брюшные сегменты (слева — сверху, справа — снизу); 43, 45, 47, 50 — сверху; 44, 48, 51–52 — снизу; 49 — спереди. Масштаб: 0,5 мм.

Head (Figs 33–34). Frontal sclerites with more developed honeycomb pattern (Fig. 55); parietal sclerites with distinct honeycomb pattern and more developed toothed microsculpture (Fig. 58); with five–six secondary setae dorsally and one–two secondary setae ventrally (Figs 33–34).

Antenna (Fig. 35) 0.8 as long as head length. Antennomere I 4.8 as long as wide. Antennomere II 1.1 as long as antennomere I and 3.0 as long as wide; conical sensorial appendage (Sa) 0.3 as long as antennomere III; additional sensilla located near AN_1 . Antennomere III 0.3 as long as antennomere II and 2.0 as long as wide.

Proxycardo and sclerotised areas of submentum partly covered in short asperities (Fig. 61).

Thorax (Figs 36–37). Pronotum partly with microgranulated sculpture, except distinct smooth strongly sclerotised areas (Fig. 64); meso- and metanotum partly covered in asperities, without group of medial asperities associated with anterior carina (Fig. 67). Prothoracic episternum, meso- and metathoracic epimeron and sternal sclerites covered with small asperities.

Chaetotaxy (Figs 36–37). Prothorax: pronotum with three–four secondary setae and additional seta PR_a ; episternum with four–five secondary setae; epimeron with single additional seta EM_a . Meso- and metathorax: meso- and metanotum with five–seven secondary setae and additional seta ME_a ; episternum with two–three secondary setae; meso- and metasternite with additional seta MS_a .

Legs (Figs 38, 76). Surface of coxa and femur partly with honeycomb pattern (Fig. 76). Femur with four–six posterior secondary setae and one additional anterior seta FE_a close to FE_b . Claw with two additional setae UN_{a-p} (Fig. 41).

Abdomen (Figs 39–42). AT I–IX covered in more asperities, which absent on strongly sclerotised areas (Fig. 70). Abdominal pleurites mostly smooth, sternites partly covered in asperities (Fig. 73). AS V–VII with incomplete anterior carina, AS VIII–IX with almost complete anterior carina. Remains of pleuropodium on AS I absent.

Urogomphi 0.25 as long as total body length; basal joint 2.7 as long and 2.3 as wide as apical one. Surface of urogomphi with more developed scale-like sculpture (Fig. 79). Dorsal surface of pygopod with larger asperities.

Chaetotaxy (Figs 39–42). AT I–VIII with four–five secondary setae and two additional setae (TE_{a-p}). AT IX with five secondary setae; basal joint of each urogomphi with five–seven secondary setae dorsally and eight–ten ventrally (Fig. 42). Hypopleurite of abdominal segments II–IV with two–three secondary setae. Abdominal sternite I consists of single large sclerite with setae ST_{1-4} . Abdominal sternites II–VIII with two–three secondary setae. Pygopod dorsally with seven–eight secondary setae, ventrally with five secondary setae.

Third-instar larva Figs 43–53.

Differences from the instar II are the following. Body length 12.3 mm; head length 1.7 mm; head width 1.8 mm, urogomphi length 2.5 mm; maximum width of thorax 2.4 mm; maximum width of abdomen 2.5 mm (Fig. 3). Most setae increase in size in comparison with second instar.

Head (Fig. 43). Frontal sclerites more sclerotised with distinct honeycomb pattern (Fig. 56); parietal sclerites with much larger asperities (Fig. 59). Chaetotaxy is the same as in second-instar larva (Fig. 43).

Antenna (Fig. 44) 0.7 as long as head length. Antennomere I 5.0 as long as wide. Antennomere II 0.8 as long as antennomere I and 3.1 as long as wide; conical sensorial appendage (Sa) 0.4 as long as antennomere III. Antennomere III 0.5 as long as antennomere II and 3 as long as wide.

Mandible (Fig. 45). Dorsal surface of each mandible in basal part with a group of small cuticular spines.

Dorsal triangular sclerite near the outer margin of stipes with medial asperities, small dorsal medial sclerite partially surrounded with asperities. Mala with asperities near the inner margin (Fig. 46). Sclerotized areas of submentum and mentum entirely covered with stout asperities (Fig. 62).

Thorax (47–48). Pronotum mostly covered in distinctly larger granulae (Fig. 65); meso- and metanotum almost entirely covered in large asperities (Fig. 68). Pretergal glands visible only on pronotum, tergal glands distinct on all segments. Thoracic pleurites and sternites with asperities arranged in short rows. Chaetotaxy is the same as in second instar (47–48).

Legs (Fig. 49). Entire surface of all joints except claw with asperities arranged in short rows (Fig. 77). Chaetotaxy is the same as in second instar.

Abdomen (50–53). Almost all surface of AT I–IX covered in stout asperities (Fig. 71). Abdominal pleurites and sternites with asperities arranged in short rows (Fig. 74). AS VIII–IX with complete anterior carina.

Urogomphi 0.2 as long as total body length; basal joint 4.0 as long and 1.6 as wide as apical one. Surface of urogomphi with more developed scale-like sculpture (Fig. 80). Dorsal surface of pygopod with stout asperities, most of them arranged in short rows; most of ventral surface with similar asperities, which are less developed in medial part.

Difference between *Apatetica* and *Nodynus* larvae

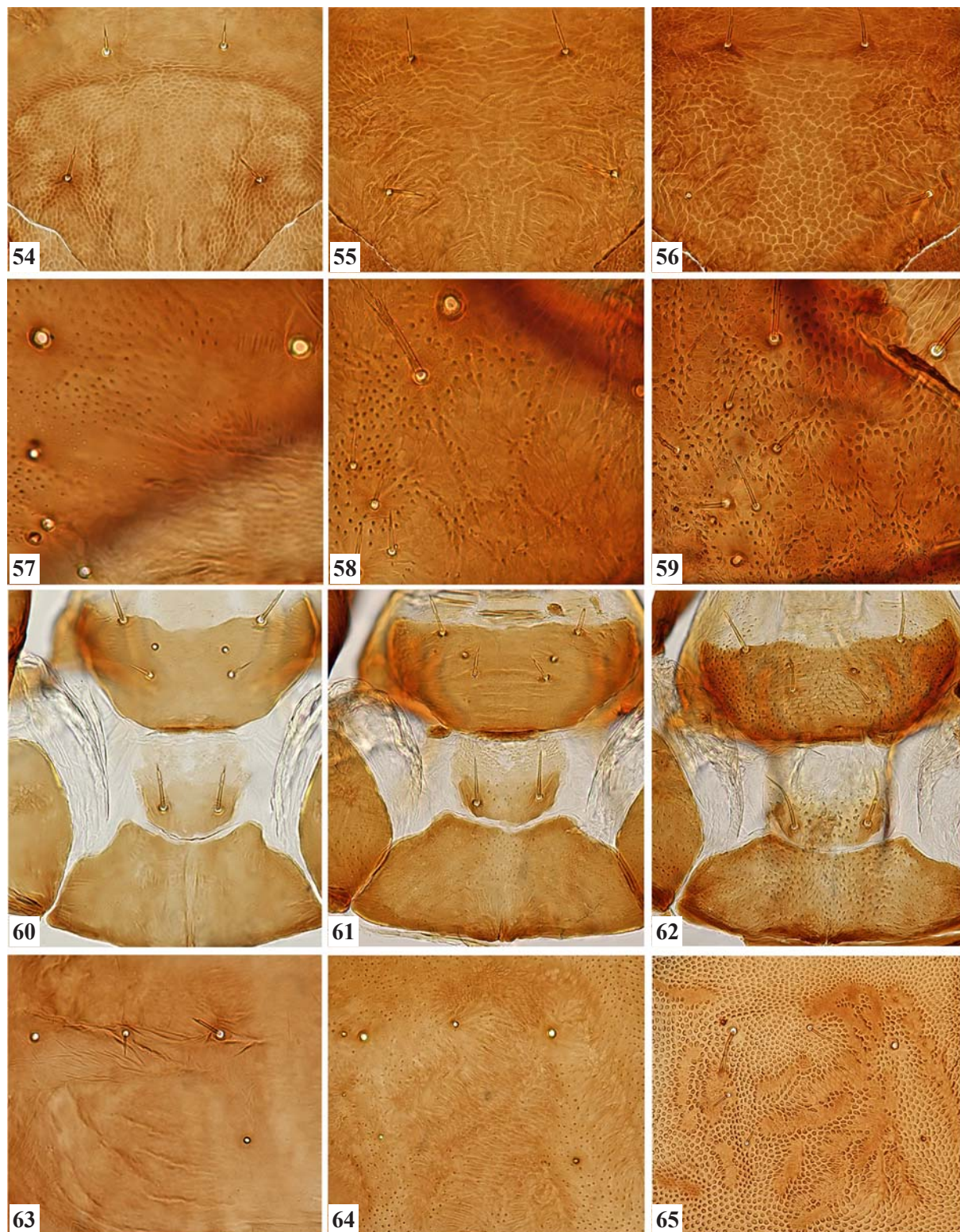
Major differences between *Apatetica* and *Nodynus* larvae were pointed out before [Grebennikov, Newton, 2012], such as antenna exceeding head capsule length (much shorter in *Nodynus*) and 1-jointed urogomphi, exceeding abdomen length (much shorter and 2-jointed in *Nodynus*). However, larvae of *Apatetica*, studied by Grebennikov and Newton, had both urogomphi broken, so the number of joints should be revised. Additional difference is ligula apically covered in numerous microtrichia in *Apatetica* (smooth in *Nodynus*).

Taxonomic position of Apateticinae based on larval characters

As was mentioned above, there are several principal views on taxonomic position of Apateticinae, which will be briefly discussed here on the basis of larval characters. It should be noted that these results are preliminary and separate study with additional data on larval morphology (including chaetotaxy) of various groups of Staphylinidae is needed.

A group within Silphidae, part of Silphinae [Madge, 1979].

Apateticinae larvae share some common features with those of Silphinae, such as six pairs of stemmata, similar shape of mandibles and hypopharyngeal sclerotization as well as presence of multiporose structures on epipharynx. But most of these attributes can also be found in other staphylinid subfamilies, so cannot be considered as the proof of close relationship. For instance, similar mandible structure is characteristic for some Aleocharinae, Omaliinae, Trigonurinae, etc [Steel, 1970; Pototskaya, 1976]; six pairs of stemmata are present in some Scaphidiinae, all Trigonurinae, Glyphommatinae and other groups [Thayer, 2005]; multi-



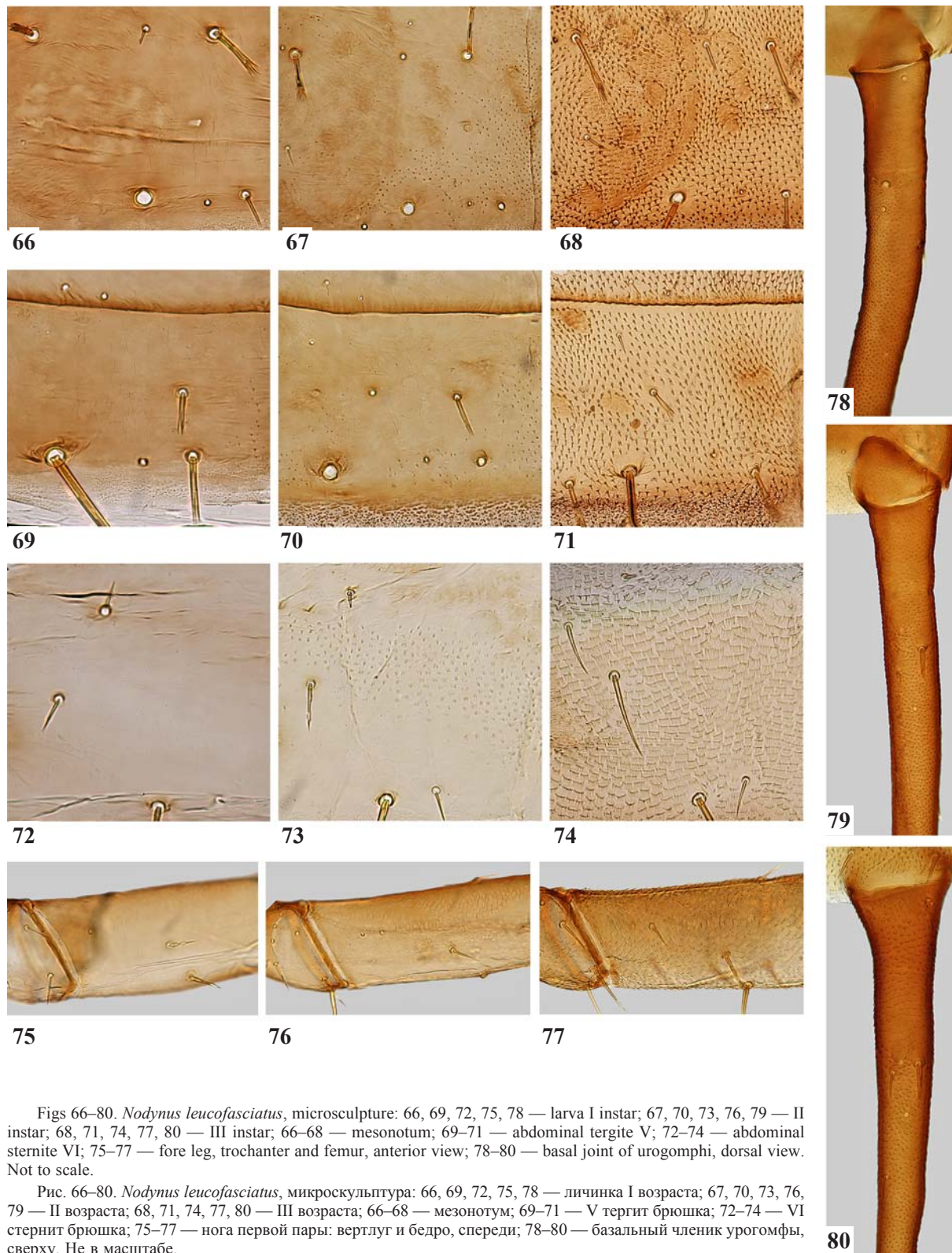
Figs 54–65. *Nodynus leucofasciatus*, microsculpture: 54, 57, 60, 63 — larva I instar; 55, 58, 61, 64 — II instar, 56, 59, 62, 65 — III instar; 54–56 — frontale; 57–59 — parietale; 60–62 — labium, submentum and mentum; 63–65 — pronotum. Not to scale.

Рис. 54–65. *Nodynus leucofasciatus*, микроскульптура: 54, 57, 60, 63 — личинка I возраста; 55, 58, 61, 64 — II возраста; 56, 59, 62, 65 — III возраста: 54–56 — фронтальный склерит; 57–59 — парietальный склерит, сверху; 60–62 — нижняя губа, субментум и ментум; 63–65 — пронотум. Не в масштабе.

porose structures on epipharynx also developed in some Tachyporinae, Aleocharinae and Phloeocharinae [Ashe, Newton, 1993; Ashe, 2005]. Hypopharyngeal sclerotisation is poorly studied in staphylinid larvae and its similar structure can be possibly found in other repre-

sentatives of the family. At the same time, Apateticinae larvae differ from those of Silphinae by presence of modified (apically frayed) setae as well as epicranial and tergal glands.

Moreover, typical Silphinae larval features such as



Figs 66–80. *Nodynus leucofasciatus*, microsculpture: 66, 69, 72, 75, 78 — larva I instar; 67, 70, 73, 76, 79 — II instar; 68, 71, 74, 77, 80 — III instar; 66–68 — mesonotum; 69–71 — abdominal tergite V; 72–74 — abdominal sternite VI; 75–77 — fore leg, trochanter and femur, anterior view; 78–80 — basal joint of urogomphi, dorsal view. Not to scale.

Рис. 66–80. *Nodynus leucofasciatus*, микроскульптура: 66, 69, 72, 75, 78 — личинка I возраста; 67, 70, 73, 76, 79 — II возраста; 68, 71, 74, 77, 80 — III возраста; 66–68 — мезонотум; 69–71 — V тергит брюшка; 72–74 — VI стернит брюшка; 75–77 — нога первой пары: вертлуг и бедро, спереди; 78–80 — базальный членик урогомфы, сверху. Не в масштабе.

the development of extending laterotergites, mala with large galeal lobe covered in numerous setae and apically bilobed ligula were not found in both *Nodynus* and *Apatetica* larvae. So, based on larval morphology, we cannot confirm close relations of Apateticinae and Silphinae.

Sister-group of Trigonurinae or Scaphidiinae [Grebennikov, Newton, 2012; McKenna et al, 2015].

Most of the shared features of Apateticinae and Trigonurinae, such as six pairs of stemmata, shape of mandibles and epipharynx with multiporose structures couldn't indicate close relations, as was mentioned above. Although Grebennikov and Newton [2012] mentioned the presence of frayed setae on head and body segments of *Trigonurus* as shared feature with Apateticine larvae, judging by figures they are actually not frayed, but clavate pubescent ones [Pototskaya, 1976; Lawrence, 1991], which are very rare in Staphylinidae. Moreover, *Trigonurus* larva differs from Apateticinae by the bilobed ligula and epipleurites fused with abdominal tergites I–IX [Pototskaya, 1976]. Another inconsistent character is the number of urogomphi joints, which is two in *Nodynus* and *Trigonurus*, but single one in *Apatetica* (see remark above). Besides, urogomphal joints in *Trigonurus* have distinct ring-shaped sculpture [Grebennikov, Newton, 2012] which is absent in Apateticinae.

According to recent molecular phylogenetic studies, Apateticinae and Scaphidiinae considered to have a sister-group relations [McKenna et al, 2015; Gusarov, 2018]. Shared features of larvae of these two subfamilies are rather hard to point out because of variable morphology of Scaphidiinae, which larvae can have five or six pairs of stemmata, one- or two-jointed urogomphi, various shape of mandibles, etc. [Kasule, 1966; Kompantsev, 1987]. Nonetheless, larvae of these two subfamilies have both epicranial and tergal glands and the structure of thoracic endoskeleton is nearly identical in *Scaphidium* and *Nodynus* larvae. However, glands mentioned above are also found in Glypholomatinae, Aleocharinae, Oxytelinae and Staphylininae larvae [Kilian, 2007]. Identity of the thoracic endoskeleton potentially could be of taxonomic significance, but knowledge of its structure within Staphylinodea is fragmentary, so this similarity should be treated with caution. Scaphidiinae larvae differ from Apateticinae by crenulate emargination on anterior margin of labrum, rounded ligula, epipleurites fused with abdominal tergites II–IX and hypopleurites fused with abdominal sternites VIII–IX [Ashe, 1984; Kompantsev, 1987]. Moreover, Scaphidiinae larvae lack frayed (and modified in general) setae and multiporose structures in epipharynx. So, in our opinion, there is no direct confirmation of close relations between Apateticinae and Scaphidiinae or Trigonurinae based on larval morphology.

Separate family in Staphylinodea [Hansen, 1997]

Based even on preliminary comparative analysis given above, it becomes quite evident, that most morphological features of Apateticinae larvae (number of stemmata, shape of mandibles, presence of apically frayed setae and mutiporose structures, set of thoracic

endoskeleton elements etc.), can be found in different combinations in various groups within the family. The only unique feature that can be established for Apateticinae is “tetra-lobed” ligula, so in our opinion there are not enough morphological evidences to count this group as separate family in Staphylinodea. It is interesting to mention though, that very similar shape of ligula is known in some Hydraenidae [Deler-Hernández, Delgado, 2017], but it requires further elaboration.

At the present time it is rather difficult to make any conclusions about the taxonomic position of Apateticinae within the Staphylinidae (except that it's almost certain they are not part of Silphinae, which are often treated as staphylinid subfamily nowadays) due to combination of characters mentioned above in various representatives within the family. Thus, we preliminary agree with Grebennikov and Newton [2012], who refer this “basal” group as Staphylinidae *incertae sedis*.

Notes on the chaetotaxy of Staphylinidae

Nowadays two main nomenclatural systems of chaetotaxy are used in studies of various groups of Coleoptera. The first one is by Ashe and Watrous [1984], proposed initially for Aleocharinae and used later for other subfamilies of Staphylinidae, as well as, with certain degree of modification, different Staphyliniformia families, such as Leiodidae, Hydraenidae, Catopidae, Ptiliidae [Wheeler, 1990; Delgado, Soler 1997; Sörensson, Delgado, 2019]. More recently this system was proposed for such distant groups as Helotidae and Monotomidae (Cucujoidea) [Lee et al, 2007; Wagner et al, 2020].

However, application of this system meets some difficulties in establishing of homologies within the family or Staphylinodea in general. Firstly, in Ashe and Watrous paper chaetotaxy nomenclature for antennae, mandibles, and labio-maxillar complex have not been provided, although their setal pattern is rather constant within the family. Secondly, this system undergo various modifications in studies of other staphyliniform families, e.g. change in the setal rows orientation from transverse to longitudinal [Wheeler, 1990; Kilian, 2007] and different principle of coding [Delgado, Soler, 1997]. It resulted in the fact that obviously homological setae were coded differently, which could lead to confusion, especially when one tries to establish the common chaetome pattern for Staphyliniformia in general. For example, seta A12 [Ashe, Watrous, 1984] located on trochanter closely to pore c4, and typical for all Staphyliniformia (and most likely beetles in a whole), is coded as Ad1 for Leiodidae [Kilian, 2005] and Hydraenidae [Delgado, Soler, 1997]; frontal seta Fd3 in Aleocharinae is coded as Da2 for Leiodidae and Fd2 for Ptiliidae [Sörensson, Delgado, 2019], etc. So, despite significant number of homological setae in larvae of these families, this similarity is unobvious due to the different coding. Moreover, the designation of chaetome elements based on the location on certain side of the body or appendage (marginal, lateral, anterolateral, posteroventral, etc) could also become the reason of different names ap-

pearing for the same setae. Such situation is rather natural, because the position of certain setae may change in comparison with *Dalotia (Atheta) coriaria* Kraatz, the model of Ashe's system, or even if orientation of the object on slide mount is different. In fact, it occurs even in studies within Aleocharinae, e.g., seta Pv1 on tibiotarsus may be coded as V1 [Staniec et al, 2018a] or Av2 [Staniec et al, 2018b]. All these difficulties resulted in the situation, when some authors rejected Ashe and Watrous system, suggesting consistent numeration of chaetome elements instead [Solodovnikov, Newton, 2005; Pietrykowska-Tudruj et al, 2011].

Also, Ashe and Watrous system is based on study of third-instar larvae, whose chaetotaxy is characterized by appearing of "secondary" setae, which number and position is significantly variable. Wheeler, in his study of Leiodidae [1990] pointed out the necessity of studying the chaetotaxy of first-instar larvae, and in subsequent works on Leiodidae, Hydraenidae and other Staphyliniformia families [Delgado, Soler, 1997; Kilian, 1998] this was performed. Unfortunately, in most papers on larval chaetotaxy of Staphylinidae, data are provided only for last-instar larvae, which makes certain difficulties in understanding common chaetome elements within the family.

The second nomenclatural system have been proposed by Bousquet and Goulet [1984] for Carabidae, and later improved by Makarov [1996]. It was subsequently used in studies of other adaphagan families, such as Dytiscidae, Haliplidae, Rhysodidae [Alarie, Harper, 1990; Makarov, 2008; Michat et al, 2020], as well as Cupedidae (Archostemata) [Grebennikov, 2004], and Hydrophilidae (Hydrophiloidea) [Fikacek et al, 2008].

In our opinion this system have the following advantages over that of Ashe and Watrous: chaetotaxy of all the body regions and appendages was coded and the designation of homological setae carried out with the help of additional methods, such as sigillotaxy and diagnostic of rather stable complexes (e.g. "seta-pore") [Makarov, 1996].

Based on our study, it appears that significant part (about 70%) of *Nodynus* chaetome elements can be reliably homologized with those of Carabidae (Table). The highest degree of congruence can be traced on body segments (except abdominal IX–X) and leg joints (except coxa). Less obvious homologies can be established for structures which undergo significant transformation comparing with Carabidae, such as labrum, labium, maxilla with galea and lacinia fused, as well as abdominal segment IX with two-jointed urogomphi. However, we believe that even on such structures more homological elements of chaetome could be found, if comprehensive study of first-instar staphylinid larvae would be performed. So, we conclude that Bousquet and Goulet system can be applied for Staphyliniformia larvae and, potentially, other groups of beetles. It can be the first step to unified nomenclatural system of chaetotaxy for beetles larvae in general, based on homological elements, which can have a certain value for phylogenetic study within the order. Moreover, if we agree with the basal position of Apateticinae within Staphylinidae (see

Discussion above), it makes us suggest that their chaetome pattern can be close to original for the family, thus making it the "starting point" when analyzing other staphylinid larvae chaetotaxy.

Acknowledgements. We are sincerely grateful to K.V. Makarov (MPGU) for permission to use photo of adult *Nodynus* and for valuable comments during our study.

Competing interests. The authors declare no competing interests.

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Table. Setal and pore homologs found in staphylinid and carabid larvae.
Таблица. Хеты и поры, гомологичные для личинок стафилинов и жуужелиц.

Body region		Ashe, Watrous [1984]	Bousquet, Goulet [1984]
Head	Frontal sclerite	Fd1, Fd2, Fd3 Fm1 F11, F12, F13, Fc1, Fc2	FR5, FR4, FR3 FR6 *FR7, FR1, FR2 *FRc/e, FRb
	Labrum	Ld1 Lm1, Lm2 Ll1	*FR11 *FR10, *FR9 *FR8
	Parietal sclerite	P2, P3, P4 Ed1, Ed2, Ed3 E11, E13 Em2 V1 V11 Ec1, Ec2, Ec3 Vc1, Vc2	PA3, PA2, PA1 PA7, PA5, PA4 PA10, PA6 PA9 *PA17 *PA12 PAd, PAb, PAa *PAn, *PAi
	Antenna	not coded*	AN1, AN2, AN3, AN4, AN5, AN6, AN7 ANa, ANb, * ANc/d, * ANd/e, ANf
	Mandible	not coded	MN1 MNa, MNb
	Maxilla	not coded	MX1, MX2, MX3, *MX9, MX10, MX11, MX12 MXe, MXf, MXg
	Labium	not coded	PA16, PA18, PA19 LA1, LA2, LA6 PAo, LAa, LAb, LAc
Thorax	Pronotum	A1, A2, A3, A5 L1, L2, L4 Da2, Dc2, Dd2 P1, P2, P3, P4, P5 C1, C2, C', C'', C3, C4, C5, C6	PR1, PR2, PR3, PR4 PR5, PR6, PR9 PR14, PR8, PR7 PR13, PR12, PRa, PR11, PR10 PRb, PRc, PRd, PRc, PRh, PRi, PRk, PRl
	Mesonotum	A1, A2, A3, A4, A5 L1, L3, L4 P1, P2, P3, P4 Da2, Db1, Db2 C1, C3, C4, C6, C'	ME4, ME3, ME5, ME6, ME7 ME9, ME10, ME11 ME14, ME13, MEa, ME12 ME1, ME2, ME8 PRa, PRd, PRb, PRg, PRc
	Cervicosternum	Pr1, Pr2, Eu1, Eu2	gPS
	Episternite I	Prehy', Prehy1, Prehy2, Ls2	ES1, ES2, ES3, ES4
	Epimerite I–III	Pohy1	EM1
	Prosternite	St1, St2	PS1, PS2
	Episternite II–III	not coded	ES1, ES5, ES6
	Meso-, metasternite	not coded	MS1, MS2, MS3, MS4
	Pleurite II–III	not coded	PL1
Leg	Coxa	Bs1, Bs2, Bs3 Ad2, Ad1, Pd1 C1, C2	CO1, CO2, CO3 CO9, CO10, CO11 COb, COa
	Trochanter, anterior	Al2, Av1, Av2 C1, C2, C3, C4, C5	TR1, TR3, TR2 TRe, TRd, TRc, TRb, TRa
	Trochanter, posterior	Pl1, Pv1, Pv2 C6, C7	TR6, TR5, TR7 TRf, TRg
	Trochanter, ventral	V1	TR4
	Femur, dorsal	D1 C1	FE1 FEa

Table. Ending
Таблица. Окончание.

Body region		Ashe, Watrous [1984]	Bousquet, Goulet [1984]
Leg	Femur, anterior	Ad1, Av1, Av2 C2	FE2, FE6, FE3 FEb
	Femur, posterior	Pd1, Pv1	FE5, FE4
	Tibiotarsus, anterior	Ad1, Ad2, Ad3, Av1, Av2 C1, C2	TA2, TA1, TI2, TI4, TI3 TA_b, TA_a
	Tibiotarsus, posterior	Pd1, Pd2, Pl1, Pv1	TA7, TI7, TI6, TI5
	Pretarsus	not coded	UN1, UN2
Abdomen	Tergite I–VIII (+epipleurite I–III)	A2, A4, A5 P1, P2, P3, P4, P5 Da2, Db2, Dd2 L1, L4, L5 C1, C5, C6	TE2, TE3, TE4 TE11, TE10, TE_a, TE_β, TE9 TE1, TE6, TE7 EP1, EP2, TE8 TE_a, TE_c, TE_d
	Tergite IX and urogomphi	A2, L1, P5 Ud1, Ud', Ud4, Uv2 not coded	UR1, UR2, UR3 UR4, UR5, UR8, UR9 UR_a, UR_d
	Sternite I	Ps1, P1, P2, D2	ST1, ST3, ST4, ST2
	Sternite II–VIII (+hypopleurite II)	Ps1, P1, P2, P4, P5, P6, D2	ST1, ST3, ST4, ST5, HY1, HY2, ST2
	Sternite IX	Ps1, P1, P2, P4	ST1, ST3, ST4, ST5
	Pygopod	not coded	PY1, PY2, PY3, PY6, PY7 PY_a, PY_f

NOTE. Reliable homologies typed in bold. Setae and pores, lacking in *Dalotia (Atheta) coriaria*, but common in *Nodynus* and Carabidae coded with '. * Although chaetotaxy of these structures not coded in Ashe and Watrous [1984] system, homology can be established.

ПРИМЕЧАНИЕ. Надёжные гомологии выделены жирным шрифтом. Хеты и поры, не указанные для *Dalotia (Atheta) coriaria*, но общие у *Nodynus* и Carabidae, обозначены с '. * Хотя номенклатура хетотаксии этих структур не приводится в системе Ashe и Watrous [1984], гомологичные элементы могут быть установлены.