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Biology and morphology of immature stages of five species of the genus *Cordilura* (Diptera: Scathophagidae)

Биология и морфология преимагинальных стадий пяти видов рода *Cordilura* (Diptera: Scathophagidae)

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КЛЮЧЕВЫЕ СЛОВА: Diptera, Scathophagidae, *Cordilura*, личинка, пупарий, описание, биология, *Carex*, Палеарктика.

ABSTRACT. The morphology of three instar larvae and puparia of five species of the genus *Cordilura* (Diptera: Scathophagidae): *C. aberrans* (Becker, 1894), *C. ciliata* (Meigen, 1826), *C. picipes* (Meigen, 1826), *C. pudica* (Meigen, 1826) and *C. rufimana* (Meigen, 1826) was studied. The morphology of the preimaginal stages of four species (except *C. pudica*) is described in this paper for the first time. Data on the biology of the studied species are presented. Larvae and puparia were collected in the Moscow Region from the stems of three species of sedges of the genus *Carex* (*C. vesicaria*, *C. rostrata*, *C. riparia*).

РЕЗЮМЕ. Изучена морфология личинок 3-его возраста и пупариев пяти видов рода *Cordilura* (Diptera: Scathophagidae): *C. aberrans* (Becker, 1894), *C. ciliata* (Meigen, 1826), *C. picipes* (Meigen, 1826), *C. pudica* (Meigen, 1826) и *C. rufimana* (Meigen, 1826). Морфология преимагинальных стадий четырех видов (кроме *C. pudica*) описаны в данной работе впервые. Приведены данные по биология изученных видов. Личинки и пупарии были собраны в Московской области в стеблях трех видов осок рода *Carex* (*C. riparia*, *C. rostrata*,*C. vesicaria*).

Introduction

Cordilura Fallén, 1810 is the largest genus within the family Scathophagidae and consists of 92 species distributed in the Northern Hemisphere: 47 species are known in Palaearctic [Iwasa, 2020; Ozerov, Krivosheina, 2020] and 36 in Nearctic [Vockeroth, 1965, 1987], with 7 species with Holarctic distribution; 2 species are recorded in Oriental Region [Ozerov, Krivosheina, 2012, 2013].

The fauna of Russia includes 38 species and 12 species known in Moscow Region, where our research was conducted [Ozerov, Krivosheina, 2020].

Adults (Fig. 1) of *Cordilura* species are often collected at locations where *Carex* plants grow: in marshy plots, at banks of lakes covered with thickets of *Carex* spp., along spring banks and in other mesophytic habitats.

Almost all species of *Cordilura* larvae whose habits are known are primary borers in stems of *Carex* and *Scirpus* spp. (Cyperaceae), and *Juncus* (Juncaceae) [Neff, Wallace, 1969; Wallace, Neff, 1971]. Besides, larvae of *Cordilura* have been found in stems of *Glyceria* (Gramineae) [Ferrar, 1987].

Life cycles, morphology of mature larvae and puparia of 14 Nearctic species of *Cordilura* were described [Neff, Wallace, 1969; Wallace, Neff, 1971], among them the three instar larva and pupa of Holarctic species *Cordilura pudica* (Meigen, 1826). With the exception of *Cordilura pudica*, the immature stages of other species in the Palaearctic are unknown.

In this paper the morphology of mature larvae and puparia of four species — *Cordilura aberrans* (Becker, 1894), *C. ciliata* (Meigen, 1826), *C. picipes* (Meigen, 1826) and *C. rufimana* (Meigen, 1826) is described for the first time. One of them, *C. rufimana*, is Holarctic and is widespread in Palaearctic [Vockeroth, 1965; Šifner, 2008; Ozerov, Krivosheina, 2020]. The other three spe-

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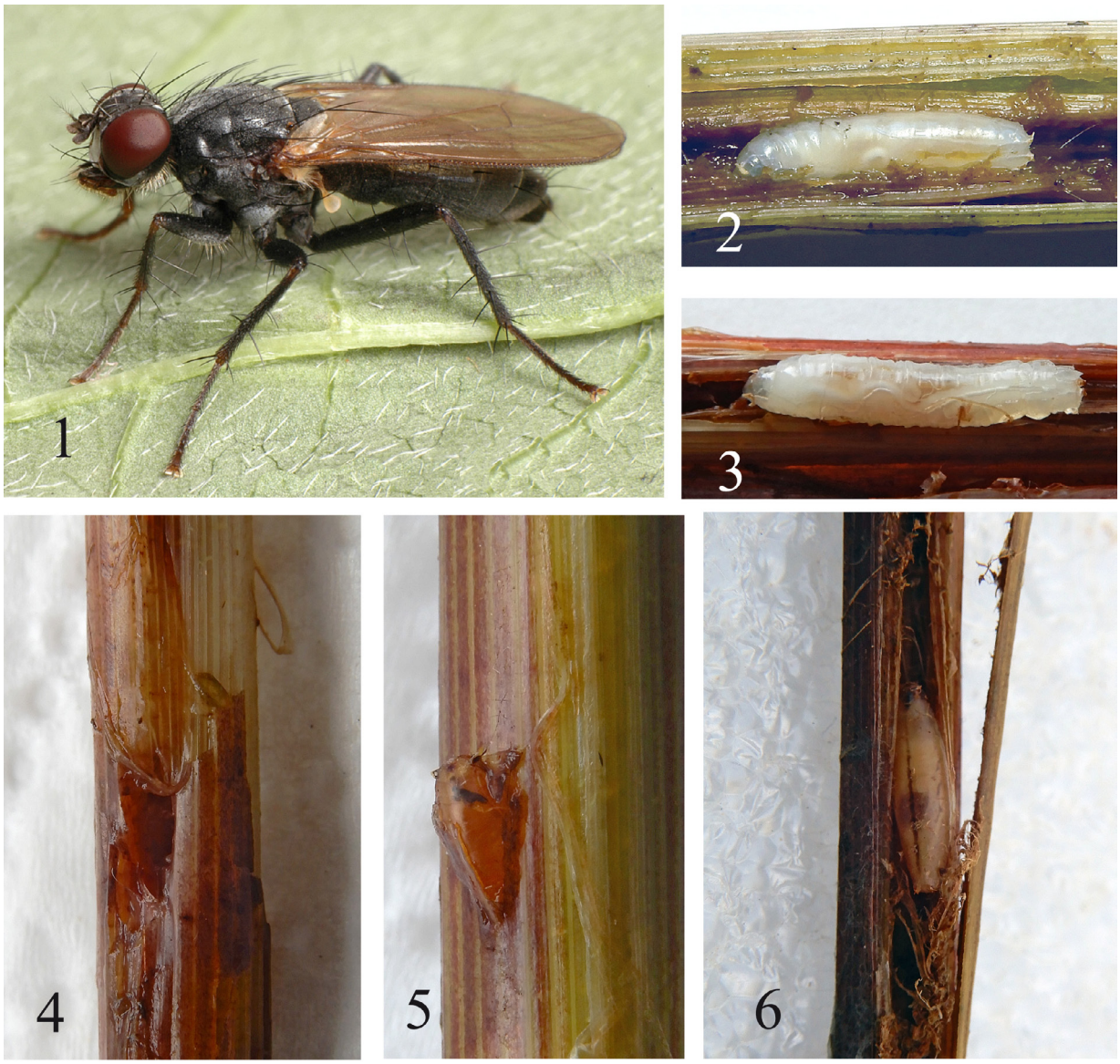
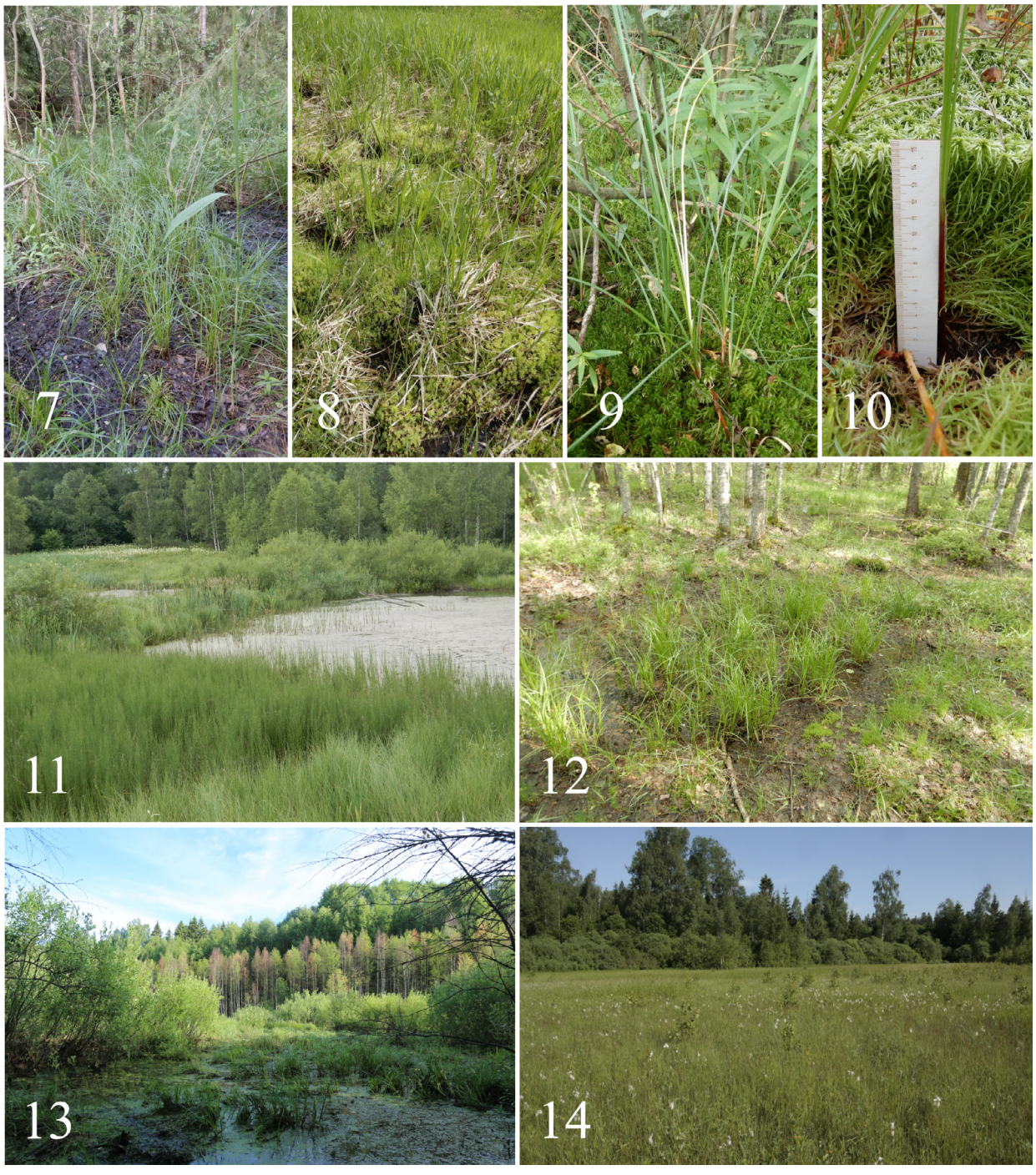
cies are Palaearctic. *C. aberrans* is noted in Scandinavia, european part of Russia and Mongolia; *C. ciliata* is widespread in Europe, also is registered in Siberia; *C. picipes* is widespread in Europe and noted in Mongolia [Šifner, 2008; Ozerov, Krivosheina, 2020].

Material and Methods

The collection of the preimaginal material (mature larvae (Figs 2, 3) and puparia (Figs 5, 6)) was carried out from stems of *Carex* spp. in Moscow Region, Shakhovskaya District, in the following locations: environs of Burtsevo (~55.9855ºN, 35.6053ºE and ~55.9842ºN, 35.5962ºE), forest bogs (Fig. 7); environs of Sizenevo (~56.0180ºN, 35.5699ºE), sphagnum bog (Figs 9, 10); environs of Yakshino (~55.9374ºN, 35.5611ºE), forest bog (Fig. 12); environs of Stepan'kovo (55.9858ºN, 35.6237ºE), bank of a lake formed by beavers and covered with *Carex* spp. (Fig. 13); environs of Ignatkovo (55.9487ºN, 35.5926ºE), sphagnum bog (Fig. 8); environs of Andreevskoe (55.9763ºN, 35.5970ºE and 55.9750ºN, 35.6037ºE)), forest bogs; environs of Shakhovskaya (56.0410ºN, 35.4561ºE), sphagnum bog (Fig. 14); environs of Ignatkovo (55.9519ºN, 35.6245ºE), forest bog; environs of Stepan'kovo (56.0044ºN, 35.6251ºE), bank of the Kolpyanka River (Fig. 11).



Figs 1–6. 1 — female of *Cordilura picipes* (Meigen); 2 — mature larva of *Cordilura picipes* (Meigen) in stem of *Carex vesicaria*; 3 — mature larva of *Cordilura aberrans* (Becker) in stem of *Carex rostrata*; 4 — exit hole of larva of *Cordilura pudica* (Meigen) in stem of *Carex riparia*; 5 — puparium of *Cordilura pudica* (Meigen) in exit hole of *Carex riparia*; 6 — puparium of *Cordilura picipes* (Meigen) in stem of *Carex vesicaria*. 1 — after Ozerov & Krivosheina, 2020, fig. 2.
Рис. 1–6. 1 — самка *Cordilura picipes* (Meigen); 2 — взрослая личинка *Cordilura picipes* (Meigen) в стебле *Carex vesicaria*; 3 — взрослая личинка *Cordilura aberrans* (Becker) в стебле *Carex rostrata*; 4 — выходное отверстие личинки *Cordilura pudica* (Meigen) в стебле *Carex riparia*; 5 — пупарий *Cordilura pudica* (Meigen) в выходном отверстии из стебля *Carex riparia*; 6 — пупарий *Cordilura picipes* (Meigen) в стебле *Carex vesicaria*. 1 — по Ozerov & Krivosheina, 2020, fig. 2.



Figs 7–14. Larval and puparia collection points of *Cordilura*: 7 — forest bog in environs of Burtsevo; 8 — sphagnum bog in environs of Ignatkovo; 9 — sphagnum bog in environs of Sizenevo (in the center infected stem of *Carex vesicaria*, with etiolated inner stems); 10 — sphagnum bog in environs of Sizenevo; 11 — bank of the Kolpyanka River; 12 — forest bog in environs of Yakshino; 13 — bank of a lake formed by beavers and covered with *Carex* spp. in environs of Stepan'kovo; 14 — sphagnum bog in environs of Shakhovskaya.
Рис. 7–14. Места сбора личинок и пупариев *Cordilura*: 7 — лесное болото в окрестностях Бурцево; 8 — сфагновое болото в окрестностях Игнатково; 9 — сфагновое болото в окрестностях Сизенево (в центре зараженный стебель *Carex vesicaria*, с этиолированными внутренними листьями); 10 — сфагновое болото в окрестностях Сизенево; 11 — берег реки Колпянка; 12 — лесное болото в окрестностях Якшино; 13 — берег озера, образованного бобрами и поросшего осокой, в окрестностях Степаньково; 14 — сфагновое болото в окрестностях Шаховской.

The forest bogs we studied are depressions in the forest with excess moisture but without a permanent water layer on the surface. Sphagnum bogs are characterized by the presence of a thick cover of moss of the genus *Sphagnum* Linnaeus, 1753 (Figs 8–10).

In areas where *Carex* spp. grew, plants with yellow or whitish inner (central) leaves were selected (Fig. 9). These plants were examined at the collection site for the presence of larvae or puparium in the stem.

In the laboratory, larvae and puparia were sorted by species, some of the larvae were removed from the stem and, after scalding with boiling water, were placed for storage in 70º alcohol.

All other stems with larvae and puparia were placed in separate test tubes with moistened sand at the bottom and a portion of sphagnum moss above the sand and were left to hatch as adults for species determination.

Throughout the summer and fall, until the first frosts, the tubes were stored at room temperature, 20–24 °C. When frosts arrived, the tubes were placed in the refrigerator for a week and kept there at approximately 4 °C. By this point, all the larvae had pupated. The refrigerator was then set to approximately –6 °C for one month. After a month, the tubes were again kept at 4 °C for a week, and then stored at room temperature (20–24 °C) until the adult flies or parasites emerged. The emerged flies and the puparia from which they emerged were pinned.

Terminology follows Zimin [1948] and Teskey [1981]. All collected material is stored in the collection of the Zoological Museum of Lomonosov Moscow State University (ZMUM).

Descriptions of immature stages

Larvae and puparia of the genus *Cordilura* share several common morphological characteristics that are difficult to distinguish at the species level. Therefore, we describe these morphological traits as common to the species we studied.

The pattern of the cephalopharyngeal skeleton is described using the example of one of the species — *C. pudica* (Fig. 16). Cephalopharyngeal skeleton strongly sclerotized. Mandibles massive, each mandible is bifid anteriorly. Dental sclerite triangular in lateral view. Hypopharynx broad, about 3 times as long as wide. Tentorial phragma broad. Dorsal cornua of pharyngeal sclerite relatively narrow with long slit-like window. Ventral cornua of pharyngeal sclerite shorter than the dorsal, broad, more sclerotized basally.

The posterior end of the body of all larvae and puparia bears the same number of paired tubercles (Fig. 15): dorsal, upper lateral, lower lateral, ventral, subventral, subanal, and unpaired anal.

The anal slit is longitudinal.

Cordilura aberrans (Becker, 1894)
Figs 3, 24, 25, 45, 46, 48, 51, 52.

MATERIAL EXAMINED. 2 larvae collected on 8.VII.2024 from environs of Sizenevo, forest bog along the edge of sphagnum bog; 4 larvae collected on 13.VII.2024 from environs of Andreevskoe (55.9750ºN, 35.6037ºE), forest bog; 6 larvae collected 18.VII. and 13.VIII.2024 from environs of Yakshino, forest bog on *Carex vesicaria*; 4 larvae emerged from larvae collected 20.IX.2024 from environs of Ignatkovo, forest bog; 3 puparia emerged from larvae collected 19.VII.2024 from environs of Ignatkovo, forest bog; 1 puparum emerged from larvae collected on *Carex vesicaria* 12.VIII.2024 from environs of Yakshino, forest bog; 3 puparia emerged from larvae collected 8.VII., 19 and 24.IX.2024 from environs of Sizenevo, forest bog along the edge of sphagnum bog.

DESCRIPTION OF THREE INSTAR LARVA. Body white, integument smooth, anterior end narrowed and rounded, posterior end truncate (Fig. 3). Body length 5.8–11.0 mm, body width 1.1–1.6 mm. Cephalic segment white, with rows of brown spines along posterior margin. Antennae and maxillary palps brown.

Thoracic segments smooth and white, dorsally marked with two triangular yellow-brown spots. Anterior spiracles yellow-brown, Y-shaped, with a distinct depression in the middle dividing spiracle into two asymmetrical branches, dorsal one longer than ventral one, bearing 28–32 papillae (Fig. 24).

Abdominal segments smooth and white, dorsally bearing sparse microscopic spinules. Creeping welts weakly developed, with 1–2 indistinct rows of transparent spinules.

Terminal segment of body has projections in form of clearly visible white conical tubercles; spiracular tubes short and white, with brown spiracular plates located at their apex, each with three curved spiracular slits of approximately equal length. Distance between spiracular plates approximately equal to diameter of spiracular plate (Fig. 25).

Anal plate white, transverse, ribbon-shaped, slightly widened in center, with rounded lateral edges. Anal opening is a longitudinal slit.

DESCRIPTION OF PUPARIUM. Puparium from light brown to dark brown, uniformly colored, without stripes or spots; body cylindrical, slightly tapering towards anterior and posterior ends, integument dense (Figs 45, 46). Body length 6.0–7.5 mm, body width 1.9–2.5 mm.

Anterior spiracles Y-shaped, with a distinct depression in the middle dividing the spiracle into two asymmetrical branches, dorsal one being longer than ventral one (Fig. 52). Posterior spiracles spaced apart by the same amount as diameter of spiracular plate. Slits of posterior spiracles approximately equal in length and curved (Fig. 51).

Anal plate dark brown, transverse, ribbon-shaped, slightly widened in center, with rounded lateral edges (Fig. 48).

Cordilura ciliata (Meigen, 1826)
Figs 15, 22, 23, 28, 29, 36, 42.

MATERIAL EXAMINED. 3 larvae collected 1.VIII. and 18.VIII.2024 on *Carex vesicaria* from environs of Stepan'kovo, bank of the Kolpyanka River; 1 larva collected 3.VII.2024 from environs of Burtsevo, forest bog; 1 larva, 3 puparia, collected 13.IX.2025 from environs of Sizenevo on *Carex rostrata*; 1 puparium emerged from larvae collected on *Carex* sp. 31.VII.2024 from environs of Stepan'kovo, bank of the Kolpyanka River on *Carex* sp.; 5 puparia emerged from larvae collected 19.IX.2024 from environs of Sizenevo; 3 puparia, collected 17.VIII. and 20.IX.2025 from environs of Sizenevo on *Carex rostrata*.

DESCRIPTION OF THREE INSTAR LARVA. Body white, integument smooth, anterior end narrowed and rounded, posterior end truncate, with two prominent posterior spiracles located on short spiracular tubes. Body length 6.6–9.5 mm, body width 1.0–2.3 mm. Thoracic segments smooth, white, with two dorsal longitudinal brown stripes. Anterior spiracles yellow, fan-shaped, with 32–45 brownish spiracular papillae (Fig. 22).

Abdominal segments smooth and white. Penultimate abdominal segment has dorsal spines that evenly cover its surface. Creeping welts are weakly developed and consist of 2–3 rows of transparent spines.

Terminal body segment has two short spiracular tubes, apexed by brown spiracular plates, each with three spiracular slits. Distance between spiracular plates less than diameter of

spiracular plate (Fig. 23). Paired tubercles of terminal body segment small, transparent, and slightly protruding; anal tubercle flat (Fig. 15).

Anal plate is transverse, 4–4.5 times longer than wide (Fig. 42). Anal opening is in the form of a longitudinal slit.

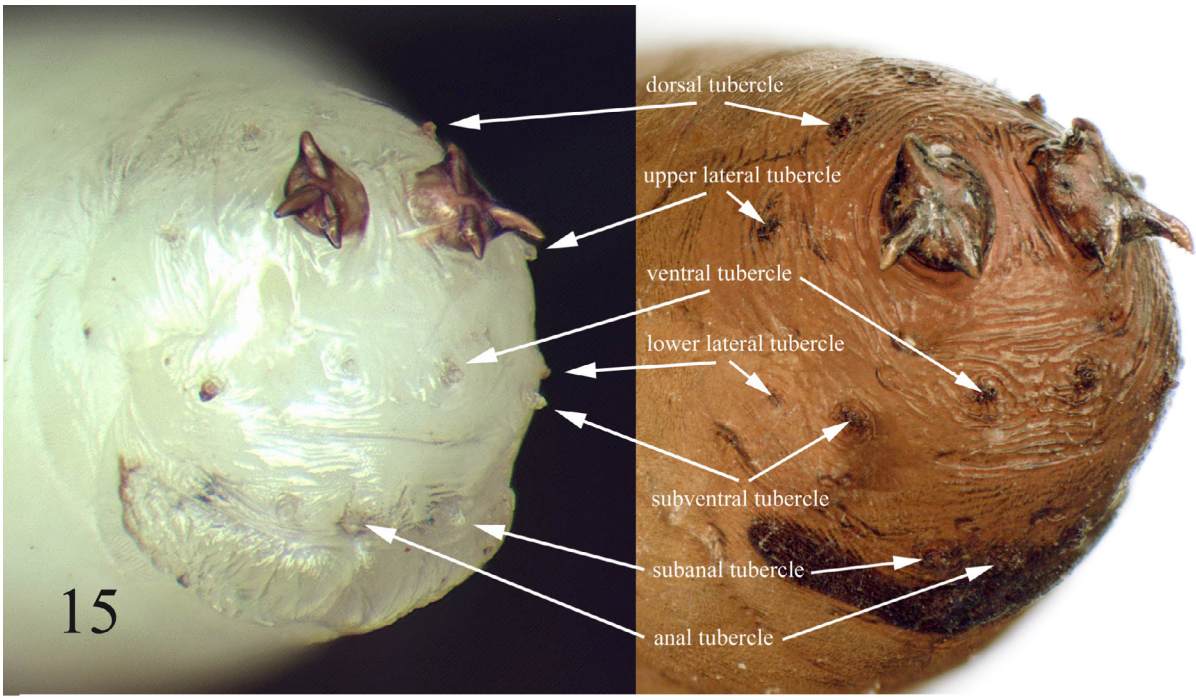
DESCRIPTION OF PUPARIUM. Puparium light brown to dark brown, uniformly colored, without stripes or spots; body cylindrical, slightly tapering towards anterior and posterior ends (Figs 28, 29), integument dense. Body length 5.7–6.9 mm, body width 1.6–2.3 mm.

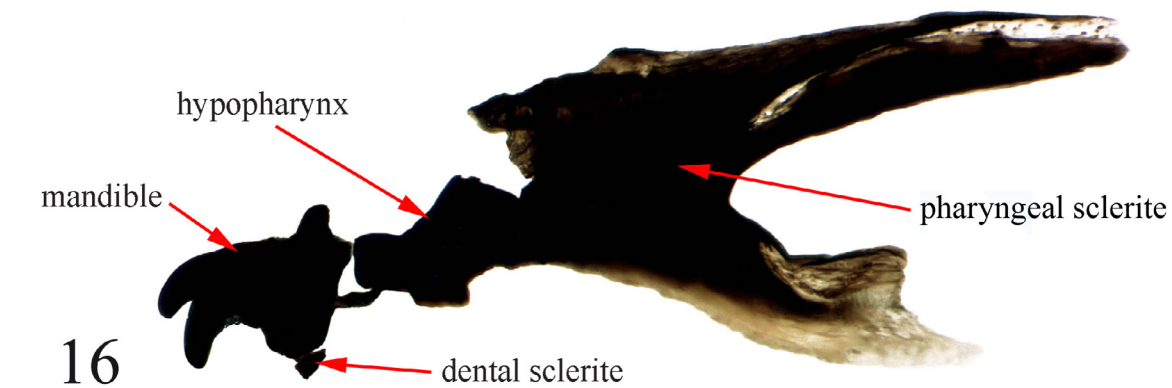
Anterior spiracles distinct and fan-shaped (Figs 28, 29). Posterior spiracles close together: distance between spiracular plates less than diameter of spiracular plate (Fig. 36). Middle slit of posterior spiracles no more than twice as long as lower slit (Fig. 36).

Anal plate dark brown, transverse, ribbon-shaped, smooth along posterior edge, protruding along anterior edge in center, with slightly widened lateral lobes (Fig. 42).

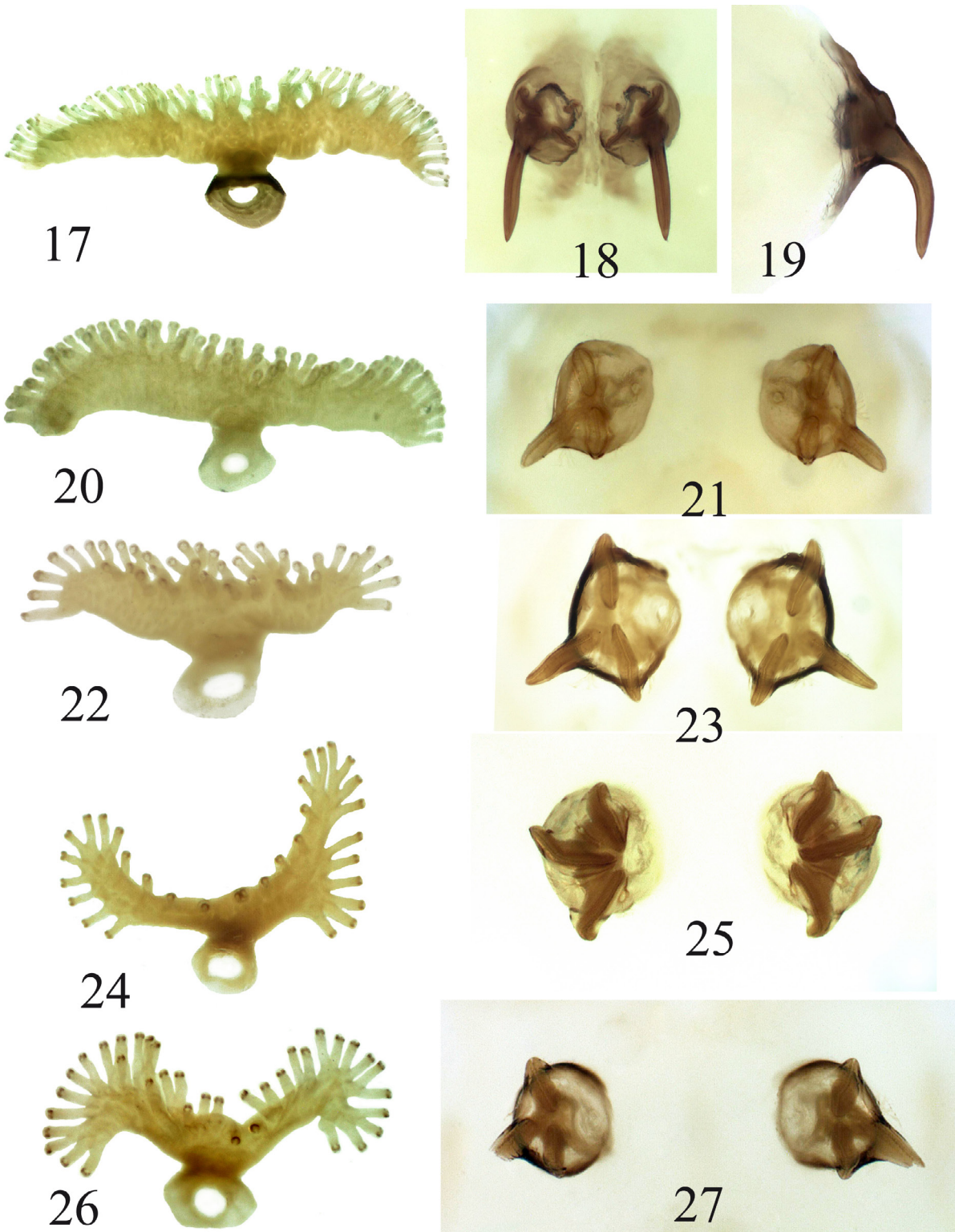
Cordilura picipes (Meigen, 1826)
Figs 1, 2, 6, 20, 21, 30, 31, 37, 40.

MATERIAL EXAMINED. 15 larvae collected 7 and 8.VII.2024 on *Carex vesicaria* from environs of Andreevskoe (55.9763ºN, 35.5970ºE), forest bog; 18 larvae collected 13.VII. and 8.VIII.2024 from environs of Andreevskoe (55.9750ºN, 35.6037ºE), forest bog; 19 larvae collected 6 and 7.IX.2024 from environs of Burtsevo, forest bog; 11 larvae collected 18.VII. and 12, 13.VIII.2024 from environs of Yakshino, forest



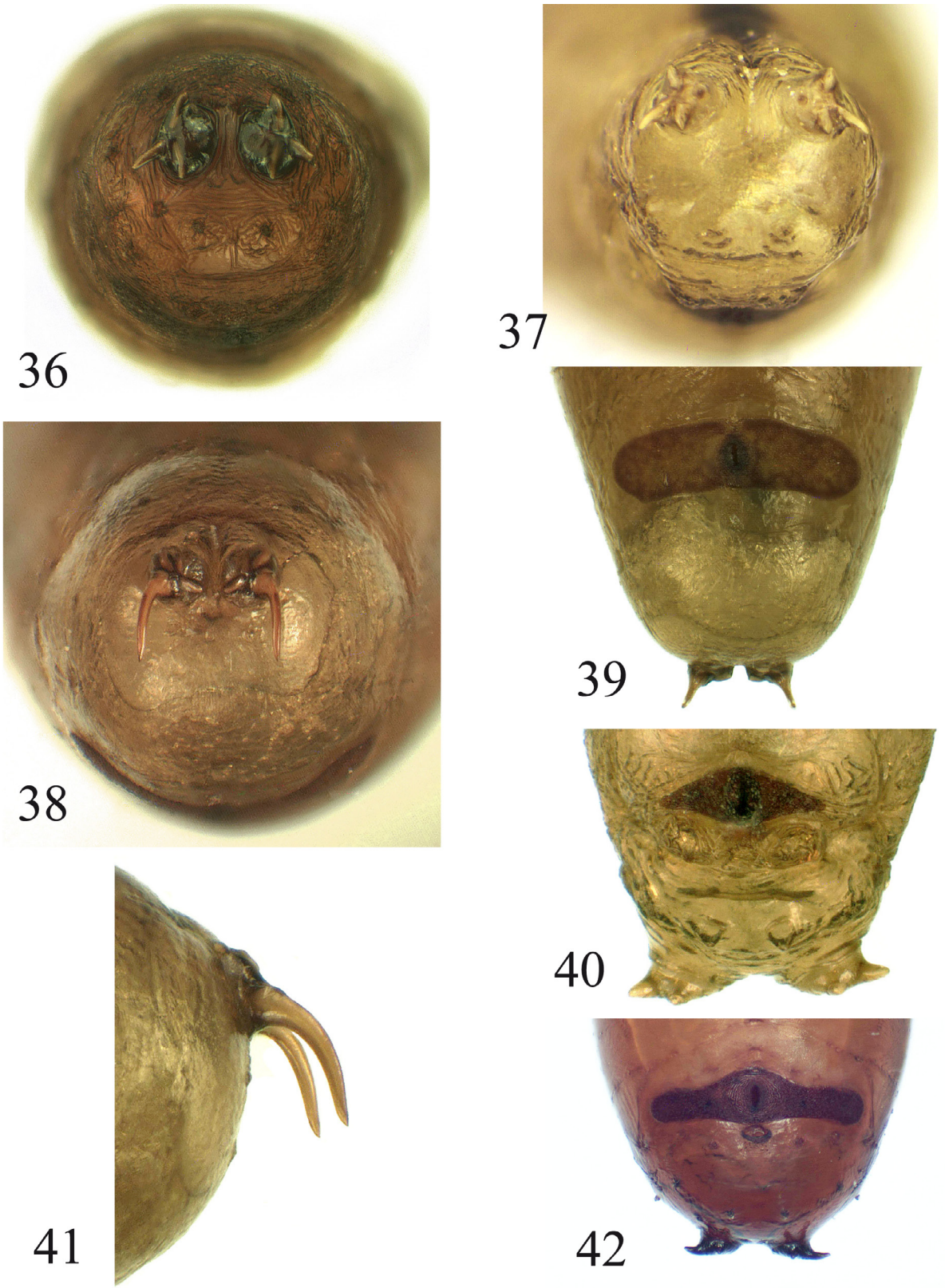


Figs 15, 16. *Cordilura ciliata* (Meigen) (15) and *Cordilura pudica* (Meigen) (16): 15 — tubercles on the posterior end of mature larva and puparium; 16 — cephalopharyngeal skeleton.
Рис. 15, 16. *Cordilura ciliata* (Meigen) (15) и *Cordilura pudica* (Meigen) (16): 15 — бугорки на заднем конце личинки и пупария; 16 — ротоглоточный аппарат.



Figs 17–27. Anterior (17, 20, 22, 24, 26) and posterior (18, 19, 21, 23, 25, 27) spiracles of mature larvae of *Cordilura*: 17–19 — *C. pudica* (Meigen); 20, 21 — *C. picipes* (Meigen); 22, 23 — *C. ciliata* (Meigen); 24, 25 — *C. aberrans* (Becker); 26, 27 — *C. rufimana* (Meigen).
Рис. 17–27. Передние (17, 20, 22, 24, 26) и задние (18, 19, 21, 23, 25, 27) дыхальца взрослых личинок *Cordilura*: 17–19 — *C. pudica* (Meigen); 20, 21 — *C. picipes* (Meigen); 22, 23 — *C. ciliata* (Meigen); 24, 25 — *C. aberrans* (Becker); 26, 27 — *C. rufimana* (Meigen).

Figs 28–35. Puparia of *C. ciliata* (Meigen) (28, 29), *C. picipes* (Meigen) (30, 31) and *C. pudica* (Meigen) (32–35): 28, 30, 32 — puparium, lateral view; 29, 31, 33 — same, dorsal view; 34 — anterior spiracles, frontal view; 35 — anterior spiracle, laterally.
Рис. 28–35. Пупарии *C. ciliata* (Meigen) (28, 29), *C. picipes* (Meigen) (30, 31) и *C. pudica* (Meigen) (32–35): 28, 30, 32 — пупарий, сбоку; 29, 31, 33 — то же, сверху; 34 — передние дыхальца, спереди; 35 — переднее дыхальце, сбоку.



Figs 36–42. Puparia of *C. ciliata* (Meigen) (36, 42), *C. picipes* (Meigen) (37, 40) and *C. pudica* (Meigen) (38, 39, 41): 36–38 — puparium, posterior view; 39, 40, 42 — posterior end of puparium, ventral view; 41 — same, laterally.
Рис. 36–42. Пупарии *C. ciliata* (Meigen) (36, 42), *C. picipes* (Meigen) (37, 40) и *C. pudica* (Meigen) (38, 39, 41): 36–38 — пупарий, сзади; 39, 40, 42 — задний конец пупария, снизу; 41 — то же, сбоку.

bog; 8 larvae collected 8.VII. and 11.IX.2024 from environs of Sizenevo along the edge of sphagnum bog; 8 larvae collected 17.VIII. and 4.IX.2024 from environs of Stepan'kovo, bank of the Kolpyanka River; 10 larvae collected 20.IX.2024 from environs of Ignatkovo (55.9519ºN, 35.6245ºE), forest bog; 1 puparium emerged from larva collected 5.VIII.2023 from environs of Andreevskoe, forest bog on *Carex vesicaria*; 2 puparia emerged from larva collected on *Carex vesicaria* 16 and 24.VIII.2023 from environs of Burtsevo, forest bog; 1 puparium emerged from larva collected 17.VIII. 2024 from environs of Stepan'kovo, bank of the Kolpyanka River; 4 puparia emerged from larvae collected 4 and 6.IX.2024 in same place; 1 puparium emerged from larva collected 12.VI.2025 from environs of Sizenevo along the edge of sphagnum bog.

DESCRIPTION OF THREE INSTAR LARVA. Body white, cylindrical, tapering towards anterior end and rounded posteriorly, with two short spiracular tubes (Fig. 2). Body length 5.9–10.1 mm, body width 1.0–1.7 mm.

Cephalic segment white, with rows of brown spines along posterior margin. Antennae and maxillary palps brown. Prothorax has two yellow-brown stripes dorsally. Anterior spiracles brownish, fan-shaped, with 60–65 papillae in 1–2 rows (Fig. 20).

Abdominal segments white and smooth, dorsally bearing sparse, microscopic, transparent spinules. Creeping welts weakly developed, with 2–3 rows of microscopic, transparent spinules. Processes on terminal segment weakly developed.

Spiracular plate and tubes brownish. Distance between spiracular plates equal to or slightly greater than diameter of spiracular plate (Fig. 21).

Anal plate transverse, diamond-shaped, and white.

DESCRIPTION OF PUPARIUM. Puparium yellow-brown, dorsally with a central dark longitudinal stripe and light coloration of the rest of dorsal surface (Figs 30, 31), oblique dark longitudinal and rounded small spots on lateral surface; ventral surface light. Body of puparium cylindrical, convex below and smoother along dorsal surface (see lateral view, Fig. 30), narrowing towards anterior and posterior ends, integument thin. Length of body 5.8–7.4 mm, width of body 1.6–2.1 mm.

Anterior spiracles distinct and fan-shaped (Figs 30, 31). Posterior spiracles spaced apart by the same amount as diameter of spiracular plate (Fig. 37).

Anal plate dark brown, diamond-shaped (Fig. 40).

Cordilura pudica (Meigen, 1826)
Figs 4, 5, 16–19, 32–35, 38, 39, 41.

MATERIAL EXAMINED. 3 larvae collected 24.VII.2024 from environs of Yakshino (~55.9374ºN, 35.5611ºE), forest bog; 36 larvae collected 31.VII., 1, 17 and 18.VIII., 4.IX.2024 from environs of Stepan'kovo (56.0044ºN, 35.6251ºE), bank of the Kolpyanka River on *Carex riparia* and *C.rostrata*; 1 larva collected 8.IX.2023 from environs of Ignatkovo, sphagnum bog on *Carex rostrata*; 1 larva collected 7.IX.2024 from environs of Burtsevo, forest bog on *Carex vesicaria*; 1 puparium emerged from larva collected 12.VIII.2024 from environs of Yakshino, forest bog on *Carex vesicaria*; 3 puparia emerged from larva collected on *Carex riparia* 28 and 31.VII. and 15.VIII.2024 from environs of Stepan'kovo (55.9858ºN, 35.6237ºE), forest bog; 1 puparium emerged from larva collected on *Carex rostrata* 9.IX.2023 from environs of Ignatkovo, sphagnum bog.

DESCRIPTION OF THREE INSTAR LARVA. Body white, cylindrical, tapering towards anterior end and rounded at the back, with two short spiracular tubes. Body length 8.2–12.8 mm, body width 1.3–2.3 mm.

Cephalic segment white, with rows of brown spines along posterior margin. Antennae and maxillary palps brown. Prothorax has two yellow-brown stripes dorsally. Anterior spiracles fan-shaped with 74–82 papillae in 1–3 rows (Fig. 17); base of spiracle black.

Cephalopharyngeal skeleton strongly sclerotized (Fig. 16). Dental sclerite triangular in lateral view. Hypopharynx broad, about 3 times as long as wide. Tentorial phragma broad. Dorsal cornua of pharyngeal sclerite relatively narrow with long slit-like window. Ventral cornua of pharyngeal sclerite shorter than dorsal, broad, more sclerotized basally.

Abdominal segments white and smooth, with sparse microscopic transparent spinules dorsally. Creeping welts undeveloped, with 2–3 rows of microscopic transparent spinules. Spiracular plate and tubes brownish. Distance between the spiracular plates smaller than diameter of spiracular plate (Fig. 18). Middle slit of posterior spiracles approximately 4 times as long as lower slit (Figs 18, 19). Processes on terminal segment poorly developed.

Anal plate transverse, rounded-ovoid, and white.

DESCRIPTION OF PUPARIUM. Puparium yellow-brown, dorsally with a central brown longitudinal stripe and a dark pattern formed by sinuous longitudinal spots directed obliquely outward; lateral and ventral surfaces with single dark short stripes (Figs 32, 33). Body of the puparium cylindrical, slightly thickened in the middle, anterior and posterior ends slightly curved upward (see lateral view, Fig. 32); integument thin. Length of body 7.7–9.6 mm, width of body 2.3–2.8 mm.

Anterior spiracles distinct and fan-shaped (Figs 34, 35). Posterior spiracles with a long, downward-curved medial slit (Figs 38, 41); in puparia found in nature, this slit is often broken off.

Anal plate dark brown, in form of a narrow transverse stripe of equal width, rounded at the ends, its length approximately 6 times greater than its width (Fig. 39).

Cordilura rufimana (Meigen, 1826)
Figs 26, 27, 43, 44, 47, 49, 50.

MATERIAL EXAMINED. 1 larva, 1 puparium collected 23.IX.2023 on *Carex rostrata* from environs of Sizenevo, sphagnum bog; 1 puparium collected 21.VI.2024 from environs of Shakhovskaya (56.0410ºN, 35.4561ºE), sphagnum bog.

DESCRIPTION OF THREE INSTAR LARVA. Body white, integument smooth, anterior end narrowed and rounded, and posterior end truncate. Body length 10.2 mm, body width 2.2 mm.

Cephalic segment white, with rows of brown spines along posterior margin. Antennae and maxillary palps brown.

Thoracic segments smooth and white, dorsally marked with two triangular yellow-brown spots. Anterior spiracles yellow-brown, Y-shaped, with a distinct depression in the middle dividing spiracle into two short, approximately equal-length branches bearing 32–37 papillae (Fig. 26).Abdominal segments smooth and white, dorsally bearing sparse microscopic spinules. Creeping welts weakly developed, with 1–2 indistinct rows of transparent spinules.

Terminal segment of body with poorly developed processes; spiracular tubes short, white, and at their apex with brown spiracular plates, each with three straight spiracular slits, the middle one being longer than the others. Distance between spiracular plates approximately 1.5–2 times greater than diameter of spiracular plate (Fig. 27).

Anal plate white, transverse, ribbon-shaped, smooth along posterior edge, and prominently protruding along anterior edge in center, with rounded lateral edges. Anal opening is a longitudinal slit.

Figs 43–52. Puparia of *C. aberrans* (Becker) (45, 46, 48, 51, 52) and *C. rufimana* (Meigen) (43, 44, 47, 49, 50): 43, 45 — puparium, lateral view; 44, 46 — same, dorsal view; 47, 48 — posterior end of puparium, ventral view; 49, 52 — anterior spiracle, laterally; 50, 51 — puparium, posterior view.

Рис. 43–52. Пупарии *C. aberrans* (Becker) (45, 46, 48, 51, 52) и *C. rufimana* (Meigen) (43, 44, 47, 49, 50): 43, 45 — пупарий, сбоку; 44, 46 — то же, сверху; 47, 48 — задний конец пупария, снизу; 49, 52 — переднее дыхальце, сбоку; 50, 51 — пупарий, сзади.

DESCRIPTION OF PUPARIUM. Puparium light brown to dark brown, uniformly colored, without stripes or spots; body is cylindrical, slightly tapering towards anterior and posterior ends (Figs 43, 44), integument dense. Body length 6.9–7.1 mm, body width 2.1–2.2 mm.

Anterior spiracles Y-shaped, with a distinct depression in the middle dividing spiracle into two short branches of approximately equal length (Fig. 49). Posterior spiracles spaced apart by the same amount as diameter of spiracular plate. Slits of posterior spiracles approximately equal in length and straight (Fig. 50).

Anal plate dark brown, transverse, ribbon-shaped, smooth along posterior edge, and noticeably protruding along anterior edge in center, with rounded lateral edges (Fig. 47).

KEY TO MATURE LARVAE OF FIVE PALAEARCTIC SPECIES OF *CORDILURA*

1. Anterior spiracles fan-shaped, convex along the upper edge (Figs 17, 20, 22) 2
– Anterior spiracles Y-shaped, with a distinct depression in the middle dividing spiracle into two branches (Figs 24, 26) 4
2. Posterior spiracles very close together, distance between spiracular plates less than diameter of spiracular plate (Figs 18, 23) 3
– Posterior spiracles spaced apart by the same amount as diameter of spiracular plate (Fig. 21) ..... *Cordilura picipes* (Meigen)
3. Middle slit of posterior spiracles no more than 2 times as long as lower slit (Fig. 23)..... *Cordilura ciliata* (Meigen)
– Middle slit of posterior spiracles approximately 4 times as long as lower slit (Figs 18, 19) ..... *Cordilura pudica* (Meigen)
4. Papillae of anterior spiracles on short, almost symmetrical processes (Fig. 26). Slits of posterior spiracles straight (Fig. 27) ..... *Cordilura rufimana* (Meigen)
– Papillae of anterior spiracles on long, asymmetrical processes (Fig. 24). Slits of posterior spiracles curved (Fig. 25) ..... *Cordilura aberrans* (Becker)

KEY TO PUPARIA OF FIVE PALAEARCTIC SPECIES OF *CORDILURA*

1. Anterior spiracles fan-shaped, convex along the upper edge (Figs 34, 35) 2
– Anterior spiracles Y-shaped, with a distinct depression in the middle dividing spiracle into two branches (Figs 49, 52) 4
2. Posterior spiracles closely spaced, distance between spiracular plates less than diameter of spiracular plate (Figs 36, 38). Anal plate ribbon-shaped with rounded edges 3
– Posterior spiracles spaced apart by the same amount as diameter of spiracular plate (Fig. 37). Anal plate diamond-shaped (Fig. 40). Puparium yellow-brown, dorsally with a central dark longitudinal stripe and light coloration of the rest of dorsal surface (Figs 30, 31) ..... *Cordilura picipes* (Meigen)
3. Middle slit of posterior spiracles no more than 2 times as long as lower slit (Fig. 36). Anal plate is transverse, 4–4.5 times longer than wide (Fig. 42) ..... *Cordilura ciliata* (Meigen)
– Middle slit of posterior spiracles approximately 4 times as long as lower slit (Figs 38, 41). Anal plate in form of a narrow transverse stripe of equal width, rounded at the ends, its length approximately 6 times greater than its width (Fig. 39) ..... *Cordilura pudica* (Meigen)
4. Anterior spiracles more or less symmetrical (Fig. 49). Slits of posterior spiracles straight (Fig. 50) ..... *Cordilura rufimana* (Meigen)
– Anterior spiracles asymmetrical (Fig. 52). Slits of posterior spiracles curved (Fig. 51) ..... *Cordilura aberrans* (Becker)

Biology

As Wallace and Neff [1971] established, a female of any species of *Cordilura* lays only one egg per plant, and the process of larval development after hatching from the egg was described by them as follows: "After hatching, the larva makes a small entry hole into the culm, burrows to the center, and makes a spiral cut clown to the culm base. This cut severs the vascular bundles and causes the leaves in the middle of the culm to wither and die. The outer portion of the culm and the outer leaf blades are unaffected. Culm as well as the inner shoots of the upper part of the culm shows a characteristic etiolation and are easily recognized. The 2nd- and 3rd-stage larvae feed on the decaying plant material in the center portion of the culm".

The larvae and puparia of the species of the genus *Cordilura* that we collected were found in the stems of three species of sedges of the genus *Carex* Linnaeus, 1753: *C. riparia* Curtis, 1783, *C. rostrata* Stokes, 1787 and *C. vesicaria* Linnaeus, 1753.

Cordilura picipes females prefer to colonize sedges (*C. rostrata* and *C. vesicaria*) growing in the shade, under the forest canopy. *Cordilura aberrans* females lay their eggs on *C. vesicaria* plants growing at the forest edge, which receive occasional sunlight. *Cordilura ciliata* colonize *C. riparia* and *C. rostrata* plants growing along the banks of water bodies.

Cordilura rufimana larvae were found only in the stems of *C. rostrata* growing in the sphagnum bog, and *Cordilura pudica* larvae can be found in the stems of three species of sedges (*Carex riparia*, *C. rostrata*, *C. vesicaria*) in all the above-mentioned stations.

When feeding on plant material in the central part of the stem, the larvae create a tunnel. The tunnel's length varies from 1 to 15 cm, and is typically 4–9 cm. Within the tunnel, the larvae can move forward and backward with equal ease and can even turn around thanks to their thin, flexible cuticle. The tunnel always extends down to the base of the stem and therefore part of the tunnel is below the soil surface.

Rainfall, in our opinion, significantly influences the egg-laying process by female *Cordilura*, as well as the development of the larva within the stem. Sedges grow in depressions, so during periods of heavy or prolonged rainfall, the water level can rise several centimeters above the base of the stem. In this case, the larva that hatches from the egg cannot reach the base of the sedge stem to cut the vascular bundles of the central leaves. If the plant has been colonized, the larva extends its tunnel upward during periods of rising water and remains at the top of the sedge stem. Conversely, during dry periods, the larva crawls to the base of the sedge stem and remains there permanently.

Cordilura rufimana in the Moscow Region was previously known from a single female from the Dmitrovsky District [Ozerov, Krivosheina, 2020]. It turns out that this species is quite common in sphagnum bogs: in early and mid-June, it was the dominant species in the sphagnum bog in Sizenevo, but larvae in *C. rostrata*

stems were found in September only. To find a suitable spot to lay an egg on the stem of a *C. rostrata* plant growing in a sphagnum bog, a female *Cordilura rufimana* must crawl 6–12 cm below the vegetation surface (Fig. 10). The species apparently has only one generation per year. Pupation occurs in the soil or in the upper part of the sedge stem. The stem sheath decomposes rapidly from autumn to spring, making it easy for the adult fly to emerge from the puparium.

Among the first to be discovered in mid-June in sedge stems were the larvae of two species—*Cordilura picipes* and *Cordilura pudica*. Both species apparently have two generations per year.

This is more evident in *Cordilura picipes*. Adult *Cordilura picipes* flies emerge from first-generation puparia in mid- to late July and begin laying eggs as early as August. Second-generation puparia typically overwinter in the soil.

In *Cordilura pudica*, the adult fly flight and female egg-laying periods are spread out. Therefore, there is some overlap between generations. *Cordilura pudica* larvae can be found in sedge stems from mid-June to late September.

Mature *C. pudica* larvae typically leave the sedge stem through an exit hole (Fig. 4) made by the larva 2–4 cm from the base of the stem and pupate near the plant, without burrowing deeply into the soil. Less frequently, a puparium forms within the stem or at the exit (Fig. 5), but parasitoid wasps often emerge from puparia found in the stem.

Cordilura aberrans and *Cordilura ciliata* apparently have only one generation per year. Larvae of both species were collected no earlier than the second half of July, and emergence from the puparium of these species was possible only after a period of stratification. Pupation of both species typically occurs in the soil, but we have also observed cases of puparium formation within the stem of a sedge.

Competing interests. The authors declare no competing interests.

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