



## Two new species of the genus *Psyllaphorura* (Collembola: Onychiuridae) from the east of European Russia

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### Abstract

Two new species of the genus *Psyllaphorura* Bagnall, 1948, namely *P. silvestris* **sp. nov.** and *P. pseudopodis* **sp. nov.**, are described from the European Russia. The former species can be compared to the Nearctic *P. obesa* (Mills, 1934) which has almost the same number of dorsal pseudocelli, but differs in having compound vesicles in PAO. *Psyllaphorura pseudopodis* **sp. nov.** is similar to *P. altaica* Weiner, Stebaeva & Kaprus<sup>7</sup>, 2019 recently described from the Altai Mountains, southern Siberia. Both these species have the same number and arrangement of the cephalic pseudocelli. Nonetheless, *P. pseudopodis* **sp. nov.** can be distinguished by the absence of pseudocelli on Abd. IV, only 2+2 dental setae and a shorter unguiculus. Besides this, *P. pseudopodis* **sp. nov.** is unique in the presence of a pair of ventral swellings on the fourth abdominal segment. Based on a revision of the types, *P. sensillifera* (Martynova, 1981) is considered a senior synonym of *P. raoheensis* Sun & Wu, 2013. Taxonomic notes on the most important diagnostic characters of the genus are given, as well as a key and a table summarizing these characters in all *Psyllaphorura* species known in the World so far.

**Key words:** *Hymenaphorurini*, morphology, main diagnostic characters

### Introduction

*Psyllaphorura* Bagnall, 1948 is a genus of the tribe Hymenaphorurini which includes only 12 species: eleven species listed on the [www.collembola.org](http://www.collembola.org) (Bellinger *et al.* 1996–2020) and very recently described *P. jiriana* Lee & Park, 2021. The genus shows disjunctive distribution, which covers the Asian part of the Palaearctic and the North America. The genus reached high diversity in East Asia, while only *P. obesa* (Mills, 1934) is represented in the Nearctic. It inhabits caves in three inner states of the United States (Iowa, Wisconsin, and Missouri) and has not been recorded beyond that region (Christiansen & Bellinger 1980). In the Palaearctic, seven described species are known from eastern and southeastern Asia, including the territories of the Northeast and Southeast of Russia, Korea, China, and Japan. Two species of the genus, *P. martynovae* (Stebaeva, 1985) and *P. altaica*, were described from the southern regions of western Siberia. *Psyllaphorura bashkirica* (Khanislamova, 1986) is presently the westernmost representative among the described congeners. Chernov *et al.* (2010), when describing peculiarities of the collembolan fauna and assemblages of the East-European broad-leaf forests, mentioned a new, still unnamed species of *Psyllaphorura* found in the vicinities of Togliatti, Samara Region. That record seems to be the truly westernmost *Psyllaphorura* in the Palaearctic. The present paper is devoted to the description of this very species, as well as one more congener from the adjacent region of European Russia.

**Abbreviations.** Abd. I–VI—abdominal segments; AC—type of labium, A—labial papilla (Fjellberg 1999); A-, T-, B-, C-, M- setae—tibiotarsal setae named according to Deharveng (1983); a-, b-, c-setae—setae on anal valves (Yoshii 1996); a-, p-setae—setae of anterior and posterior rows on terga; Ant. I–IV—antennal segments; AIII—antennal organ on Ant. III; AS—anal spines; BA, OR, MN—baso-antennal, outer and median complexes, types of cephalic pseudocelli arrangement (see Taxonomic remarks), d0—unpaired dorsal seta on head; m—medial pso on the head; ms—microsensillum(a); or—organite on antennal tip; PAO—postantennal organ; pso—pseudocellus(i);

psx—parapseudocellus(i); S—lanceolate sensorial seta; Sc—subcoxa; Th. I–III—thoracic segments; Ti—tibiotarsus(i); UIII—unguis on hind leg, VT—ventral tube; MSPU—Zoology and Ecology Department of the Moscow State Pedagogical University; ZIN—Zoological Institute, Russian Academy of Sciences (Saint Petersburg); ISEAS—Institute of the Systematics and Ecology of Animals, Siberian Branch of the Russian Academy of Sciences (Novosibirsk).

## Taxonomy

### *Psyllaphorura silvestris* sp. nov.

Figs 1–10

**Type material.** Russia: holotype, male, European part, Middle Volga River Basin, Samara Region, “Samarskaya Luka” National Park, calcareous stone-pit near cave, *Acer* and *Betula* forest [N 53.4059°, E 50.0794°], soil, 02.05.2011, Yu. Shveenкова leg. Paratypes: **1** female and **4** males, same data as holotype; **1** juvenile, same biotope, but 13.06.2011; **2** males, **7** females and **1** juvenile, *ibid.*, but 04.05.2019, Yu. Shveenкова leg. The types are kept in the collection of MSPU.

**Other material.** **1** juvenile, European part of Russia, Penza Region, “Privolzhskaya Lesostep” State Nature Reserve, upper reaches of Sura River, floodplain *Pinus* forest [N 53.3169°, E 46.8866°], soil, 30.09.2014; **1** female and **2** juveniles, Penza Region, near Leonidovka settlement, nearby Lake “Mertvoe”, mixed forest, 21.07.2006; **2** juveniles, *ibid.*, but *Pinus* forest. All Yu. Shveenкова leg.; **2** females and **4** juveniles, Penza Region, Zarechny town, *Populus tremula* and *Betula* forest, 01.05.2010, T. Gorbushina leg.; **1** male and **2** juveniles, European part of Russia, Kaluga Region, “Kaluzhskie Zaseki” State Nature Reserve, near Kireykovo settlement, broad-leaved forest, soil, 17.10.2005, A. Chernov leg.; **1** female, Republic of Bashkortostan, foothills of southern Urals, Burzyansky Region, “Shulgan-Tash” State Nature Reserve, “Shulgan-Tash” (“Kapova”) Cave, 17–23.07.2008, S. Kapralov leg.; **2** females and **4** juveniles, Middle Urals, Sverdlovsk Region, low reaches of Serga River, left bank, “Olenyi Ruchyi” National Nature Park, “Bolshaya Arakaevskaya” Cave, moss, 08.08.2002, M. Potapov and A. Potapov leg.; **1** male and **5** females, Mordovian Republic, Temnikovskiy Region, Mordovian State Nature Reserve, floodplain *Quercus robur* forest, 18.08.1983, N. Kuznetsova leg.

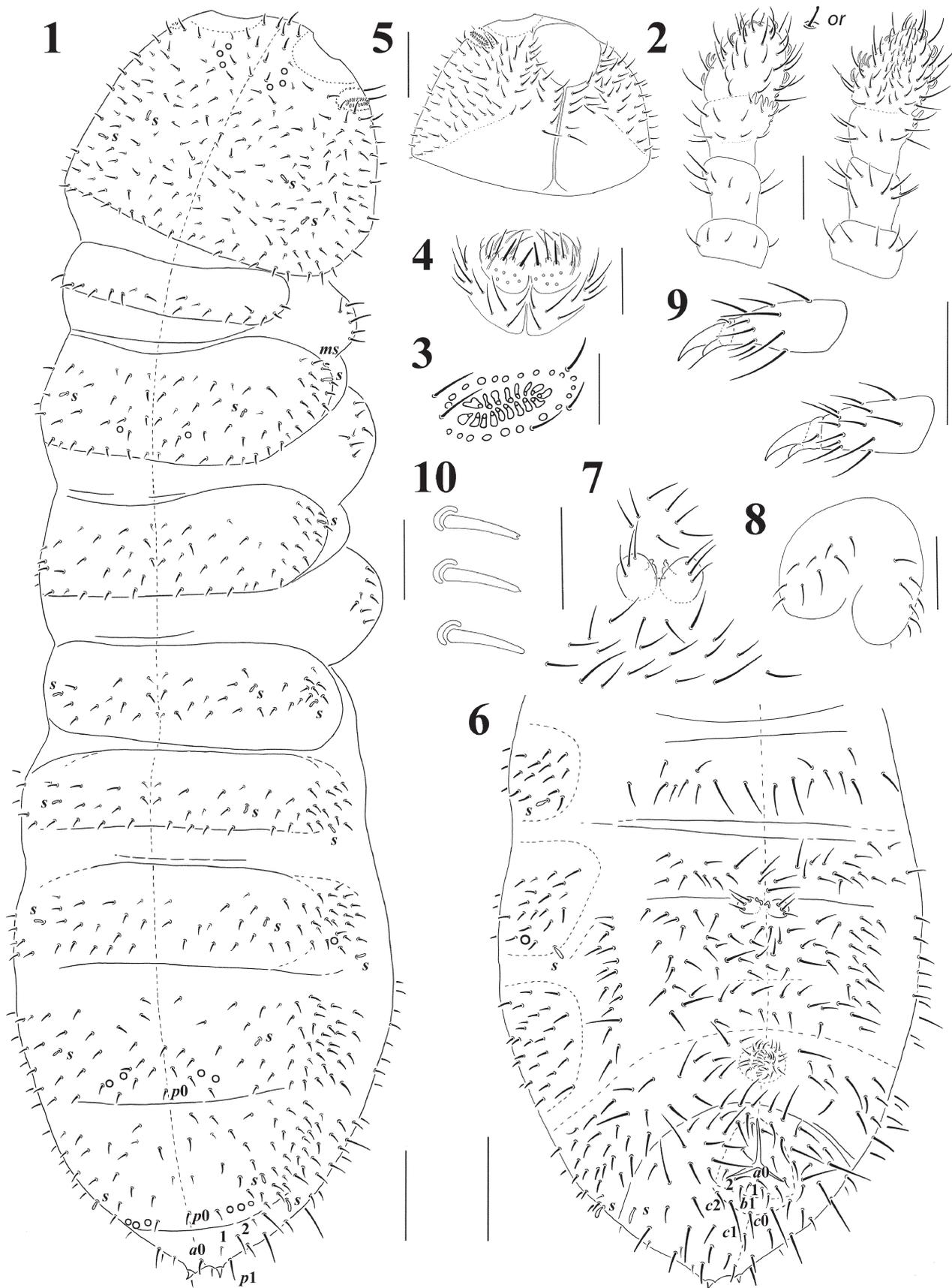
**Diagnosis.** A species of the genus *Psyllaphorura*, which can be distinguished from the congeners due to the presence of 30/010/00123 dorsal pso (3+3 cephalic pso are located outside of antennal bases in the form of two half-arches along the axial line) and PAO with 16–22 simple vesicles. It is also characterized by: mid-sized cuticular granulation, relatively distinct dorsal sensilla, AO with 5 papillae and 4 guard setae, Ant. IV with an elongated subapical organite, labium of AC-type, only Th. II with lateral ms, furcal remnant of usual shape typical of genus with 3+3 setae, retinaculum with 1+1 teeth and a long unguiculus with a broad basal lamella.

**Description.** Size 1.2–1.6 mm in females, 0.9–1.3 mm in males; holotype: 1.38 mm. Colour white. Habitus typical of the genus (Fig. 1), body ovoid, Abd. VI short with relatively small anal spines. Cuticular granulations not too coarse, with 9–11 cuticular granules around each pso on abdominal tip, and 11–13 granules between p1 setae on Abd. V.

Dorsal pseudocelli as 30/010/00123, 3+3 cephalic pso located outside antennal bases in two semi-arcs along axial line (Fig. 1). Psx invisible.

Antennae club-like, clearly shorter than head diagonal. Antennal base distinctly marked. Ant. IV with unusually long subapical organite (Fig. 2), 2–3 thickened blunt sensilla laterally and 5–6 similar sensilla on its inner side, basolateral microsensillum set in line with proximal whorl of setae. AIIIIO consisting of 5 cuticular papillae, two sensory rods, two smooth sensory clubs, 4 guard setae, and lateral microsensillum (Fig. 2). Ant. I–II with 10 and 13–14 setae respectively. PAO with 16–22 simple vesicles (Fig. 3). Labrum with 4/9 setae, maxillary outer lobe simple with two sublobal setae. Labium of AC type (sensillum on papilla A clearly thicker) with 7 long and 4 spiniform guards and 6 proximal setae (Fig. 4). Basomedian and basolateral fields of labium with 4 and 6 setae, respectively. Usually 5+5 postlabial setae present along ventral mid line (Fig. 5).

Chaetotaxy plurichaetotic and usually not symmetrical, dorsal setae slightly differentiated: most setae blunt and rather thick (Figs. 1, 10), besides few pointed, thin and curved microsetae present on most terga, dorsal sensilla relatively distinct: 2(1)/021/222111, sensilla on Abd. VI located ventro-laterally on pleura (Figs. 1, 6). Seta d0 on



**FIGURES 1–10.** *Psyllaphorura silvestris* sp. nov.: 1, dorsal chaetotaxy; 2, antenna, different views; 3, PAO; 4, labial palp (small guards not shown); 5, ventral chaetotaxy of head; 6, ventral chaetotaxy of abdomen; 7, furcal remnant; 8, ventral tube; 9, tip of leg II; 10, dorsal mesosetae. Scales: Figs 1, 5, 6—0.1 mm; 2, 4, 7–9—0.05 mm; 3—0.025 mm; 10—0.01 mm.

head present or absent. Th. I with up to 12 setae on each side. Only Th. II with a lateral microsensillum. Upper subcoxae of legs 1–3 prominent, with 6(7)–7(6)–7(8) setae, respectively. Abd. IV with 1–3 unpaired or paired m-setae, setae p0 present also on both Abd. IV and V. Axial seta a0 on Abd. VI slightly shorter than p1 and a2, seta a2 about twice as long as a1 (Fig. 1). Sterna of Th. I–III without setae along ventral line. Ventral chaetom on abdomen composed of pointed meso- and macrosetae (Figs. 5, 6).

Furcal remnant as usual for genus: mucro absent, dens knob-like with 3+3 long setae, retinaculum present with 1+1 teeth (Fig. 7). Chaetotaxy of furcal field in adults highly variable and usually not symmetric: in largest specimens 3–4 irregular rows of manubrial setae present posteriorly to dental remnant. VT with 8–9 distal setae on each side and without proximal setae at base (Fig. 8). Tibiotarsi with complete distal whorl (7A + 4T), 7–7–6 setae in B-whorl, M seta present, C-whorl variable. Unguis toothless, unguiculus as long or slightly longer than inner edge of unguis, with wide basal lamella (Fig. 9). Upper anal valve with setae a0, 2a1, 2a2, 2b1, c0, 2c1, 2c2, each lateral valve with setae a0 and 2a1 (Fig. 6). AS short and conical, about as long as papillae.

**Etymology.** The species is named after its ecological preferences, i.e. different types of forest habitats.

**Affinities.** *Psyllaphorura silvestris* **sp. nov.** shares the presence of 3+3 anterior cephalic pso with only three known congeners (see Table 1), namely *P. obesa*, *P. altaica* and *P. pseudopodis* **sp. nov.**, the latter species described below. Among them only in *P. obesa* the position of these pso is the same as in *P. silvestris* **sp. nov.**, namely in the form of two separate half-arcs outside of the bases of the antennae along the midline of the head (OR-pattern, see below). Contrary, in both *P. altaica* and *P. pseudopodis* **sp. nov.** cephalic pso are located in a common axial group. There are also some additional similarities between *P. silvestris* **sp. nov.** and *P. obesa*, for instance, the presence of thoracic pso (absent in all other congeners) or rather long unguiculus with a distinct basal lamella. Despite all these similarities *P. silvestris* **sp. nov.** and *P. obesa* can be easily distinguished by pso formulas (30/010/00123 pso in the former vs 30/011(0)/00023 in the latter) and the shape of PAO vesicles (simple in *P. silvestris* **sp. nov.** vs compound in *P. obesa*). *Psyllaphorura silvestris* **sp. nov.** is characterized by two probably unique traits that are not mentioned for all other known congeners, namely the absence of lateral microsensillum on Th. III and an unusually long subapical organite on Ant. IV.

**Distribution.** Apparently, the new species is widespread in the forest belt of the East-European part of Russia where it mainly inhabits riparian forests, as well as in the entrance of caves and their environs.

### ***Psyllaphorura pseudopodis* sp. nov.**

Figs 11–19

**Type material.** Russia: holotype, female, European part, Middle Volga River Basin, Penza Region, “Privolzhskaya Lesostep” State Nature Reserve, middle reaches of Kadada River, near Shatkino settlement, *Alnus glutinosa* floodplain forest [N 52.9322°, E 46.3022°], soil, 15.09.2017, Yu. Shveenkov leg. Paratypes: 4 males and 5 females, same data as holotype; 1 male, *ibid.*, but 10.10.19; 1 female, *ibid.*, but 18.09.20, Yu. Shveenkov leg. The types are kept in the collection of MSPU.

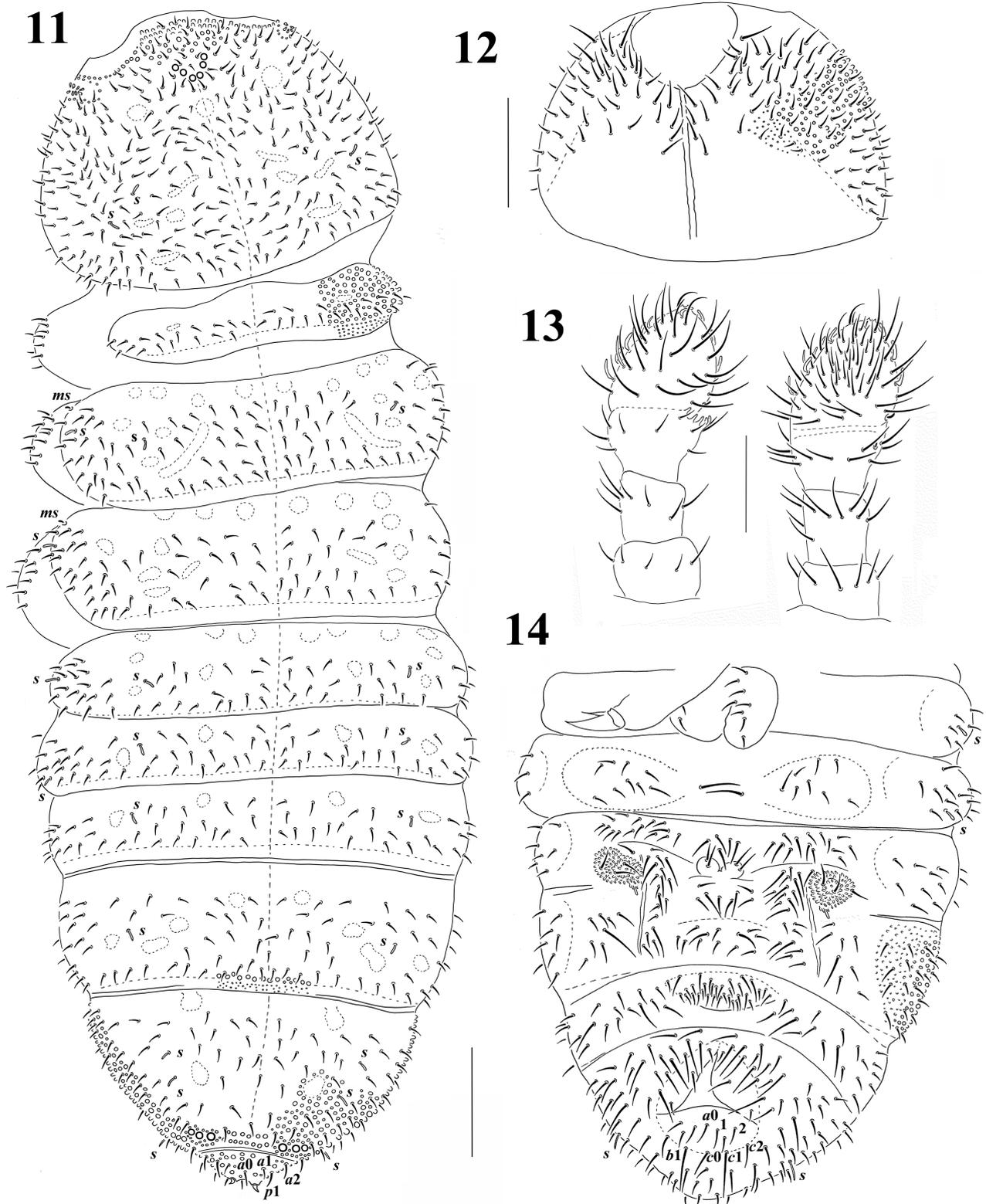
**Diagnosis.** A species of the genus *Psyllaphorura*, which can be distinguished from the congeners due to the presence of 30/000/00003 dorsal pso (3+3 cephalic pso are located as a common axial group on the median part of the head), only 2+2 dental setae and a pair of ventral swellings on Abd. IV. It is also characterized by coarse dorsal granulation, rather distinct dorsal sensilla, AO with 5 papillae and 4 guard setae, PAO with 12–15 simple vesicles, labium of AC-type, the presence of lateral ms on both Th. II–III, rather short unguiculus and the absence of retinaculum.

**Description.** Size: 1.0–1.2 mm in females, 0.87–0.97 mm in males, holotype: 1.06 mm. Colour white. Habitus typical of the genus (Fig. 11), body ovoid with a short Abd. VI armed by small anal spines. Cuticular granulation very coarse, especially in middle parts of terga, with 8–9 cuticular granules around each abdominal pso and only 5–6 granules between p1 setae on Abd. V.

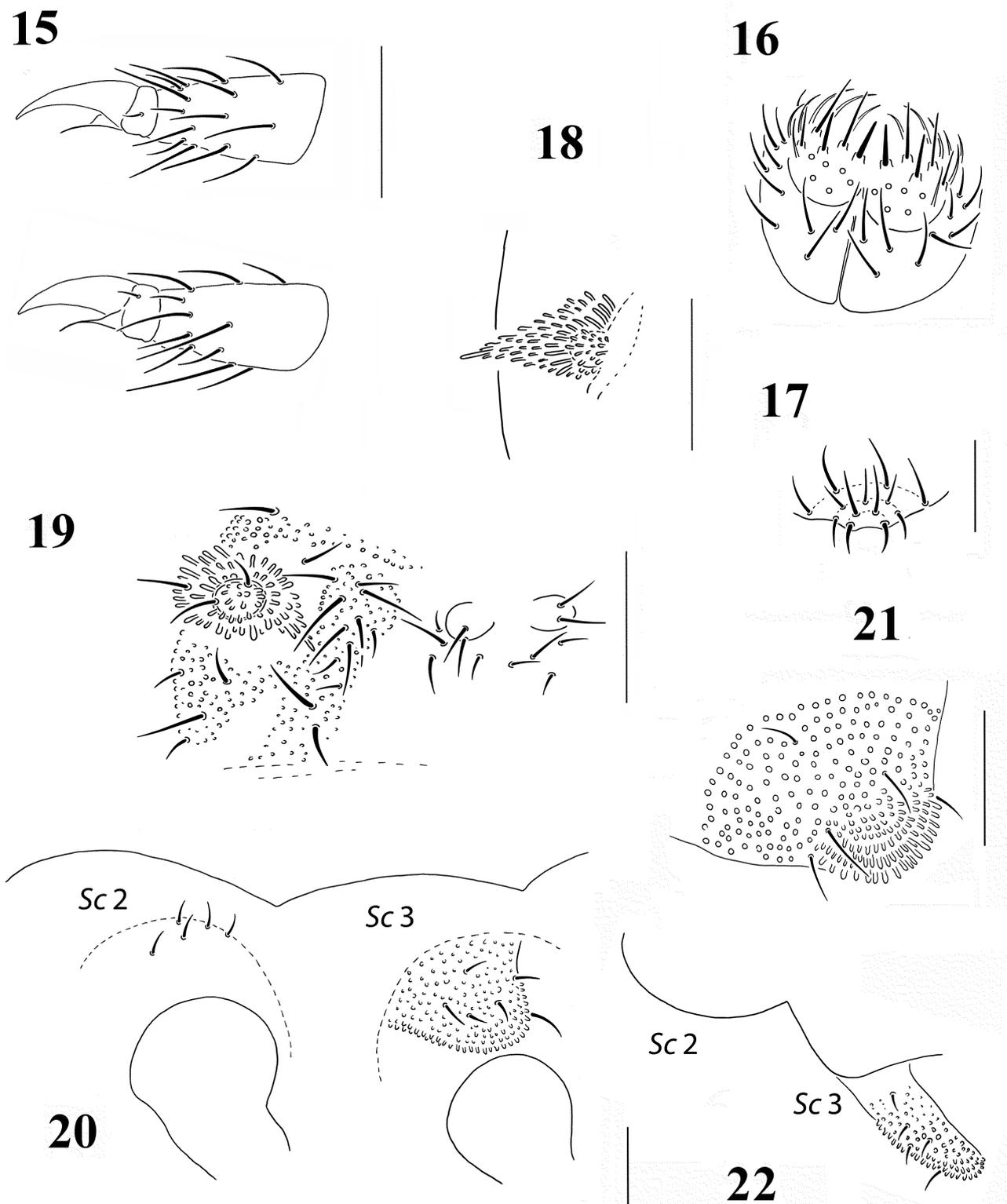
Dorsal pseudocelli as 30/000/00003, 3+3 cephalic pseudocelli located on head front in the form of a single “V-shaped” complex (Fig. 11). Psx invisible.

Antennae club-like, distinctly shorter than head diagonal. Small area of antennal bases clearly marked with finer granulation. Ant. IV with small, peg-like subapical organite, 3 curved blunt sensilla laterally and up to 8 sensilla on its inner side, basolateral microsensillum present in line with proximal whorl of setae (Fig. 13). AIIIO typical, with

5 cuticular papillae, 4 guard setae, two sensory rods, two smooth sensory clubs and lateral microsensillum (Fig. 13). Ant. I–II with 10 and 13–14 setae, respectively. PAO with 12–15 simple vesicles. Labrum with 4/9 setae (Fig. 17), maxillary outer lobe simple with two sublobal setae. Labium of AC type (sensillum on papilla A clearly thicker) with 7 long and 4 spiniform guards and 6 proximal setae (Fig. 16). Basomedian and basolateral fields of labium with 4 and 6 setae, respectively. Usually 4+4 postlabial setae present along ventral midline (Fig. 12).



**FIGURES 11–14.** *Psyllaphorura pseudopodis* sp. nov.: 11, dorsal chaetotaxy; 12, ventral chaetotaxy of head; 13, antenna, different views; 14, ventral chaetotaxy of abdomen. Scales: Figs 11, 12, 14—0.1 mm; 13—0.5 mm.



**FIGURES 15–22.** *Psyllaphorura pseudopodis* sp. nov.: (15–19), *P. altaica* (20–22): 15, tip of leg III; 16, labial palp (small guards not shown); 17, labrum; 18, ventral swelling (lateral view); 19, sterna of Abd. III-IV (lateral parts) with ventral swelling and furca; 20, subcoxae of legs II, III; 21, subcoxa of leg III (dorsal view); 22, subcoxa of leg III (lateral view). Scales: Figs 15, 18, 19—0.05 mm; 16, 17—0.025 mm; 20–22—0.5 mm.

Chaetotaxy plurichaetotic and usually not symmetrical, dorsal setae weakly differentiated (Fig. 11). Most dorsal sensilla relatively distinct, but masked by coarse granulations, 2/021/221121(0) in number, sensilla on Abd. VI, if present, located ventro-laterally on pleura. The presence/absence of dorsal seta d0 on head often obscure due to

chaetotic asymmetry. Th. I with up to 17 setae on each side set in two irregular rows. Both Th. II and Th. III with lateral microsensillum. Upper subcoxae prominent on all legs with up to 10 setae. Chaetotaxy of Abd. IV very plurichaetotic, axial m-setae present or absent. Abd. V with seta p0. Axial seta a0 on Abd. VI about as long as p1 and a2 setae, seta a1 shorter than a2 (~0.7 : 1). Sterna of Th. I–III without setae along ventral line. Ventral chaetom on abdomen composed of pointed meso- and macrosetae (Fig. 14).

Furcal remnant without mucro, dens knob-like with 2+2 long setae, retinaculum absent. Chaetotaxy of furcal field in adults highly variable and usually not symmetric: in largest specimens 2–3 irregular rows of manubrial setae present posterior to dental remnant. VT with 7(8) distal setae on each side and without proximal setae at base. Sternum of Abd. IV on each side of furcal remnant with two specific protuberances covered with modified (long and thin) cuticular granules (Figs. 14, 18, 19). Tibiotarsi with a complete distal whorl (7A+4T), 7–7–6 setae in B-whorl, M seta present, C-whorl variable. Unguis toothless, unguiculus about as long as half of inner edge of unguis (Fig. 15). Upper anal valve with setae a0, 2a1, 2a2, 2b1, c0, 2c1, 2c2, each of lateral valve with setae a0 and 2a1 (Fig. 14). AS short and conical, about as long as papillae.

**Etymology.** The species name is derived from the unique ventral swellings located on the fourth abdominal segment, which is somewhat reminiscent of pseudopodia.

**Affinities.** In having 3+3 cephalic pso arranged in a single group on the median part of the head, *Psyllaphorura pseudopodis* **sp. nov.** is the most similar to *P. altaica*, which has recently been described from southern Siberia. *P. pseudopodis* **sp. nov.** can be easily distinguished from the latter species by the absence of pso on Abd. IV (*P. altaica* has 00013 abdominal pso), only 2+2 dental setae (vs 3+3 setae in *P. altaica*) and a shorter unguiculus (~ 0.5–0.6 UIII vs 0.8 UIII in *P. altaica*).

The only other congener with not 3+3, but 2+2 setae on the furcal knobs as in *P. pseudopodis* **sp. nov.**, is *P. bashkirica* (Khanislamova, 1986), described from a more easterly region (at a distance of ~ 700 km). Although the description of the latter species does not fully correspond to modern standards and clearly requires verification, its conspecificity with the new species is unlikely. These species clearly differ by the number of dorsal pso (5/000/00023 in *P. bashkirica* vs 3/000/00003 pso in the new species), structure of PAO (15–17 divided vesicles in *P. bashkirica* vs 12–15 simple vesicles in *P. pseudopodis* **sp. nov.**), the number of dorsal sensilla (??/11/11112?, sensilla on Th. III in medial position in *P. bashkirica* vs 2/021/221120(1), sensilla on Th. III in lateral position in the new species) and guard setae in AIIIO (5 setae in *P. bashkirica* vs 4 setae in *P. pseudopodis* **sp. nov.**).

*P. pseudopodis* **sp. nov.** is also characterized by one unique feature, namely the development of a pair of ventral swellings on the fourth abdominal segment, which seem to have never been observed in any other species of Collembola. These swellings are covered with modified cuticular granules, representing a structure of unknown origin with a duct system or a hole inside visible under them.

**Distribution and ecology.** The species has only been registered at the type locality.

## Taxonomic remarks

The genus *Psyllaphorura* was established by Bagnall (1948) for *Onychiurus obesus* Mills, 1934 described from Iowa (USA). He listed several distinguishing characters of the genus, i.e. the presence of both a furcal remnant and a retinaculum, PAO with compound vesicles, few pseudocelli, antero-dorsal pseudocelli of head set outside the antennal bases and arranged vertically, postero-marginal pseudocelli of head absent and AIIIO with smooth sensory clubs. Like many other genera of Onychiuridae erected by Bagnall, *Psyllaphorura* was “forgotten” and regained recognition only half a century later (Weiner 1996). However, its diagnosis has been changed significantly, and some species presently included in this genus may have simple or only slightly divided vesicles in the PAO (all known species except *P. obesa*). Two species, *P. martynovae* (Stebaeva, 1985) and *P. olga* Babenko & Fjellberg, 2016, show a different arrangement of cephalic pseudocelli (inside the antennal bases), which is more typical of the closely related genus *Kalaphorura* Absolon, 1901. As a result, only two distinguished characters remained shared by these two genera (Weiner *et al.* 2019): “...body shape (ovoid in *Psyllaphorura* vs fusiform in *Kalaphorura*) and Abd. VI very short with chaetae in two rows in *Psyllaphorura* and elongated with 6–7 rows of chaetae in *Kalaphorura*...”. Below we discuss the most important characters used to distinguish between species within the genus *Psyllaphorura*.

**TABLE 1.** Main diagnostic characters of *Psyllaphorura* species

Species	Dorsal pso	Type of cephalic pso localization	Number of papillae / guard setae in AIII	Lateral ms on Th. III	Setae on furcal knobs	Retinaculum	Unguiculus / unguis	Setae on VT	Vesicles in PAO	Sensilla on Abd. V	Dorsal sensilla	Others
<i>P. altaica</i>	3/000/0001(2)3 <sup>a</sup>	MN	4/4	+	3+3	- <sup>a</sup>	0.8	7+7	9–14, simple	2+2	4/032/222121(0) <sup>a</sup>	enlarged upper subcoxae of leg III <sup>a</sup>
<i>P. bashkirica</i>	5/000/00023 <sup>b</sup>	?	5/5	?	2+2	?	0.5	?	17–19, divided	2+2	?/11/11112?	very coarse granulation, sensilla on Th. III in medial position
<i>P. jiangsuensis</i>	2/000/00013	OR, convergent	4/5	+	3+3	?–	0.8–0.9	5+5	20–22, simple or divided	1+1	1/011/11111	
<i>P. jirisana</i>	2/000/00023	OR, convergent	5/5	+	3+3	+	1.0–1.1	8+8	19–22, simple	2+2	2/011/11112	unguis with clear lateral teeth
<i>P. martynovae</i>	2/000/00013	BA <sup>c</sup>	4/5	+ <sup>c</sup>	3+3	+ <sup>c</sup>	0.5 or 0.9–1.0 <sup>c</sup>	7+7	18, simple	2+2 <sup>c</sup>	3/021/222121 <sup>c</sup>	
<i>P. obesa</i>	3/011(0)/00023	OR, arched	4(5)/4(5)	?	3+3	+	0.8–0.9	?	compound	?	?	unguiculus with broad basal lamella
<i>P. okafujii</i>	2/000/0001(2)3	OR, straight	5/5	?	3+3	+	0.5–0.6	7+7	20–25, simple or divided	2+2	?	
<i>P. olga</i>	2/000/00023	BA	5(4)/5	+	3+3	+	1.1–1.2	8(9)+8(9)	17–21, slightly divided	2+2	?/021/222121(0) <sup>a</sup>	
<i>P. pseudopodis</i> sp. nov.	3/000/00003	MN	5/4	+	2+2	–	0.5–0.6	7(8)+7(8)	12–15, simple	2+2	2/021/221121(0) <sup>d</sup>	very coarse granulation, ventral swellings on Abd. IV

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TABLE 1. (Continued)

Species	Dorsal pso	Type of cephalic pso localization	Number of papillae / guard setae in AIIIO	Lateral ms on Th. III	Setae on furcal knobs	Retinaculum	Unguitulus / unguis	Setae on VT	Vesicles in PAO	Sensilla on Abd. V	Dorsal sensilla	Others
<i>P. ryozoyoshii</i>	2/000/00023	MN	5/5	+	3+3	+	0.7–0.8	8+8	18–20 simple	2+2	3/022/2222 <sup>a</sup> 21 <sup>d</sup>	
<i>P. silvestris</i> sp. nov.	3/010/00123	OR, arched	5/4	–	3+3	+	1.0–1.1	8(9)+8(9)	16–22, simple	1+1	2(1)/021/222111 <sup>d</sup>	elongated or on Ant. IV, unguiculus with broad basal lamella
<i>P. sensillifera</i> <sup>f</sup>	2(1)/000/001(0)23	OR, straight	5(4)/5	+	3+3	+	1.1–1.2	8+8	20–26, simple or divided	2+2	3–5/021/222120	
<i>P. uenoi</i>	2/000/00023	OR, straight	5/5	?	3+3	+	0.6–0.7	?	15–18, simple	? not distinct	?	
<i>Psyllaphorura</i> sp. undet. [Kuznetsk Alatau]	2/000/00013	OR, divergent	4/5	+	?	?	0.9–1.0	7+6	?	2+2	at least 3/011/21112	

a – according to our study of type or topotype material

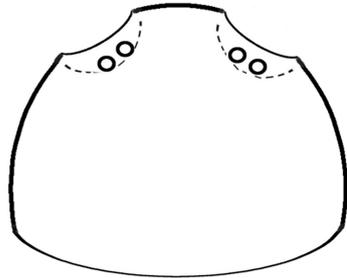
b – the number of cephalic pso given in the original description is doubted to be correct

c – based on our study of a single specimen from the NE Altai

d – a lateral sensillum is located on the pleuron of this segment

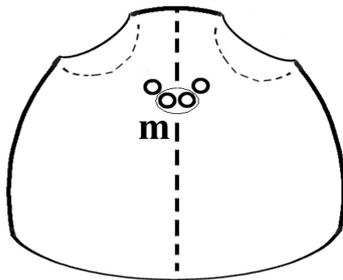
f – in combination with data on *P. raoheensis* as a junior synonym

**23 BA - baso-antennal complex**

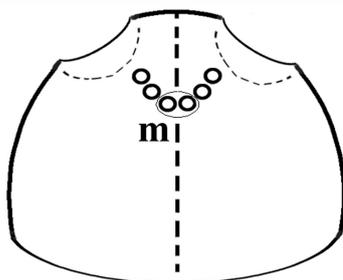


*P. olga, P. martynovae*

**24 MN - median complex**

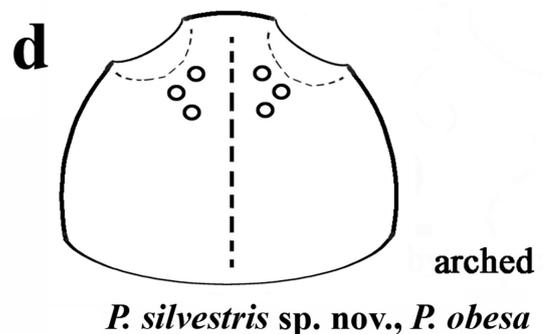
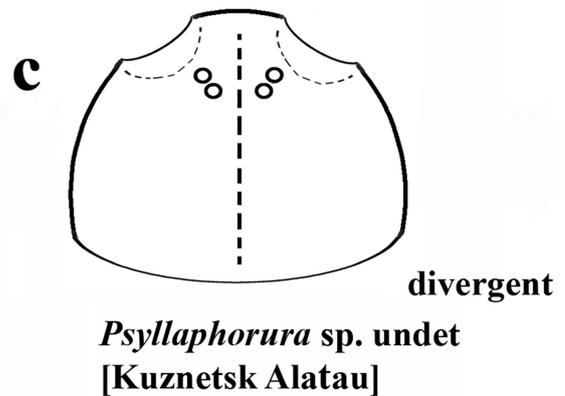
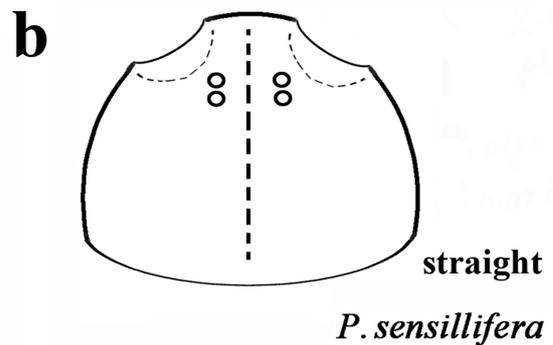
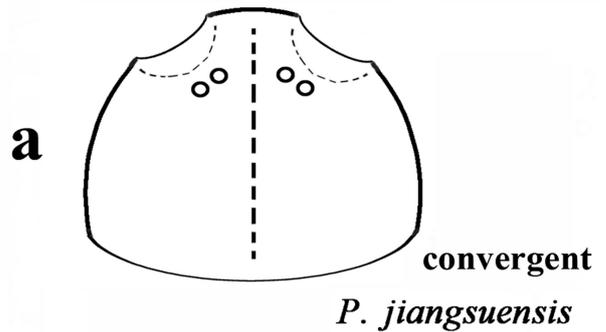


*P. ryozyoshii*



*P. altaica, P. pseudopodis sp. nov.*

**25 OR - outer complex**



FIGURES 23–25. Patterns of the cephalic pso arrangement in *Psyllaphorura*: 23, baso-antennal complex; 24, median complex; 25, outer complex.

**Arrangement of cephalic pseudocelli.** Contrary to the majority of Onychiurinae, the position of the anterior pseudocelli on the head is a variable character in *Psyllaphorura*. At least three main types of its arrangement may be distinguished (Figs 23–25).

The ancestral type, which is typical of all other genera of Hymenaphorurini having pso, may be named as BA, or “baso-antennal” complex. Cephalic pso in this type of arrangement are located within the antennal bases at their border with the field of coarser granulations (Fig. 23). Among *Psyllaphorura* this type is known only for two species, namely *P. martynovae* and *P. olga*.

The most unique and, probably, apomorphic pattern (Fig. 24), which was never revealed in any other Onychiuridae, was first found in *P. ryozoyoshii* Weiner & Najt, 2000 and then in *P. altaica*. The same type is also typical of *P. pseudopodis* **sp. nov.** All these three species are characterized by the frontal localization of cephalic pseudocelli in a unified “V-shaped” group (medial or m-pso present). This pattern may be termed MN or “median” complex.

In all other known congeners, the cephalic pso are located in an intermediate position, i.e. in two separate groups on both sides of the head between the antennal bases and axial line. We suggest terming such a position of pso as OR-type, which means “outer” complex (Fig. 25). Four variants of this pattern may be distinguished:

1) “convergent” (Fig. 25a), when the lines passing through the pso on opposite sides of the head converge anteriorly (*P. jiangsuensis* Yan, Huang & Chen, 2007; *P. jirisana* Lee & Park, 2021);

2) “straight” (Fig. 25b), when pso are located vertically one under the other, parallel to the axial line. (*P. sensillifera* (Martynova, 1981))

3) “divergent” (Fig. 25c), lines diverge anteriorly (undescribed *Psyllaphorura* sp. from Kuznetsk Alatau, southern Siberia, found in the ISEAS collection);

4) “arched” (Fig. 25d). In the latter case pso are located in semicircles (*P. obesa*, *P. silvestris* **sp. nov.**).

A certain level of intraspecific variability in all these variants, especially in “convergent” and “straight” ones, is highly probable which must be taken into account.

Species that formally have the same number of pseudocelli can sometimes be easily distinguished by the position of the cephalic pso, because such a character as “2+2 pso on head” can actually mean several different cases in *Psyllaphorura*: BA- (*P. martynovae*), OR- (*P. sensillifera*) or MN-type (*P. ryozoyoshii*). *Psyllaphorura olga* and *P. sensillifera* may have the same number of pso (20/000/00023), but they clearly differ in the position of cephalic pseudocelli (OR-type in *P. sensillifera* vs BA-type in *P. olga*). The same is the case of *P. martynovae* (20/000/00013 pso, BA-type) and *P. jiangsuensis* (the same number of pso, but OR-type). All above clearly indicates the urgent need to specify in the keys or tables with diagnostic characters not only the number of cephalic pseudocelli, but also a pattern of their location. It should be noted that such a different arrangement of antennal cephalic pseudocelli among species of the same genus is generally quite unusual and is not observed among Onychiurinae (Pomorski 1998, Weiner 1996).

**Variability of abdominal pso.** As in most Onychiurinae, the taxonomic descriptions of *Psyllaphorura* species are mainly based on the number of dorsal pso. Nonetheless, it is noteworthy that, despite the low number of pso in *Psyllaphorura*, variations in pso formulas have been detected in some species. All known *Psyllaphorura* species have 3+3 pso on Abd. V, but analyses of representative number of specimens may show pso variability on Abd. IV as well as on Abd. III. For example, while studying a recent collection from a site close to the type locality of *P. altaica*, we found not only specimens with 1+1 pso on Abd. IV (as in the types) but also one individual with 1+2 pso, and three specimens with 2+2 pso in that position. The same type of variation was noted for *P. okafujii* (Yosii, 1967), which has, according to the original description, 2/000/0001(2)3 dorsal pso.

A similar intraspecific variability in the number of pso is apparently characteristic of *P. sensillifera*. During our investigation of Collembola in the forests of the Russian Far East including those of Southern Primor’e (close to the type locality of *P. sensillifera*) two very similar forms were found. The most common form with lateral pso on Abd. III (2/000/00123 pso, totally), could be identified as *P. raoheensis* Sun & Wu, 2013, described from northeastern China. The distribution range of another form with 2/000/00023 pso as described for *P. sensillifera* appears to be more restricted. It was found only in the Khabarovsk Territory (near Gorin, about 80 km northwest of Komsomolsk-on-Amur), where both forms can coexist in the same biotope. We studied the holotype and two paratypes of the latter species, stored in ZIN, and found that 1+1 pso on Abd. III were overlooked during the original description as they are definitely present at least in two of the three types restudied, including the holotype. Thus, *P. sensillifera* appears to have the same (although variable) number of abdominal pso as *P. raoheensis*. According to Sun & Wu

(2013), the latter also differs "...by dorsal S-chaetae formula (3–5/021/222120 in *P. raoheensis*... and 0/111/111120 in *P. sensillifera*)..., teeth on tenaculum (2+2 in *P. raoheensis*... and 1+1 in *P. sensillifera*), number of vesicles in PAO (20–22 in *P. raoheensis*... and 24–26 in *P. sensillifera*) and ratio of AS/unguis (0.2 in *P. raoheensis* and 0.5 in *P. sensillifera*)...". Our study of the *P. sensillifera* types showed that most of these "differences" are due to a deficient original description. The types have at least 3/021/22?12 dorsal sensilla (whereas the holotype has 4+4 S on the head), 2+2 teeth on the retinaculum, and AS are clearly smaller than 0.5U (ranging from 0.32 to 0.36). In other words, in our opinion *P. raoheensis* is an obvious junior synonym of *P. sensillifera*.

**Dorsal sensilla.** The formulas of dorsal and ventral sensilla on the body are usually used as an additional character for species distinctions. In our opinion, this must be done with due caution, because there is a high possibility of misinterpretation due to similarity between sensilla and common setae. In addition, the number of sensilla can vary both at intra- and interspecific levels and clearly depends on age: juveniles possess significantly fewer sensilla. As a result, the formulas given in the original descriptions are somewhat subjective. Naturally, this primarily concerns a number of "old" descriptions, in which the absence of direct indications of the presence of sensilla cannot be considered reliable. For example, Yosii (1967), comparing *P. okafujii*, with *P. uenoi* (Yosii, 1954), wrote that the former has "...two small sensory setae of abd. V... very distinct". Unfortunately, we cannot be sure that it means their complete absence from *P. uenoi*. This may be also applied to some modern descriptions. Thus, Babenko & Fjellberg (2016) indicated the presence of only two distinct sensilla on Abd. V for *P. olga*. In fact, all dorsal setae in this species are slightly widened and obtuse; therefore, it is difficult to distinguish "sensilla" from ordinary setae on other terga. Sometimes some of the setae are widened and thickened somewhat more than others, and when these setae are taken into account, one can obtain a more or less common sensillar formula: ?/021/22212; sometimes even a "sensillum" on the ventro-lateral part of Abd. VI is also visible. Nevertheless, such a formula would be highly subjective, whereas 2+2 sensilla on Abd. V can always be distinguished for sure. Therefore, we suggest paying more attention to the number of sensilla on Abd. V: the presence of 2+2 or 1+1 sensilla on this tergum appears to be a stable and easily distinguishable feature.

In light of the variability described above, we believe that the status of *P. jirisana*, requires further confirmation. The postulated differences of this Korean species from *P. sensillifera* are limited by the dorsal s-chaetae formula, as well as "...by shape of vesicles in PAO..., ratio of AS/unguis... and lateral teeth of claw (present in *P. jirisana*; absent in *P. sensillifera*).". (see also Table 1). Among these characters only the last one, namely the presence/absence of lateral teeth on unguis, seems to be quite reliable.

**Axial setae on head and abdominal tip.** The presence of an unpaired seta d0 on the head is a rather stable character for many genera within Onychiurinae. In most *Psyllaphorura* this axial seta may be present or absent, as well as simply overlooked due to plurichaetosis. The number of axial setae on Abd. IV is also variable. Therefore, these characters are poorly applicable for separating the *Psyllaphorura* species. The axial chaetotaxy of Abd. V and Abd. VI may be more useful, although the designation of setae differs among authors. The axial seta located in front of AS on Abd. VI considered either as a0 or m0 could be the case.

**Number of papillae in AIII and PAO vesicles.** The number of papillae in AIII is also used in taxonomy for clear determination of Onychiurinae species (for example, within such multispecies genera as *Allonychiurus*, *Oligaphorura*, *Onychiuroides*, *Protaphorura*, *Thalassaphorura*) or even for separating the genera, i.e. *Deuteraphorura* and *Orthonychiurus*. However, intraspecific variability of this trait occurs quite frequently among *Hymenaphorurini* (*Heteraphorura conjungens* (Börner, 1909), *Hymenaphorura polonica* Pomorski, 1990, *H. pseudosibirica* (Stach, 1954), *H. submontana* (Denis, 1926)). Some species of *Psyllaphorura* (*P. obesa*, *P. olga* and *P. sensillifera*) are also characterized by a variable number (5–4) of papillae in AIII.

The number of PAO vesicles is constantly used to separate Onychiurinae species, including *Psyllaphorura*. The importance of this character cannot be denied. Nevertheless, intraspecific variability of this feature can be relatively high in some species, especially when individual size is directly related to the number of PAO vesicles.

**Retinaculum.** We have never seen a direct indication of the absence of retinaculum in any available description of the *Psyllaphorura* species. Therefore, its complete absence was unexpected in *P. pseudopodis* sp. nov. Nevertheless, this is not a unique character for the genus. The same can probably be expected for *P. jiangsuensis*. No retinaculum has been mentioned, nor has it been depicted, in its description, but the furcal knobs in fig. 11 in Yan *et al.* (2007) are so widely separated that the retinaculum should have been visible, if present at all. This structure is also absent from *P. altaica*, despite the authors' indication of its presence. This was first discovered in specimens from recent samples within the type locality (Russia, Altai Republic, N-E Altai, N-W shore of Teletskoye Lake, near Artybash

village) and then confirmed from types by I. Kaprus' and W. Weiner (pers. comm.). Such a discrepancy between the original description and our data is likely to be due to a mixed nature of the type series. This assumption is based on the discovery in the materials of S. Stebaeva (with a label identical to the type's one) not only typical *P. altaica* having no retinaculum, but also a single specimen of another congener which has a retinaculum. The latter specimen can be identified as *P. martynovae* although it has a longer unguiculus (about as long as the unguis) than it was indicated in the original description. This has allowed us to clarify some morphological characters typical of *P. martynovae* (Table. 1).

**Unique characters.** Some species of this genus are characterized by unique morphological features of unknown origin or function. Among them peculiar swellings on ventral side of Abd. IV in *P. pseudopodis* **sp. nov.** are the most interesting. Each of these swellings appears to be a spherical cavity covered with modified cuticular granules. At the top of these swellings the granules are thinner and longer forming a kind of cone-shaped “tail” (Figs. 14, 18, 19). Such a structure has not been found in any other Collembola. The greatly enlarged upper subcoxae of leg III in *P. altaica* (Figs. 20–22) are also worth mentioning. Their outer surface is covered with similarly modified granules (high and thin), but, contrary to *P. pseudopodis* **sp. nov.**, no additional formations are visible beneath.

Such rare features as the strongly elongated subapical organite on Ant. IV in *P. silvestris* **sp. nov.** and the absence of lateral ms on Th. III in the same species also deserve special mention.

### Key to the *Psyllaphorura* species

1	Furcal knobs with 2+2 setae . . . . .	2
-	Furcal knobs with 3+3 setae . . . . .	3
2	AIIIO with 5 guard setae; PAO vesicles divided; Abd. IV without ventral swellings; 5+5 cephalic pso . . . . .	<i>P. bashkirica</i> (Khanislamova, 1986); Russia, southern Urals
-	AIIIO with 4 guard setae; PAO vesicles simple; Abd. IV with ventral swellings; 3+3 cephalic pso in MN position . . . . .	<i>P. pseudopodis</i> <b>sp. nov.</b> ; Russia, European part
3	Head with 3+3 <i>pso</i> . . . . .	4
-	Head with 2+2 <i>pso</i> . . . . .	6
4	Cephalic pso in OR position . . . . .	5
-	Cephalic pso in MN position . . . . .	<i>P. altaica</i> Weiner, Stebaeva & Kaprus', 2019; Russia, southern Siberia
5	PAO vesicles compound; Abd. III without pso . . . . .	<i>P. obesa</i> (Mills, 1934); United States, Iowa, Wisconsin, and Missouri
-	PAO vesicles simple or bilobed; lateral pso present on Abd. III . . . . .	<i>P. silvestris</i> <b>sp. nov.</b> ; Russia, European part
6	Cephalic pso in MN position . . . . .	<i>P. ryozoyoshii</i> Weiner & Najt, 2000; North Korea
-	Position of cephalic pso different . . . . .	7
7	Cephalic pso in BA position . . . . .	8
-	Cephalic pso in OR position . . . . .	9
8	VT with 8(9)+8(9) setae; 2+2 pso on Abd. IV . . . . .	<i>P. olga</i> Babenko & Fjellberg, 2016; Russia, North-East
-	VT with 7+7 setae; 1+1 pso on Abd. IV . . . . .	<i>P. martynovae</i> (Stebaeva, 1985); Russia, southern Siberia
9	Unguiculus about as long as unguis . . . . .	10
-	Unguiculus shorter than unguis . . . . .	11
10	Unguiculus without inner or lateral teeth . . . . .	<i>P. sensillifera</i> (Martynova, 1981); Russia, Far East; northeastern China
-	Unguiculus with clear lateral teeth . . . . .	<i>P. jirisana</i> Lee & Park, 2021; South Korea
11	PAO with 15–18 vesicles; dorsal sensory setae invisible . . . . .	<i>P. uenoi</i> (Yosii, 1954); Japan
-	PAO with 20–25 vesicles; dorsal sensory setae distinct . . . . .	12
12	VT with 5+5 setae; unguiculus as long as 0.8–0.9 of unguis . . . . .	<i>P. jiangsuensis</i> Yan, Huang & Chen, 2007; China
-	VT with 7+7 setae; unguiculus as long as 0.5–0.6 of unguis . . . . .	<i>P. okafujii</i> (Yosii, 1967); Japan

### Conclusion

In total, together with the newly described species and taking into account the proposed synonymy, the genus *Psyllaphorura* presently encompasses 13 species. The known distributions of most species of the genus are rather limited, whereas that of the whole genus covers the major part of the Palearctic except Western Europe. *Psyllaphorura obesa*, the type species of the genus that comes from the center of the Nearctic, represents the only exception of this rule. Despite such a low species diversity, the genus is quite diverse morphologically, being characterized by a rather unusual set of varying characters including the arrangement of cephalic pseudocelli, the number of dental setae, the length of unguiculus and the presence/absence of a retinaculum and ms on Th. III.

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