# Four new genera of the North American Hymenaphorurini (Collembola: Onychiuridae) with a description of new species and key to World genera of the tribe

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Insect Syst. Evol. Pomorski, R. J. & Steinmann, D.: The onychiurid Collembola Dinochiurus reus (Christiansen & Bellinger, 1980) gen. n. & comb. n., Reducturus christianseni gen. n. & sp. n., Sacaphorura parapseudocellata gen. n. & sp. n. and Vexaphorura robustiseta gen. n. & sp. n. are redescribed and described from North America. An identification key to the World genera of Hymenaphorurini is given. Insect Syst. Evol. 35: 15-27. Copenhagen, April 2004. ISSN 1399-

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#### Introduction

Pomorski (2000, 2001, 2002, 2003), in series of studies on North American Hymenaphorurini, made a review of species belonging to the genera Hymenaphorura Bagnall, 1949; Heteraphorura Bagnall, 1948; Paronychiurus Bagnall, 1948 and he described the new genus Arneria Pomorski, 2000. The materials for these studies came of personal collections of Prof. Kenneth Christiansen, Dr. Arne Fjellberg and Mr. David Steinmann, and from collection of Harvard Museum of Comparative Zoology and Illinois Natural History Survey. Among these materials we also found 4 species that we can not classify to any existing genera.

### Taxonomy

## Genus Dinochiurus gen. n.

Type species: - Onychiurus reus Christiansen & Bellinger, 1980

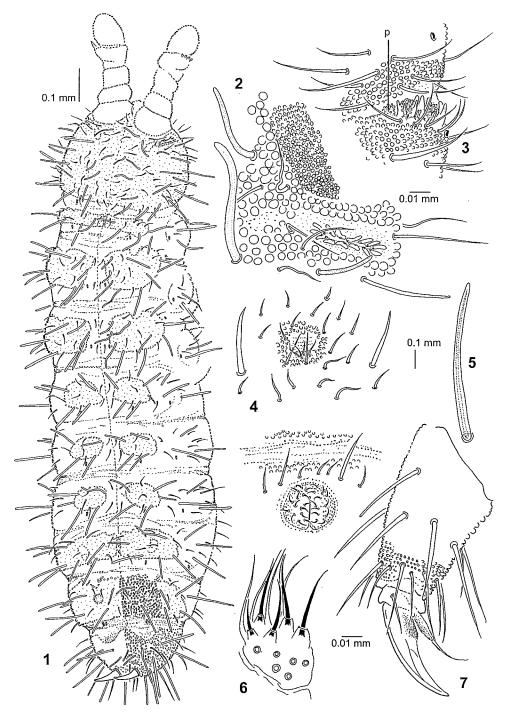
Diagnosis. - Dorsal side of body with areas of stronger granulation. Body with parapseudocelli only, always located outside of granular areas. Antennal III sense organ with 5 forked and branched papillae, 5 guard setae and additional

papilla-like cuticular prominence. Furca reduced to a small concavity without granulation, with 4 setulae posteriorly arranged in one row. Anal spines inserted on distinct papillae. All macrosetae large, rod-like, apically blunt. Distal whorl of setae on tibiotarsi with 11 setae. Vesicles in postantennal organ simple and bilobed. Labium O type with 5 sharply pointed papillae. Setae sensuales on head and body not marked. Seta do on head absent, abdominal terga I-IV with 2+2 submedial setae, abdominal tergum VI with 2 medial setae.

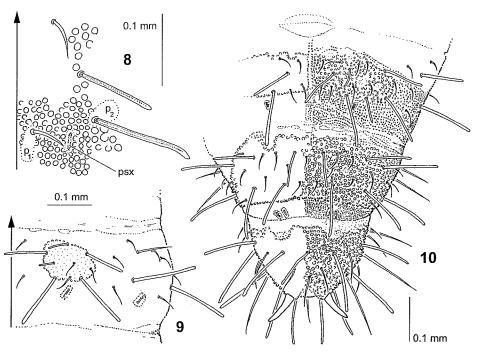
Etymology. - The new genus name is derived from the Greek word "deinos" - terrible.

Discussion. – The genus Dinochiurus gen. n. is a monophyletic group within Hymenaphorurini with the lack of pseudocelli and presence of parapseudocelli always outside of granular areas and exceptional build of macrosetae as autapomorphic characters. The genus shares with Arneria Pomorski, 2000 and Reducturus gen. nov., described below, the synaphomorphy of presence of additional papilla-like prominence in the antennal III sense organ. Apart from Dinochiurus, also Reducturus have 2+2 submedial setae on the thoracic III and abdominal I-IV terga, and the same tendency to having branched papillae on the antennal III sense

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Figures 1-7. *Dinochiurus reus* (Christiansen & Bellinger, 1980) (paratype): (1) habitus and dorsal chaetotaxy; (2) postantennal organ; (3) antennal III sense organ, p – papilla-like prominence; (4) remnant of furca and genital plate; (5) macroseta; (6) labium; (7) tibiotarsal chaetotaxy and claw.



Figures 8-10. Dinochiurus reus (Christiansen & Bellinger, 1980): (8) submedial part of thoracic tergum III, psx - prapseudocellus; (9) chaetotaxy and localisation of parapseudocelli on abdominal tergum I; (10) chaetotaxy and localisation of parapseudocelli on abdominal terga IV-VI.

## Dinochiurus reus (Christiansen & Bellinger, 1980) comb. nov.

(Figs 1-10).

Redescription. - Colour white. Size without antennae: Unreproductive male (holotype) 2.2 mm, females 2.3-2.6 mm. Shape of body Hymenaphorura-type (Fig. 1). Antennae as long as head or a little shorter. Furca reduced to a small depression, with 2 small posterior setae (Fig. 4). Cuticular granulation on the dorsal surface of the body regular and strong, with distinct areas of very coarse granules.

Antennal III sense organ with 5 guard setae, 5 forked or branched papillae, 2 sensory rods, 2 distinctly granulated sensory clubs and additional cuticular prominence (Fig. 3).

Antennal segment IV with subapical organ and microsensillum located distinctly above the row of the posterior setae. Microsensillum of antennal segment III minute, situated lateral and slightly posterior to the antennal III sense organ (Fig. 3).

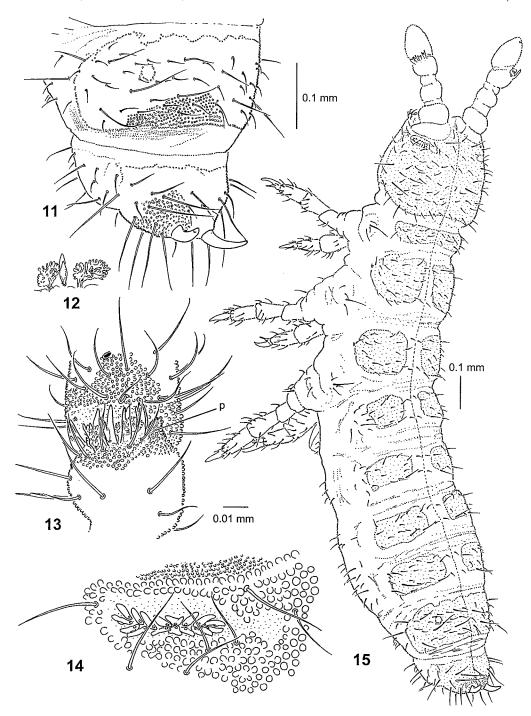
Postantennal organ in a cuticular groove with 2 acuminate border setae, consisting of 16-19 simple and bilobed vesicles arranged obliquely and parallel to the long axis of the organ (Fig. 2).

Pseudocelli absent. Dorsal parapseudocellar formula 01/111/22222, ventral 0/000/111111. All subcoxa with 1 parapseudocellus. Submedial parapseudocelli always located outside of areas of strong granulation (Figs. 1, 8, 9). On thoracic terga II and III submedian pseudocelli located exceptionally between setae  $p_1$  and  $p_2$  (Fig. 8).

Labium O type with all 5 papillae apically pointed. (Fig. 6).

Dorsal chaetotaxy very well differentiated into pointed microsetae and large, rod-like, apically blunt macrosetae, as in Figs 1, 5, 8 and 10. Head wi thout seta do. Thoracic tergum III and abdominal terga I-IV with 2+2 submedial setae located outside of areas of coarse granulation. Abdominal tergum V with a<sub>0</sub> seta, abdominal tergum VI with 2 medial setae. Thorax II-III with lateral microsensilla. Subcoxae with 4, 7, 6 setae. No setae between legs on pro-, meso- and metasternum. Ventral tube with 11+11 setae, without setae at base. Sensory setae invisible.

Male ventral organ absent.



Figures 11-15. *Reducturus christianseni* sp. n. (holotype): (11) tibiotarsal chaetotaxy and claw; (12) sensory rods and sensory clubs; (13) antennal III sense organ, p – papilla-like prominence; (14) postantennal organ; (15) habitus and dorsal chaetotaxy.

Claw without inner tooth. Empodial appendage shorter than inner edge of the claw, with small basal lamella (Fig. 7). Distal whorl of setae on tibiotarsi symmetrical, with 11 setae.

Anal spines on distinct basal papillae, weakly curved and about 1.5 times the length of the hind claw.

Type material. - Holotype is an unreproductive male on slide; USA, Illinois, Hillcrest, Culhoun Co.; 20 XI 1958; forest debris. Leg. J. Stannard (Illinois Natural History Survey - insect collection no. #0017). Paratype - unreproductive male on the same slide; the same data as holotype.

Other material. - 2 females (9684) USA, Indiana, Orange Co. Splorin hole cave, 1 mi. south of Chambersburg, 29 III 2002, leaf litter, Leg. J. Lewis et al. 3 females (9686) USA, Indiana, Lawrence Co, Little African Pleasure Palace cave, ~ 1 mile south of Chambersburg, 16 III 2002, Leg. J. Lewis et al.

## Genus Reducturus gen. n.

Type species: – Reducturus christianseni sp. n.

Diagnosis. - Dorsal side of body with granular areas. Body without pseudocelli and parapseudocelli. Antennal III sense organ with 5 forked and branched papillae, 5 guard setae and additional papilla-like cuticular prominence. Furca reduced to a small concavity without granulation with 2 setulae posteriorly. Anal spines inserted on distinct papillae. Distal whorl of setae on tibiotarsi with 11 setae. Vesicles in postantennal organ simple and bilobed. Labium with 5 sharply pointed papillae. Setae sensuales on head and body not marked. Seta d<sub>0</sub> on head absent, abdominal terga I-IV with 2+2 submedial setae, abdominal tergum VI with 2 medial setae.

Discussion. - All known members of the Onychiuridae family, as a rule, possess cuticular secretive structures - pseudocelli and parapseudocelli. The genus Reducturus gen. n. is a monophyletic group with an exceptional autapomorphy - lack of pseudocelli and parapseudocelli. All other important morphological characters (shape of body, postantennal organ, antennal III sense organ and remnant of furca) clearly show that this genus belongs to the tribe Hymenaphorurini within the subfamily Onychiurinae. The genus shares with Arneria and Dinochiurus, described above, the synaphomorphy of the presence of additional papilla-like prominence in the antennal III sense organ. Besides, the build of the furcal rest of the new genus is similar to the furcal rest of Arneria.

# Reducturus christianseni sp. n.

(Figs 11-18).

Description. - Colour white. Size without antennae: Reproductive male (holotype) 2.05 mm, juveniles of III instar 1.25 mm. Shape of body Hymenaphorura-like (Fig. 15). Antennae as long as head or a little shorter. Furca reduced to a small depression, with 2 small posterior setae (Fig. 16). Cuticular granulation on dorsal surface of the body regular, with distinct areas of coarser granules.

Antennal III sense organ with 5 guard setae, 5 forked or branched papillae, 2 fluke-like sensory rods, 2 distinctly granulated sensory clubs and additional cuticular prominence (Fig. 12-13).

Antennal segment IV with subapical organ and microsensillum located distinctly above the row of posterior setae. Microsensillum of antennal segment III minute, situated lateral and slightly posterior to the antennal III sense organ (Fig. 13).

Postantennal organ in a cuticular groove with 2 acuminate border setae, consisting of 15-16 simple and bilobed vesicles arranged obliquely and parallel to the long axis of the organ (Fig. 14).

Pseudocelli and parapseudocelli absent. Labium O type with all 5 papillae (Fig. 17).

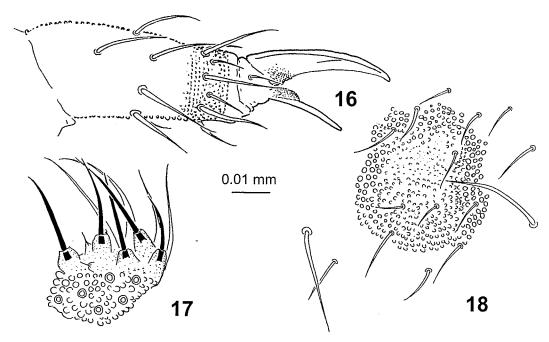
Dorsal chaetotaxy poorly differentiated into microsetae and macrosetae. Macrosetae distinct only on abdominal terga IV-VI and laterally on head, as in Figs 11 and 15. Head without seta d<sub>0</sub>. Thoracic tergum II and abdominal terga I-IV with 2+2 submedial setae located outside of areas of coarse granulation. Abdominal tergum V with a<sub>0</sub> seta, abdominal tergum VI with 2 medial setae. Thorax II-III with lateral microsensilla. Subcoxae with 4, 4, 5 setae. No setae between legs on pro-, meso- and metasternum. Ventral tube with 8+8 setae, without setae at base. Sensory setae invisible.

Male ventral organ absent.

Claw without inner tooth. Empodial appendage relatively thick and blunt, shorter than inner edge of the claw, with small basal lamella (Fig. 16). Distal whorl of setae on tibiotarsi symmetrical, with 11 setae.

Anal spines on distinct basal papillae, slender, weakly curved and about 0.5 times the length of the hind claw.

Type material. - Holotype is a reproductive male (9401); USA, Colorado, Garfield Co., Bair cave; 11 I 2000, under marmot scat in dark zone, leg. D. Steinmann. 2 paratypes (juv.) USA, Colorado, Garfield Co., Bair cave; 10 000' elevation (approximately 107° 39°), 22 IX 2001, in dark zone and under rocks near marmot scat, leg. D. Steinmann. (in the Illinois Natural History Survey collection, and in the collection of the Department of



Figures 16-18. Reducturus christianseni sp. n. (holotype): (16) tibiotarsal chaetotaxy and claw; (17) labium; (18) remnant of furca.

Systematic Zoology and Zoogeography, Wrocław University).

Etymology. – The new species is named in honor of Prof. Kenneth Christiansen, eminent apterygotologist, for his inspiration and guidance. The new genus name is derived from the Latin word "reductor" – "one who brings back".

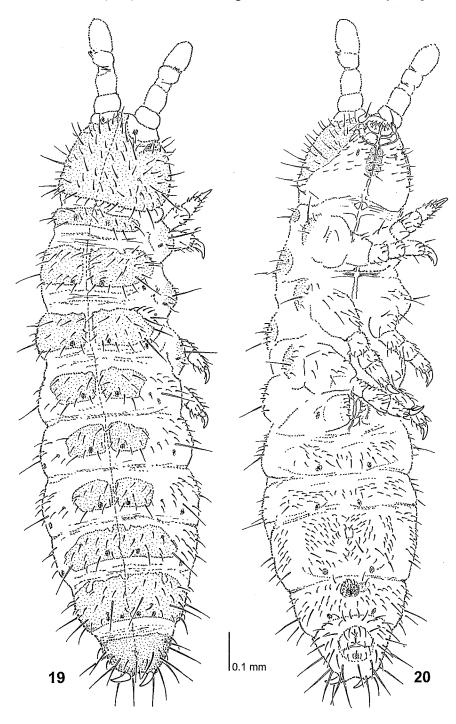
Biological remarks. - R. christianseni lives in the dark zone of Bair Cave (limestone, two separate entrances, 250 meters of passageway with several small extensions, the temperature is 2-4°C) and probably is a troglobite. It feeds at organic nutrients imported by rodents and bats also living in the cave. Together with R. christianseni over 20 invertebrate species have been found. They belong to the following taxa: Diplopoda, Chilopoda, Acari, Araneae, Collembola, Diptera, Coleoptera, and Psocoptera. Among Collembola four species were collected: Onychiurus n. sp., Tomoceus (Plutomurus) n. sp., Tomocerus (Lethemurus) n. sp., and Tomocerus (Pogonognathellus) flavescens Tullberg, 1871 (det. K. Christiansen and R. J. Pomorski).

# Genus Sacaphorura gen. n.

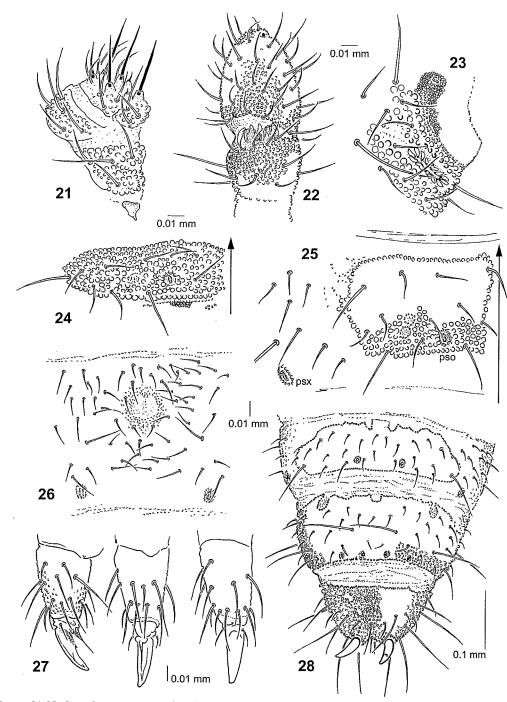
Type species: - Sacaphorura parapseudocellata sp. n.

Diagnosis. - Dorsal side of body with very distinct areas of coarser granulation. Granulated areas of abdominal tergum IV fused together midline into one plate. Pseudocelli and parapseudocelli present. Antennal III sense organ with 5 papillae, 5 guard setae. Vesicles in postantennal organ simple and bilobed. Labium with 5 sharply pointed papillae. Furca reduced to a small area without granulation, with 2 setulae posteriorly located outside of this area. Anal spines inserted on distinct papillae. Distal whorl of setae on tibiotarsi with 11 setae. Setae sensuales on head and body well marked. Seta do on head absent. Submedial setae on thoracic and abdominal terga located inside areas of stronger granulation. Abdominal tergum VI with 2 medial setae.

Discussion. – Within Hymenaphorurini the genus Sacaphorura gen. n. is a monophyletic group with 2 apomorphies: The presence of one tergal plate of coarser granulation on abdominal tergum IV and



Figures 19-20. Sacaphorura parapseudocellata sp. n.: (19) habitus and dorsal chaetotaxy; (20) habitus and ventral chaetotaxy.



Figures 21-28. Sacaphorura parapseudocellata sp. n.: (21) labium; (22) antennomere III-IV with antennal III sense organ; (23) postantennal organ and pseudocellus at base of antenna; (24) thoracic tergum I; (25) abdominal tergum I, psx – parapseudocellus, pso – pseudocellus; (26) chaetotaxy of abdominal sternum IV, remnant of furca and parapseudocelli; (27) tibiotarsal chaetotaxy and claw; (28) chaetotaxy of abdominal terga IV-VI.

the location of pseudocellus inside granular area of thoracic tergum I. The most likely candidate for a sister group to the new genus is Hymenaphorura, because both taxa share a similar build of the furcal rest and postantennal organ.

# Sacaphorura parapseudocellata sp. n.

(Figs 19-28).

Description. - Colour white. Size without antennae: Reproductive males 1.65 mm, females 1.75 mm. Shape of body Hymenaphorura-like (Figs. 19-20). Antennae as long as head or a little shorter. Furca reduced to a small depression, with 2 small posterior setae (Fig. 26). Cuticular granulation on dorsal surface of the body regular, with very distinct areas of coarser granules (usually 9-10 granules around each pseudocellus). Granulated areas of abdominal tergum IV fused to one median plate.

Antennal III sense organ with 5 guard setae, 5 papillae, 2 sensory rods, 2 smooth sensory clubs (Fig. 22).

Antennal segment IV with subapical organ and microsensillum at the level of the row of the posterior setae. Microsensillum of antennal segment III minute, situated lateral and slightly posterior to the antennal III sense organ (Fig. 22).

Postantennal organ in a cuticular groove with 1 acuminate border seta, consisting of 13-16 simple and bilobed vesicles arranged obliquely and parallel to the long axis of the organ (Fig. 23).

Pseudocelli weakly chitinised and very similar to parapseudocelli. Dorsal pseudocellar formula 10/111/11112. On thoracic tergum I pseudocellus located inside granular area (Fig. 24). On abdominal tergum IV pseudocelli located as in Figs. 19 and 28. Parapseudocelli well developed and very distinct. Dorsal parapseudocellar formula 0/011/ 1111, ventral 1/000/111111. All subcoxae with 1 parapseudocellus.

Labium O type with all 5 papillae apically pointed (Fig. 21).

Dorsal chaetotaxy well differentiated into microsetae and macrosetae. Macrosetae are distinct on the body only laterally and on abdominal terga V-VI, as in Fig. 19. Head without seta d<sub>0</sub>. Thoracic and abdominal terga with submedial setae located inside areas of coarse granulation. Abdominal tergum V with a<sub>0</sub> seta, abdominal tergum VI with 2 medial setae. Thorax II-III with lateral microsensilla. Subcoxae with 4, 5, 5 setae. No setae between legs on pro-, meso- and metasternum. Ventral tube with 12+12 setae, without setae at base. Sensory setae invisible.

Male ventral organ absent.

Claw with inner tooth. Empodial appendage relatively short, without basal lamella (Fig. 27). Distal whorl of setae on tibiotarsi symmetrical, with 11 setae.

Anal spines on distinct basal papillae, weakly curved and about 1.1 times the length of the hind claw (Fig. 28).

Type material. – Holotype is a reproductive male on slide; USA, Alaska, Eagle Creek; 27 VII 1980, Alnus litter on mining tips, leg. A. Fjellberg. 5 paratypes on 3 slides (2 reproductive males, 3 females) and 13 paratypes in alcohol; same data as holotype (in the Illinois Natural History Survey collection, and in the collection of the Department of Systematic Zoology and Zoogeography, Wrocław University).

Etymology. - The new species is named after very distinct parapseudocelli. The new genus name is derived from the Greek word "sacos" - shield.

## Genus Vexaphorura gen. n.

Type species: - Vexaphorura robustiseta sp. n.

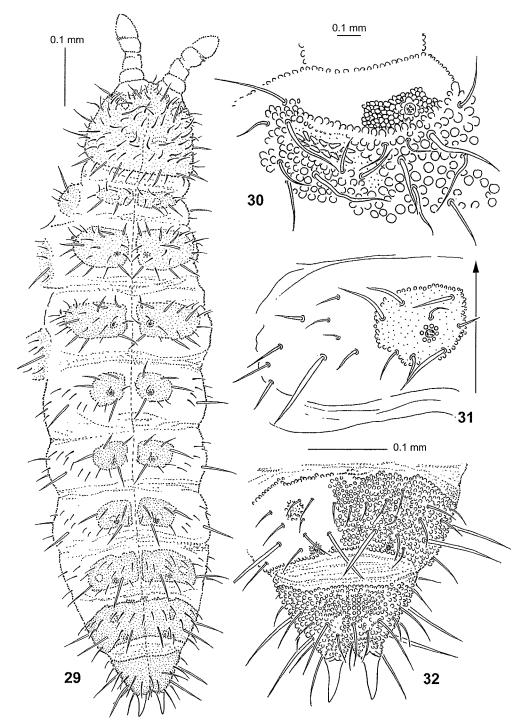
Diagnosis. – Dorsal side of body with granular areas. Body without parapseudocelli. Antennal III sense organ with 5 simple papillae, 5 guard setae. Furca reduced to a small area without granulation, with 2 setae located posteriorly on this area. Anal spines inserted on distinct papillae. Distal whorl of setae on tibiotarsi with 11 setae. Vesicles in postantennal organ simple and bilobed. Labium A-type with all 5 papillae. Setae sensuales on head and body not marked. Seta do on head absent. Submedial setae on thoracic and abdominal terga located inside areas of stronger granulation. Abdominal tergum VI with 2 medial setae.

Discussion. - Within Hymenaphorurini the new genus is characterised by two apomorphies - lack of parapseudocelli and lack of "free" submedial setae, located outside areas of stronger granulation. The genus shares with Hymenaphorura the synaphomorphies of the same shape of the furcal rest and postantennal organ.

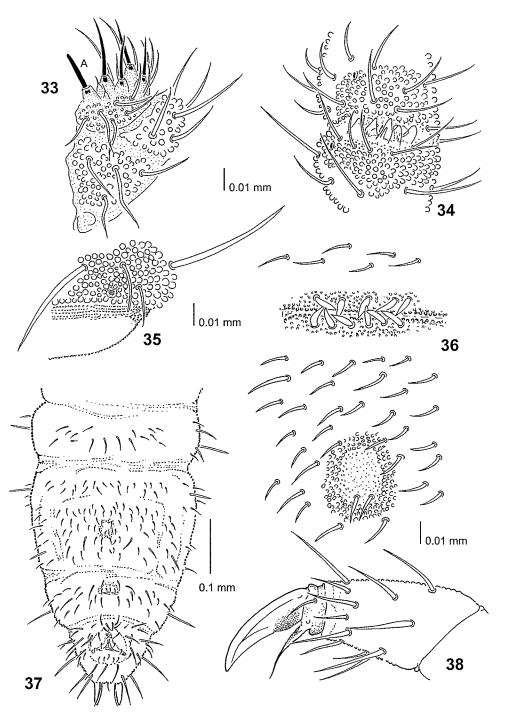
## Vexaphorura robustiseta sp. n.

(Figs 29-38).

Description. - Colour white. Size without antennae: Reproductive males 1.2-1.25 mm, females 1.5 mm. Shape of body Hymenaphorura-like (Fig. 29). Antennae as long as head or a little shorter. Furca reduced to a small depression, with 2 posterior setae (Fig. 36). Cuticular granulation on the dorsal surface of the body strongly regular, with distinct areas of coarser granules. Usually there are 8-9



Figures 29-32 *Vexaphorura robustiseta* sp. n.: (29) habitus and dorsal chaetotaxy; (30) postantennal organ and pseudocellus at base of antenna; (31) chaetotaxy of abdominal tergum I; (32) chaetotaxy of abdominal terga V-VI.



Figures 33-38 *Vexaphorura robustiseta* sp. n.: (33) labium, A – thickened labial papilla; (34) antennal III sense organ; (35) pseudocellus and surrounding setae on abdominal tergum V; (36) remnant of furca, and male ventral organ (reproductive male); (37) chaetotaxy of abdominal sterna II-VI; (38) tibiotarsal chaetotaxy and claw.

granules around each pseudocellus. Granular areas on abdominal tergum IV separated by 2 medial parallel rows of smaller granules.

Antennal III sense organ with 5 guard setae, 5 simple papillae, 2 small sensory rods and 2 smooth sensory clubs (Fig. 34).

Antennal segment IV with subapical organ and microsensillum located distinctly above the row of the posterior setae. Microsensillum of antennal segment III minute, situated lateral and slightly posterior to the antennal III sense organ (Fig. 34).

Postantennal organ in a cuticular groove with 2 acuminate border setae, consisting of 10-13 simple and bilobed vesicles arranged obliquely and parallel to the long axis of the organ (Fig. 30).

Pseudocelli 10/011/11111. Parapseudocelli absent

Labium A type with all 5 papillae (papilla A thickened and apically blunt) (Fig. 33).

Dorsal chaetotaxy well differentiated into microsetae and macrosetae. Macrosetae and most microsete relatively robust and always apically pointed. Head without seta  $d_0$ . Thoracic and abdominal terga without setae located outside areas coarse granulation. Abdominal tergum V with  $a_0$  seta, abdominal tergum VI with 2 medial setae. Thorax II-III with lateral microsensilla. Subcoxae with 4, 4, 5 setae. No setae between legs on pro-, mesoand metasternum. Ventral tube with 8+8 setae, without setae at base. Sensory setae invisible.

Male ventral organ consists of 5-6 thickened setae situated on the posterior edge of abdominal sternum III and 6 of the same kind on anterior edge of abdominal sternum IV (Fig. 36).

Claw without inner tooth. Empodial appendage shorter on inner edge of the claw, without basal lamella (Fig. 38). Distal whorl of setae on tibiotarsi symmetrical, with 11 setae.

Anal spines very strong on distinct basal papillae, weakly curved and about 2 times longer than the hind claw.

Type material. – Holotype is a reproductive male on slide; USA, Alaska, Bonanza Creek Exp. Forest; 8 VIII 1980, Betula/Alnus litter, leg. A. Fjellberg. 5 paratypes on 2 slides (2 unreproductive males, 3 females) same data as holotype (in the Illinois Natural History Survey collection, and in the collection of the Department of Systematic Zoology and Zoogeography, Wrocław University).

Other material. – 3 unproductive males, 4 females (on 7 slides); USA, Alaska, Bonanza Creek Exp. Forest; 8 VIII 1980, moss in white spruce forest, leg. A. Fjellberg.

Etymology. – The new species is named after the robust setae on the dorsal side of the body. The new genus name is derived from the Latin word "vexator" - tormentor.

## Key to genera of Hymenaphorurini

Within Onychiurinae the tribe Hymenaphorurini is characterized by absence of pseudocelli on the hind margin of the head and the lateral part of body. A key to the genera of Hymenaphorurini was presented in the Checklist of the Collembola (http://www.geocities.com/~fransjanssens/taxa/on ycinae.htm). We have decided to give a new key because of the description of four new genera in this paper. (Note: The tribe Hymenaphorurini probably also comprises the genus *Probolaphorura* Dunger, 1976 but we have not included it in the key because it needs redescription).

the key because it needs redescription).	
1.	Antennal III sense organ with 5 or 4 papilla, no papilla-like prominence
_	Antennal III sense organ with 5 papilla and
2.	additional papilla-like cuticular prominence 8 Abdominal tergum III with submedial pseudo-
2.	celli
-	Abdominal tergum III without submedial pseudocelli
3.	Furca reduced to two knobs with 3+3 (4+4)
	setulae, tenaculum present
	setulae posteriorly, tenaculum absent
4.	Antennal area with pseudocelli, body fusiform
_	
	of antennal area, body oval-elliptical
5.	
٦.	sent, antennal III sense organ with 4 guard
	setae
	(syn. Hymenaphorurodes Bagnall, 1949; syn. Sibirichiurus Stach, 1954)
	Labium with all 5 papilla (E present), antennal
	III sense organ with 5 guard setae
6.	
	um 0 type - with all 5 papillae apically pointed. Granular areas of abdominal tergum IV
	ed. Granular areas of abdominal tergum IV
	fused together midline into one plate
_	Body without parapseudocelli, labium A type -
	with papilla A thickened and apically blunt
	Granular areas on abdominal tergum IV sepa-
	rated by 2 medial parallel rows of smaller gran-
~	ules
7.	Furca reduced to a small depression with 2
	small, posterior setae, in contact with the bor-

der between abdominal sterna III and IV.

Vesicles in PAO compound. Chaetotaxy on

terga consists of two kinds of setae: blunt rod-

tion with 4 setulae arranged in one row or an

arch located in a middle part of sternum IV.

Vesicles in PAO of three kinds (simple, bilobed

or multilobed) located perpendicularly or

obliquely to the long axis of the organ. All setae apically pointed ....... Heteraphorura Bagnall, 1949 (syn. Subgenus: Japonychiurus Yosii, 1996)

like mesosetae and pointed microsetae.. Paronychiurus Bagnall, 1948 (syn. Ramonychiurus Stach, 1954) Furca reduced to a small area of fine granula-

- 8. Body without pseudocelli and parapseudocelli, with areas of stronger granulation. All setae apically pointed. Furca reduced to a small concavity without granulation with 2 setulae posteriorly. Tibiotarsi with 11 distal setae .....
- Pseudocelli absent. Body with parapseudocelli always located outside of areas of coarser granulation. Macrosetae rod-like and apically blunt. Furca reduced to a small concavity without granulation, with 4 setulae posteriorly arranged in one row. Tibiotarsi with 11 distal setae ...... Dinochiurus gen. n.
- Body with pseudocelli, parapseudocelli and areas of stronger granulation absent. All setae typical, apically pointed. Furca reduced to a small depression without granulation with 2 setulae posteriorly. Tibiotarsi with distal 9 setae ...... Arneria Pomorski 2000

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Comparative Zoology and Illinois Natural History Survey who made it possible to examine North American onychiurids material. Permission to collect invertebrates from Bair Cave was authorized under a Special Use Permit issued by the White River National Forest, U.S. Forest Service, with the help of Bill Kight.

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