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A new troglobiont species of Rhagidiidae (Acari: Eupodoidea) from cave sites in the Ural Mountains (Russia)

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Original research

ABSTRACT

A new troglobiont species, *Foveacheles uralensis* **n. sp.**, is described from the Gremutshaya, Rossiyskaya, and the Shulgan-Tash caves of the Ural Mountains. The new species is characterized by intermediate character states between the genera *Foveacheles* and *Traegaardhia* and its taxonomic position is discussed. The current state of the troglobiont and stygobiont arthropod fauna of the Ural Mountain caves is also discussed.

Keywords Acariformes; Prostigmata; *Foveacheles*; *Traegaardhia*; systematics; troglobionts **Zoobank** http://zoobank.org/AEEDBF76-3C11-438C-ACOF-DF3B23B17EF2

Introduction

The cosmopolitan family Rhagidiidae Oudemans, 1922 (Acari: Eupodoidea) currently includes 29 genera, one of which is in a fossil form (Zhang *et al.* 2011; Khaustov 2015). Rhagidiid mites inhabit soil, forest litter, mosses, lichens, etc. Many rhagidiid species are troglobionts, i.e., they live in caves. This group includes all representatives of the genera *Traegaardhia* Zacharda, 1980; *Troglocheles* Zacharda, 1980; *Elliotia* Zacharda, 1980; and *Flabellorhagidia* Elliott, 1976, as well as some species of the genera *Rhagidia* Thorell, 1872; *Foveacheles* Zacharda, 1980; *Robustocheles* Zacharda, 1980; and *Poecilophysis* Cambridge, 1876 (Zacharda 1980, 1985, 1987; Zacharda, Elliott 1981; Zacharda, Pugsley 1988; Walter *et al.* 2009; Zacharda *et al.* 2011). Some troglobiont species of Rhagidiidae are characterized by troglomorphism that is expressed in an unusually large quantity and size of rhagidial solenidia and unusually long legs (Zacharda 1980). Rhagidiid mites are predators of small arthropods and nematodes (Zacharda 1980).

The family Rhagidiidae on the territory of Russia is insufficiently studied. Zacharda (1983) described and recorded 13 species of Rhagidiidae from various regions of Russia: *Foveacheles* (*Foveacheles*) caucasica Zacharda, 1983; *F.* (*F.*) cegetensis Zacharda, 1983; *F.* (*F.*) brevichelae Zacharda, 1980; and Poecilophysis (Procerocheles) pseudoreflexa Zacharda, 1980 from Central Caucasus; *P.* (Soprocheles) pratensis (C.L. Koch, 1835) from Central Caucasus and Central Siberia; *P.* (Dentocheles) pratensis (C.L. Koch, 1835) from Central Siberia; Robustocheles (Robustocheles) mucronata (Willmann, 1936) from Central Siberia; *Robustocheles* (Robustocheles) mucronata (Willmann, 1936) from Central Siberia; Evadorhagidia bezdezensis Zacharda, 1980 from Central Siberia;

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(Canestrini, 1886) from Central Caucasus; *C. pittardi* Strandtmann, 1971, *Thoria uniseta* (Thor, 1909) and *Th. brevisensilla* Zacharda, 1980 from Central Caucasus and Central Siberia. Also, Makarova (2002) recorded *Robustocheles hilli* (Strandtmann, 1971) from the Severnaya Zemlya Archipelago, and *Hammenia macrostella* Zacharda, 1980 from the Taymyr Peninsula (Makarova 2015). Khaustov (2015) described a new genus and species, *Paracrassocheles clavisetosus* Khaustov, 2015, from Crimea. Troglobiont species of Rhagidiidae have never been described from Russia.

The genus *Foveacheles* is one of the largest in the family Rhagidiidae and currently comprises 34 species grouped into 10 subgenera and one species group (Zacharda 1996, 2000). The subgenera *Hirschmanniella* Zacharda, 1980, *Proxistella* Zacharda, 1980, *Spelaeocheles* Zacharda, 1988, *Trofocheles* Zacharda, 1982, and *Usitorhagidia* Zacharda, 1980 include troglobiont species (Zacharda 1980, 1982, 1988).

This paper presents the first description of a troglobiont species, *Foveacheles uralensis* **n. sp.**, from three caves located in the Ural Mountains of Russia.

Material and methods

Mites were collected by hand inside the caves and immediately fixed in 96% alcohol. The collected mites were mounted in Hoyer's medium. The notations for the prodorsal and leg setae follow those of Lindquist and Zacharda (1987) and Baker (1995), while the remaining nomenclature is that applied to eupodoids by Baker (1990). All measurements are given in micrometers (μ m) for the holotype; paratypes were not measured because their soft bodies are strongly damaged. In the descriptions of leg setation, the number of solenidia is given in parentheses (μ m). Mite morphology was studied using a Carl Zeiss Axio Imager A2 compound microscope with phase contrast and DIC optics, as well as a Bioptic C-400 microscope with DIC optics. Photomicrographs were taken with an AxioCam ICc5 digital camera.

Photographs of the live specimens of *Foveacheles uralensis* **n. sp.** were made using a Sony Alpha NEX-5T digital camera equipped with a Sony E 3.5/30 MACRO lens.

The distribution map (Fig. 1) was created using Google Earth Pro (ver. 7.3.4.8248) and Adobe Photoshop CS6 (ver. 13.0.1.3).

Systematics

Family Rhagidiidae Oudemans, 1922

Genus Foveacheles Zacharda, 1980

Type species: Foveacheles osloensis (Thor, 1934), by original designation

Foveacheles uralensis n. sp.

Zoobank: 4862C3D6-E3C8-44FA-A0A3-BC184B30E6B7 (Figures 2–11)

Description

Female — Body white in color (Fig. 11). Length of idiosoma 1340, width 560.

Idiosoma (Figs 2A, B). Cuticle finely striated. All dorsal and ventral setae uniform in shape, densely pilose. Trichobothria *sc1* thin, with large barbs; setae *v1* situated in bothridia on welldeveloped anteriorly rounded naso. Transverse furrow visible posteriad setae *f1* and *f2*. Setae *f2* present. Lyrifissures *ia* situated posterolaterally to bases of setae *c1*; *im* situated posterolaterad bases of setae *d*; *ip* situated anterolaterad bases of setae *f2*; *ih* located anterolaterally to setae *ps3*. Three pairs of pseudanal, one pair of adanal, five pairs of both aggenital and genital setae present. Epimeral formula: 3-1-5-3; in some specimens coxisternal fields I and III with



Figure 1 The distribution of Foveacheles uralensis n. sp. in the caves (yellow circles) of the Urals.

asymmetrical presence of four and six setae, respectively (Fig. 6A). Progenital chamber with two pairs of large, oval genital papillae and well-developed ovipositor with numerous eugenital setae. Lengths of idiosomal setae: *v1* 102, *v2* 65, *sc1* 145, *sc2* 195, *c1* 80, *c2* 187, *d1* 80, *e1* 77, *f1* 123, *f2* 77, *h1* 180, *h2* 107, *ps1* 148, *ps2* 95, *ps3* 65, *ad* 64, *1a* 53, *1b* 62, *1c* 73, *2b* 79, *3a* 34, *3b* 72, *3c* 84, *3d* 135, *3e* 125, *4a* 49, *4b* 67, *4c* 74, *ag1* 52, *ag2* 45, *ag3* 47, *ag4* 45, *ag5* 42, *g1* 37, *g2* 36, *g3* 28, *g4* 23, *g5* 35.

Gnathosoma (Figs 3, 7A). Integument papillate. Subcapitulum (Fig. 3C) roughly triangular, with two pairs of smooth adoral setae (*or1-2*), located subapically; subcapitular setae *sbc1-2* densely pilose, located at level of proximal margin of palp trochanters; labrum (LS) acuminate; external malae (EM) weakly sclerotized, with several small projections. Lengths of subcapitular setae: *sbc1* 97, *sbc2* 51, *or1* 85, *or2* 89. Chelicera (Fig. 3A) 410 in length; length of movable digit 155. Movable digit with smooth inner margin. With lyrifissure-like structure located near articulation of movable digit with fixed digit. Seta *chb* situated dorsolaterally in shallow depression (Fig. 7A), seta *cha* situated dorsally at level of articulation of movable digit with fixed digit; tip of fixed digit with three short cusps. Palps (Fig. 3B) with supracoxal seta *ep* smooth, baculiform. Length of palp 405. Palp setation: Tr 0, FeGe 2 (*dFe*, *dGe*), Ti 3 (*d*, *l'*, *l''*), Ta 10 (1) (*d*, *l'*, *l''*, *acm*, *sl''*, *p'*, *p''*, *v'*, *ba*, ω). All palpal setae densely pilose; solenidion ω small, rod-like.

Legs (Figs 4, 5, 7B–F). Lengths of legs: leg I 1470, leg II 1050, leg III 1160, leg IV 1415. All leg setae densely pilose. Tarsal claws with large basal clawlets (Fig. 7F). Distal part of claws on tarsi II-IV weakly sclerotized, distinctly flattened and rounded in dorso-ventral aspect. Leg I (Figs 4A, B, 7B): Supracoxal setae *el* of the same shape and length as palpal supracoxal setae *ep*. Femur completely divided into basi- and telofemur. Leg setation: Tr 1 (v'), Fe 5+5 (*d*, *l'*, *l''*, v', v'', *d1*, *l'1*, *l''1*, v''1, *bv''*), Ge 11(1 σ) (*d*, *l'*, *l''*, v', v'', *d1*, *l'1*, *l''1*, v'1, *l'2*, *l''2*, σ), Ti 11(2 ϕ) (*k*, *d*, *l'*, *l''*, v', *v''*, *l'1*, v'1, v'1, v'2, v''2, ϕ 1, ϕ 2), Ta 19(4 ω , ε) (*p'*, *p''*, *it'*, *it''*, *tc'*, *tc''*, *ft'*, *ft''*, *pl''*, *u'*, *u''*, *pv'*, *vv''*, *v''*1, *v''*2, *v''2*, *v'*3, ε , ω 1- ω 4). Rhagidial organ I with four rhagidial solenidia arranged obliquely in separate pits; famulus ε (stellate seta) located near the base of rhagidial solenidion ω 2 (Fig. 7B). Rhagidial solenidion ϕ 1 situated in





shallow depression just posterolaterad seta k; small erect solenidion φ^2 located dorsodistally, posteromesad rhagidial solenidion φ^1 at level of seta l' (Fig. 7D). Small erect solenidion σ on genu located anteroventrally, almost at level of seta (l). Leg II (Figs 4C, D, 7C, E): Femur incompletely divided into basi- and telofemur. Leg setation: Tr 1 (v'), Fe 6+5 (d, l', l'', v', v'', d1, l'1, l''1, v'1, v''1, bv''), Ge 9(1 σ) (d, l', l'', v', v'', l'1, l''1, v'1, l'2, σ), Ti 8(2 φ) (d, l', l'', v', v'', l'1, l''1, v'1, φ^1 , φ^2), Ta 16(4 ω , ε) (p', p'', it', it'', tc', tc'', ft', ft'', pl', u', u'', pv', pv'', v'1, v''1, v'2, ε , $\omega 1$ - $\omega 4$). Rhagidial organ II with four rhagidial solenidia arranged obliquely in separate pits; spiniform famulus ε located laterad basal part of rhagidial solenidion $\omega 1$ (Fig. 7C). Dorsodistal rhagidial solenidion φ 1 large, lanceolate, situated in deep depression with large dorsal opening (Fig. 7E); small erect solenidion φ 2 located anteroventrally, almost at level of seta v'. Leg III (Figs 5A, B, 6B, 7C): Leg setation: Tr 2 (l', v'), Fe 4+4 (d, l', l'', v', d1, l'1, v'1, ev'), Ge 7 (1 σ) (d, l', l'', v', v'', l''1, v'1, σ), Ti 7 (2 φ) (d, l', l'', v', v'', l'1, v'1, φ 2, Ta 14 (p', p'', it', it'', tc', tc'', ft', u'', u'', pv', pv'', v'1, v''); femur completely divided into basi- and telofemur; erect solenidia φ 2 very small, located dorsomedially, distance between bases of solenidia variable (Fig.



Figure 3 Foveacheles uralensis n. sp., female: A – left palp, dorsolateral aspect; B – chelicera, antiaxial aspect; C – subcapitulum, ventral aspect.

6B); one female paratype with only one solenidion on tibia III. Small erect solenidion σ on genu located ventrodistally, slightly anteriad seta v'. Leg IV (Fig. 5C, D): Leg setation: Tr 2 (v', v"), Fe 3+4 (d, l', l", v', d1, v'1, ev'), Ge 6 (d, l', l", v', v", l"1), Ti 7 (1 φ) (d, l', l", v', v", l'1, v'1, φ), Ta 14 (p', p", it', it", tc, ft', ft", u', u", pv', pv", v'1, v"1, v'2); femur completely divided into basi- and telofemur. Minute erect solenidion φ situated middorsally.

Male — Differs from female in having elongate sperm sac typical for rhagidiids, as illustrated for *F. halltalensis* Zacharda, (2000, Fig. 4A).

Deutonymph — (Figs 8–10). In general similar to adults with the following differences: three pairs of aggenital and two pairs of genital setae; eugenital setae absent; rhagidial organs I and II with three oblique solenidia each; famulus ε on tarsus I located near basal part of solenidion ωI ; basifemur I with five setae (v'I absent); genu I with 10 setae (v'I absent); tibia I with 10 setae (l'I absent); genu II with eight setae (v'I absent); tibia III with one solenidion.

Other stages unknown.

Type material

Holotype female, slide N° T-Rhag-1, Russia, Chelyabinsk Oblast, Gremutshaya Cave, ca. 56°17′ N 59°18′ E, 03 January 2024, collected by E.V. Lyubavina and L. Pshennikova. Paratypes: one female and one male, same data; one deutonymph and three females, Russia, the Republic of Bashkortostan, Shulgan-Tash Cave, ca. 53°03′ N 57°04′ E, 19 February 2018, collected by O.Ya. Chervyatsova; two males and one female, Russia, Perm Krai, Rossiyskaya Cave, ca. 58°49′ N 57°37′ E, 12 December 2020, collected by P.V. Somchenko.



Figure 4 Foveacheles uralensis n. sp., female: A - right leg I, dorsal aspect; B - right leg I, ventral aspect; C - left leg II, dorsal aspect; D - left leg II, ventral aspect.



Figure 5 Foveacheles uralensis n. sp., female: A – right leg III, dorsal aspect; B – right leg III, ventral aspect; C – right leg IV, dorsal aspect; D – right leg IV, ventral aspect.



Figure 6 Foveacheles uralensis **n. sp.**, female: A – specimen with an abnormal number of setae on coxisternal fields I and III (arrows point at additional setae); B – variability in the location of solenidia on tibia III.

Type deposition

The holotype and one paratype deutonymph, along with four female and two male paratypes are deposited in the mite collection of the Zoological Institute of RAS, St. Petersburg, Russia; one female and one male paratype are deposited in the mite collection of the Tyumen State University Museum of Zoology, Tyumen, Russia.

Etymology

The name of the new species refers to its geographical distribution, i.e., the caves of the Ural Mountains.

Differential diagnosis

The new species is placed in the genus *Foveacheles* as it possesses: filiform trichobothria; chelicerae that have, in lateral aspect, a distinct dorsal saddle-shaped depression, the fixed digit with a soft, sharp dorsal ridge at the base of which seta *chb* is inserted dorsolaterally in a shallow depression (Fig. 3B, 7A), and dorsal *cha*; rhagidial organs I and II with four rhagidial solenidia and, respectively, a stellate and spiniform famulus, and the epimeral formula 3-1-5-3 (Zacharda 2000).

Foveacheles comprises 10 subgenera and one species group (Zacharda 1996, 2000).

According to the key to the subgenera and their species (Zacharda 1996), the new species does not match any subgenus. In the presence of four rhagidial solenidia in each of the rhagidial organs (I and II) and erect solenidia $\varphi 2$ on tibiae I and II, the new species is similar to the species from the subgenera *Proxistella* Zacharda, 1980, *Usitorhagidia* Zacharda, 1980, and *Foveacheles* Zacharda, 1980. It differs from the representatives of these subgenera in having the epimeral formula 3-1-5-3 (vs. 3-1-6-3 in the aforementioned subgenera). The new species differs from all subgenera in having solenidion $\varphi 2$ on tibiae I and II located dorsodistally, just posteriad solenidia $\varphi 1$ (vs. solenidia $\varphi 2$ on tibiae I and II located dorsomedially in the other



Figure 7 DIC photomicrographs of *Foveacheles uralensis* **n. sp.**, female: A – distal part of fixed digit with setae *cha* and *chb*, posterolateral aspect; B – rhagidial organ I, dorsal aspect; C – rhagidial organ II, dorsal aspect; D – distal part of tibia I, dorsal aspect; E – distal part of tibia II, posterolateral aspect; F – distal part of tarsus III, anterolateral aspect.





subgenera). The new species differs from the representatives of the subgenera *Foveacheles*, *Proxistella*, and *Hirschmannetta* in having solenidion φI on tibia II located in a deep depression with a small terminal pore in the aforementioned subgenera). The new species is most similar to the *gigantea* species group (Zacharda 2000) and the monotypic subgenus *Spelaeocheles* Zacharda, 1988 in having a lyrifissure-like structure on the fixed digit of the chelicera. Zacharda (2000) remarked that the chelicerae and rhagidial organs of another monotypic subgenus, *Hirschmannetta* Zacharda, 1980, are strikingly similar to those of the *gigantea* species group, but the presence of the cheliceral lyrifissure-like structure is yet to be confirmed. The new species differs from all species with a lyrifissure-like structure on the chelicerae in having solenidia $\varphi 2$ on tibiae I and II located dorsodistally, just posteriad solenidia $\varphi 1$ (vs. solenidia $\varphi 2$ on tibiae I and II located dorsomedially in the other species).

The new species is also similar to the representatives of the genus *Traegaardhia* Zacharda, 1980 in general appearance (discussed further below) and ecology (all species of *Traegaardhia* are troglobionts). Among *Traegaardhia*-species, the new species is most similar to *T. dis*-tosolenidia Zacharda, 2010 in having solenidia $\varphi 2$ on tibiae I and II located dorsodistally. The new species differs from *T. distosolenidia* in having four obliquely aligned solenidia in the rhagidial organ II (vs. three solenidia arranged in tandem in *T. distosolenidia*).

Discussion

In the key to the genera of Rhagidiidae (Zacharda 1980), the genera *Foveacheles* and *Traegaard*hia were separated at the couplet concerning two character states: 1) the number of aggenital setae (6-7 pairs in *Traegaardhia* and 5 pairs in *Foveacheles*), and 2) the shape of the insertion pit of solenidion φl on tibia II (longitudinally opened in *Traegaardhia* and in a deep insertion





pit with terminal pore in Foveacheles). However, Zacharda et al. (2010), in the revision of the genus Traegaardhia, redescribed the type species Traegaardhia dalmatina (Willmann, 1939) with solenidion φI on tibia II in a deep depression with a small terminal pore. Solenidion φI on tibia II in the other species described was either of the latter form or recessed in a deep pit with an elongated, broadly open surface pore. The above authors also described several new species with five pairs of aggenital setae. Zacharda et al. (2010) noted that the genera Foveacheles and Traegaardhia are very similar; in fact, he even moved a couple of troglobiont species from Foveacheles to Traegaardhia. According to the latest diagnosis of the genus Traegaardhia (Zacharda et al. 2010), the main differences between Traegaardhia and Foveacheles are as follows: "Traegaardhia species have the cheliceral digits elongated and attenuated, the distal cheliceral seta is inserted laterodorsally in a weakly expressed depression (as seen in lateral aspect); in Foveacheles species the distal cheliceral seta is also inserted laterodorsally but in the distinct, well-developed, distally bounded and proximally open depression, and the cheliceral digits are usually much shorter and thick". The length and width of the cheliceral digits is a subjective character which is difficult to apply at generic level. However, the location of the cheliceral seta *chb* in the new species is, undoubtedly, as in the genus *Foveacheles*. In view of the variability, and sometimes overlapping, of character states within each genus, the generic boundary between the two genera warrants re-examination.

Not much is known about the ecology of *Foveacheles uralensis* **n. sp.** Most often, *F. uralensis* specimens were found in the aphotic parts of caves, on the surfaces of microponds. Springtails (Hexapoda: Collembola) are noted among its food items (see Fig. 11).

In accordance with recent reviews of the cave biota of Russia (Turbanov *et al.* 2016a, b, c; Golovatch *et al.* 2018) the core of the cave fauna of the Urals consists of a variety of troglophile and trogloxene elements. At the same time, the fauna of the caves of the Urals is significantly depleted in specialized stygobionts and troglobionts in comparison with those of Crimea, the



Figure 10 Foveacheles uralensis n. sp., deutonymph: A – right leg I, dorsolateral aspect; B – right leg II, posterolateral aspect; C – right leg III, anterolateral aspect; D – right leg IV, dorsal-posterolateral aspect.



Figure 11 Live Foveacheles uralensis n. sp. (in situ) in the Shulgan-Tash Cave, attacking springtail Plutomurus baschkiricus (Skorikow, 1900). Photo by Olga Ya. Chervyatsova.

Caucasus, and the Far East of Russia. Thus, among stygobionts, the only species known is the amphipod *Uralocrangonyx chlebnikovi* Borutzky, 1928 (Amphipoda: Crangonyctidae) from caves in the Perm Region (Borutzky 1928; Marin, Palatov 2022); and among the known troglobiont springtails (Collembola), *Philotella olgae* Kniss and Thibaud, 1995 (Poduromorpha: Neanuridae), *Ceratophysella kapoviensis* (Babenko, 1994), *Schaefferia baschkirica* Kniss, 1985 (Poduromorpha: Hypogastruridae), *Plutomurus baschkiricus* (Skorikow, 1900) (Entomobryomorpha: Oncopoduridae), and *Sericeotoma knissi* Potapov, 1991 (Entomobryomorpha: Isotomidae) from caves in the Republic of Bashkortostan (Skorikow 1900; Kniss 1985; Potapov 1991; Babenko *et al.* 1994; Kniss and Thibaud 1995). Also, the presence of the troglobiont *Foveacheles* sp. – described in this paper as a new species – has been repeatedly indicated in the Shulgan-Tash Cave (Bashkortostan) (Abdullin *et al.* 2012; Kapralov 2015; Turbanov *et al.* 2016b; Golovatch *et al.* 2018; Lyakhnitsky, Chervyatsova, 2019). Among other Rhagidiidae, *Rhagidia breviseta* Zacharda, 1995 and *Rhagidia* sp. were cited as troglophiles for caves in the Ural Mountains of Bashkortostan (Kniss 1984; Kapralov 2015). However, in regards to the latter statement, the record of *R. breviseta* is doubtful because it was originally described from caves in the Nearctic region, and troglobiont species of Rhagidiidae are usually endemic for the region.

The reason for rather impoverished troglobiont fauna of the Urals lies in the global climatic changes associated with the glacial and interglacial periods. The above notion stems from the fact that the most likely sources of terrestrial troglobiont fauna consisted of forest litter inhabitants, as well as soil invertebrates, including those sheltering under rocks and in rock crevices. During periods of cold weather and ice sheet formation, a number of species found refuge in karst cavities where the temperature regime is more stable (a kind of refugium). Having penetrated caves and acquired specific adaptations, organisms became specialized (troglobionts, stygobionts) and began to occupy their ecological niches (Jeannel 1959, 1965; Vandel 1964; Birstein, Ljovuschkin 1967).

Recent studies in the Ural Mountain caves based on calcite dating (Dublyansky *et al.* 2018, 2021) have shown that in the Late Pleistocene (ca. 0.078-0.010 Ma) the growth of speleothems in caves ceased, which is associated with the spread of permafrost in northern Eurasia at this time. In our opinion, the beginning of this Late Pleistocene glaciation has provoked the ancestral terrestrial form of *Foveacheles uralensis* **n. sp.** –inhabiting the Urals in the interglacial period– to go into caves in search of stable suitable habitat conditions. This also explains the occurrence of the same species in caves over such a vast area, from the Middle to the Southern Urals – ca. 670 km from north to south (see Fig. 1). The temporally insignificant allopatric isolation of a number of cave populations seems insufficient for species divergence. However, this problem can be more reliably addressed by molecular genetic analysis.

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References

Abdullin Sh.R., Kapralov L.I., Kuzmina L.I., Ryss A.Yu., Snitko V.P., Chervyatsova O.Ya., Chertoprud E.S. 2012. The biota of Shulgan-Tash (Kapovaya) Cave: A popular science essay. Shulgan-Tash Reserve, Irgizly. 25 pp [in Russian]. Babenko A.B., Potapov M.B., Stebaeva S.K., Chernova N.M. 1994. Keys to Collembola of the fauna of Russia and adjacent countries: Family Hypogastruridae. Moscow: Nauka. Pp. 336 [in Russian].

Baker A.S. 1990. A survey of external morphology of mites of the superfamily Eupodoidea Banks, 1894 (Acari: Acariformes). J. Nat. Hist., 24: 1227-1261. https://doi.org/10.1080/00222939000770741

Baker A.S. 1995. A redescription of *Halotydeus destructor* (Tucker) (Prostigmata: Penthaleidae) with a survey of ontogenetic setal development in the superfamily Eupodoidea. Int. J. Acarol., 21: 2 61-282. https://doi.org/10.1080/01647959508684069

Borutzky E.W. 1928. Materialien über die Fauna der unterirdischen Gewässer: Crangonyx chlebnikovi sp. n. (Amphipoda) aus den Höhlen der mittleren Urals. Zool. Anz., 77 (9-10): 253-259.

Birstein J.A., Ljovuschkin S.I. 1967. Some results and problem in studying of the subterranean fauna of the USSR. Zool. Zh., 46 (10): 1509-1535 [in Russian, with English summary].

Dublyansky Y., Moseley G.E., Lyakhnitsky Y., Cheng H., Lawrence Edwards R., Scholz D., Koltai G., Spötl C. 2018. Late Palaeolithic cave art and permafrost in the Southern Ural. Scient. Rep., 8 (1): 12080. https://doi.org/10.1038/s41598-018-30049-w

Dublyansky Y., Shirokov V., Moseley G.E., Kosintsev P.A., Lawrence Edwards R., Spötl C. 2021. ²³⁰Th dating of flowstone from Ignatievskaya Cave, Russia: Age constraints of rock art and paleoclimate inferences. Geoarchaeology, 36: 532-545. https://doi.org/10.1002/gea.21851

Golovatch S.I., Palatov D.M., Turbanov I.S., Kniss V.A., Gazaryan S., Snit'ko V.P., Decu, V., Juberthie Ch., Nazareanu G. 2018. Subterranean biota of the European part of Russia: A review. Invert. Zool., 15 (2): 153-213. https://doi.org/10.15298/invertzool.15.2.01

Jeannel R. 1959. Situation geographique et peuplement des caverns. Ann. Spéléol., 14: 333-338.

Jeannel R. 1965. Le genèse du peuplement des milieux souterrains. Rev. ècol. boil. sol, 2: 1-22. Kapralov S.A. 2015. Arthropods of caves in the European part of Russia and the Southern Urals. In:

Turbanov J.X., 2015. Artin I.N., Gongalsky K.B. (Eds.), Materials of the All-Russia Youth Conference (Biospeleology of the Caucasus and other regions of Russia», Moscow, December 3-5, 2015. Severtzov Institute of Ecology and Evolution of RAS, Papanin Institute of Biology of Inland Waters of RAS & Speleological Club «Zelenye Kamneyedy», P. 21-23 [in Russian].

Khaustov A.A. 2015. A new genus and species of the family Rhagidiidae (Acari: Eupodoidea) from Crimea. Int. J. Acarol., 41(7): 617-623. https://doi.org/10.1080/01647954.2015.1085899

Kniss V.A. 1984. On the fauna of karst caves of southeastern Bashkiria. Fauna and ecology of springtails (Collembola). Moscow: Nauka. P. 123-128 [in Russian].

Kniss V.A. 1985. Springtails of the genus Schaefferia (Collembola, Hypogastruridae) from caves of south-west Bashkiria. Zool. Zh., 64 (6): 934-937 [in Russian, with English summary].

Kniss V.A., Thibaud J.-M. 1995. Une nouvelle espèce de *Philotella* des grottes d'Oural du Sud (Collembola, Neanuridae, Pseudachorutidae). Rev. Fr. Entomol., 17 (2): 49-51.

Lindquist E.E., Zacharda M. 1987. A new genus and species of Rhagidiidae (Acari: Prostigmata) from Chihuahuan Desert litter in New Mexico. Can. J. Zool., 65: 2149-2158. https://doi.org/10.1139/z87-328 Lyakhnitsky Y.S., Chervyatsova O.Ya. 2019. Kapova Cave (Shulgan-Tash). Atlas of Russian caves.

Moscow: Russian Geographical Society, Russian Union of Speleologists. P. 421-429 [in Russian].

Makarova O.L. 2002. Acarocenoses (Acariformes, Parasitiformes) in polar deserts: 1. Mite assemblages of the Severnaya Zemlya Archipelado: structure of fauna and abundance. Entomol. Rev., 82 (7): 839-856.

Makarova O.L. 2015. 18.3. Acari. In: The Greenland Entomofauna. An Identification Manual of Insects, Spiders and their Allies (Böcher J. et al., eds). Leiden: Koninklijke Brill NV. P. 705-856.

Marin I.N., Palatov D.M. 2022. Uralocrangonyx gen.n. (Amphipoda: Crangonyctidae) from the Southern Ural, Russia. Arthr. Sel., 31 (2): 183-195. https://doi.org/10.15298/arthsel.31.2.07

Potapov M.B. 1991. Species of the genus *Isotoma* subgenus *Parisotoma* Bagnall, 1940 and *Sericeotoma* subgen. nov. (Collembola, Isotomidae) of USSR fauna. Acta Zool. Cracov., 34 (1): 267-301.

Skorikow A.S. 1900. On the systematics of the genus *Tomocerus* (Collembola) with description of a new species from Eastern Russia. Tr. Obshch. Ispyt. Prir. Khark. Univer., 35: 73-82 [in Russian].

Turbanov I.S., Palatov D.M., Golovatch S.I. 2016a. The present state of the art of biospeleology in Russia and the countries of the former Soviet Union: A review of the cave (endogean) invertebrate fauna.
1. Introduction - Crustacea. Zool. Zh., 95 (10): 1136-1159 [in Russian, with English summary]. https://doi.org/10.1134/S0013873816070162

- Turbanov I.S., Palatov D.M., Golovatch S.I. 2016b. The present state of the art of biospeleology in Russia and the countries of the former Soviet Union: A review of the cave (endogean) invertebrate fauna. 2. Arachnida - Acknowledgments. Zool. Zh., 95 (11): 1283-1304 [in Russian, with English summary]. https://doi.org/10.7868/S0044513416110064
- Turbanov I.S., Palatov D.M., Golovatch S.I. 2016c. The present state of the art of biospeleology in Russia and the countries of the former Soviet Union: A review of the cave (endogean) invertebrate fauna.
 Bibliography and summary. Zool. Zh., 95 (12): 1399-1426 [in Russian, with English summary]. https://doi.org/10.7868/S0044513416120187

Vandel A. 1964. Biospéologie. La Biologie des Animaux Cavernicoles. Paris: Gauthier-Villars. pp. 679. Walter D.E., Lindquist E.E., Smith I.M., Cook D.R., Krantz G.W. 2009. Order Trombidiformes In: Krantz

G.W., Walter D.E. (Eds.) A Manual of Acarology. Third Edition. Texas: Texas Tech University Press, Lubbock. p. 223-420.

Zacharda M. 1980. Soil mites of the family Rhagidiidae (Actinedida: Eupodoidea). Morphology, systematics, ecology. Acta Univ. Carol. Biol., 1978: 489-785.

Zacharda M. 1982. The cavernicolous fauna of Hawaiian lava tubes. 13. A new subgenus and two new species of Rhagidiidae (Acari: Eupodoidea). Pacif. Ins., 24(3-4): 275-280.

Zacharda M. 1983. The Rhagidiidae (Acarina: Prostigmata) from the central Caucasus, Siberia, and some other parts of the USSR. Věst. Čs. Společ. Zool., 47: 304-318.

Zacharda M. 1985. New Rhagidiidae (Acarina: Prostigmata) from caves of the U.S.A. Věst. Čs. Společ. Zool., 49: 67-80.

Zacharda M. 1987. New taxa of Rhagidiidae (Acari: Prostigmata) from Pyrenean caves. Can. J. Zool., 65(8): 2051-2056. https://doi.org/10.1139/z87-313

Zacharda M. 1988. *Foveacheles (Spelaeocheles) troglodyta* sp. n., subgen. n. (Acari: Prostigmata: Rhagidiidae) from Stratenska Cave, the Western Carpathians, Slovakia. Věst. Čs. Společ. Zool., 52: 73-78.

Zacharda M. 1996. New taxa of Rhagidiidae (Acari: Prostigmata) from North America. Part IV. Genus *Foveacheles* Zacharda, with a key to world species. Can. J. Zool., 74(2): 343-356. https://doi.org/10.1139/z96-042

Zacharda M. 2000. New species of the rhagidiid genus *Foveacheles* (Acari: Prostigmata: Eupodoidea) with a lyrifissure-like structure on the chelicerae. J. Nat. Hist., 34: 247-265. https://doi.org/10.1080/ 002229300299624

Zacharda M., Elliott W.R. 1981. New species of the family Rhagidiidae (Acarina: Actinedida: Eupodoidea) from California Caves. Acta Univ. Carol. - Biol., 30(9): 463-475.

Zacharda M., Fong D., Hobbs III H.H., Piva E., Slay M.L., Taylor S.G. 2010. A review of the genus *Traegaardhia* (Acari, Prostigmata, Rhagidiidae) with descriptions of new species and a key to species. Zootaxa, 2471: 1-64. https://doi.org/10.11646/zootaxa.2474.1.1

Zacharda M., Grafitti J., Piva E. 2011. New taxa of *Rhagidia* and *Foveacheles* (Acari: Prostigmata: Rhagidiidae) from Italian and French caves, with keys to adults of subgenera *Deharvengiella* and *Mediostella*. J. Nat. Hist., 45(11-12): 667-683. https://doi.org/10.1080/00222933.2010.535915

Zacharda M., Pugsley C.W. 1988. *Robustocheles occulta* sp.n., a new troglobitic mite (Acari: Prostigmata: Rhagidiidae) from North American caves. Can. J. Zool., 66(3): 646-650. https://doi.org/10.1139/288-096

Rhagidiidae) from North American caves. Can. J. Zool., 66(3): 646-650. https://doi.org/10.1139/z88-096
Zhang Z.-Q., Fan Q.-H., Pesic V., Smit H., Bochkov A.V., Khaustov A.A., Baker A., Wohltmann A., Wen T.-H., Amrine J.W., Beron P., Lin J.-Z., Gabrys G., Husband R. 2011. Order Trombidiformes Reuter, 1909. In: Zhang, Z.-Q. (Ed.), Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa, 3148: 129-138. https://doi.org/10.11646/zootaxa.3148.1.24