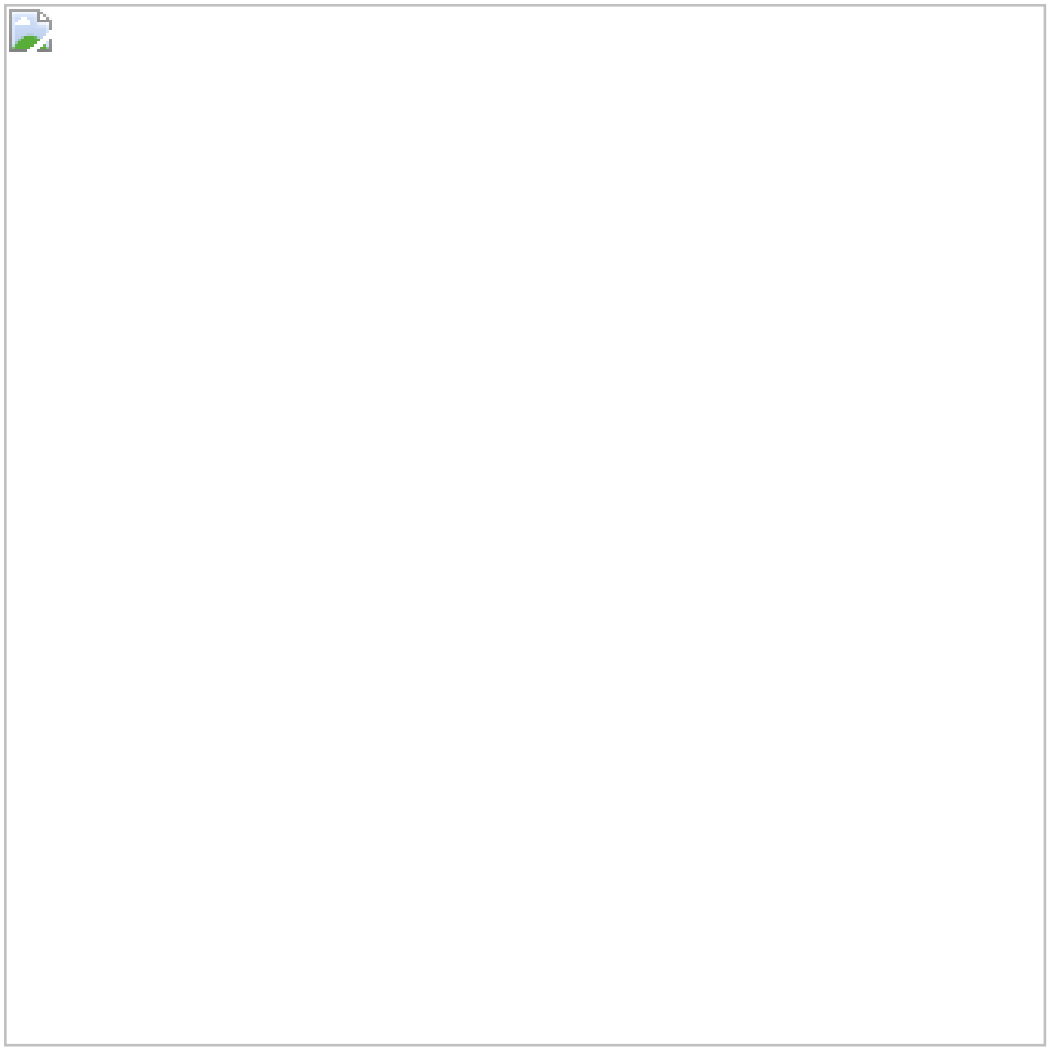

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Source: Systematic and Applied Acarology, 24(12) : 2409-2426

Published By: Systematic and Applied Acarology Society

URL: https://doi.org/10.11158/saa.24.12.9

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*Systematic & Applied Acarology* 24(12): 2409–2426 (2019) ISSN 1362-1971 (print)
http://doi.org/10.11158/saa.24.12.9 ISSN 2056-6069 (online)

Article http://zoobank.org/urn:lsid:zoobank.org:pub:F0ED8D90-EBBB-445C-AF21-B859515E4E8C

# Molecular and ontogeny studies clarify systematic status of *Chamobates borealis* (Acari, Oribatida, Chamobatidae): an integrated taxonomy approach

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## Abstract

*Chamobates borealis* (Trägårdh 1902) has been considered by some authors as a junior synonym of *Chamobates pusillus* (Berlese 1895). In this study we used an integrated taxonomy approach, comparing mitochondrial coding gene COI and morphological ontogeny of these species to clarify their systematic status. The Bayesian inference tree based on COI sequences of *C. borealis* and *C. pusillus*, as well as *C. birulai* (Kulczyński 1902), *C. bispinosus* Mahunka, 1987, *C. cuspidatus* (Michael 1884) and *C. rastratus* (Hull 1914) separated all these species. In terms of the morphology, the adults of *C. borealis* and *C. pusillus* have similar body size and shape, thin aggenital setae and two lateral teeth on the rostrum, but *C. borealis* has the medial incision between these teeth, which is absent in *C. pusillus*. The adults of these species differ also from each other by the shape of bothridial setae, size of area porose *Aa*, location of seta *lm* and lyrifissure *im*, and the shape of most setae on the hysterosoma. The morphological ontogeny of these species is similar, but the larva and nymphs of *C. borealis* differ from those of *C. pusillus* by the length of some prodorsal and gastronotal setae, and the nymphs of *C. borealis* have a humeral organ, which is absent in *C. pusillus*. The presence of a humeral organ in some *Chamobates* species supports a clade inferred by COI sequence data.

**Keywords:** oribatid mites, COI, phylogeny, morphology, juveniles

## Introduction

*Chamobates borealis* (Trägårdh 1902) was firstly described as *Notaspis cuspidatus borealis* Trägårdh, 1902, but this description, as well as a later redescription (Trägårdh 1910) were brief and concerned mainly the anterior part of the body, whereas the location of setae and porose areas on the notogaster were not indicated. Later, however, most authors (Shaldybina 1975; Karppinen & Krivolutsky 1982; Golosova *et al*. 1983; Schatz 1983; Marshall *et al*. 1987; Pavlichenko 1994; Bernini *et al*. 1995; Olszanowski *et al*. 1996; Niemi *et al*. 1997; Weigmann 2006; Siepel *et al*. 2009; Miko 2016; Murvanidze & Mumladze 2016) considered *C. borealis* as a separate species, whereas some (Mahunka and Mahunka-Papp 1995; Subías 2004, 2019; Bayartogtokh 2010; Weigmann *et al*. 2015; Arroyo *et al*. 2017) treated it as a junior synonym of *Chamobates pusillus* (Berlese 1895). According to Weigmann (2006), *C. borealis* has a medial incision between the two lateral teeth, while this incision is absent in *C. pusillus*. The adult of *C. borealis* has thin aggenital setae, and Subías (2004, 2019) included it in *Chamobates sensu stricto*, with 21 nominative species.

The morphological ontogeny—an often useful systematic and taxonomic data—of *C. borealis* has not been investigated, yet. Based on the catalogue of Norton and Ermilov (2014) and papers of

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Seniczak and Seniczak (2014) and Seniczak *et al*. (2018), the full ontogeny of six species of *Chamobates* is known, which constitutes a third of all species of this genus. These species are: *C. cuspidatus*, *C. pusillus*, *C. rastratus* (Hull 1914), *C. schuetzi* (Oudemans 1902), *C. subglobulus* (Oudemans 1900) and *C. voigtsi* (Oudemans 1902).

The aim of this paper is to clarify the systematic status of *C. borealis*, based on mitochondrial COI gene sequences and morphological ontogeny of this species, which was investigated in detail for the first time.

## Materials and Methods

*Sampling*

*Chamobates borealis* was collected in broadleaf forests in Norway, *C. pusillus* in a peatland in Ireland, from which the juveniles of this species were described previously (see Seniczak *et al*. 2018), while other species included in the phylogeny analyses originated from Norway and Greece (Table 1). Sampling was carried out during 2012–2018, in mainland Norway by Anna Seniczak, Steffen Roth and Per Djursvoll, in Svalbard by Steffen Roth, in Ireland by Anna Seniczak and Thomas Bolger, and in Greece by Stanislaw Seniczak and Stefanos Sgardelis. Samples of mosses, each of a volume of 500 $cm^3$, were collected by hand from the ground. Additionally, in order to study the ecology of *C. borealis*, several microhabitats (mosses from tree bark at ground level and 1.5 m above it, from stumps and dead tree trunks and dead wood) were sampled in one forest (Norway, Hordaland, Kvam: Mundheim, 60.155°, 5.896°, 97 m a. s. l., 8 June 2017). This was a low-herb deciduous forest dominated by gray alder [*Alnus incana* (L.) Moench], ash (*Fraxinus excelsior* L.), hazel (*Corylus avellana* L.), wych elm (*Ulmus glabra* Hudson) and birch (*Betula pendula* Roth), while the forest floor was mostly overgrown by mosses. The detailed habitat characteristics were presented earlier (Seniczak *et al*. 2019). Mites were extracted in Tullgren funnels for 14 days, because the samples were relatively large and originated from wet forest (Seniczak *et al*. 2019), and preserved in 90% ethanol.

*Studies of type material*

Type specimens of *C. borealis* (2 adults, slide label: "*Oribata cuspidata* var. *borealis*. Rör 3 Kårsonjuonje I.T-dh.", 1 adult, slide label:"*Oribata cuspidata* var. *borealis*. N01, 07 I.T-dh."), and one adult of *C. pusillus* collected by K.H. Forsslund in the type locality [label:"*Chamobates pusillus* (Berl.) ♀ K.-H.F. leg. det. Ital. Toscana, Vallombrosa 24.9.1961. mf. 1006"] were borrowed from the Swedish Museum of Natural History, Stockholm, Sweden. The type specimen from the Berlese collection (single specimen, slide 28/10) was not in a good condition to be studied, so instead the measurements and photographs of other material from the type locality from this collection (slides 68/11 and 12) were kindly provided by Dr. Roberto Nannelli (CREA-DC, Research Centre for Plant Protection and Certification, Florence, Italy).

*Molecular analyses*

Thirty-five specimens of six *Chamobates* species (Table 1) were analyzed. We used species of putatively close genera as outgroups, *Ceratozetes parvulus* Sellnick, 1922, *Euzetes globulus* (Nicolet 1855), *Fuscozetes fuscipes* (C.L. Koch 1844) and *Mycobates sarekensis* (Trägårdh 1910). Each specimen was photographed and the photos are the vouchers that are available at Barcode of Life Data System (BOLD, http://boldsystems.org/). The specimens were subsequently placed in a well containing 50 ml of 90% ethanol in a 96-well microplate, and send to the Canadian Centre for DNA Barcoding (CCDB). Mites were sequenced for the barcode region of the COI gene according to



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standard protocols at CCDB (CCDB 2019), using either LepF1/LepR1 (Hebert *et al.* 2003) or LCO1490/HCO2198 (Folmer *et al.* 1994) primer pairs. The DNA extracts were placed in archival storage at -80°C at the University Museum of Bergen (UiB). The sequences are available in GenBank (accessions numbers in Table 1).

**TABLE 1.** Information about specimens used in this study; labels correspond to specimen numbers in BOLD database.

| Species | Label | GeneBank access No | Locality | Coordinates | Sampling date |
|---|---|---|---|---|---|
| *Ceratozetes parvulus* Sellnick, 1922 | UMNFO593-18_*Ceratozetes parvulus* | MN520698 | NO: Hardanger, Finse | 60.59°N 7.51°E | 06.08.18 |
| *Chamobates bispinosus* Mahunka, 1987 | UMNFO012-18_*Chamobates bispinosus* | MN520673 | GR: Olympos Mtn. | 40.05°N 22.24°E | 25.06.15 |
| *C. birulai* (Kulczynski, 1902) | UMNFO198-18_*Chamobates birulai* | MN520691 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO108-18_*Chamobates birulai* | MN520672 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| | UMNFO109-18_*Chamobates birulai* | MN520692 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| *C. borealis* (Trägårdh, 1902) | UMNFO001-18_*Chamobates borealis* | MN520677 | NO: Kvam, Mundheim | 60.15°N 5.90°E | 08.06.17 |
| | UMNFO002-18_*Chamobates borealis* | MN520684 | NO: Kvam, Mundheim | 60.15°N 5.90°E | 08.06.17 |
| | UMNFO110-18_*Chamobates borealis* | MN520679 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| | UMNFO148-18_*Chamobates borealis* | MN520671 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| | UMNFO149-18_*Chamobates borealis* | MN520668 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| | UMNFO233-18_*Chamobates borealis* | MN520680 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO234-18_*Chamobates borealis* | MN520694 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO420-18_*Chamobates borealis* | MN520686 | NO: Bergen, Fløyen | 60.22°N 5.14°E | 15.06.18 |
| | UMNFO421-18_*Chamobates borealis* | MN520682 | NO: Bergen, Fløyen | 60.39°N 5.34°E | 15.06.18 |
| | UMNFO422-18_*Chamobates borealis* | MN520664 | NO: Bergen, Fløyen | 60.39°N 5.34°E | 15.06.18 |
| | UMNFO588-18_*Chamobates borealis* | MN520670 | NO: Bergen, Lydehorn | 60.37°N 5.24°E | 06.10.18 |
| | UMNFO589-18_*Chamobates borealis* | MN520695 | NO: Bergen, Lydehorn | 60.37°N 5.24°E | 06.10.18 |
| | UMNFO590-18_*Chamobates borealis* | MN520697 | NO: Bergen, Lydehorn | 60.37°N 5.24°E | 06.10.18 |
| | UMNFO591-18_*Chamobates borealis* | MN520681 | NO: Bergen, Lydehorn | 60.37°N 5.24°E | 06.10.18 |

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**TABLE 1.** (Continued)

| Species | Label | GeneBank access No | Locality | Coordinates | Sampling date |
|---|---|---|---|---|---|
| *C. cuspidatus* (Michael, 1884) | UMNFO019-18_*Chamobates cuspidatus* | MN520690 | NO: Kvam, Mundheim | 60.15°N 5.90°E | 08.06.17 |
| | UMNFO020-18_*Chamobates cuspidatus* | MN520687 | NO: Kvam, Mundheim | 60.15°N 5.90°E | 08.06.17 |
| | UMNFO023-18_*Chamobates cuspidatus* | MN520667 | NO: Kvam, Mundheim | 60.15°N 5.90°E | 08.06.17 |
| | UMNFO180-18_*Chamobates cuspidatus* | MN520685 | NO: Flekkefjord, Eide | 58.36°N 6.64°E | 10.06.17 |
| | UMNFO181-18_*Chamobates cuspidatus* | MN520661 | NO: Flekkefjord, Eide | 58.36°N 6.64°E | 10.06.17 |
| | UMNFO197-18_*Chamobates cuspidatus* | MN520662 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO239-18_*Chamobates cuspidatus* | MN520693 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO240-18_*Chamobates cuspidatus* | MN520675 | NO: Flekkefjord, Leirvik | 58.46°N 6.67°E | 10.06.17 |
| | UMNFO692-18_*Chamobates cuspidatus* | MN520674 | NO: Halden, Kjeøya | 59.09°N 11.22°E | 12.06.17 |
| *C. pusillus* (Berlese, 1895) | UMNFO004-18_*Chamobates pusillus* | MN520696 | IR: Leinster, Lullymore | 53.28°N 6.95°W | 09.12.14 |
| | UMNFO005-18_*Chamobates pusillus* | MN520683 | IR: Leinster, Lullymore | 53.28°N 6.95°W | 09.12.14 |
| | UMNFO006-18_*Chamobates pusillus* | MN520669 | IR: Leinster, Lullymore | 53.28°N 6.95°W | 09.12.14 |
| | UMNFO007-18_*Chamobates pusillus* | MN520678 | IR: Leinster, Lullymore | 53.28°N 6.95°W | 09.12.14 |
| | UMNFO008-18_*Chamobates pusillus* | MN520666 | IR: Leinster, Lullymore | 53.28°N 6.95°W | 09.12.14 |
| *C. rastratus* (Hull, 1914) | UMNFO693-18_*Chamobates rastratus* | MN520676 | NO: Halden, Kjeøya | 59.09°N 11.22°E | 12.06.17 |
| | UMNFO694-18_*Chamobates rastratus* | MN520663 | NO: Halden, Kjeøya | 59.09°N 11.22°E | 12.06.17 |
| *Euzetes globulus* (Nicolet, 1855) | UMNFO071-18_*Euzetes globulus* | MN520689 | NO: Kvam, Neshalvøya | 60.15°N 5.93°E | 08.06.17 |
| *Fuscozetes fuscipes* (Koch, 1844) | UMNFO277-18_*Fuscozetes fuscipes* | MN520688 | NO: Arendal, Verpåsen | 58.45°N 8.70°E | 10.06.17 |
| *Mycobates sarekensis* (Trägårdh, 1910) | UMNFO292-18_*Mycobates sarekensis* | MN520665 | NO: Svalbard, Longyearbyen | 78.19°N 15.59°E | 05.06.18 |

COI sequences (sequence length a ≥ 407 bp) were blasted against GenBank in order to detect and exclude possible contaminations. Sequence variation within *Chamobates* species and between-species was calculated in BOLD, using Kimura 2 Parameter distance model, pairwise deletion, and BOLD Aligner (Amino Acid based HMM).



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The sequences were aligned by eye in BioEdit v7.0.5 sequence alignment editor (Hall 2011). The search for the best fitting substitution model was carried out in PAUP* 4.0 a164 (Swofford 2002) using ModelTest (Posada & Crandall 1998). Phylogenetic Bayesian inference (BI) analysis was conducted in MrBayes 3.2 (Ronquist *et al.* 2012). Posterior probabilities were generated from Markov chain Monte Carlo (MCMMC) sampling over 10 million generations in two independent runs using 4 chains, HKY+I+G model (Hasegawa *et al.*1985) and 25% burn-in. The trace files generated by Bayesian MCMC runs were analyzed in Tracer v.1.6. (Rambaut & Drummond 2007) in order to assess chain convergence. After this step a 50% majority rule consensus tree was summarized from post burn-in trees and BI topologies were visualized in FigTree 1.4.2 (available at http://tree.bio.ed.ac.uk/software/figtree).

*Illustrations and photomicrographs*

Illustrations were prepared from individuals macerated in lactic acid, using the open-mount technique (Grandjean 1949). We measured total length (from tip of rostrum to posterior edge of notogaster) and width (widest part of notogaster without pteromorphs), and length of setae and some parts of the body of mites in μm. The illustrations of instars are limited to the body regions of mites that show substantial differences between instars, including the dorsal and lateral aspect of the larva, tritonymph and adult, some leg segments of these stages and ventral regions of all instars. Palp and chelicera of the adult are also illustrated. In the text and figures, we use the following abbreviations: rostral (*ro*), lamellar (*le*), interlamellar (*in*) and exobothridial (*ex*) setae, lamella (*La*), bothridium (*bo*), bothridial seta (*bs*), notogastral or gastronotal setae (*c*-, *d*-, *l*-, *h*-, *p*-series), lyrifissures or cupules (*ia*, *im ip*, *ih*, *ips*, *iad*), porose areas (*Aa*, *A1–A3*), opisthonotal gland opening (*gla*), pteromorph (*Ptm*), pedotecta (*Pd1*), tutorium (*Tut*), Claparède organ (*Cl*), subcapitular setae (*a*, *m*, *h*), genal tooth (*gt*), genal notch (*gn*), discidium (*Dis*), cheliceral setae (*cha*, *chb*), palp setae (*sup*, *inf*, *l*, *d*, *cm*, *acm*, *lt*, *vt*, *ul*, *su*) and solenidion ω, epimeral setae (*1a–c*, *2a*, *3a–c*, *4a–c*), adanal and anal setae (*ad*-, *an*-series), aggenital seta (*ag*), leg solenidia (σ, φ, ω), famulus (ε) and setae (*bv*, *ev, d*, *l*, *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl*, *v*). Terminology used follows that of Grandjean (1953, 1962) and Norton and Behan-Pelletier (2009).

For scanning electron microscopy (SEM), mites were fixed in 90% ethanol and placed on Al-stubs with a double-sticky carbon tape and coated with Au/Pd in a Polaron SC502 Sputter coater. Observations and micrographs were made with a ZEISS Supra 55VP scanning electron microscope.

## Results

*Molecular analyses*

The Bayesian inference tree based on COI sequences showed that *C. borealis* forms a separate clade from *C. pusillus* (Fig. 1). Each of the two taxa obtained maximum posterior probability and were separated from each other by other *Chamobates* species with high node support. The two species were separated by a minimum of 14.33% COI sequence divergence (Table 2), whereas intraspecific COI variation in any of the included *Chamobates* species did not exceed 3.77%.



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**TABLE 2.** COI-based maximum P-distances within *Chamobates* species (underlined) and minimum P-distances between species, na – only one specimen was available and it was not possible to calculate P-distance within species.

| Species | *C. birulai* | *C. bispinosus* | *C. borealis* | *C. cuspidatus* | *C. pusillus* | *C. rastratus* |
|---|---|---|---|---|---|---|
| *C. birulai* | 0.62 | 23.72 | 16.64 | 18.68 | 17.98 | 17.31 |
| *C. bispinosus* | - | na | 18.66 | 19.26 | 19.74 | 19.93 |
| *C. borealis* | - | - | 3.77 | 16.09 | 14.33 | 16.79 |
| *C. cuspidatus* | - | - | - | 1.08 | 17.33 | 18.71 |
| *C. pusillus* | - | - | - | - | 1.26 | 15.58 |
| *C. rastratus* | - | - | - | - | - | 0.19 |

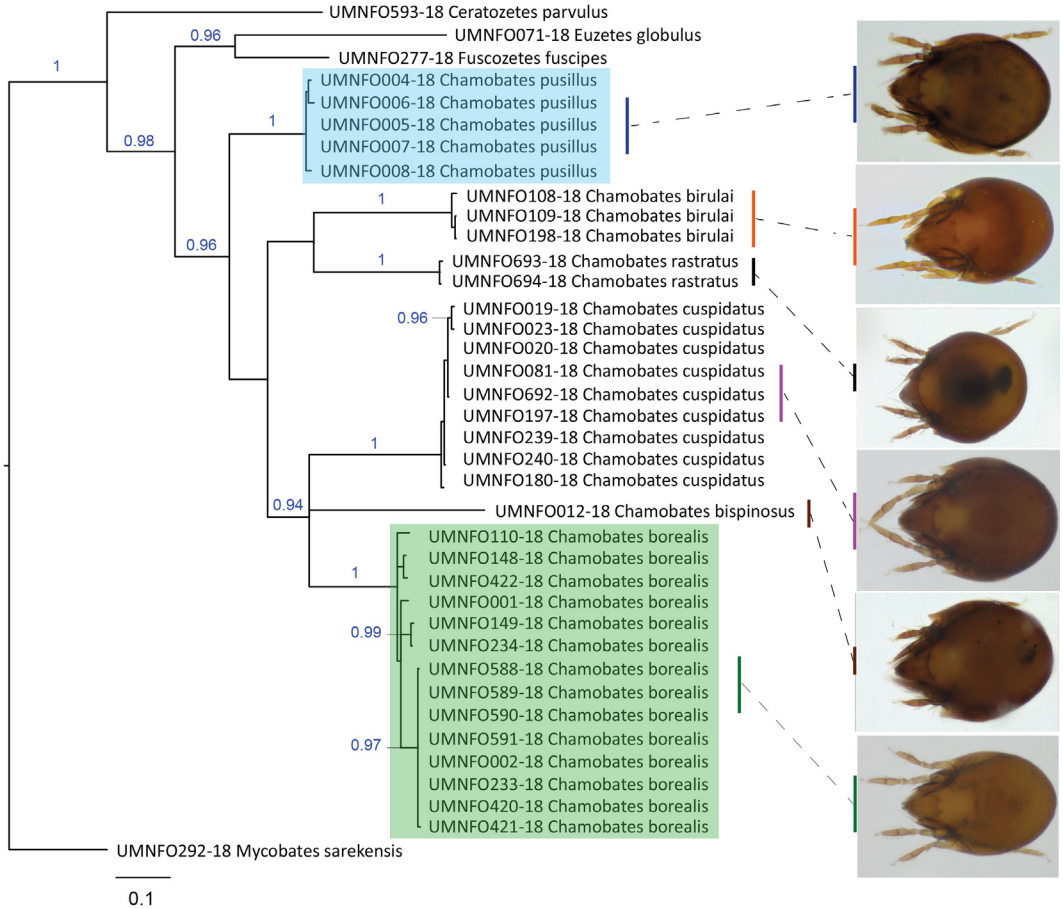


**FIGURE 1**. Bayesian inference tree based on COI sequences (658 bp). Specimen numbers correspond to BOLD database (http://boldsystems.org/) and the photographs are vouchers of the sequenced animals. Information about specimens used for sequencing with Gene Bank accession numbers are in Table 1. Node support values < 0.90 are not presented in the graph.



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## Systematics

### *Chamobates borealis* (Trägårdh, 1902)

(Figs. 2a, 2b, 3–12)

*Notaspis cuspidata* var. *borealis* Trägårdh, 1902.

*Oribata cuspidata* var. *borealis*: Trägårdh 1910.

*Chamobates borealis*: Shaldybina 1975; Karppinen and Krivolutsky 1982; Golosova *et al*. 1983; Schatz 1983; Marshall *et al*. 1987; Pavlichenko 1994; Bernini *et al*. 1995; Olszanowski *et al*. 1996; Niemi *et al*. 1997; Weigmann 2006; Siepel *et al*. 2009; Miko 2016; Murvanidze and Mumladze 2016.

*Chamobates schuetzi* (Oudemans 1902): Willmann 1931.

*Diagnosis*

Adult rather small (length 325–384, width 202–247; n= 60). Rostrum with medial incision and two lateral teeth. Bothridial seta clavate, finely barbed. Prodorsal seta *le* long, *ro* and *in* of medium size and *ex* short. Lamella well developed, cusp with outer tooth, translamella absent. Notogastral setae minute. Porose area *Aa* distinctly larger than other porose areas. Seta *lm* located posterior-medially to porose area *Aa* at distance equal to diameter of *Aa*. Lyrifissure *im* placed midway between seta *lm* and porose area *A1*. Aggenital setae thin, adanal and anal setae short.

Juveniles unpigmented. Gastronotal shield absent in larva, but present in nymphs, with 10 pairs of setae (*d*-, *l*-, *h*-series and $p_1$), setae $p_2$, $p_3$ and of *c*-series inserted on unsclerotized cuticle. In larva, seta *in* shorter than *ro*, seta *lp* almost two times longer than *la*, but of similar length as $h_1$. Humeral organ present only in nymphs. Gastronotal setae short in nymphs, except for longer $c_3$, *dp* and $h_1$.

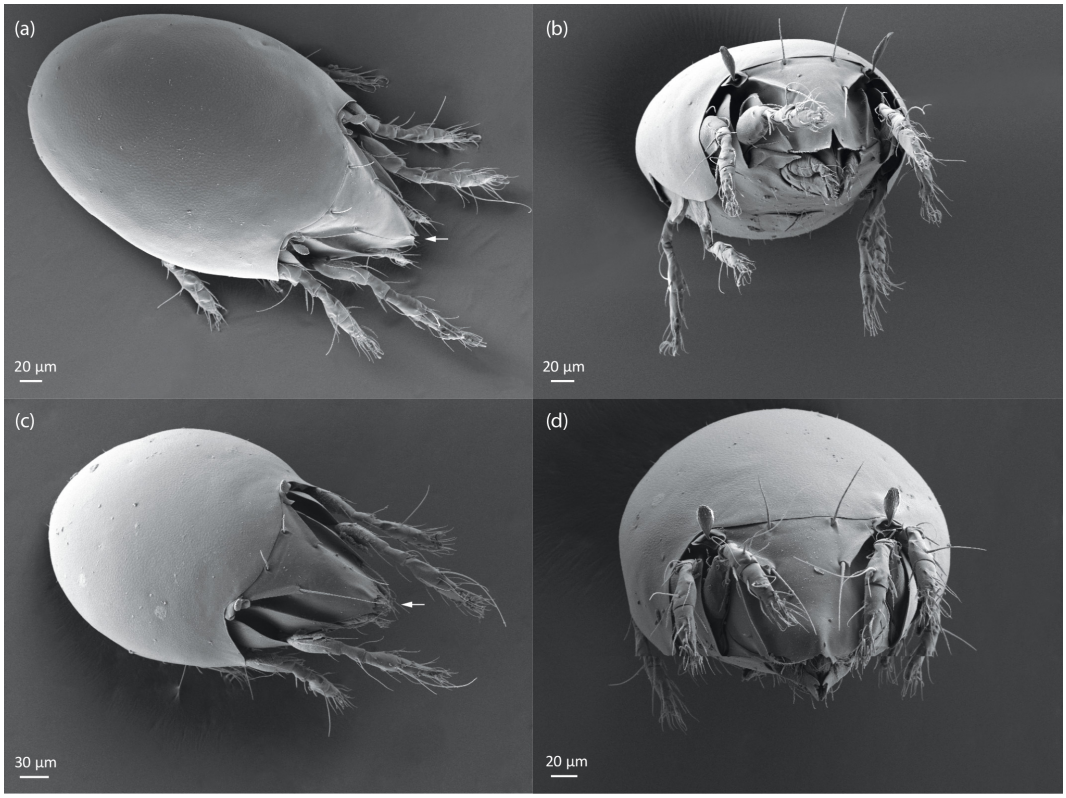


**FIGURE 2.** Adults of *Chamobates* species, SEM micrographs, arrow points differences in rostrum of species. (a) *C. borealis*, dorso-lateral aspect, (b) *C. borealis*, frontal aspect, (c) *C. pusillus*, dorso-lateral aspect, (d) *C. pusillus*, frontal aspect.



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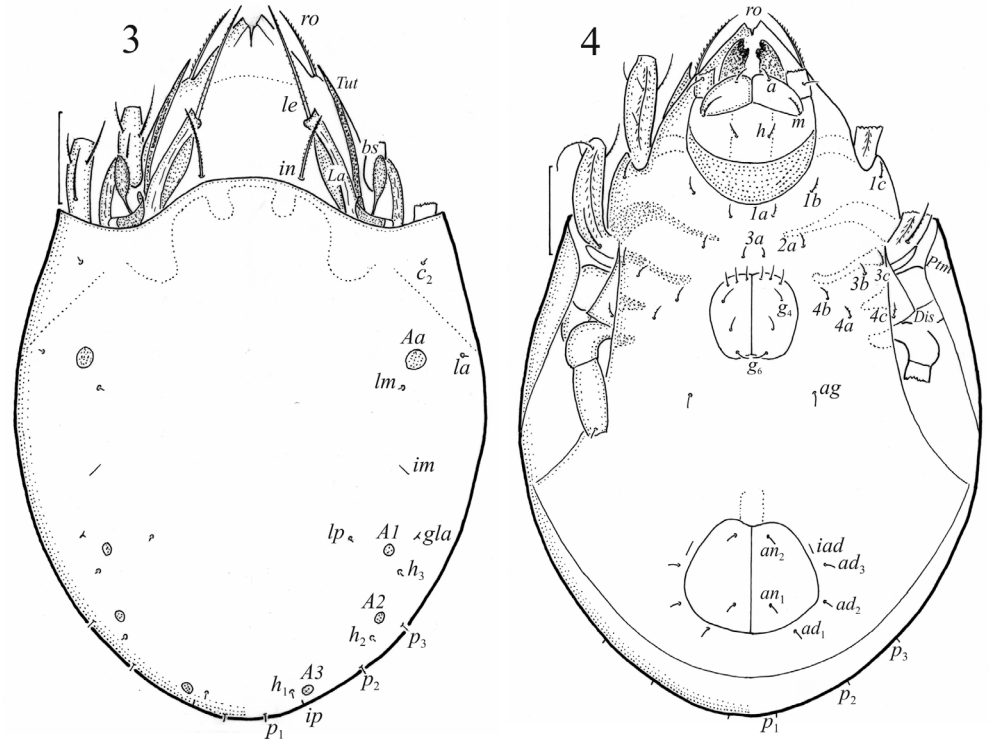


**FIGURES 3–4.** *Chamobates borealis*, female, legs partially drawn, scale bar 50 μm. 3. Dorsal aspect. 4. Ventral aspect.

## Description of morphological ontogeny

*Adult*

Morphology of adult (Figs. 2a, 2b, 3–6) similar to that investigated by Weigmann (2006), with triangular prodorsum and almost spherical, convex notogaster. Mean length of females 368.1 (range 356–384, n=30) and width 238.5 (228–247), and mean length of males 346.7 (range 325–358, n= 30) and width 209.4 (202–215). All notogastral setae minute. Porose area *Aa* rounded and larger than other porose areas. Seta *lm* located closer to *Aa* than seta *la*, lyrifissure *im* located midway between seta *lm* and *gla* opening. Cheliceral setae *cha* longer than *chb*, both barbed (Fig. 5b). Most palp setae barbed, except for smooth tarsal setae (Fig. 5c). Anteroventral apophysis on genua I and II absent, tibia I with anterodorsal apophysis (Fig. 6). Most leg setae with short barbs, setae *pv* and *s* on all tarsi with longer barbs. Formulae of leg setae [trochanter to tarsus (+ solenidia)]: I—1-5-3(1)-4(2)-20(2); II—1-5-3(1)-4(1)-15(2); III—2-2-1(1)-3(1)-15; IV—1-2-2-3(1)-12. Tarsi heterotridactylous.

*Juvenile stages*

Larva oval (Fig. 7a), unpigmented. Prodorsum subtriangular, prodorsal seta *ro* longer than *in* and *le* (Table 3), all barbed; seta *ex* short and smooth. Mutual distance between pair *le* about two times longer, and between pair *in* about three times longer than between pair *ro*. Setal pair *le* inserted closer to *in* than *ro*. Opening of bothridium rounded, bothridial seta clavate, with barbed head.



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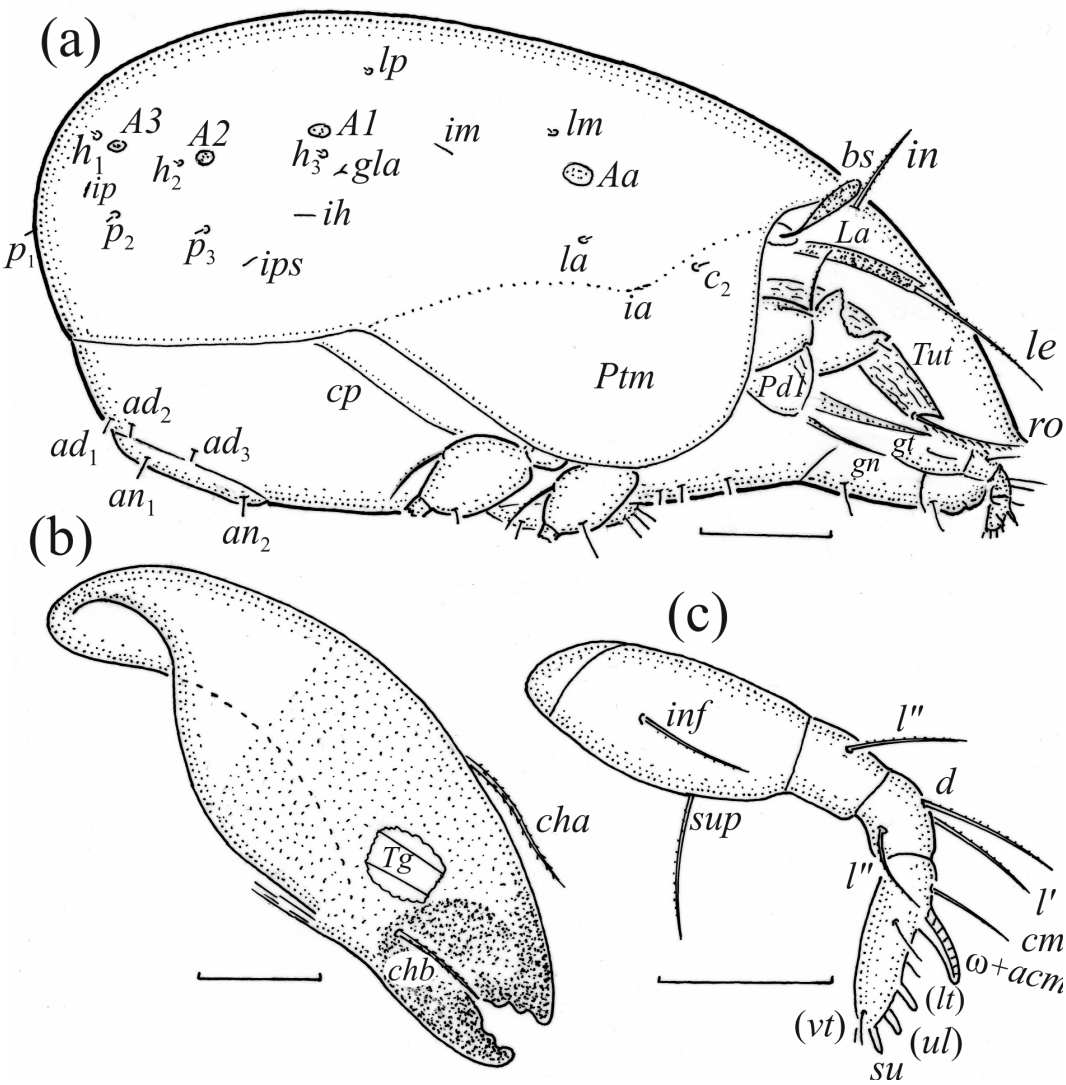


**FIGURE 5.** *Chamobates borealis*, female. (a) Lateral aspect, legs partially drawn, scale bar 50 μm; mouthparts, right side, scale bars 20 μm, (b) chelicera, (c) palp.

Gastronotum of larva with 12 pairs of setae, including $h_3$ inserted laterally to posterior part of anal valves (Figs. 8a, 9a); most of medium size (Table 3) and barbed, except for short and smooth $h_3$, length of setae increasing from anterior to posterior. Longer gastronotal setae darkly pigmented, except for light basal part (Fig. 7b). Gastronotal shield absent. Cupule *ia* located posterior to seta $c_3$, cupule *im* between setae *lm* and *lp*, cupule *ip* between setae $h_1$ and $h_2$, and gland opening anterolateral to seta *lp*. Anal valves (segment PS) glabrous (Figs. 8a, 9a).

Nymphs with relatively shorter prodorsum and slimmer bothridial seta than in larva, length of prodorsal setae increasing during ontogeny (Table 3). Gastronotum of protonymph with 15 pairs of setae because setae of *p*-series appear in protonymph (Fig. 8b), and remain in other nymphs (Figs. 10a, 10b). Gastronotal shield present, with 10 pairs of setae (*d*-, *l*-, *h*-series and $p_1$), setae $p_2$, $p_3$ and of *c*-series inserted on unsclerotized cuticle. Seta $c_3$ of medium size and barbed, other gastronotal setae short, except for slightly longer *dp* and $h_1$ (Table 3); longer setae with short barbs, other setae smooth (Fig. 11). Longer gastronotal setae dark pigmented, except for light basal part. In



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protonymph, one pair of setae appears on genital valves (Fig. 8b), and two pairs are added in deutonymph and tritonymph each (Figs. 10a, 10b); all short and smooth. In deutonymph, one pair of aggenital setae and three pairs of adanal setae appear and remain in tritonymph; all short and smooth. Anal valves of protonymph (segment AD) and deutonymph (segment AN) glabrous, but in tritonymph two pairs of small, smooth setae present (Fig. 10b). In nymphs cupules *ia* and *im* placed as in larva, cupule *ip* located between seta $h_2$ and $p_2$ (protonymph) or between $p_1$ and $h_2$ (other nymphs), cupule *iad* located lateral to anterior part of anal valves, cupules *ips* and *ih* displaced posterolateral and lateral to *iad* (Figs. 8a, 8b, 10a, 10b). Gland opening as in larva. Leg setae of tritonymph with short barbs or smooth (Fig. 12).

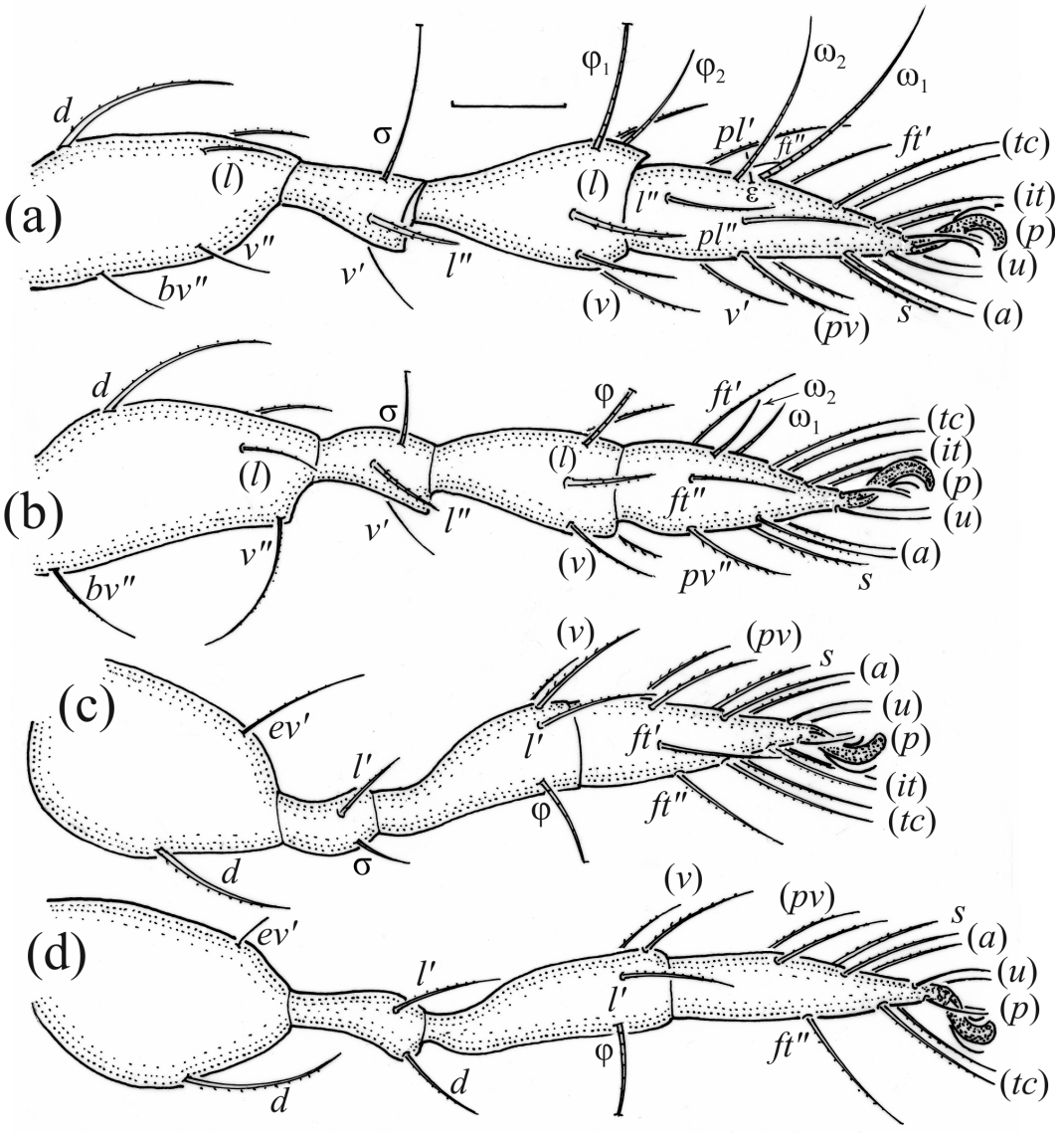


**FIGURE 6.** *Chamobates borealis*, leg segments of adult (femur to tarsus), right side, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, genu (*l′*); (b) leg II, genu (*l′*), tarsus (*pv′*); (c) leg III; (d) leg IV.



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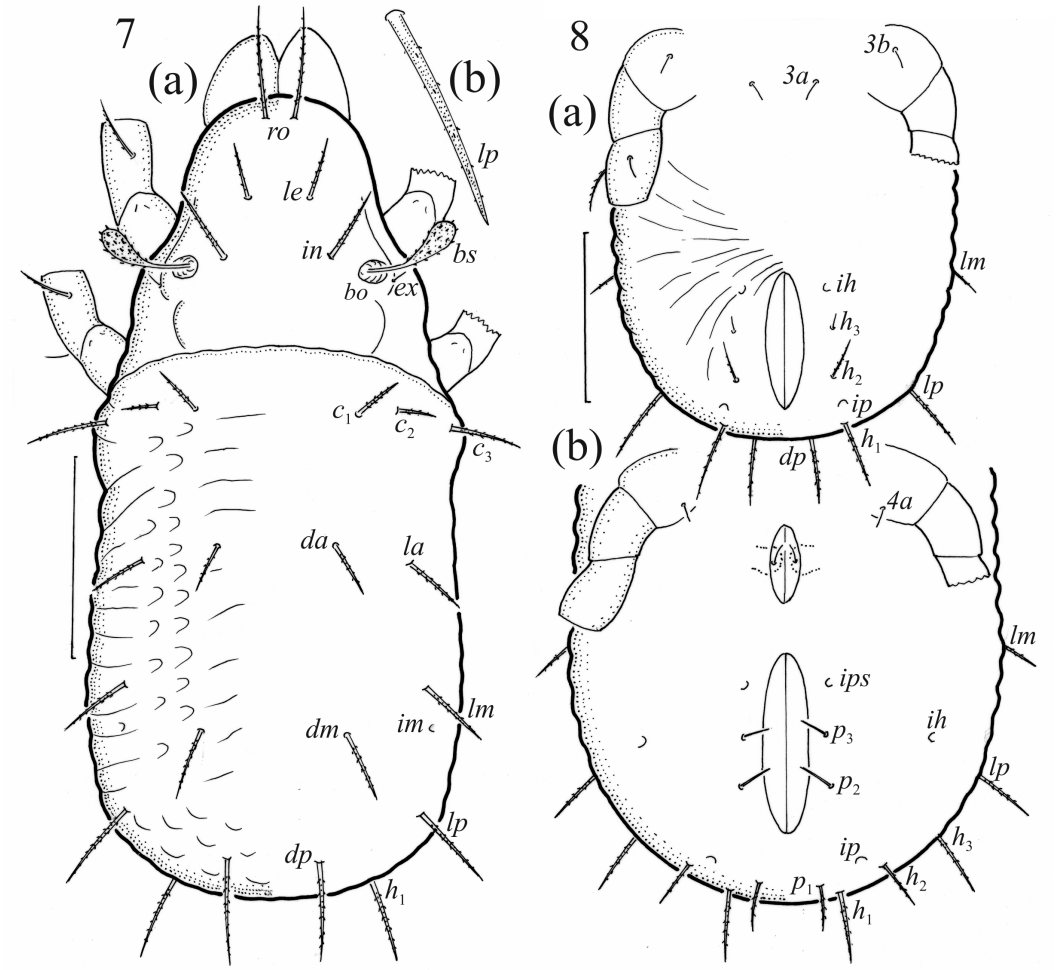
*Ontogenetic transformation*

The relative length of prodorsal setae *ro*, *in* and *le* changes during the ontogeny. In the larva, the longest of these three setae is *ro*, in the nymphs *in*, and in the adult *le*. In all instars, seta *ex* remains short. The opening of bothridium is rounded in all instars, but in the adult it is larger and has lateral and medial scales. In all instars, the bothridial seta is clavate and barbed, but in the nymphs its head is slimmer than in the larva and adult. The larva has 12 pairs of gastronotal setae, the nymphs have 15 pairs (*p*-series appears), whereas the notogaster of the adults loses setae $c_1$, $c_3$ and *d*-series, such that 10 pairs of setae ($c_2$, *l*- and *h*- and *p*-series) remain. The formula of gastronotal setae of *C. borealis* is 12-15-15-15-10 (from larva to adult). Formulae of epimeral, genital, aggenital setae and segments PS–AN are as in *C. pusillus* (Seniczak *et al*. 2018). The ontogeny of leg setae and solenidia of *C. borealis* is similar to that of *C. pusillus* (Seniczak *et al*. 2018).

*Distribution and ecology of Chamobates borealis*

*Chamobates borealis* is considered a Holarctic species (Weigmann 2006), typically found in soils in forests of different humidity (Weigmann 2006). It is a silvicolous, microphytophagous (Schatz 2016) and secondary decomposer (Schneider *et al*. 2004). It was also reported on feathers of birds (Lebedeva & Krivolutsky 2003).




**FIGURES 7–8.** *Chamobates borealis*, legs partially drawn, scale bar 50 μm. 7. Larva, (a) dorsal aspect, (b) shape of seta *lp* (enlarged). 8. Ventral part of hysterosoma, (a) larva, (b) protonymph.



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**TABLE 3.** Measurements of some morphological characters of juvenile stages and adults of *Chamobates borealis* (mean measurements of 2–10 individuals per instar in μm); Nd – not developed.

| Morphological character | Larva | Protonymph | Deutonymph | Tritonymph | Adult |
|---|---|---|---|---|---|
| Body length | 198 | 248 | 290 | 345 | 384 |
| Body width | 93 | 122 | 136 | 191 | 234 |
| Length of: seta *bs* | 27 | 22 | 27 | 39 | 42 |
| seta *ro* | 28 | 24 | 26 | 33 | 42 |
| seta *le* | 18 | 18 | 25 | 34 | 53 |
| seta *in* | 24 | 25 | 30 | 44 | 43 |
| seta $c_1$ | 16 | 11 | 14 | 8 | Lost |
| seta $c_3$ | 22 | 24 | 26 | 32 | Lost |
| seta *da* | 16 | 12 | 14 | 15 | Lost |
| seta *dp* | 28 | 21 | 16 | 25 | Lost |
| seta *la* | 14 | 11 | 12 | 8 | 2 |
| seta *lp* | 25 | 15 | 17 | 13 | 2 |
| seta $h_1$ | 24 | 19 | 17 | 24 | 2 |
| seta $p_1$ | Nd | 14 | 14 | 11 | 2 |
| genital opening | Nd | 22 | 31 | 45 | 50 |
| anal opening | 38 | 48 | 67 | 75 | 55 |

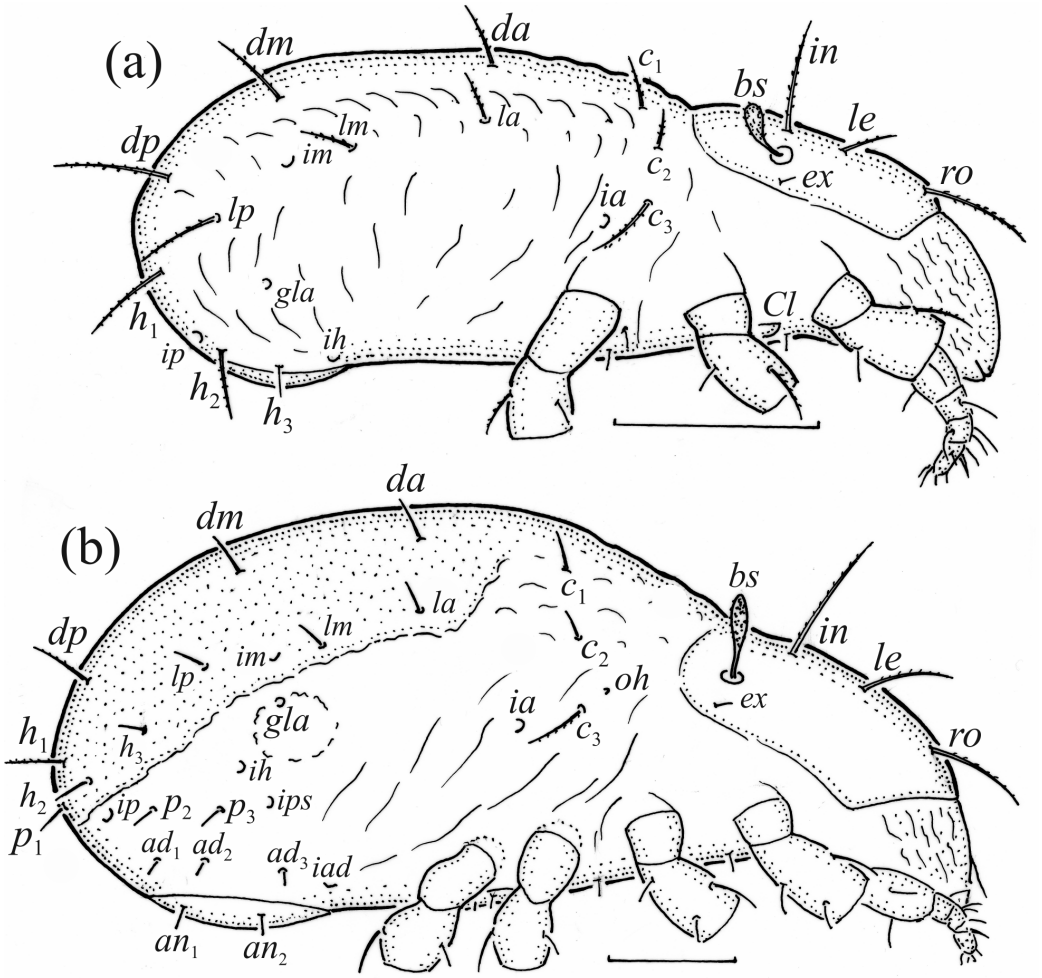


**FIGURE 9.** *Chamobates borealis*, lateral aspect, legs partially drawn, scale bars 50 μm. (a) Larva, (b) tritonymph.



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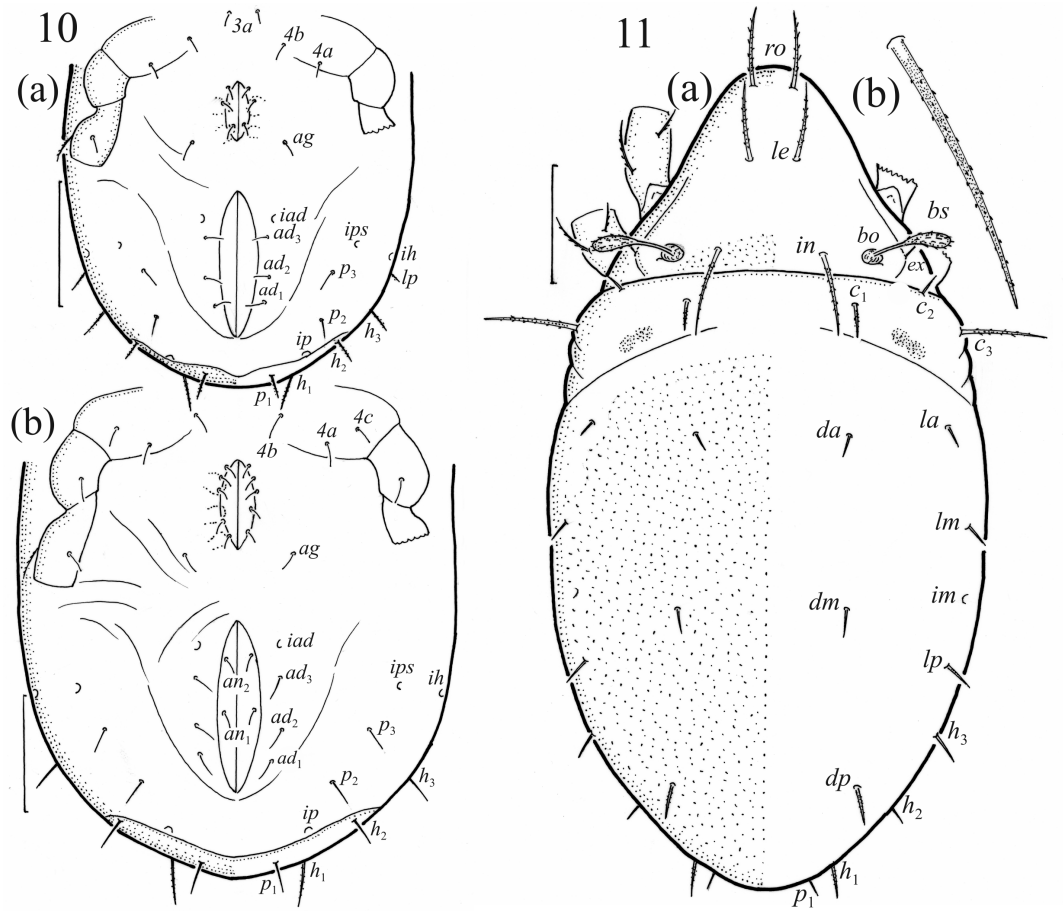


**FIGURE 10–11.** *Chamobates borealis*, legs partially drawn, scale bars 50 μm. 10. Ventral part of hysterosoma, (a) deutonymph, (b) tritonymph. 11. Tritonymph, (a) dorsal aspect, (b) shape of seta *in* (enlarged).

*Chamobates borealis* was the second most abundant oribatid species in a rich broadleaf forest in western Norway (dominance index, 17%; average density 83 individuals per 500 $cm^3$). It was found in all microhabitats studied (mosses from soil, tree bark, stump, dead wood, and in dead wood) but was most abundant in mosses growing on dead wood (Seniczak *et al*. 2019). The juveniles made on average 10% of the population, but were most abundant in mosses on ground and absent from tree bark and dead wood. In mosses on the ground (total of five samples, sampled 8 June), the stage structure of *C*. *borealis* was the following: 17 larvae (3%), seven protonymphs (1%), 22 deutonymphs (4%), 19 tritonymphs (4%) and 457 adults (88%). The sex ratio (females: males) calculated for one sample (120 adults) was 1:1.3 and 50% of females were gravid, carrying one to four large eggs (160 x 77), which made about 43% of their total body length.

*Note on* Chamobates pusillus *(Berlese, 1895)*

Seniczak *et al*. (2018) described morphological ontogeny of *Chamobates pusillus* (Berlese, 1895) but did not provide diagnosis of this species. To facilitated future identification, we supplementary present it as follows: *Diagnosis of adult*: Adult of similar size (length 345–390, width 234–267 (n= 35), rostrum with two teeth, medial incision absent (Figs. 2c, 2d). Most notogastral setae alveolar, except minute $c_2$ and *p*-series. Porose area *Aa* slightly larger than other porose areas.



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Seta *lm* located medially from porose area *Aa* at distance of two times diameter of *Aa*; lyrifissure *im* placed closer to porose area *A1* than to seta *lm*; aggenital setae thin, adanal and anal setae alveolar. *Diagnosis of juveniles*: Gastronotal shield absent in larva, present in nymphs, with 10 pairs of setae (*d*-, *l*-, *h*-series and $p_1$), setae $p_2$, $p_3$ and of *c*-series inserted on unsclerotized cuticle. In larva, seta *in* longer than *ro*, in nymphs humeral organ absent and gastronotal setae fine and short, except for distinctly longer and thicker $c_3$.

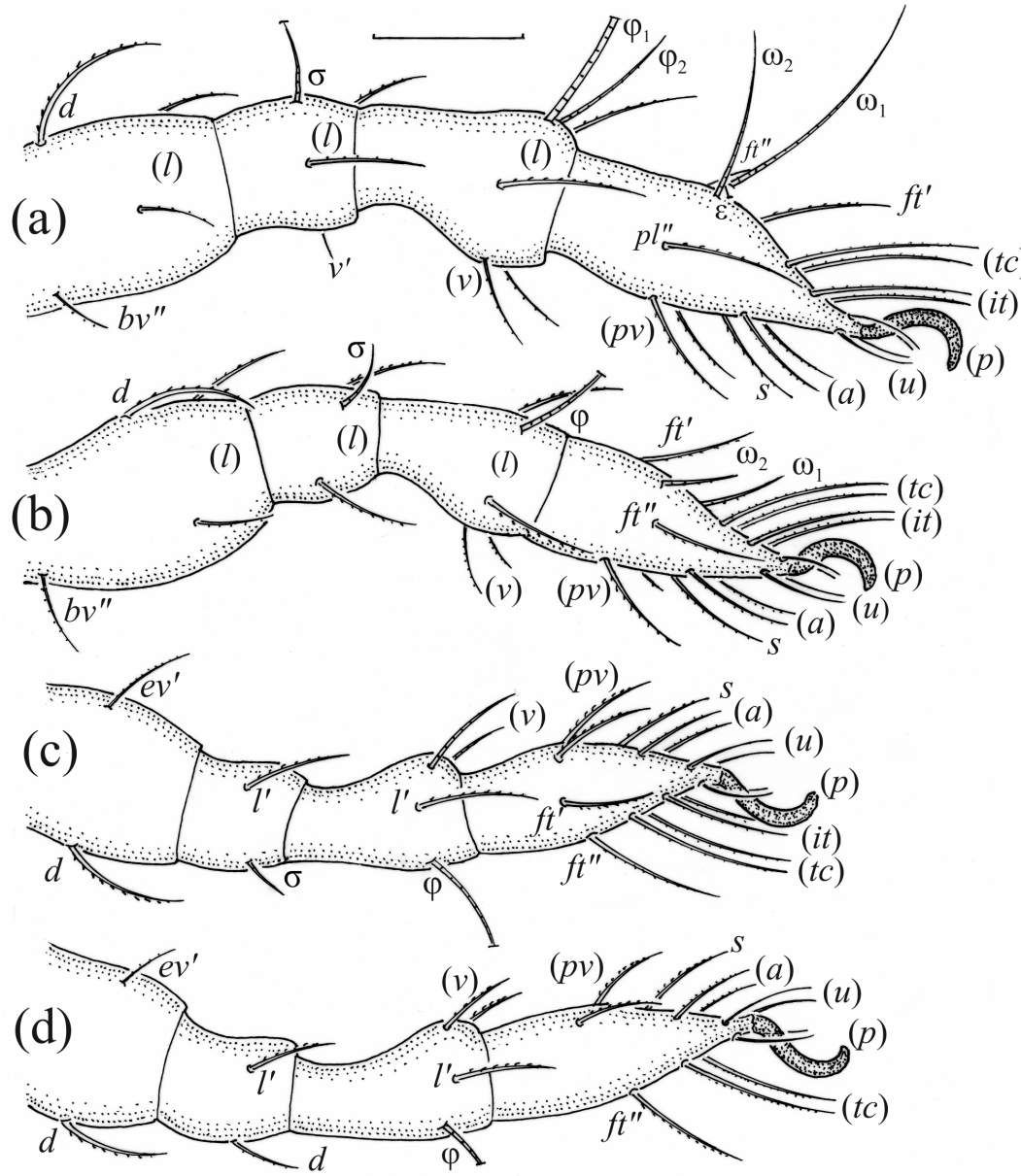


**FIGURE 12.** *Chamobates borealis*, leg segments of tritonymph (femur to tarsus), right side, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, tarsus (*pl′*); (b) leg II (genu *v′*); (c) leg III; (d) leg IV.



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## Discussion

*Chamobates borealis* has been considered a junior synonym of *C. pusillus* by some authors, but in the light of our investigations these species differ clearly from each other, both on the molecular and morphological level (Tables 2, 4). Although not so common in the field of acarology, yet, morphology-based species identification should be accompanied by DNA characters. There is an increasing number of studies using COI sequence data to assess species boundaries in Oribatida (Schäffer *et al*. 2010; Lienhard *et al*. 2014; Kreipe 2015; Pfingstl *et al*. 2019a, 2019b). The level of sequence divergence in the *Chamobates* species analyzed here is generally similar to species in those studies. Although the threshold between intra- and interspecific variance for many groups can be much higher than 2% (Hebert *et al*. 2003; Cognato 2006), the more than 14% observed here between *C. borealis* and *C. pusillus* is far beyond what can be accepted within a species. More importantly, the phylogenetic analysis clearly set apart *C. borealis* from *C. pusillus*, with several taxa separating the two with a strong support.

The morphology of adult *C. borealis* differs from *C. pusillus* by several distinct characters (Weigmann 2006; Seniczak *et al*. 2018). *Chamobates borealis* has the medial incision between the rostral teeth, whereas *C. pusillus* has no such incision. The former species has more slender bothridial seta, and larger porose area *Aa* than the latter species. In *C. borealis*, the seta *lm* is located closer to *Aa* than in *C. pusillus*. In the latter species, lyrifissure *im* is placed closer to the *gla* opening than in the former species. Moreover, in *C. borealis* all setae of the hysterosoma are short, whereas in *C. pusillus* most notogastral setae and setae of *ad*- and *an*-series are alveolar.

Also the juveniles of *C. borealis* differ from those of *C. pusillus*. The larva of the former species has longer prodorsal setae *ro* than *in*, while in the latter species it is the opposite. The nymphs of *C. borealis* have longer setae *dp* and $h_1$ than *C. pusillus* and possess a humeral organ, which is absent in the latter species. This organ is also present in the nymphs of *C. cuspidatus*, *C. rastratus* and *C. subglobulus*, whereas it is absent in *C. schuetzi* and *C. voigtsi* (Seniczak & Solhøy 1988; Seniczak & Żelazna 1994; Seniczak & Seniczak 2014; Seniczak *et al*. 2018). It is interesting to note that the presence or absence of a humeral organ in these taxa at least partly fit with the clades inferred by COI sequence data (Fig. 1). The gastronotal shield is on the other hand present in the nymphs of both *C. borealis* and *C. pusillus*, and additionally in *C. rastratus* and *C. schuetzi*, whereas absent in other species. In the nymphs of *C. borealis*, *C. pusillus* and *C. schuetzi*, most gastronotal setae are short (Seniczak & Solhøy 1988; Seniczak *et al*. 2018), in *C. rastratus* and *C. subglobulus* they are long (Seniczak & Żelazna 1994; Seniczak & Seniczak 2014), whereas in *C. cuspidatus* they are of medium size (Seniczak & Solhøy 1988). In the larvae of most species, most gastronotal setae are of medium size, except for *C. subglobulus*, in which these setae are very long. Our molecular data have indicated that these characters are of limited value in phylogenetic studies, but can be of great taxonomic value.

Willmann (1931) considered *C. borealis* a synonym of *C. schuetzi*, but in the former species the porose area *Aa* is larger than in the latter species, and seta *in* is shorter than in *C. schuetzi*. Therefore, *C. schuetzi* needs more studies, also on the molecular level to confirm the systematic status.

## Acknowledgements

We thank two anonymous reviewers for helpful suggestions and Dr. Marut Fuangarworn, a section Editor of Systematic & Applied Acarology for editorial suggestions that improved the scientific value of this paper. We are grateful to Ms. Gunvi Lindberg (Swedish Museum of Natural History, Stockholm, Sweden) for the loan of the material used in this study, and to Dr. Roberto Nannelli



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(CREA-DC, Research Centre for Plant Protection and Certification, Florence, Italy) for the photographs and measurements of *C. pusillus* from the Berlese Collection, and to Dr. Steffen Roth (University Museum of Bergen, Bergen, Norway) for collecting samples in Svalbard. This study was supported by grant No. 811030 from The Norwegian Taxonomy Initiative – KR 35-16 (Norwegian Forest Oribatida (NFO) - highly diverse, but poorly known). DNA barcode data in this publication was generated in collaboration with the Norwegian Barcode of Life Network (NorBOL) funded by the Research Council of Norway and the Norwegian Biodiversity Information Centre. Part of the study was done within the program of Polish Minister of Science and Higher Education "Regional Initiative of Excellence" in 2019–2022 (Grant No. 008/RID/2018/19).

## References

Arroyo, J., O Connell T. & Bolger T. (2017) Oribatid mites (Acari: Oribatida) recorded from Ireland: Catalogue, historical records, species habitats and geographical distribution, combinations, variations and synonyms. *Zootaxa*, 4328, 1–174.
https://doi.org/10.11646/zootaxa.4328.1.1

Bayartogtokh, B. (2010) Oribatid mites of Mongolia (Acari: Oribatida). *Russian Academy of Sciences*. Moscow, KMK Scientific Press Ltd., pp. 1–400. (In Russian)

Berlese, A. (1895) Acari, Myriapoda et Scorpiones hucusque in Italia reperta, vol. 77.

Bernini, F., Castagnoli, M. & Nannelli, R. (1995) Arachnida, Acari. *In*: Minelli, A., Rufo, S. & La Posta, S. (Eds.), *Checklist delle specie della fauna italiana*, Calderini, Bologna, 24, 1–131.

Cognato, A.I. (2006) Standard percent DNA sequence difference for insects does not predict species boundaries. *Journal of Economic Entomology*, 99(4), 1037–1045.
https://doi.org/10.1093/jee/99.4.1037

CCDB (2019) The Canadian Centre for DNA Barcoding website. Available: www.ccdb.ca (Accessed May 2019).

Dhora, D. (2009) Register of species of the fauna of Albania. *Botimet Camaj – Pipa*, Tirana, pp. 1–130.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3(5), 294–299.

Golosova, L.D., Karppinen, E. & Krivolutsky, D.A. (1983) List of oribatid mites (Acarina, Oribatei) of northern Palaearctic region. II. Siberia and the Far East. *Acta Entomologica Fennica*, 43, 1–14.

Grandjean, F. (1949) Observation et conservation des tres petits Arthropodes. *Bulletin du Muséum National d'Histoire Naturelle*, Series 2, 3, 363–370.

Grandjean, F. (1953) Essai de classification des Oribates (Acariens). *Bulletin de la Société zoologique de France*, 78, 421–446.

Grandjean, F. (1962) Nouvelles observations sur les Oribates (2e série). *Acarologia*, 4, 396–422.

Hall, T.A. (2011) BioEdit: An important software for molecular biology. *GERF Bulletin of Biosciences*, 2(1), 60–61.

Hasegawa, M., Kishino, H. & Yano, T. (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, 22 (2), 160–174.
https://doi.org/10.1007/BF02101694

Hebert, P.D.N., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences*, 270, 313–321.
https://doi.org/10.1098/rspb.2002.2218

Hull, J.E. (1914) British Oribatidae. Notes on new and critical species. *The Naturalist*, 215–288.

Karppinen, E. & Krivolutsky, D.A. (1982) List of oribatid mites (Acarina, Oribatei) of northern Palaearctic region. I. Europe. *Acta Entomologica Fennica*, 41, 1–18.

Koch C.L. (1844) Deutschlands Crustaceen, Myriapoden und Arachniden. Regensburg, Vol. 33–40.

Kreipe, V., Corral-Hernández, E., Scheu, S., Schaefer, I. & Maraun, M. (2015) Phylogeny and species delineation in European species of the genus *Steganacarus* (Acari, Oribatida) using mitochondrial and nuclear markers. *Experimental and Applied Acarology*, 66, 173–186.

Kulczyński, V. (1902) Zoologische Ergebnisse der russischen Expeditionen nach Spitzbergen. *Annuaire du*



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*Musée zoologique de l'Académie Imperiale des sciences de St. Pétersbourg*, 77, 335–355.
Lebedeva, N.V. & Krivolutsky, D.A. (2003) Birds spread soil microarthropods to Arctic islands. *Doklady Biological Sciences*, 391, 329–332.
https://doi.org/10.1023/A:1025150500875
Lienhard, A., Schäffer, S., Krisper, G. & Sturmbauer, C. (2014) Reverse evolution and cryptic diversity in putative sister families of the Oribatida (Acari). *Journal of Zoological Systematics and Evolutionary Research*, 52, 86–93.
https://doi.org/10.1111/jzs.12037
Mahunka, S. (1987) A survey of the oribatids of Kiskunság National Park (Acari: Oribatida). *In*: Mahunka, S. (Ed.) *Fauna of Kiskunság National Park vol. 2*. Akadémiai Kiadó, Budapest, pp. 346–397.
Mahunka, S. & Mahunka-Papp, L. (1995) The oribatid species described by Berlese (Acari). *Hungarian Natural History Museum*, Budapest, pp. 1–325.
Marshall, V.G., Reeves, R.M. & Norton, R.A. (1987) Catalogue of the Oribatida (Acari) of Continental United States and Canada. *Memoirs of the Entomological Society of Canada*, 139, 1–418.
https://doi.org/10.4039/entm119139fv
Michael, A.D. (1884) British Oribatidae. London, Vol. I. *Ray Society*, pp. 1–336.
Miko, L. (2016) Oribatid mites (Acarina, Oribatida) of the Czech Republic. Revised check-list with a proposal for Czech oribatid nomenclature. *Klapalekiana*, 52 (Suppl.), 1–302.
Murvanidze, M. & Mumladze, L. (2016) Annotated checklist of Georgian oribatid mites. *Zootaxa*, 4089(1), 1–81.
https://doi.org/10.11646/zootaxa.4089.1.1
Nicolet, H. (1855) Histoire naturelle des Acariens qui se trouvent aux environs de Paris. *Archives du Museum d'Histoire naturelle*, Paris 7, 381–482.
https://doi.org/10.5962/bhl.title.66066
Niemi, R., Karppinen, E. & Uusitalo, M. (1997) Catalogue of the Oribatida (Acari) of Finland. *Acta Zoologica Fennica*, 207, 1–39.
Norton, R.A. & Behan-Pelletier, V.M. (2009) Suborder Oribatida. *In*: Krantz, G.W., Walter, D.E. (Eds.), *A manual of acarology 3rd Edition*. Lubbock, Texas Tech University Press, pp. 430–564.
http://dx. doi.org/10.1653/024.092.0323
Norton, R.A. & Ermilov, S.G. (2014) Catalogue and historical overview of juvenile instars of oribatid mites (Acari: Oribatida). *Zootaxa*, 3833, 1–132.
https://doi.org/10.11646/zootaxa.3833.1.1
Olszanowski, Z., Rajski, A. & Niedbała, W. (1996) Roztocze Acari – Mechowce Oribatida. Katalog Fauny Polski - Catalogus faunae poloniae, *Sorus*, Poznań, 34(9), 1–243.
Oudemans, A.C. (1900) New list of Dutch Acari, 1st part. *The Tijdschrift voor Entomologie*, 43, 150–171.
Oudemans, A.C. (1902) New list of Dutch Acari. Second part. With remarks on known and descriptions of a new subfamily, new genera and species. *The Tijdschrift voor Entomologie*, 45, 1–52.
Pavlichenko, P.G. (1994) A guide to the Ceratozetoid mites (Oribatei, Ceratozetoidea) of Ukraine. Kiev, *National Academy of Sciences of the Ukraine*, pp. 1–144.
Pfingstl, T., Lienhard, A. & Baumann, J. (2019a) New and cryptic species of intertidal mites (Acari, Oribatida) from the Western Caribbean – an integrative approach. *International Journal of Acarology*, 45(1–2), 10–25.
https://doi.org/10.1080/01647954.2018.1532458
Pfingstl, T., Lienhard, A., Shimano, S., Bin Yasin, Z., Shau-Hwai, A.T., Jantarit, S. & Petcharad, B. (2019b) Systematics, genetics, and biogeography of intertidal mites (Acari, Oribatida) from the Andaman Sea and Strait of Malacca. *Journal of Zoological Systematic and Evolutionary Research*, 57, 91–112.
https://doi.org/10.1111/jzs.12244
Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* 14(9), 817–818.
https://doi.org/10.1093/bioinformatics/14.9.817
Rambaut, A. & Drummond, A. (2007) Tracer v1.4. Retrieved from http:// beast.bio.ed.ac.uk/Tracer
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539–542.
https://doi.org/10.1093/sysbio/sys029
Schatz, H. (1983) U.-Ordn.: Oribatei, Hornmilben. *Catalogus Faunae Austriae*, Wien. Teil IXi, 1–118.
Schatz, H. (2016) Oribatid mites (Acari, Oribatida) from the biodiversity days in South Tyrol (Prov. Bolzano,



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Italy). *Gredleriana*, 16, 113–132.
Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A. & Maraun, M. (2004) Trophic niche differentiation in oribatid mites (Oribatida, Acari): evidence from stable isotope ratios (15N / 14N). *Soil Biology & Biochemistry*, 36, 1769–1774.
https://doi.org/10.1016/j.soilbio.2004.04.033
Schäffer, S., Koblmüller, S., Pfingstl, T., Sturmbauer, C. & Krisper, G. (2010) Contrasting mitochondrial DNA diversity estimates in Austrian *Scutovertex minutus* and *S. sculptus* (Acari, Oribatida, Brachypylina, Scutoverticidae). *Pedobiologia*, 53, 203–211.
https://doi.org/10.1016/j.pedobi.2009.09.004
Sellnick, M. (1922) Eine neue Oribatide und Berichtigungen zu einer meiner Arbeiten. *Schriften der physikalisch–ökonomische Gesellschaft*, Königsberg, 63, 97–98.
Seniczak, A. & Seniczak, S. (2014) Comparison of morphology and ontogeny of *Chamobates subglobulus* (Oudemans, 1900) and *Euzetes globulus* (Nicolet, 1855) (Acari: Oribatida). *International Journal of Acarology*, 40(4), 274–295.
https://doi.org/10.1080/01647954.2014.914971
Seniczak, A., Seniczak, S., Kaczmarek, S. & Bolger, T. (2018) Morphological ontogeny of *Chamobates pusillus* (Acari, Oribatida, Chamobatidae), with comments on some species of *Chamobates* Hull. *Systematic & Applied Acarology*, 23(2), 339–352.
http://doi.org/10.11158/saa.23.2.9
Seniczak, A., Bolger, T., Roth, S., Seniczak, S., Djursvoll, P. & Jordal, B.H. (2019) Diverse mite communities (Acari) from a rich broadleaf forest in Western Norway. *Annales Zoologici Fennici* 56, 121–136.
Seniczak, S. & Solhøy, T. (1988) The morphology of juvenile stages of moss mites of the family Chamobatidae Thor (Acarida: Oribatida), I. *Annales Zoologici*, 41, 491–502.
Seniczak, S. & Żelazna, E. (1994) The morphology of juvenile stages of moss mites of the family Chamobatidae Thor (Acarida: Oribatida), II. *Zoologischer Anzeiger*, 232, 223–236.
Shaldybina, E.S. (1975) Family Chamobatidae Thor, 1938. *In*: Ghilarov, M.S. (Ed.), *Key to soil-inhabiting mites – Sarcoptiformes*. Moscow, Nauka Publisher, pp. 313–316. (In Russian)
Siepel, H., Zaitsev, A. & Berg, M. (2009) Checklist of the oribatid mites of the Netherlands (Acari, Oribatida). *Nederlandse Faunistische Mededelingen*, 30, 83–111.
Subías, L.S. (2004) Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1758−2002). *Graellsia*, 60 (número extraordinario), 3–305.
https://doi.org/10.3989/graellsia.2004.v60.iExtra.218
Subías, L.S. (2019) Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes: Oribatida) del mundo (Excepto fósiles), 14ª actualización, 536 pp. Available from: http://bba.bioucm.es/cont/docs/RO_1.pdf (accessed 13 May 2019).
Swofford, D.L. (2002) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland.
https://doi.org/10.1111/j.0014-3820.2002.tb00191.x
Trägårdh, I. (1902) Beiträge zur Kenntnis der schwedischen Acaridenfauna. I. Lappländische Trombidiiden und Oribatiden. *Bihang till Svenska vetenskaps-akademiens handlingar*, 28 (4–5), 1–26.
Trägårdh, I. (1910) Acariden aus dem Sarekgebirge. Naturwissenschaftliche Untersuchungen des Sarekgebirges in Schwedisch Lappland. *Zoologie (Stockholm)*, 4, 375–586.
Weigmann, G. (2006) Hornmilben (Oribatida). *In*: Dahl F., series founder. *Die Tierwelt Deutschlands* part 76. Goecke & Evers, Keltern, pp. 1–520.
Weigmann, G., Horak, F., Franke, K. & Christian, A. (2015) Verbreitung und Ökologie der Hornmilben (Oribatida) in Deutschland. *Senckenberg, Museum Für Naturkunde, Görlitz*, Peckiana, 10, 1–171.
Willmann, C. (1931) Moosmilben oder Oribatiden (Cryptostigmata). *In*: Dahl, F., series founder. *Die Tierwelt Deutschlands*. Gustav Fischer Jena, 22, 79–200.

*Submitted: 10 Jul. 2019; accepted by Marut Fuangarworn: 03 Oct. 2019; published: 20 Dec. 2019*



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