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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

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

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

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

.....continued on the next page

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).

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%.

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

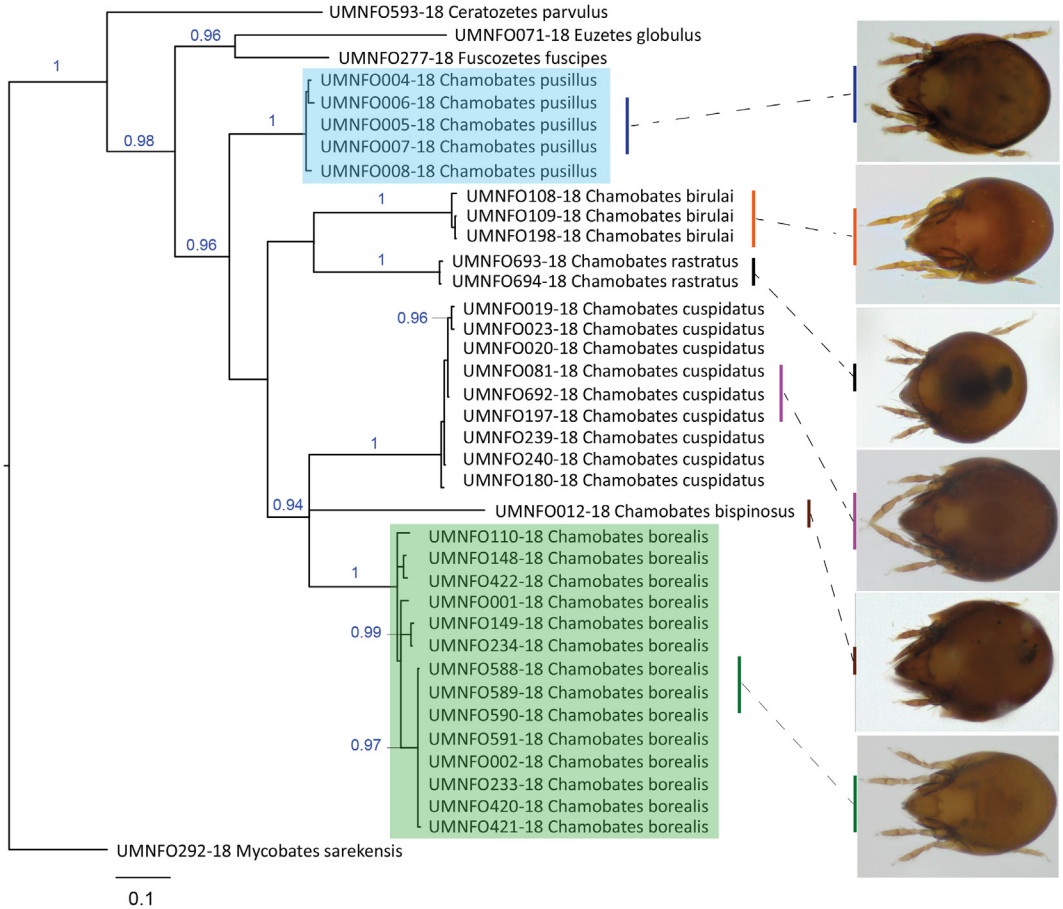


FIGURE 1. Bayesian inference tree based on COI sequences (658 bp). Specimen numbers correspond to BOLD database (http://boldsystems.org/) and the photographs are vouchers of the sequenced animals. Information about specimens used for sequencing with Gene Bank accession numbers are in Table 1. Node support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

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.

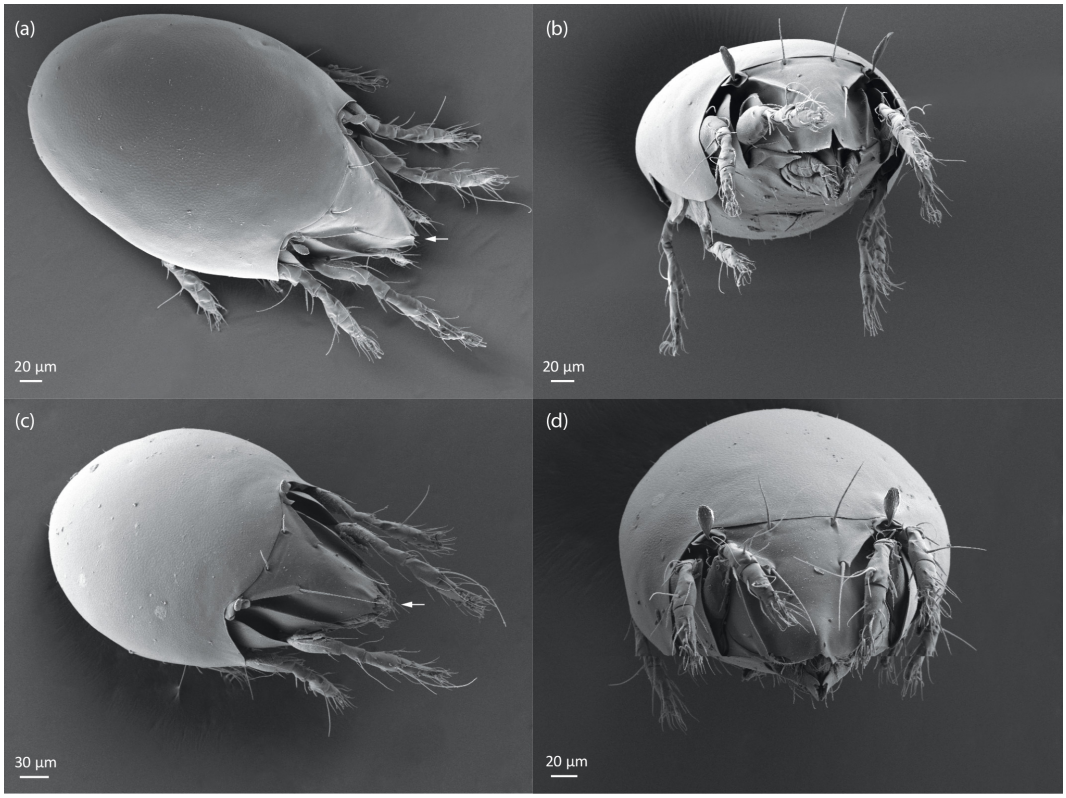
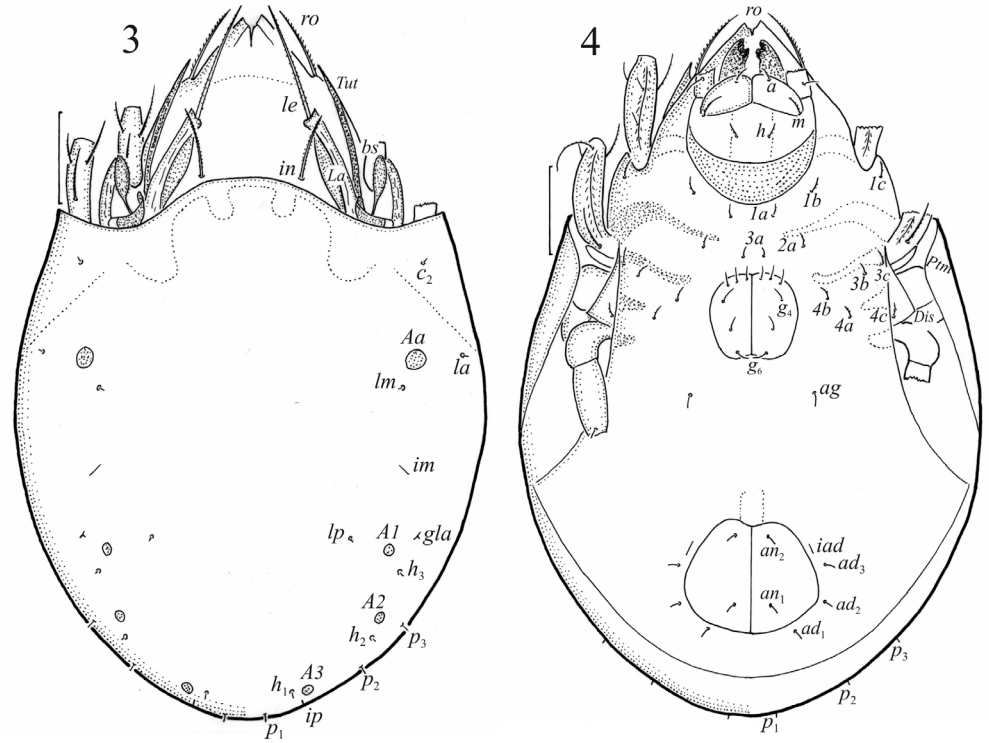


FIGURE 2. Adults of *Chamobates* species, SEM micrographs, arrow points differences in rostrum of species. (a) *C. borealis*, dorso-lateral aspect, (b) *C. borealis*, frontal aspect, (c) *C. pusillus*, dorso-lateral aspect, (d) *C. pusillus*, frontal aspect.



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.

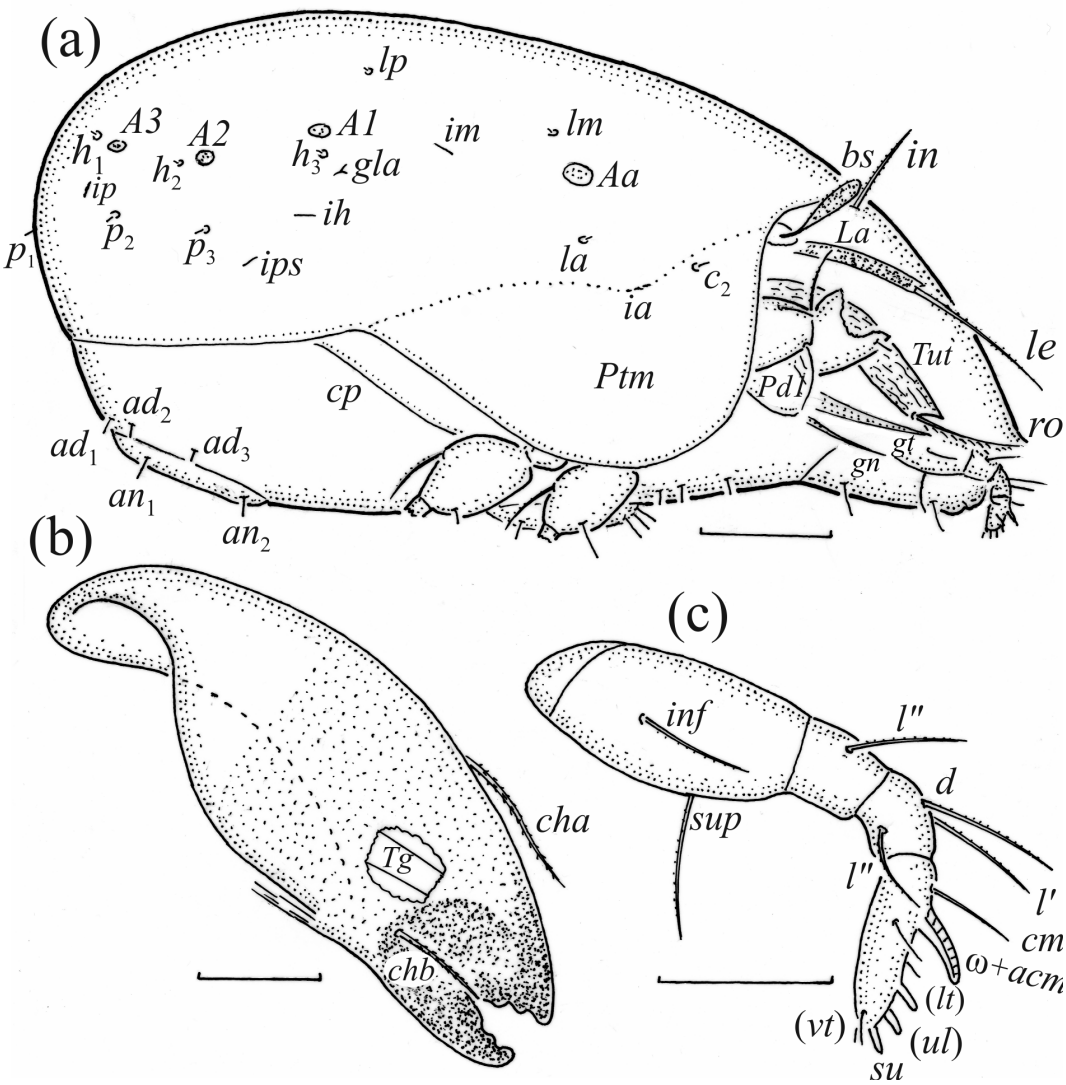


FIGURE 5. *Chamobates borealis*, female. (a) Lateral aspect, legs partially drawn, scale bar 50 μm; mouthparts, right side, scale bars 20 μm, (b) chelicera, (c) palp.

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

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).

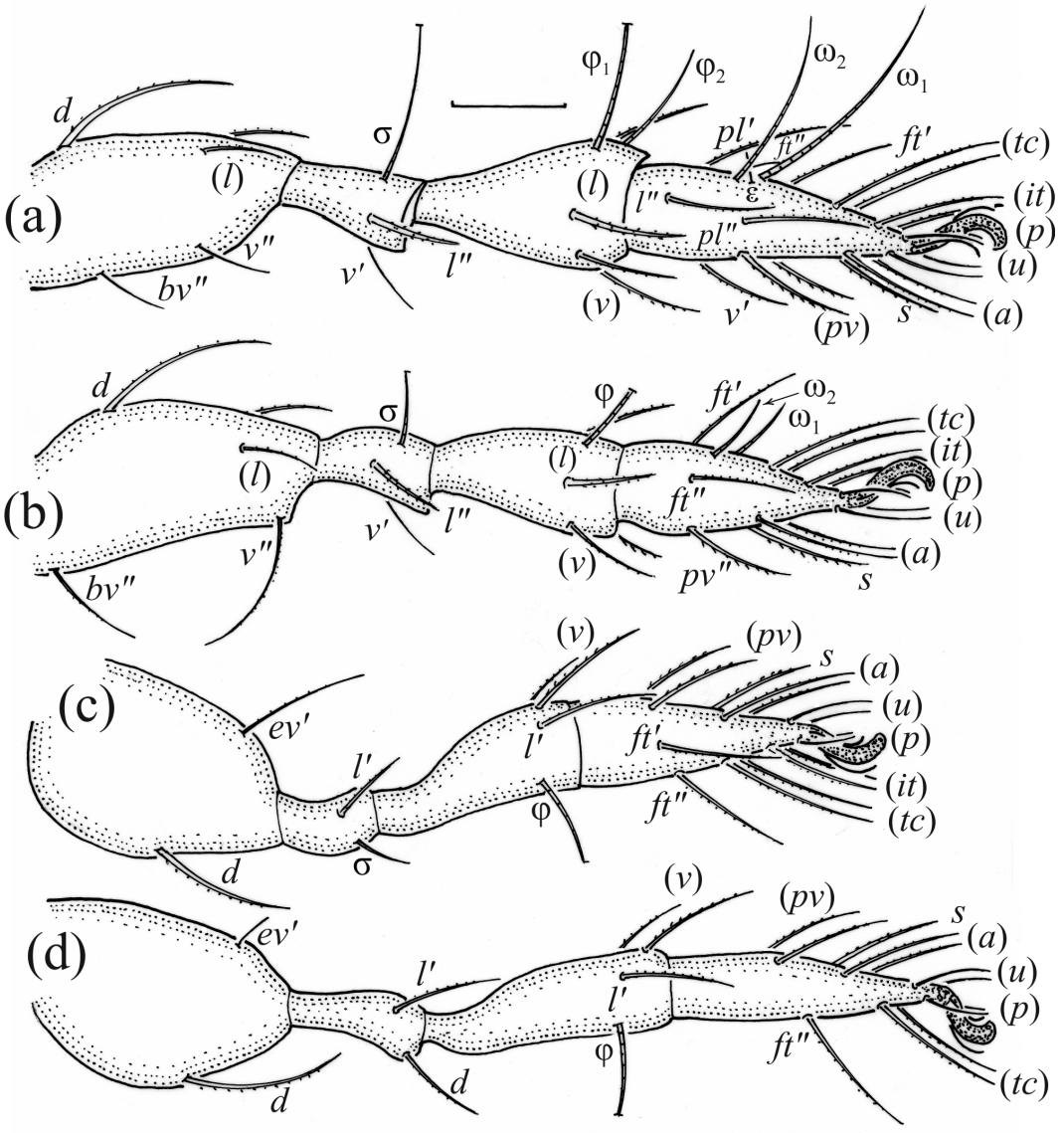


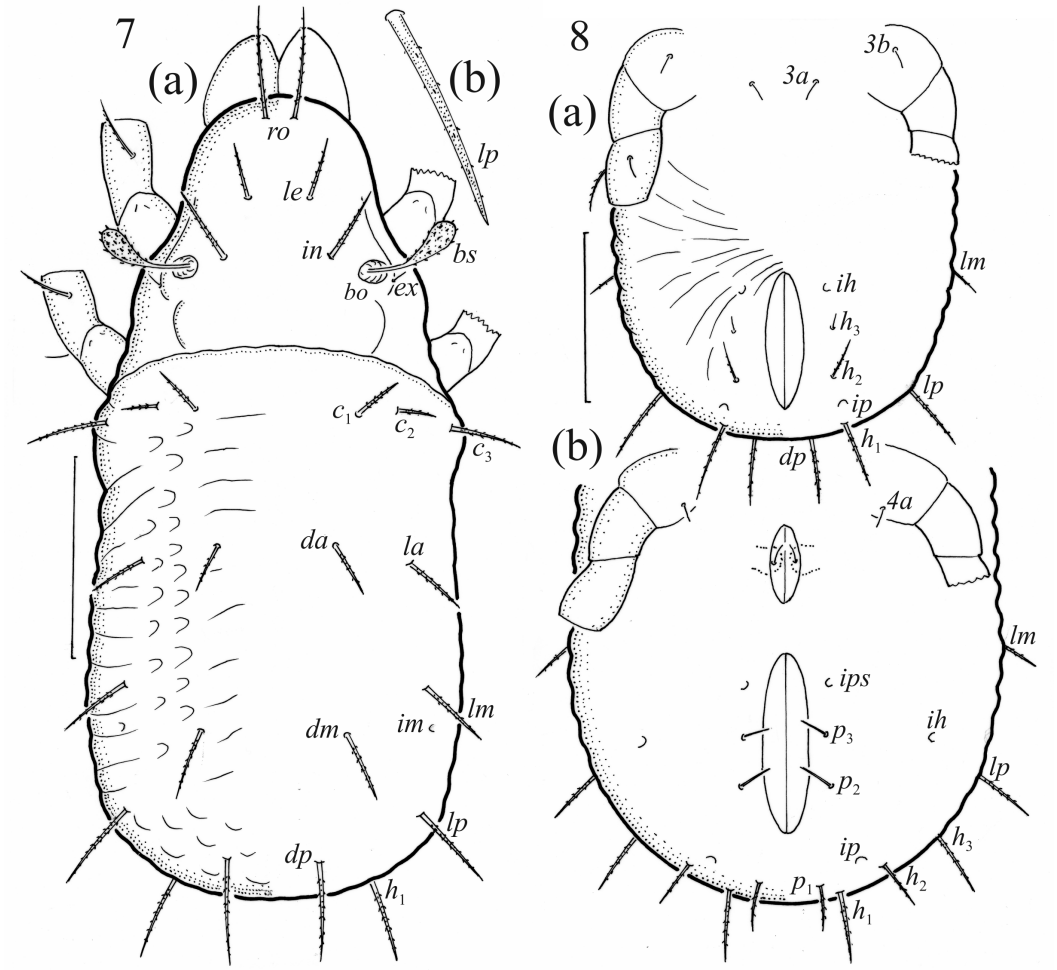
FIGURE 6. *Chamobates borealis*, leg segments of adult (femur to tarsus), right side, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, genu (*l′*); (b) leg II, genu (*l′*), tarsus (*pv′*); (c) leg III; (d) leg IV.

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.

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

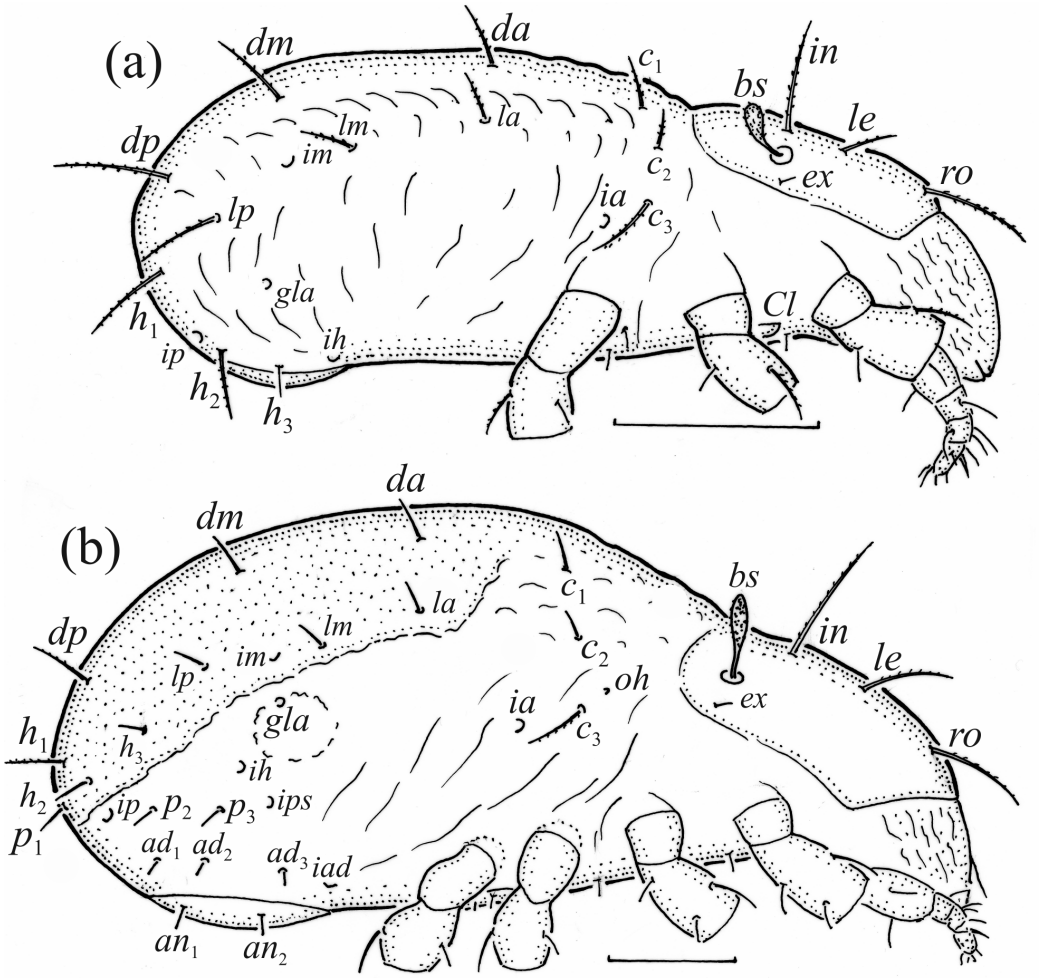


FIGURE 9. *Chamobates borealis*, lateral aspect, legs partially drawn, scale bars 50 μm. (a) Larva, (b) tritonymph.

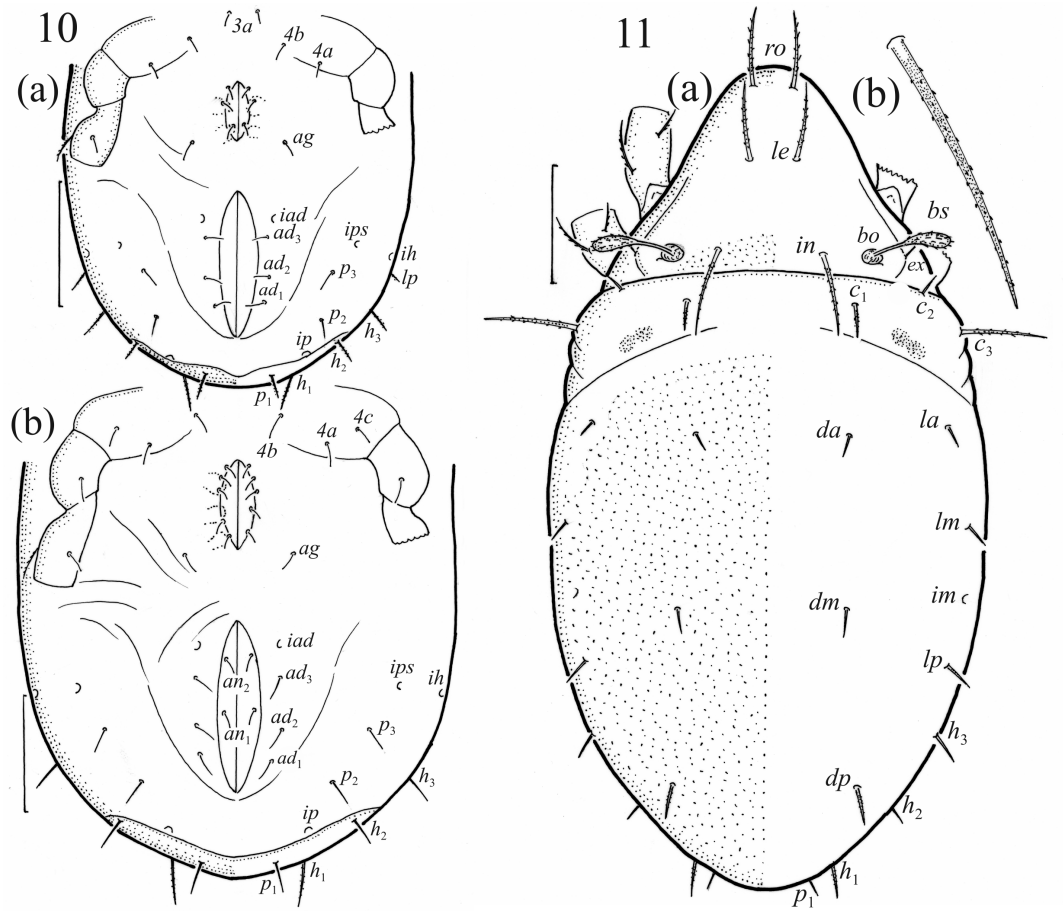


FIGURE 10–11. *Chamobates borealis*, legs partially drawn, scale bars 50 μm. 10. Ventral part of hysterosoma, (a) deutonymph, (b) tritonymph. 11. Tritonymph, (a) dorsal aspect, (b) shape of seta *in* (enlarged).

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.

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.

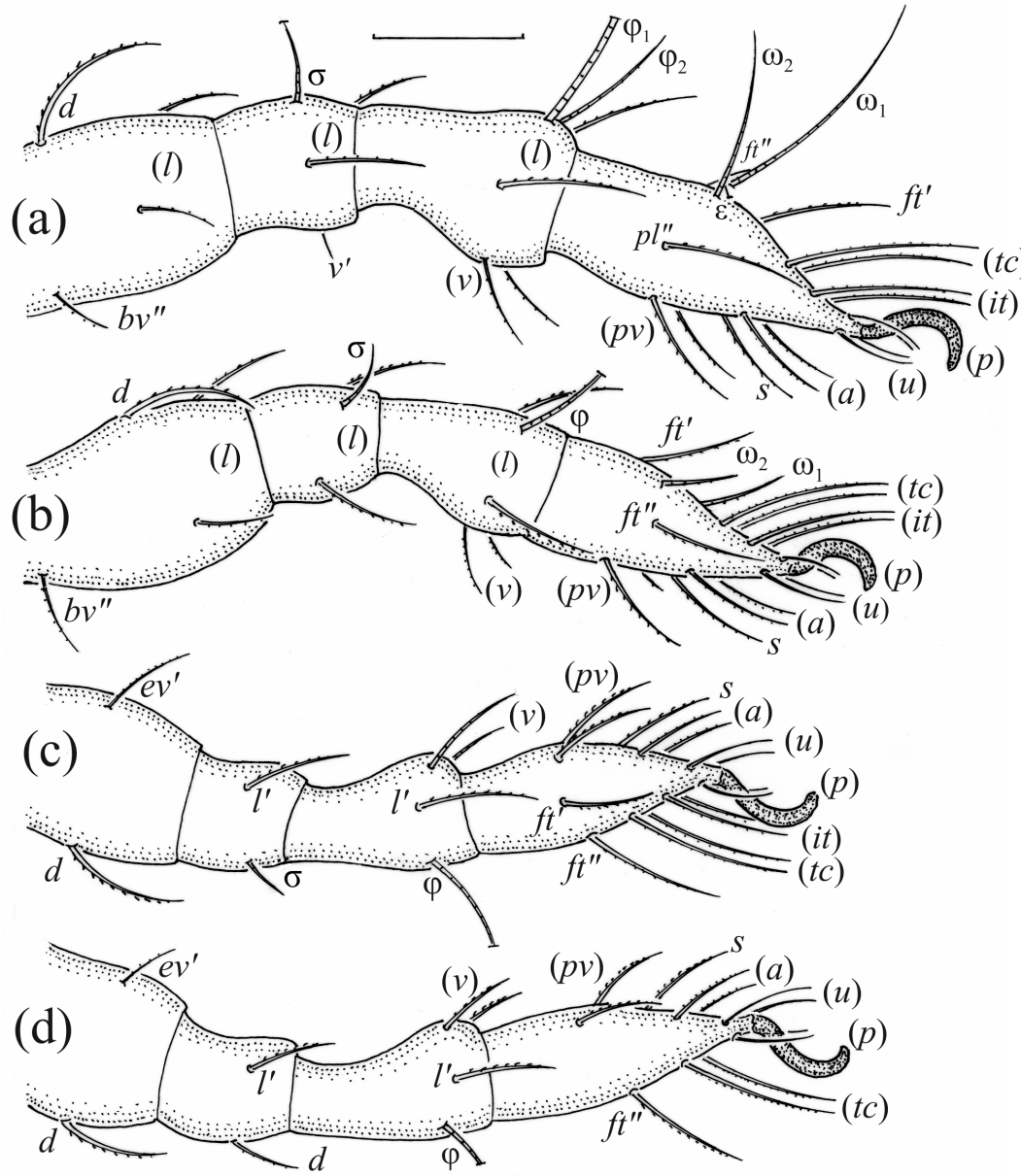


FIGURE 12. *Chamobates borealis*, leg segments of tritonymph (femur to tarsus), right side, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, tarsus (*pl′*); (b) leg II (genu *v′*); (c) leg III; (d) leg IV.

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

(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).

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