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Morphological ontogeny of *Limnozetes solhoyorum* sp. nov. (Acari: Oribatida: Limnozetidae) from Norway, with comments on *Limnozetes* Hull

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Abstract

The morphological ontogeny of *Limnozetes solhoyorum* **sp. nov.** from Norway is described and illustrated. This species is most similar to *L. guyi* Behan-Pelletier, 1989 as adult, but differs from it mainly by the sculpture of notogaster, shorter prodorsal seta *in* and notogastral setae, especially p_1, and the distribution of posterior notogastral setae. The tritonymph of *L. solhoyorum* differs from that of *L. guyi* by shorter gastronotal setae c_3, *dm*, *dp*, *lm* and *lp*. In the deutonymph, tritonymph and adult of both species, setae *d* and *l′* from genu IV are absent.

Keywords: oribatid mites, juveniles, leg setation, ecology, stage structure

Introduction

The mites of *Limnozetes* Hull, 1916 live abundantly, including the juveniles, in semiaquatic and aquatic habitats, bogs, fens and at the edges of lotic habitats (Behan-Pelletier 1989; Seniczak 2011; Seniczak *et al*. 2016, 2019a, b; Lehmitz *et al*. 2019). Behan-Pelletier (1989) gave the diagnosis of the genus *Limnozetes*, from which the main diagnostic characters are well-developed pteromorph, presence of dorsal expansion of bothridium, tutorium and genal tooth, weakly developed bothridial seta, lack of lenticulus and one or two setae *a* from tarsi, and presence of very long and curved seta *d* on femora I–III. By contrast, the juveniles of *Limnozetes* have long bothridial seta, but the gastronotum can be rounded, with plicate cuticle and short, thin setae or elongated, with slightly folded cuticle and blade-like marginal setae. Based mainly on the morphology of juveniles of nine species of *Limnozetes* from North America and Europe, Seniczak and Seniczak (2009a) divided *Limnozetes* species in '*rugosus* group', with stocky juveniles, plicate cuticle, and short and thin gastronotal setae, and '*ciliatus* group', with boat-shaped juveniles, slightly folded cuticle and blade-like marginal setae on the gastronotum.

The morphological ontogeny of *Limnozetes* species is insufficiently known. According to the catalogue of juvenile oribatid mites by Norton and Ermilov (2014), the full morphological ontogeny of four species of this genus is known: *L. ciliatus* (Schrank 1803), *L. foveolatus* Willmann, 1939 (= *L. palmerae* Behan-Pelletier, 1989), *L. lustrum* Behan-Pelletier, 1989 and *L. rugosus* (Sellnick, 1925). The morphological ontogeny of *L. amnicus* Behan-Pelletier, 1989, *L. borealis* Behan-Pelletier, 1989, *L. feuerborni* Willmann, 1932b, *L. guyi* Behan-Pelletier, 1989, *L. latilamellatus* Behan-Pelletier, 1989 and *L. onondaga* Behan-Pelletier, 1989 is only partially known.

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While working on the oribatid mite fauna from a poor bog carpet near lake Langvotnevatnet (Kvam, Vestland, Norway), we found in a bog pool in submerged moss *Warnstorfia fluitans* (Hedw.) a large population of undescribed *Limnozetes* species, with all juvenile stages. These juveniles have plicate cuticle on the gastronotum, indicating their membership in the '*rugosus* group'.

The aim of this paper is to describe and illustrate the morphological ontogeny of this species, as *Limnozetes solhoyorum* **sp. nov**., and to compare its morphology with congeners.

Materials and methods

The juveniles and adults of *L. solhoyorum* **sp. nov.** were collected on 25th June 2008 by the senior author from a bog pool, from submerged moss *Warnstorfia fluitans*, in a poor bog carpet near lake Langvotnevatnet (Kvam, Vestland, Norway: 60.370718°N, 6.024418°E, 340 m a. s. l.). For a better understanding of the morphology of the '*rugosus* group', we also investigated the ontogeny of leg setae and solenidia of *L. rugosus* and the shape of chelicerae and palp of this species, which were omitted by Seniczak and Seniczak (2010). We also present the scanning electron microscopy (SEM) micrographs of both species because they illustrate better than the line drawings the surface of the body – an important diagnostic character of *Limnozetes* species. The latter species was collected from mire in Finse (Vestland, Norway, 60.585722°N, 7.516167°E, 1300 m a. s. l.).

The illustrations of instars are limited to the body regions that show substantial differences between instars, including the dorsal and lateral aspects of the larva, tritonymph and adult, ventral regions of all instars and some leg segments of the adult and tritonymph. The chelicera and palp of the adult are also illustrated. We measured the 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. Illustrations were prepared from specimens mounted temporarily on slides in lactic acid (Grandjean 1949a). In the text and figures, we used 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*), opisthonotal gland opening (*gla*), subcapitular setae (*a*, *m*, *h*), cheliceral setae (*cha*, *chb*) and Trägårdh organ (*Tg*), palp setae (*sup*, *inf*, *l*, *d*, *cm*, *acm*, *lt*, *vt*, *ul*, *su*) and solenidion ω, genal tooth (*gt*), pedotectum 1 (*Pd1*), tutorium (*Tut*), discidium (*Dis*), epimeral setae (*1a–c*, *2a*, *3a–b*, *4a–b*), 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*, *v*). The terminology used follows that of Grandjean (1949b, 1951, 1953) and Norton and Behan-Pelletier (2009). The species nomenclature follows Subías (2004, 2019).

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.

Limnozetes solhoyorum sp. nov.

(Figs. 1–17)

Diagnosis

Adults of medium size (344–364), with characters of *Limnozetes*. Lamella narrow, with well developed cusp, translamella absent. Seta *in* reaching half length of lamella, sensillus short, setiform. Notogaster convex, with elongated and rounded foveae, short and thin setae, length to width of

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notogaster and length to width of pteromorph similar (1.2:1). Famulus on tarsus I present, but setae *d* and *l′* from genu IV absent.

Juveniles plicate, with characters of *Limnozetes*. Prodorsal setae *le* and *in* and bothridial seta long and thin, whereas gastronotal setae short and thin, except slightly longer *lp*, h_1 and h_2 in larva, and p_1 and *h*-series in nymphs. In deutonymph and tritonymph, setae *d* and *l′* from genu IV absent.

Adult. Measurements: mean body length (and range): females 353.9 (344–364, n= 50) and width 240.1 (234–244).

Prodorsum. Rostrum rounded, lamella long, without translamella, lamellar cusp of medium size (14), rounded, with lamelar seta (Figs. 1a, 2, 3a, 4a, 4b, 4c, 5a, Table 1). Setae *le* and *in* longer (46–48) than *ro* (33–35), and *in* thinner than *le* and *ro*. Seta *ro* inserted on lateral part of rostrum, whereas seta *in* inserted close to inner border of lamella and anterior border of notogaster. Bothridium rounded, with well developed dorsal expansion (Figs. 1a, 5a), bothridial seta short, setiform. Medial and posterior parts of prodorsum punctate.

TABLE 1. Measurements of some morphological characters of juvenile stages and adult of *Limnozetes solhoyorum* **sp. nov.** (mean values of 10 individuals in μm); Nd: not developed.

Morphological character	Larva	Protonymph	Deutonymph	Tritonymph	Adult
Body length	185	228	281	347	353
Body width	110	149	182	244	240
Length of prodorsum	48	57	72	81	64
Length of: seta *le*	28	33	45	50	48
seta *in*	29	35	46	51	40
seta *bs*[1]	42	35	55	56	10
seta c_1	2	4	5	7	Lost
seta c_2	2	4	5	7	12
seta c_3	2	4	5	7	Lost
seta *da*	5	4	6	8	Lost
seta *dp*	12	8	9	11	Lost
seta *la*	5	4	5	8	12
seta *lm*	5	5	7	10	12
seta *lp*	18	8	13	12	15
seta h_1	9	11	14	16	17
seta h_3	1	7	13	15	15
seta p_1	Nd	5	14	16	18
genital opening	Nd	25	29	40	48
anal opening	52	56	70	89	80

[1]Broken seta is omitted.

Notogaster. Convex, ratio length to width of notogaster similar to ratio length to width of pteromorph (1.2:1, Figs. 4a, 5c). Ten pairs of notogastral setae present, including c_2, all short (Table 1) and thin. Notogaster with elongated and rounded foveae, anterior part and pteromorphs with more elongated foveae than central part (Figs. 1–3a, 4, 5a). Lyrifissures *ia* and *im* posterolateral to seta c_2 and posterior to seta *la*, respectively, *ip* posterolateral to seta h_1, *ips* and *ih* anterior and anteromedial to seta p_3, respectively, and *iad* anteromedial to seta ad_3 (Figs. 1a, 2, 3a).

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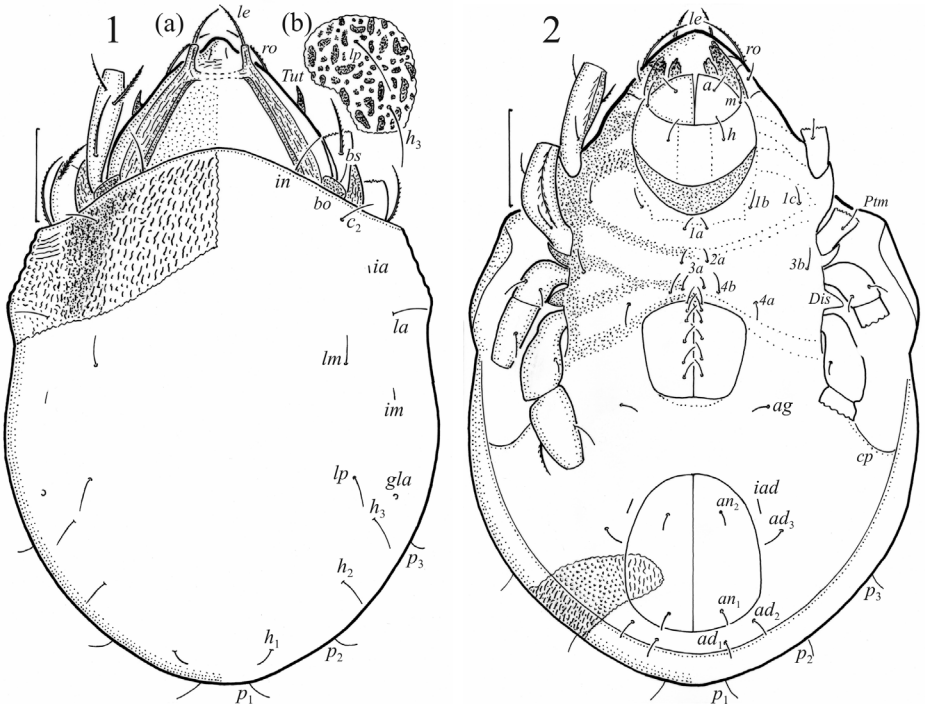

FIGURES 1–2. *Limnozetes solhoyorum* **sp. nov.**, adult, legs partially drawn, scale bar 50 μm. 1. (a) Dorsal aspect, (b) region of setae *lp* and h_3 (enlarged). 2. Ventral aspect.

Gnathosoma. Subcapitular seta *h* as long as *m* (23), seta *a* slightly shorter (16), all smooth (Figs. 2, 5b). Chelicera (length 87–89, width 38) with setae of similar length (12), *cha* thicker than *chb*, both barbed (Fig. 3b). Palp (length 55–57) with short and smooth setae (Figs. 3c, 5b, 6b, 6d), palpal eupathidium *acm* fused with solenidion ω at some distance from insertion of solenidion, eupathidia ul_1, ul_2 and *su* short (Figs. 3c, 6b, 6d). Formula of palp setae (trochanter to tarsus + solenidion ω): 0-2-1-3-9(1).

Ventral aspect. All epimeral setae short and smooth (Figs. 2, 4d), formula of epimeral setae 3-1-2-2. Six pairs of genital setae, all short and smooth, inserted on inner part of genital plates. One pair of aggenital setae as short as genital setae. Anadal setae short, but slightly longer than anal setae. Ventral and anal plate with elongated and rounded foveae (Figs. 4d, 5c).

Legs. Seta *d* on femora I–III very long, curved and barbed (Fig. 7). Seta *l″* on genua I and II relatively thick, famulus ε on tarsus I short, solenidia ω_1 and ω_2 on tarsi I and II fused at some distance from insertions (Figs. 6a, 7a, 7b, 7e), setae *d* and *l′* absent from genu IV, distal setae on tarsi short, thick and barbed (Fig. 6c, 7). Formulae of leg setae [trochanter to tarsus (+ solenidia)]: I—1-4-3(1)-4(2)-15(2); II—1-4-3(1)-4(1)-14(2); III—2-3-1(1)-3(1)-13; IV—1-2-0-3(1)-10. Tarsi heterotridactylous.

Juvenile stages

Larva oval in dorsal aspect, light brown, cuticle plicate (Fig. 8). Prodorsum subtriangular, all prodorsal setae thin and smooth; *ro* of medium size, *le* and *in* long and *ex* short. Mutual distance between setal pair *le* about two times longer than between setal pair *ro*, and mutual distance between setal pair *in* about four times longer than between pair *ro*. Pair *le* inserted closer to pair *ro* than to

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pair *in*. Opening of bothridium small, oval, bothridial seta setiform and longer than seta *in*. Area between bothridia with transverse folds, lateral parts with longitudinal folds.

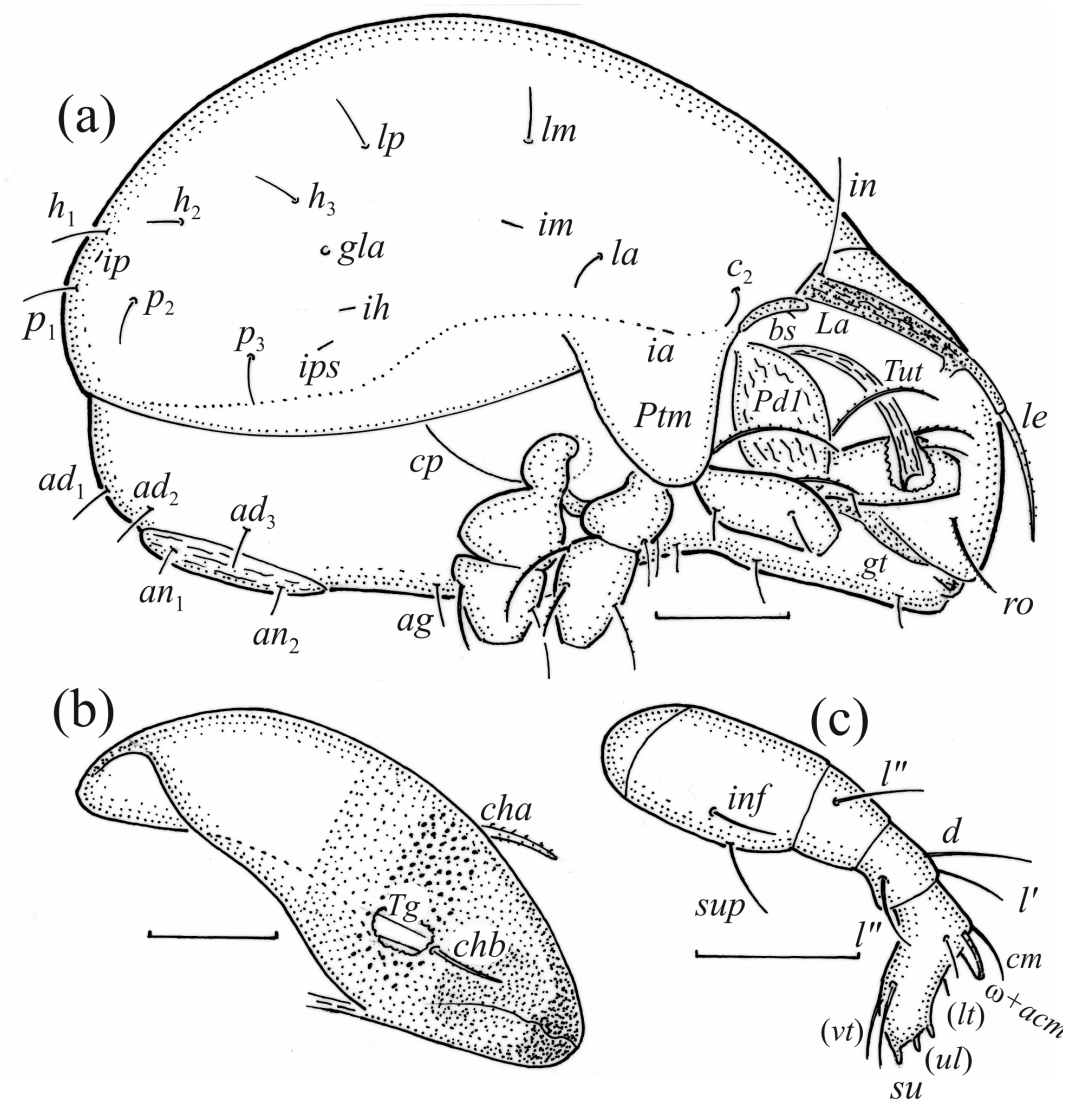

FIGURE 3. *Limnozetes solhoyorum* **sp. nov.**, adult. (a) Lateral aspect, legs partially drawn, scale bar 50 μm; mouthparts, right side, antiaxial aspect, scale bars 20 μm, (b) chelicera (Trägårdh organ indicated in 'transparent' area), (c) palp.

Gastronotum of larva with 12 pairs of setae, including h_3 inserted laterally to medial part of anal valves (Figs. 9a, 10a). Setae of *c*-series and h_3 minute, other gastronotal setae short, but posterior setae, especially seta *lp*, longer than other setae (Fig. 8, 10a, Table 1), all smooth. Cupules not observed in plicate cuticle. Opisthonotal gland opening anterolateral to *lp* (Fig. 10a). Paraproctal valves (segment PS) glabrous. Most leg setae short, setae *l′* and *l″* on all genua and tibiae thicker than *v′* on tibiae (Fig. 11).

Prodorsum of protonymph porose, prodorsal setae and bothridial seta as in larva. Gastronotum of protonymph with 15 pairs of setae due to appearance of setae of *p*-series (Fig. 9b), retained in subsequent stages (Figs. 12a, 12b); all short and smooth. In protonymph, one pair of genital setae

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present on genital valves, and two pairs added in deutonymph and tritonymph each, all short and smooth. In deutonymph, one pair of aggenital setae and three pairs of adanal setae added, and retained in tritonymph (Figs. 12a, 12b), all short and smooth. In protonymph and deutonymph, anal valves glabrous, in tritonymph two pairs of short and smooth anal setae present. Cupules not observed in plicate cuticle, opisthonotal gland opening anterolateral to seta *lp* (Fig. 10b). Some anterior and medial setae hardly visible in plicate cuticle, posterior marginal setae on gastronotum longer than other setae (Figs. 10b, 12a, 12b, 13, 14, 15a). Palp of tritonymph with short and smooth setae, palpal eupathidium *acm* fused with solenidion ω at some distance from insertion, eupathidia ul_1, ul_2 and *su* short (Figs. 15c, 15d). Leg segments stocky, most leg setae short, setae *l′* and *l″* on genua I and II and tibiae I and II thicker than seta *v′* on tibiae I and II (Fig. 16a, 16b). Famulus ε on tarsus I short, solenidia ω_1 and ω_2 on tarsi I and II fused together at some distance from insertions (Figs. 16a, 16b, 16e, 17a, 17b). In tritonymph, seta *l″* on femora I–III present or absent, and setae *d* and *l′* from genu IV absent (Fig. 16).

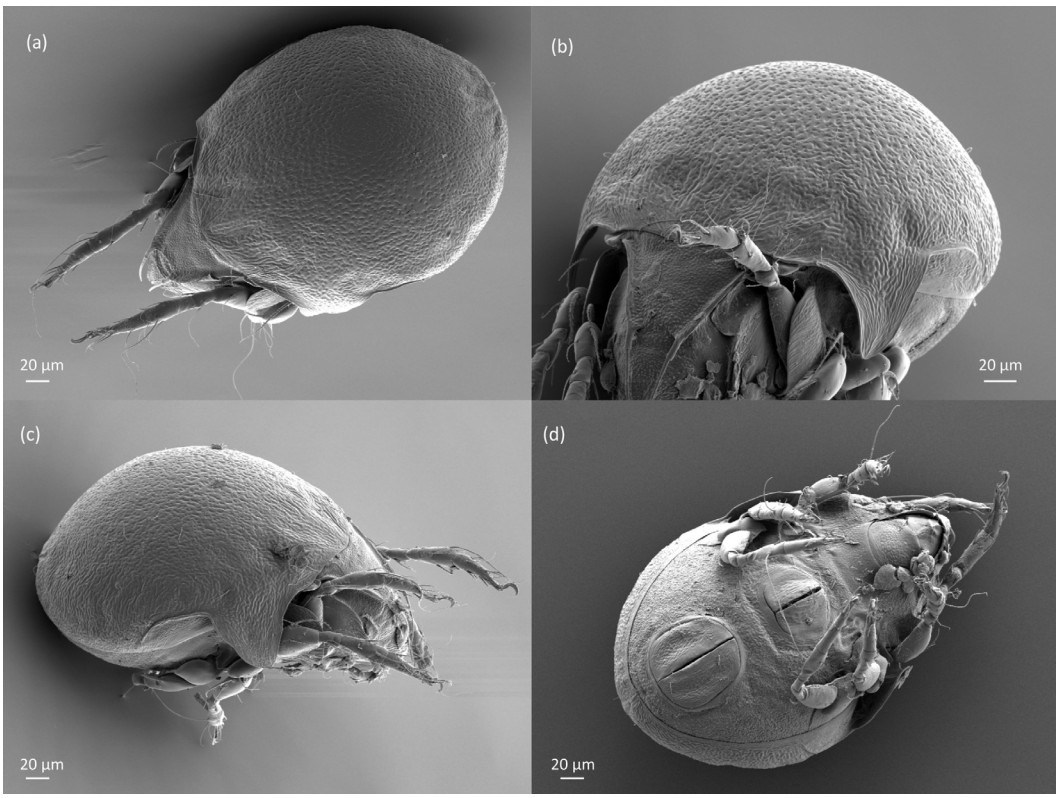

FIGURE 4. *Limnozetes solhoyorum* **sp. nov.**, adult, SEM micrographs. (a) Dorsal aspect, (b) fronto-lateral aspect, (c) lateral aspect, (d) ventral aspect.

Summary of ontogenetic transformations

In all juveniles of *L. solhoyorum*, setae *le* and *in* are long, *ro* is of medium size and *ex* is short, whereas in the adult *in*, *le* and *ro* are long, and *ex* is short. The bothridium is small and rounded in all juveniles, but in the adult it gets larger, and develops a dorsal expansion. In all juveniles, the bothridial seta is long, setiform, whereas in adults it is short, setiform or absent. In all instars, the gastronotal setae are short. The larva has 12 pairs of gastronotal setae, including h_3, the nymphs have 15 pairs (*p*-series is added). The notogaster of adult loses setae c_1, c_3 and of *d*-series, such that 10 pairs of setae remain, all are short and smooth. The formula of gastronotal setae of *L. solhoyorum* is

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12-15-15-15-10 (from larva to adult), formulae of epimeral setae are 2-1-2 (larva), 3-1-2-1 (protonymph) and 3-1-2-2 (deutonymph, tritonymph and adult). Formula of genital setae is 1-3-5-6 (protonymph to adult) and formula of aggenital setae is 1-1-1 (deutonymph to adult). Fomula of segments PS–AN is 03333-0333-022. The ontogeny of leg setae and solenidia of *L. solhoyorum* is given in Table 2.

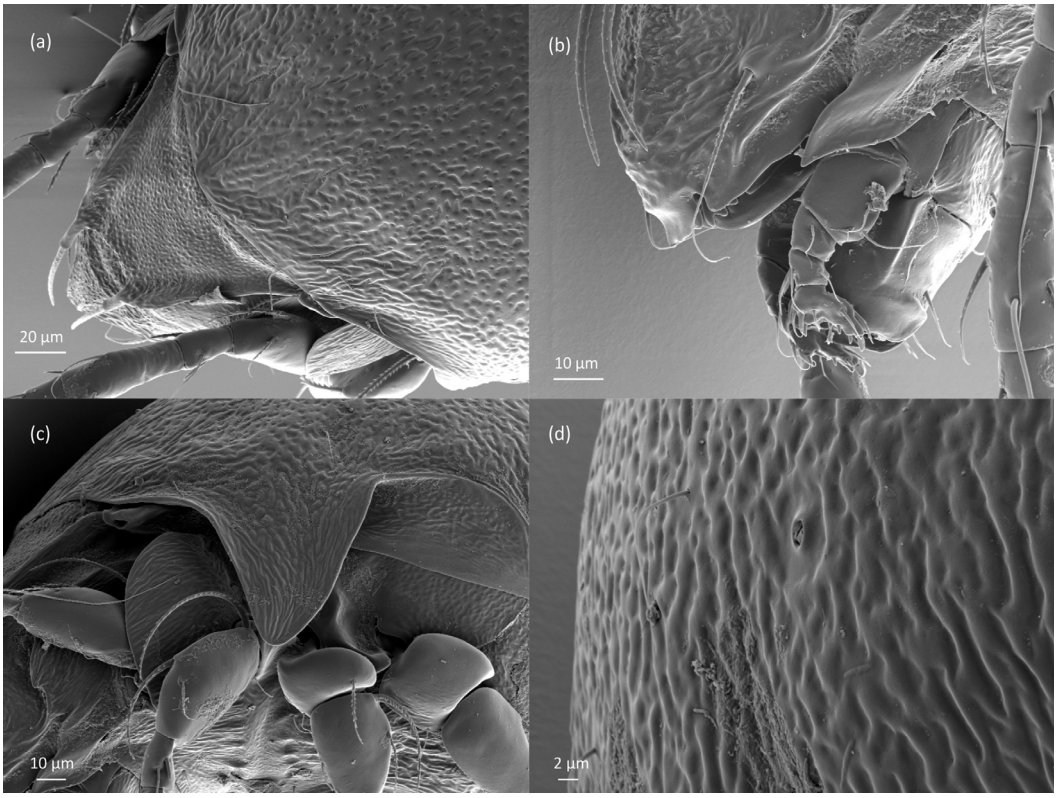

FIGURE 5. *Limnozetes solhoyorum* **sp. nov.**, adult, SEM micrographs. (a) Prodorsum and anterior part of notogaster, dorsal aspect, (b) palp and hypostomatic plate, lateral aspect, (c) pteromorph, ventrolateral aspect, (d) region of *gla* opening.

Distribution, ecology and biology

We found a large population of *L. solhoyorum* **sp. nov.** in a small pool in submerged moss *Warnstorfia fluitans*. In this pool, 5,994 individuals of *L. solhoyorum* were collected in 2 dm^3 of moss, corresponding to density 150,000 individuals per m^2. This species constituted 82% of all Oribatida, being accompanied by *Hydrozetes octosetosus* Willmann, 1932a (17% of Oribatida) and single individuals of *Hydrozetes lacustris* (Michael 1882), *Limnozetes foveolatus* Willmann, 1939, *Tyrphonothrus maior* (Berlese 1910), *Oppiella nova* (Oudemans 1902) and *Diapterobates humeralis* (Hermann 1804). Juveniles of *L. solhoyorum* constituted 24% of all individuals of this species and the stage structure was: 119 larvae, 539 protonymphs, 732 deutonymphs, 50 tritonymphs and 4,554 adults. In the same bog, one adult of *L. solhoyorum* was also found in *Sphagnum pulchrum* (Lindb. ex Braithw.) Warnst and two adult individuals were found in *S. riparium* Ångstr. (mentioned as *Limnozetes*. sp. 1 in Seniczak *et al*. 2019b). Only females were noted, and 70% of them were gravid, carrying one or two large eggs. The eggs were relatively large (157 x 94), comprising 44% of total body length of females.

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TABLE 2. Ontogeny of leg setae (Roman letters) and solenidia (Greek letters) in *Limnozetes solhoyorum* **sp. nov.**

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	–	*d*, *bv″*	(*l*), σ	(*l*), *v′*, φ_1	(*ft*), (*tc*), (*p*), (*u*), *a′*, *s*, (*pv*), ε, ω_1
Protonymph	–	–	–	–	ω_2
Deutonymph	–	*l′*	–	φ_2	–
Tritonymph	*v′*	*l″*[1]	–	–	(*it*)
Adult	–	*l″*[2]	*v′*	*v″*	–
Leg II					
Larva	–	*d*, *bv″*	(*l*), σ	*l′*, *v′*, φ	(*ft*), (*tc*), (*p*), (*u*), *a′*, *s*, (*pv*), ω_1
Protonymph	–	–	–	–	–
Deutonymph	–	*l′*	–	–	ω_2
Tritonymph	*v′*	–	–	*l″*	(*it*)
Adult	–	*l″*	*v′*	*v″*	–
Leg III					
Larva	–	*d*, *ev′*	*l′*, σ	*v′*, φ	(*ft*), (*tc*), (*p*), (*u*), *s*, (*pv*)
Protonymph	–	–	–	–	–
Deutonymph	*l′*	–	–	–	–
Tritonymph	–	*l*[1]	–	*l′*	(*it*)[1]
Adult	*v′*	*l*[2]	–	*v″*	(*it*)[2]
Leg IV					
Protonymph	–	–	–	–	*ft″*, (*p*), (*u*), (*pv*)
Deutonymph	–	*d*, *ev′*	–	*v′*, φ	(*tc*), *s*
Tritonymph	*v′*	–	–	*l′*	–
Adult	–	–	–	*v″*	–

Note: structures are indicated where they are first added and are present through the rest of ontogeny; pairs of setae in parentheses, dash indicates no additions; [1]present in some individuals, [2]added if absent in previous stage.

Type material

The holotype (female) and five paratypes (females) with above collection data are deposited in University Museum of Bergen, University of Bergen, Bergen, Norway.

Etymology

This species is named in honour of two oribatologists working in Norway: Dr. Ingrid Wunderle-Solhøy and Prof. Torstein Solhøy, University of Bergen.

Comparison of the morphology of *Limnozetes solhoyorum* with congeners

Limnozetes Hull, 1916, with the type species *L. ciliatus*, comprises medium sized mites as adults (266–390 µm), with *Limnozetes* characters. Subías (2019) listed 14 species in *Limnozetes*, including *Limnozetes palmerae* Behan-Pelletier, 1989, but the latter species we consider a junior synonym of *L. foveolatus* Willmann, 1939, as suggested by Siepel *et al*. (2009) and supported by Lehmitz *et al*. (2019). Among these species, the largest is *L. similis* Pérez-Íñigo & Baggio, 1989 and the smallest is *L. foveolatus*. The body length of most species overlaps (Table 3). These 14 species also differ one

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from another by the presence of translamella, shape of bothridial seta, shape of notogaster and pteromorph, length of some setae and presence of setae *d* and *l′* on genu IV.

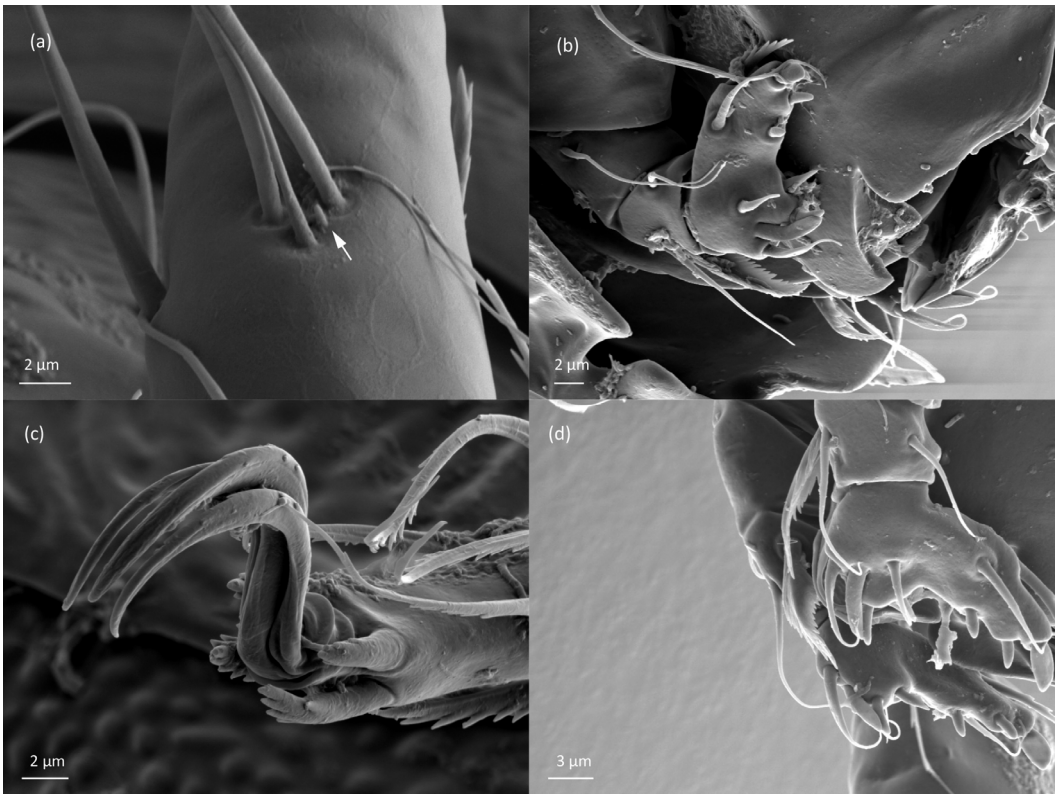

FIGURE 6. *Limnozetes solhoyorum* **sp. nov.**, adult, SEM micrographs. (a) Region of solenidia ω_1 and ω_1 on tarsus I, arrow points famulus ε, (b) shape of palpal tarsus, ventrolateral aspect, (c) shape of claws of leg IV, lateral aspect, (d) part of palpal tibia and tarsus, lateral aspect.

Based on the ontogeny of leg setae (Table 2), setae *d* and *l′* are also absent from genu IV in deutonymphs and tritonymphs of the '*rugosus* group' (*L. borealis*, *L. guyi*, *L. latilamellatus*, *L. rugosus*, *L. solhoyorum* **sp. nov.**), with plicate cuticle (Behan-Pelletier 1989; Seniczak & Seniczak 2010), whereas these nymphs of the '*ciliatus* group', with boat-shaped juveniles, have these setae. Among the adults of the '*rugosus* group', with plicate juveniles, *L. borealis* and *L. rugosus* have an incomplete translamella, whereas other species lack the translamella. However, in *L. latilamellatus* the lamella is wide, without lamellar cusp, which is unique in *Limnozetes*, whereas in *L. solhoyorum* and *L. guyi* the lamella is narrow, with lamellar cusp. From this comparison it is evident that *L. solhoyorum* is most similar to *L. guyi*, but differs from it mainly by shorter prodorsal seta *in* and notogastral setae, especially p_1, and by the distribution of posterior setae on the notogaster. In *L. solhoyorum*, seta h_1 is inserted more medially than in *L. guyi* (Behan-Pelletier 1989). The tritonymph of *L. solhoyorum* differs from that of *L. guyi* mainly by shorter gastronotal seta c_3, *dm*, *dp*, *lm* and *lp*. The body size of the adult of *L. solhoyorum* overlaps with that of *L. rugosus*, and the shape of body, pteromorph, leg setae, solenidia and famulus ε is also similar in both species (Figs. 4, 5a, 5c, 6a, 7, 18, 19, 20). The latter species has incomplete translamella, which in the former species is absent, and differs from it also by the length:width ratio of the notogaster and pteromorph (Table 3).

The tritonymph of *L. solhoyorum* differs from that of *L. rugosus* in few morphological characters (Table 4). The former species has higher number of longer setae on the gastronotum than

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the latter species both in the larva (*lp*, h_1, h_2, and *lm*, respectively) and nymphs (p_1, *h*-series, and *lp*, h_1, h_2, respectively), and differs also from it by the shape of setae *in* and h_3 in the larva. Moreover, the shape of leg setae and solenidia of the adult and tritonymph of *L. rugosus* (Figs. 20, 21) is similar as in *L. solhoyorum* presented above, but the ontogeny of setae differs in these species. In *L. rugosus*, seta *l″* is more often added on femora I and II than in *L. solhoyorum*, *l″* can appear on tibia II in the deutonymph or tritonymph (versus in tritonymph in *L. solhoyorum*), and *l′* appears in the deutonymph (versus in the tritonymph in adult of *L. solhoyorum*). The shape of body, palp and leg setae, solenidia and famulus ε of tritonymph of *L. rugosus* (Figs. 21, 22) is similar as in the tritonymph of *L. solhoyorum* (Figs. 14–17).

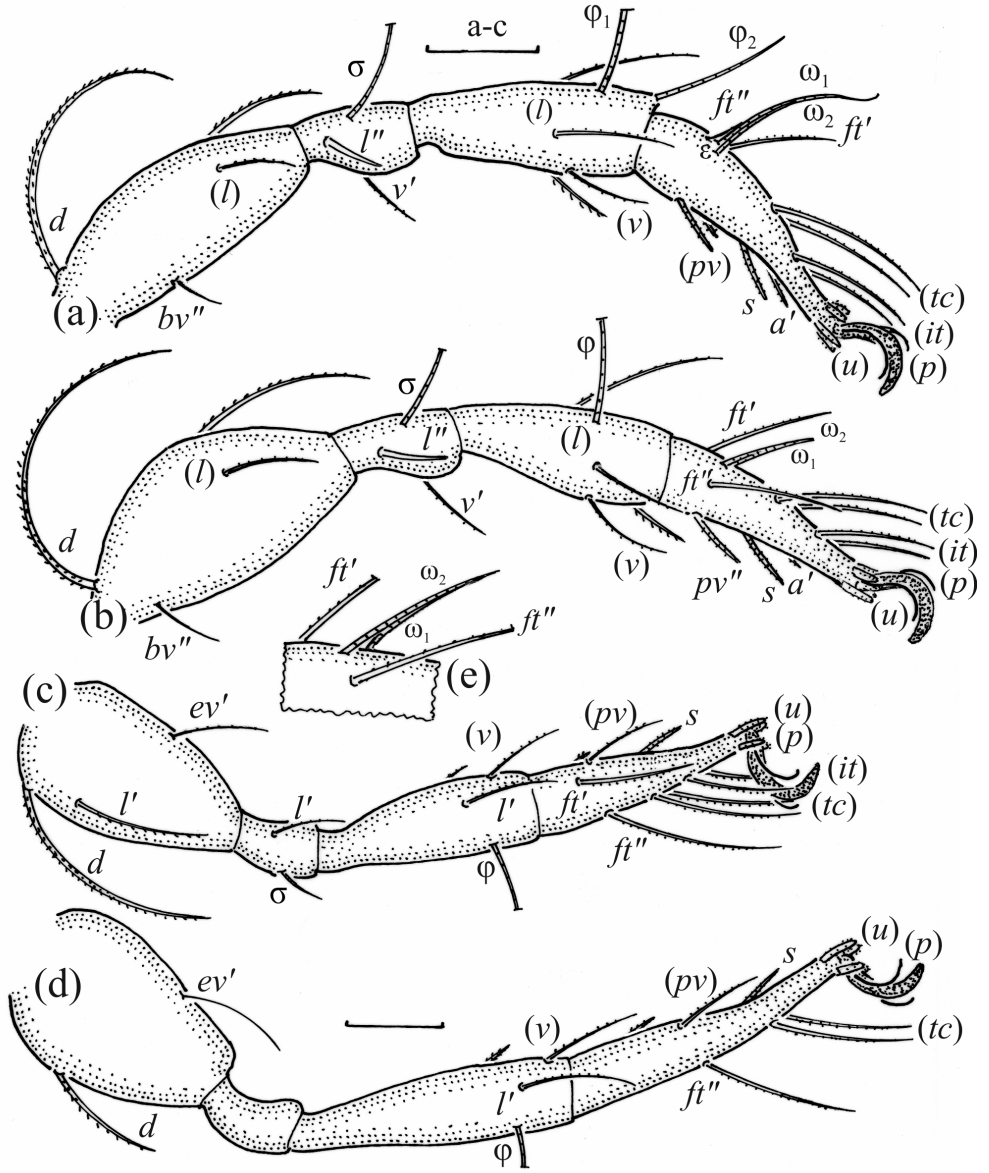

FIGURE 7. *Limnozetes solhoyorum* **sp. nov.**, leg segments of adult (part of femur to tarsus), right side, antiaxial aspect, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, genu (*l′*); (b) leg II, genu (*l′*), tarsus (*pv′*); (c) leg III; (d) leg IV; (e) solenidia ω_1 and ω_2 on tarsus II, lateral aspect.

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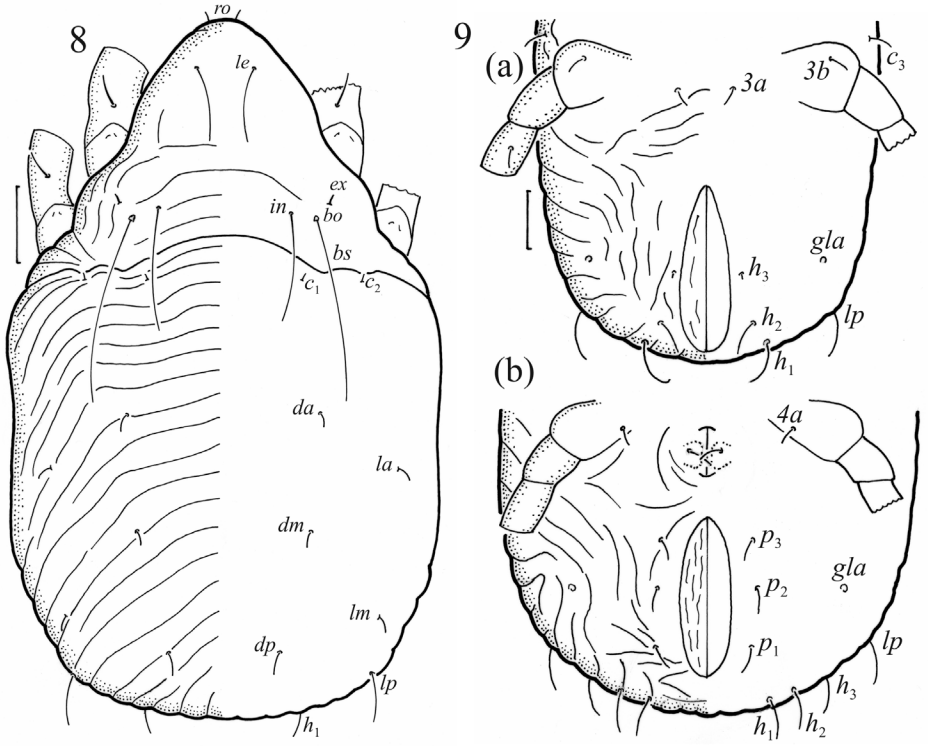

FIGURES 8–9. *Limnozetes solhoyorum* **sp. nov.**, legs partially drawn, scale bar 50 µm. 8. Larva, dorsal aspect. 9. Ventral aspect of hysterosoma, (a) larva, (b) protonymph.

TABLE 3. Selected morphological characters of *Limnozetes* species.

Species	Body length in µm	Presence of *Tr*	Shape of *bs*	Convex Ng	Length/width of:		Length of seta:		Setae on genu IV	Cuticle of juveniles
					Ng	Ptm	*in*	*lp*		
L. amnicus Behan-Pelletier, 1989	343–373	Absent	Clavate	No	1.3:1	0.6:1	Medium sized[a]	Medium sized[b]	Present	Rare folds
L. atmetos Behan-Pelletier, 1989	363–365	Present	Setiform	No	1.1:1	1.2:1	Short	Medium sized[b]	Present	?
L. borealis Behan-Pelletier, 1989	343–376	Incomplete	Setiform	Yes	1.2:1	1.4:1	Long	Short	Absent	Plicate
L. ciliatus (Schrank, 1803)	270–330	Present	Clavate	No	1.3:1	?	Short	Medium sized[b]	Present	Rare folds
L. feuerborni Willmann, 1932b	300–330	Present	Setiform	No	?	?	Short	?	?	Rare folds
L. foveolatus Willmann, 1939	266–292	Present	?	No	1.3:1	0.6:1	Short	Short	Present	Rare folds
L. guyi Behan-Pelletier, 1989	324–343	Absent	Clavate/ setiform	Yes	1.2:1	0.9:1	Long	Medium sized[b]	Absent	Plicate
L. latilamellatus Behan-Pelletier, 1989	324–343	Absent[c]	Setiform	Yes	1.1:1	1.9:1	Medium sized[a]	Medium sized[b]	Absent	Plicate
L. lustrum Behan-Pelletier, 1989	343–365	Incomplete	Clavate	No	1.2:1	0.9:1	Short	Short	Present	Rare folds
L. onondaga Behan-Pelletier, 1989	311–343	Incomplete	Clavate	No	1.3:1	0.7:1	Short	Short	Present	Rare folds
L. pustulatus (Mahunka, 1987)	310–312	Incomplete	Clavate	No	1.3:1	0.8:1	Short	Medium sized[b]	?	?
L. rugosus (Sellnick, 1925)	350	Incomplete	Setiform	Yes	1.3:1	1.0:1	Medium sized[a]	Short	Absent	Plicate
L. silvicola Hammer, 1961	390	Incomplete	Clavate	No	1.2:1	?	Short	Short	?	?
L. similis Pérez-Íñigo & Baggio, 1989	370–378	Incomplete	Setiform	No	1.3:1	1.2:1	Long	Short	?	?
L. solhoyorum **sp. nov.**	344–364	Absent	Setiform	Yes	1.2:1	1.2:1	Medium sized[a]	Short	Absent	Plicate

[a]Does not reach a half length of the lamella, [b]reaches insertion of seta h_3, [c]this species has wide lamella, without lamellar cusp, which is unique in *Limnozetes*.

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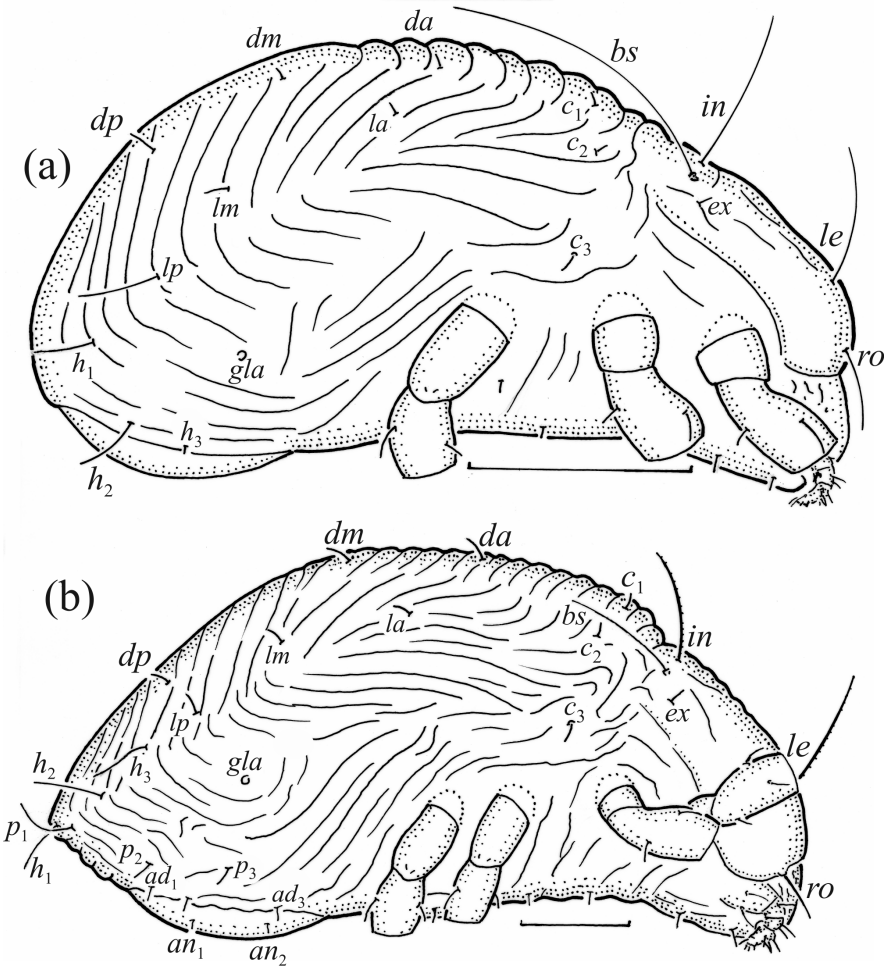

FIGURE 10. *Limnozetes solhoyorum* **sp. nov.**, lateral aspect, legs partially drawn, scale bars 50 μm. (a) Larva, (b) tritonymph.

Discussion

The juveniles of *L. solhoyorum* **sp. nov.** are stocky, with plicate cuticle and short setae on the gastronotum, as other species of the '*rugosus* group' of *Limnozetes* proposed by Seniczak and Seniczak (2009a). All species also lack setae *d* and *l′* on genu IV in the deutonymph and tritonymph (Behan-Pelletier 1989; Seniczak & Seniczak 2010). By contrast, the juveniles of the '*ciliatus* group' are boat-shaped, with slightly folded cuticle and blade-like marginal setae on the gastronotum, and they have setae *d* and *l′* on genu IV in the deutonymph and tritonymph.

In the adults of *Limnozetes*, only the presence of setae *d* and *l′* on genu IV supports the division of *Limnozetes* in '*rugosus* group' and '*ciliatus* group', whereas using the other morpholological characters is risky. For example, in most species of the '*rugosus* group', the notogaster of adults is more convex than in most species of the '*ciliatus* group', but it is also convex in *L. lustrum* from the '*ciliatus* group' (see Seniczak & Seniczak 2010). In the '*rugosus* group', the range of length to width ratio of notogaster is smaller (1.1:1–1.3:1) than in the '*ciliatus* group' (1.2:1–1.3:1), and this ratio of pteromorph is larger (0.9:1–1.9:1) than in the '*ciliatus* group' (0.6:1–0.9:1), but in several species of both groups each ratio overlaps.

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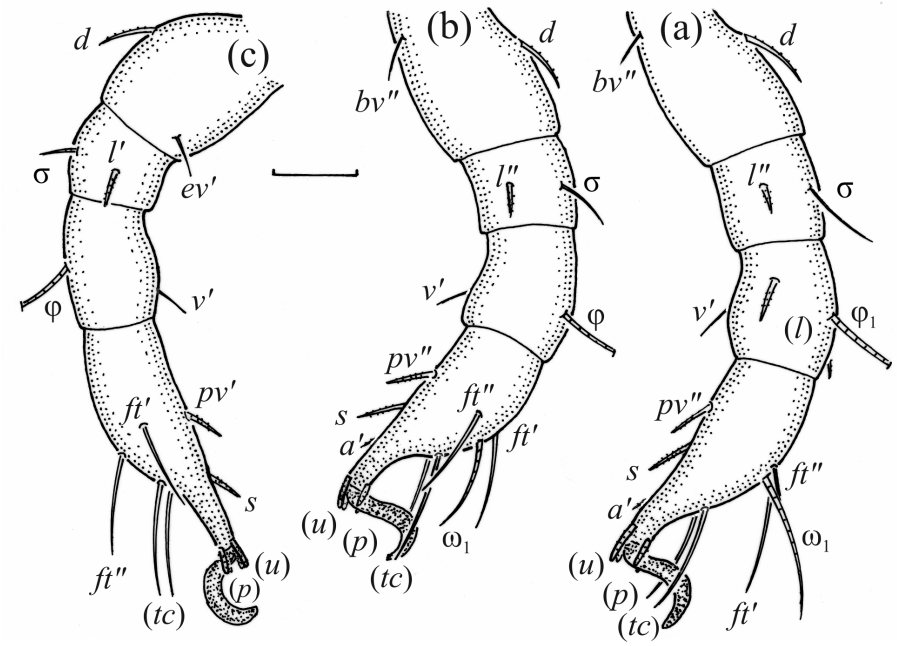
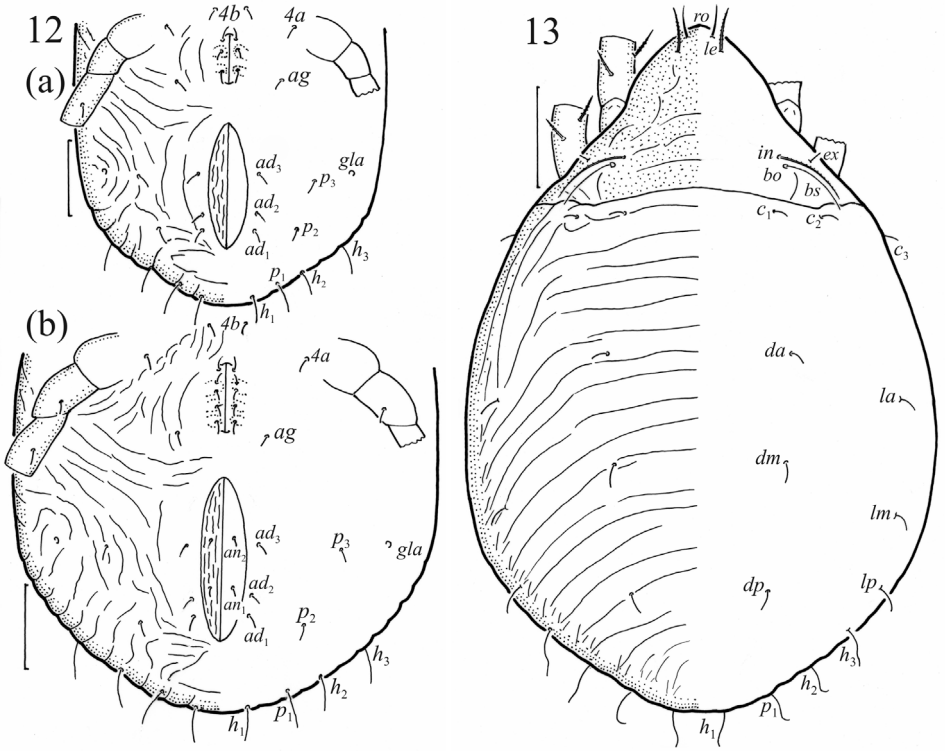


FIGURE 11. *Limnozetes solhoyorum* **sp. nov.**, leg segments of larva (part of femur to tarsus), right side, antiaxial aspect, setae on the opposite side not illustrated, but indicated in the legend, scale bar 10 μm. (a) Leg I, genu (*l′*), tarsus (*pv′*); (b) leg II, tibia (*l′*), tarsus (*pv′*); (c) leg III, tarsus (*pv″*).



FIGURES 12–13. *Limnozetes solhoyorum* sp. nov., legs partially drawn, scale bar 50 μm. 12. Ventral aspect of hysterosoma, (a) deutonymph, (b) tritonymph. 13. Tritonymph, dorsal aspect.

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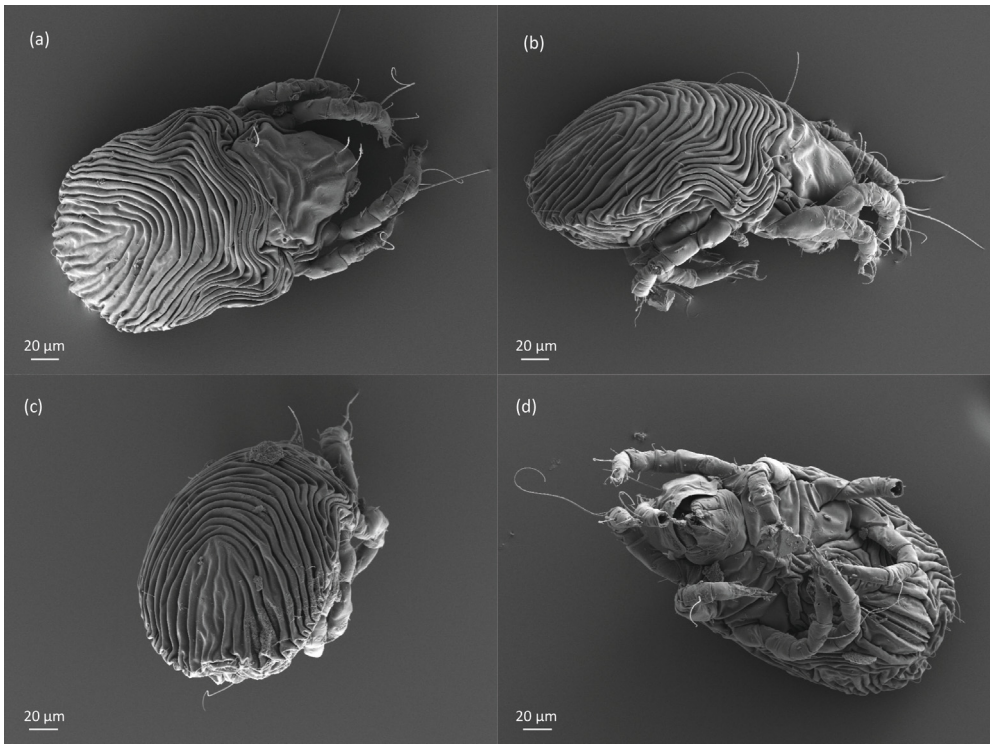

FIGURE 14. *Limnozetes solhoyorum* **sp. nov.**, tritonymph, SEM micrographs. (a) Dorsal aspect, (b) lateral aspect, (c) dorsoposterior aspect, (d) ventral aspect.

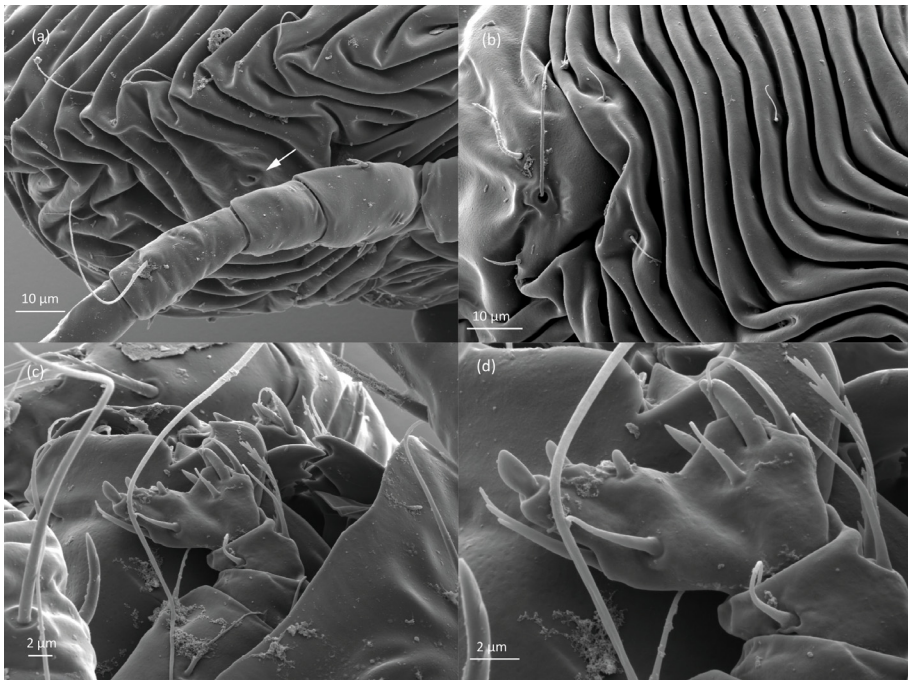

FIGURE 15. *Limnozetes solhoyorum* **sp. nov.**, tritonymph, SEM micrographs. (a) Posterior part of hysterosoma, lateral aspect, arrow points *gla* opening (b) region of bothridium, dorsolateral aspect, (c), part of palpal femur, genu, tibia and tarsus, ventral aspect (d) part of palpal tibia and tarsus, ventral aspect.

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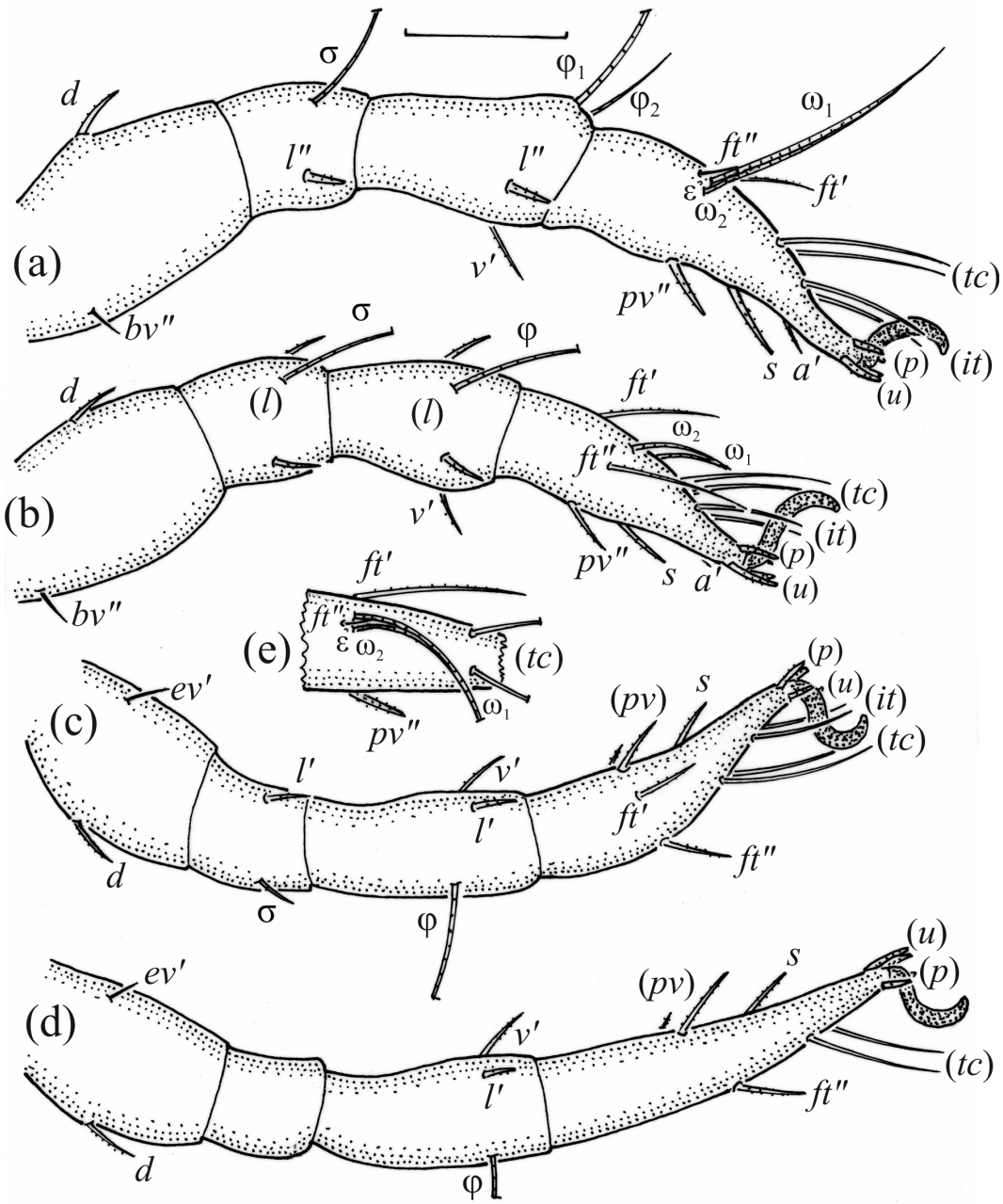

FIGURE 16. *Limnozetes solhoyorum* **sp. nov.**, leg segments of tritonymph (part of femur to tarsus), right side, antiaxial aspect, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, femur (*l'*), genu (*l'*), tibia (*l'*), tarsus (*pv'*); (b) leg II, femur (*l'*), tarsus (*pv'*); (c) leg III; (d) leg IV; (e) region of solenidia ω_1 and ω_2 on tarsus I.

Grandjean (1951) compared several morphological characters of *Limnozetes* and *Hydrozetes* Berlese, 1902 and stated that these genera are closely related, and morphological characters are more derived in *Limnozetes* than in *Hydrozetes*. This relationship is also well-observed in a similar way of loss of setae of *c*-series in these genera, which reflects their phylogeny and was supported by molecular studies (Krause *et al*. 2016). In both genera, the loss of these setae starts with seta c_1 and

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continues to c_3, according to the hypothesis of Shaldybina (1972). However, in some species of *Hydrozetes*, all setae of *c*-series are present (Seniczak *et al*. 2007, 2009), whereas in some individuals of *L. rugosus* only c_2 and c_3 are present (Seniczak & Seniczak 2010), indicating more derived character than in some species of *Hydrozetes*.

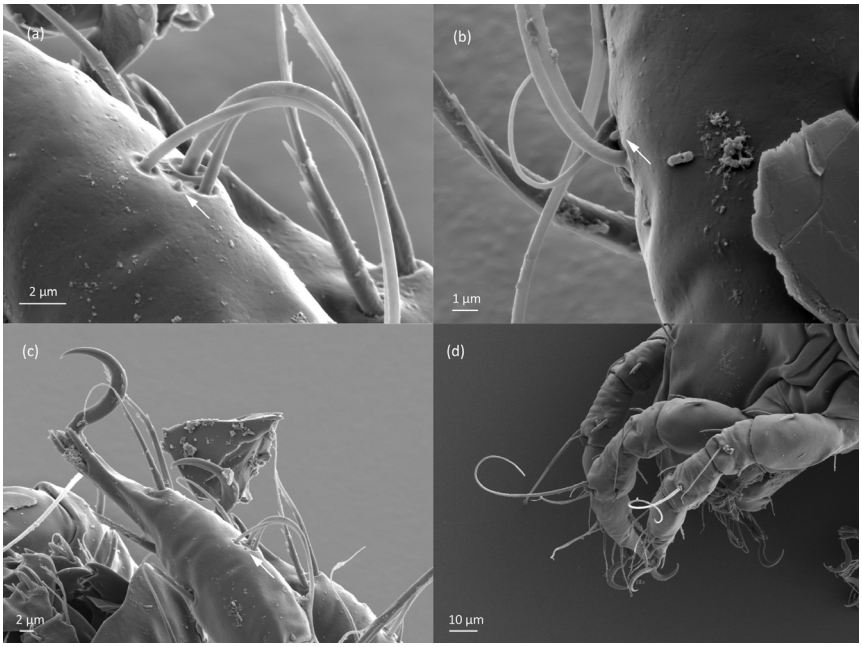

FIGURE 17. *Limnozetes solhoyorum* sp. nov., tritonymph, SEM micrographs, arrow points famulus ε, (a) region of solenidia ω_1 and ω_1 on tarsus I, lateral aspect, (b) the same as in a, lateral aspect, (c) tarsus I, lateral aspect, (d) solenidion φ on tibiae I and II.

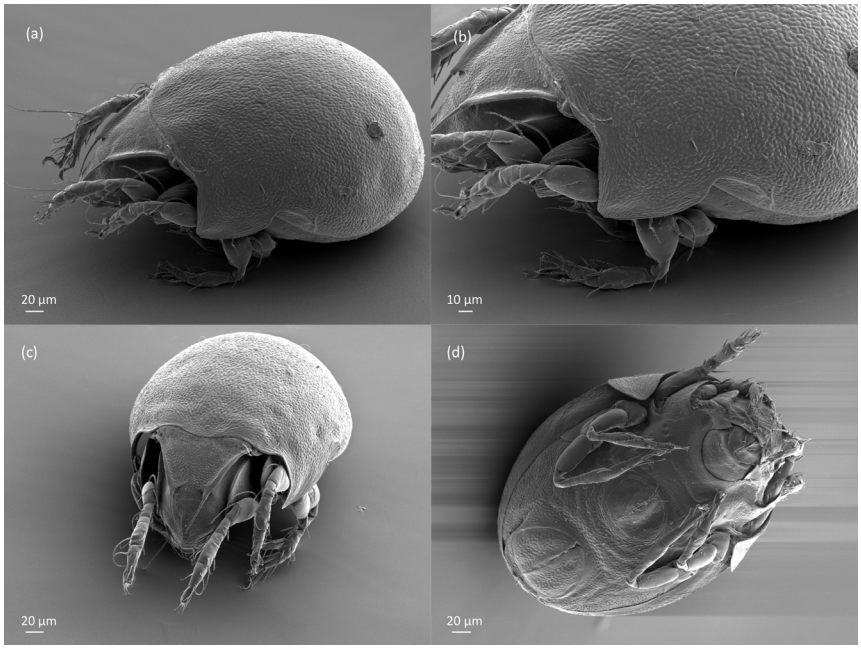

FIGURE 18. *Limnozetes rugosus*, adult, SEM micrographs. (a) Dorsolateral aspect, (b) anterior and medial part of body, dorsolateral aspect, (c) frontal aspect, (d) ventral aspect.

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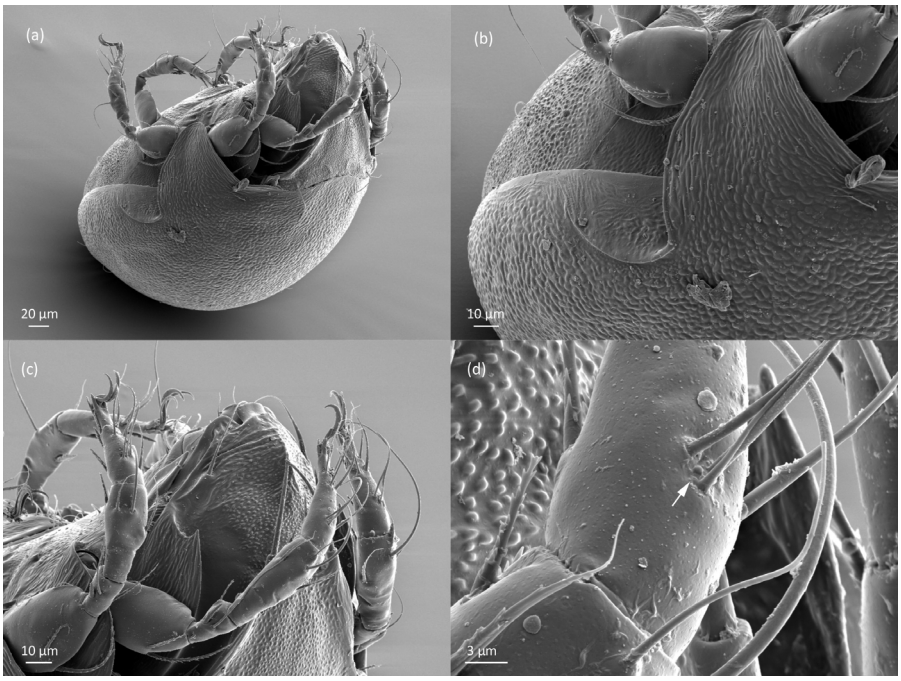

FIGURE 19. *Limnozetes rugosus*, adult, SEM micrographs. (a) Anterior part of body, lateral aspect, (b) shape of pteromorph, (c) shape of solenidia of legs I and II, (d) region of solenidia ω_1 and ω_1 on tarsus I, arrow points famulus ε.

TABLE 4. Selected morphological characters of juveniles of *Limnozetes solhoyorum* **sp. nov.** and *L. rugosus*.

Morphological characters	*L. solhoyorum*	*L. rugosus*[a]
Tritonymph		
Longer gastronotal setae	p_1, *h*-series	*lp*, h_1, h_2
Seta *l′* on femur III	Present/Absent	Present
Larva		
Shape of seta *in*	Smooth	Barbed
Longer gastronotal setae	*lp*, h_1, h_2	*lm*
Shape of seta h_3	Minute	Short

[a]According to Seniczak and Seniczak (2010).

The ontogeny of leg setae of *Limnozetes* also differs from that of *Hydrozetes*. For example, some species of *Limnozetes* lost the famulus ε on tarsus I and many leg setae (setae *pl* on tarsus I, *a″* on tarsi I and II, setae *a′* and *a″* on other tarsi, *l′* and *d* on genu IV in deutonymph to adult), which are present in *Hydrozetes* (Seniczak *et al*. 2017). However, in *Limnozetes* species, tarsal setae *u* and *p* are short, thick and barbed, similarly as in *Hydrozetes* species (Seniczak & Seniczak 2008, 2009b; Seniczak *et al*. 2007, 2009, 2017), and these setae reflect their ecological importance. They cooperate with claws and help the mites to stick to water plants, which can be easily observed when manipulating the mites with the needle.

Our study shows the importance of SEM micrographs for better understanding of the morphology of *Limnozetes* species. For example, the hand made figures show similar sculpture of the adult of *L. solhoyorum* to that of *L. rugosus* and *L. borealis* (Behan-Pelletier 1989; Seniczak &

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Seniczak 2010), whereas the SEM micrographs clearly differentiate these species. The famulus ε on tarsus I is small and can be easily overlooked in light microscopy, but is well observed in SEM micrographs. The latter micrographs also show the shape of leg and palp setae, fusion of solenidia ω_1 and ω_2 on tarsi I and II in a certain distance from their insertions. However, some palp setae observed in SEM micrographs look thicker than those in the hand made figures, which probably results from coating the mites for the SEM study.

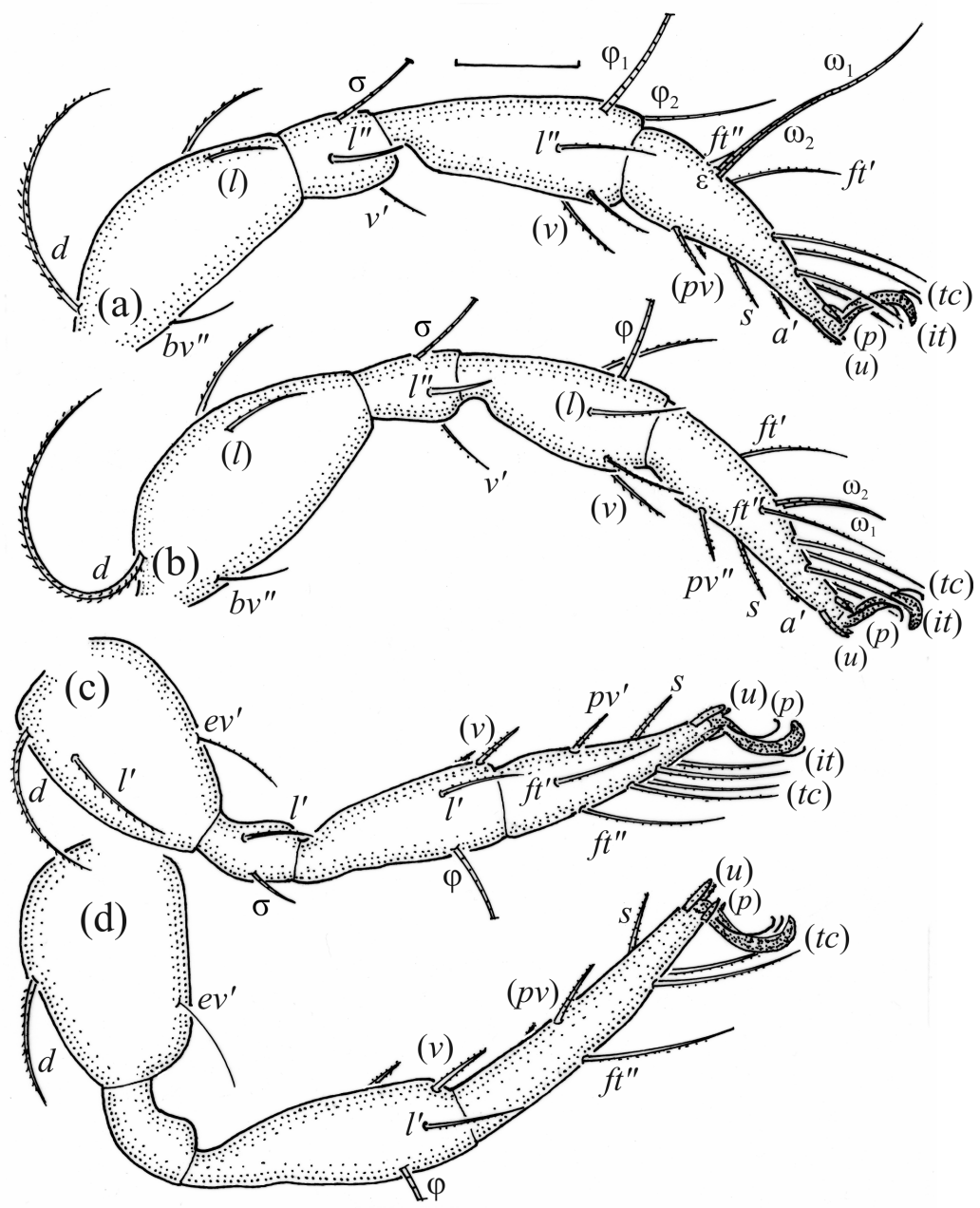

FIGURE 20. *Limnozetes rugosus*, leg segments of adult (part of femur to tarsus), right side, antiaxial aspect, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, genu (*l′*), tibia (*l′*); (b) leg II, genu (*l′*), tarsus (*pv′*); (c) leg III, tarsus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

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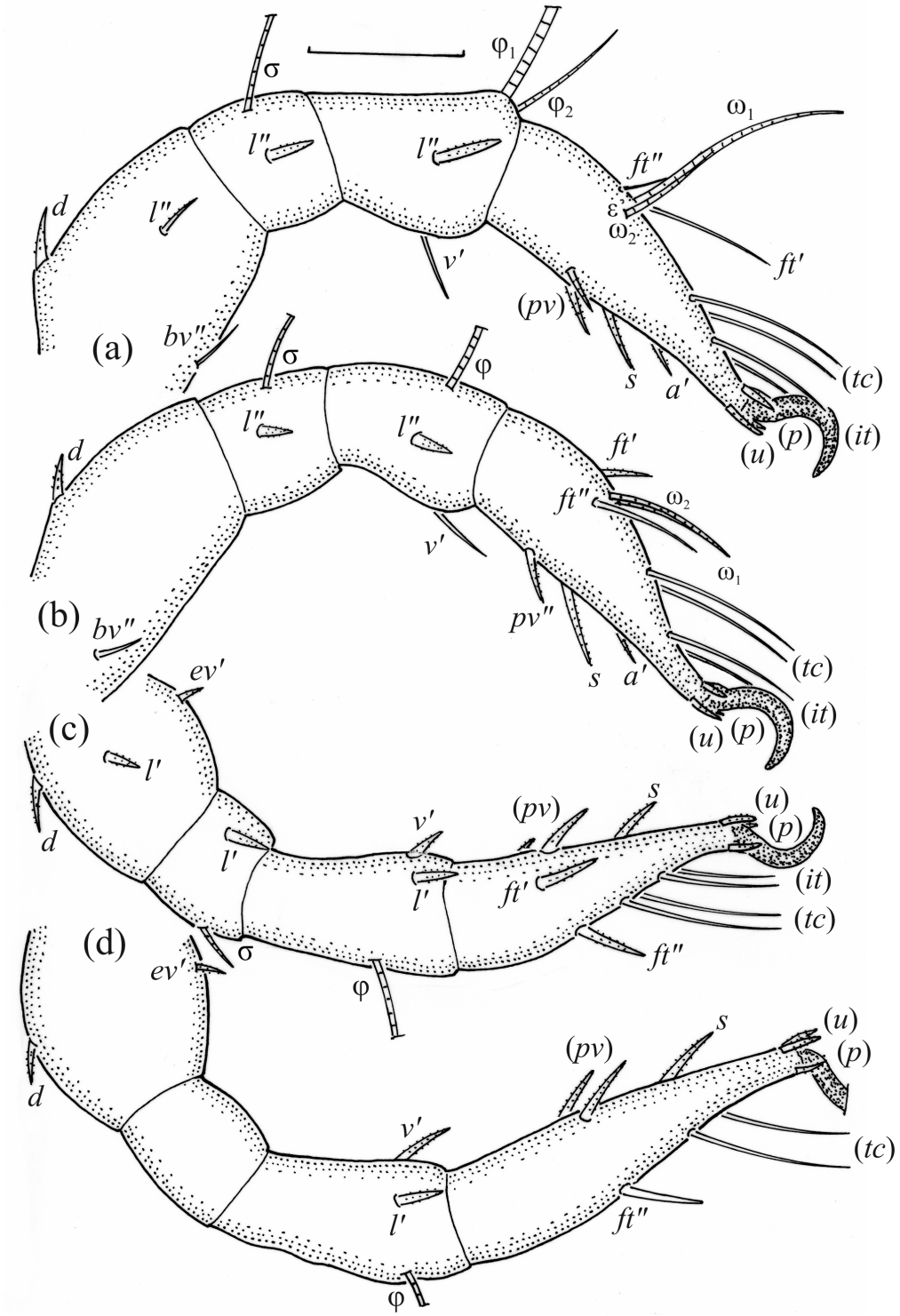

FIGURE 21. *Limnozetes rugosus*, leg segments of tritonymph (part of femur to tarsus), right side, antiaxial aspect, setae on the opposite side not illustrated, but indicated in the legend, scale bar 20 μm. (a) Leg I, femur (*l'*), genu (*l'*), tibia (*l'*); (b) leg II, femur (*l'*), genu (*l'*), tibia (*l'*), tarsus (*pv'*); (c) leg III; (d) leg IV.

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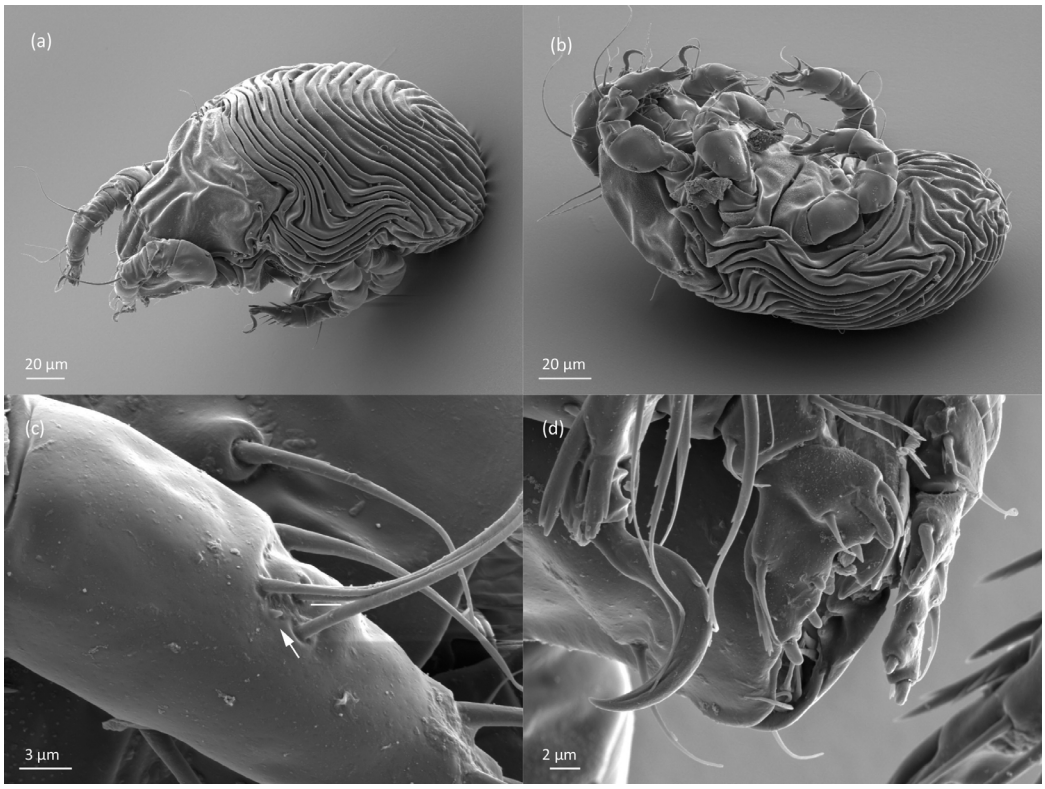

FIGURE 22. *Limnozetes rugosus*, tritonymph, SEM micrographs. (a) Dorsolateral aspect, (b) ventrolateral aspect, (c) region of solenidia ω_1 and ω_2 on tarsus I, arrow points famulus ε, (d) part of palpal tibia and tarsus, lateral aspect.

Acknowledgements

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