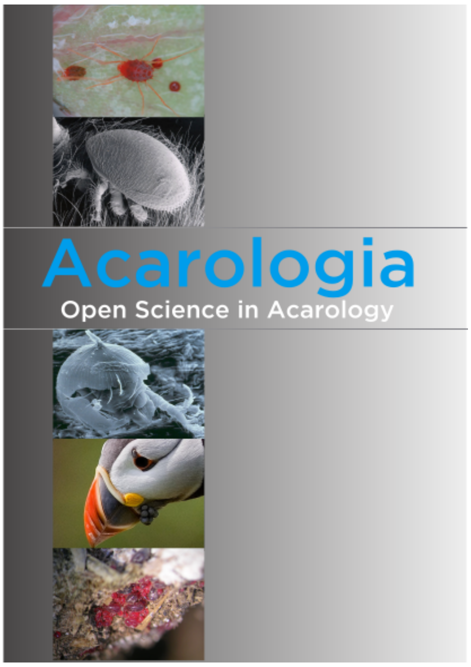

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Morphological ontogeny, distribution of *Hermannia scabra* (Acari: Oribatida: Hermanniidae) in Svalbard and descriptive population parameters

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ABSTRACT — The morphological ontogeny and distribution of *Hermannia scabra* (L. Koch, 1879) in Arctic Svalbard and descriptive population parameters were investigated. All instars of *H. scabra* are stocky, as in other species of *Hermannia* Nicolet, 1855, and have the same gastronotal setal ontogeny (12 pairs in the larve and 16 pairs in the nymphs and adults). In this species, the prodorsal setae are similar to other species of *Hermannia*, except for the bothridial seta which is clavate, as in *H. reticulata* Thorell, 1871. In other species of *Hermannia* the bothridial seta is setiform. Most prodorsal and gastronotal setae of *H. scabra* are phylliform whereas in other *Hermannia* species they are thickened. The number of epimeral setae in the nymphs and adults and the ontogeny of leg setae are characteristic for *H. scabra*. This species has a holarctic distribution and in Svalbard is not as common as *H. reticulata*, but it achieves higher density than the latter species, mainly due to the abundance of juveniles. *Hermannia scabra* prefers moist and wet localities, and in Svalbard the highest density is achieved in vegetation class 8 (wet vegetated flats, beaches, slopes and river fans with some exposed *Dryas* vegetation and graminoids *Luzula* sp.).

KEYWORDS — Oribatid mites; soil mites; Arctic area; stage structure; leg setation

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INTRODUCTION

Hermannia Nicolet, 1855 (Hermanniidae) is included in the cohort Nothrina (Norton and Behan-Pelletier 2009) but due to the brachypyline venter of the adult it is also treated as an intermediate genus between the lower (macropyline) and higher (brachypyline) oribatid mites (Norton and Behan-Pelletier 2009; Colloff 2011; Seniczak *et al*. 2017). Seniczak *et al*. (2017) compared the morphological ontogeny of three species of *Hermannia* with two species of *Phyllhermannia* Berlese, 1916 and 16 other species of Crotonioidea and stated that the latter group is highly differentiated and insufficiently known, and therefore it is difficult to determine the correct systematic position of *Hermannia* in this superfamily. For example, *Hermannia* retains seta f_1, which is ancestral in Nothrina, but loses the second pair of exobothridial seta (*exi*), which is progressive in early-derivative oribatid mites. *Hermannia* also retains seta f_2 in all instars, as most species of Brachypylina, but the ontogeny of leg setae of *Hermannia* species more closely resembles the macropyline than the brachypyline oribatid mites. Subías (2017) listed in *Hermannia* sensu stricto a total of 17 species, but six of them he considered inquirenda.

The diagnostic characters of *Hermannia* species are based exclusively on the morphology of adults, mainly the forms of the bothridial seta and prodorsal seta *in*, the ornamentation of the cuticle, and the form of the setae on the notogaster and legs (Sitnikova 1975; Woas 1978, 1981; Weigmann 2006). The body length of adults of most *Hermannia* species overlaps and only have a diagnostic value in comparing the small and large species. The nymphs are strikingly similar to adults, except for the smaller body size and folded and less sclerotized cuticle (Bäumler 1970; Travé 1977a; Ermilov *et al.* 2012; Seniczak *et al.* 2017).

The juveniles of *Hermannia* are inadequately known. According to Norton and Ermilov (2014) and Seniczak *et al.* (2017), the full morphological ontogeny of only three species is studied:

(1) *Hermannia gibba* (C. L. Koch, 1839): Nicolet (1855) described and illustrated a nymph, Grandjean (1933) studied the formulae of gastronotal, genital, aggenital and anal regions, and line of dehiscence and hysterosomal setation (Grandjean 1947) in a wide phylogenetic context. Bäumler (1970) investigated the larva and nymphs, and Ermilov *et al.* (2012) described and illustrated the morphological ontogeny of juveniles, including leg setae and solenidia.

(2) *Hermannia jesti* Travé, 1977: Travé (1977a) described all juvenile stages and numerical ontogeny of leg setae, illustrated the tritonymph and leg I of the larva, and studied epimeral setae in a wide phylogenetic context (Travé 1977b).

(3) *Hermannia reticulata* Thorell, 1871: Thor (1930) gave photos of a nymph in ventral and lateral aspects, Grandjean (1949) studied the formulae of gastronotal, genital, aggenital and anal regions of this species and Seniczak *et al.* (2017) described and illustrated the morphological ontogeny, including leg setae.

The known morphological ontogeny of some other *Hermannia* species is incomplete. According to Norton and Ermilov (2014), Oudemans (1900) and Willmann (1931) described and illustrated a nymph of *Hermannia convexa* (C. L. Koch, 1839), and Hammen (1978) described and illustrated the ventral aspect of all juvenile stages of this species, including the prelarva, and discussed the morphology and development of chelicera in a wide phylogenetic context. However, in our opinion a nymph described and illustrated by Willmann (1931) belongs to *Hermannia scabra* (L. Koch, 1879) because it has similar body shape and the pattern of the cuticle on the gastronotum is as in the nymphs investigated here. However, the description of a nymph by Willmann (1931) is general and omits important diagnostic characters. We therefore redescibe this stage and describe the morphology of the other juvenile instars that are currently undescribed. *Hermannia scabra* is a large species, similarly to congener *H. reticulata* (Woas 1978), but was rarely recorded from Svalbard (Coulson and Refseth 2004; Coulson 2008; Bayartogtokh *et al.* 2011), its presence in Svalbard was even uncertain (Coulson *et al.* 2014); its distribution and ecology in this archipelago is poorly known.

The aim of this paper is to describe the morphological ontogeny of *H. scabra*, expand the diagnosis of this species to include morphological characters of the juveniles and compare its ontogeny with that of congeners. We also present the distribution of *H. scabra* in Svalbard, population density, and stage structure of this species.

MATERIAL, METHODS AND TERMINOLOGY

Sampling, mite extraction, determination and analysis

We investigated the distribution of *H. scabra* in the Svalbard archipelago (Figure 1A) using 174 samples from 33 locations (Table 1, Figure 1B). Samples were collected by S. J. Coulson during the polar summer, in a period of around six weeks (from late June to early August) between 2009 – 2014. Soil samples were collected in the typical vegetation communities at each location, and the number of samples

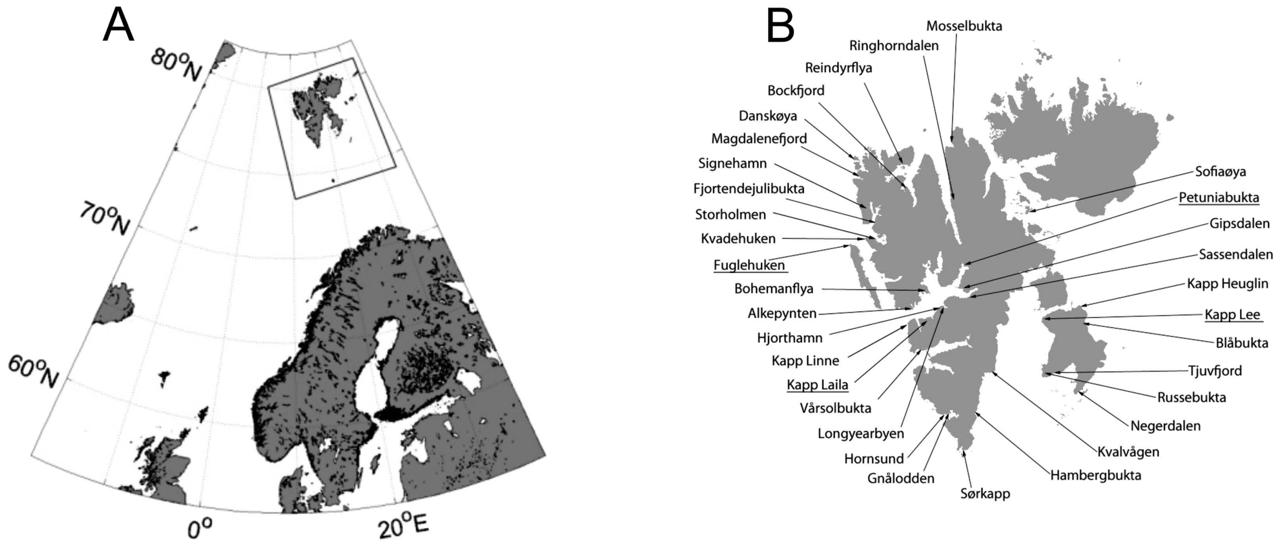

FIGURE 1: Sampling locations: A – location of the Svalbard archipelago (box) in the European High Arctic; B – *Hermannia scabra* was found in locations underlined.

TABLE 1: Mean density (individuals per 1 m^2) of *Hermannia scabra* in vegetation classes and locations of Svalbard, where this species occurred.

Vegetation class	Locations (samples)	Coordinates (WGS 84)	Density	Range
Class 8. Wet vegetated flats, beaches, slopes and river fans with some exposed *Dryas* vegetation and graminoids (*Luzula* sp.)	Kapp Lee (4)	78°04′53.3″N 20°49′06.7″E	11800	200-45800
Class 11. Moss tundra	Kapp Laila (10)	78°06′44.6″N 14°50′57.7″E	100	–
Class 13. Arctic meadows (rich vegetation)	Fuglehuken (6)	78°53′47.2″N 10°28′41.7″E	100	–
Class 16. Established dense *Dryas* heaths	Petuniabukta (12)	78°42′04.8″N 16°37′34.2″E	15000	–

Vegetation classes after Johansen *et al*. (2012).

from each location varied between 2 – 12. Each sample had dimensions of 10 x 10 cm by ca. five cm deep (the usual maximum depth of the organic soil). The samples (soil and plant cover) were kept cool until being extracted in Tullgren funnels (Burkard Scientific Ltd., Uxbridge, UK) at the University Centre in Svalbard (UNIS) within five days from collection and preserved in 96% ethanol. We determined the density, stage structure and the body length using all mites, but in the abundant two samples (Kapp Lee b, Petuniabukta a) we measured 15 individuals selected randomly.

Statistical calculations were done on the body length of *H. scabra* in vegetation classes 8 and 16, where this species was abundant. Normality of data was examined by the Kolmogorov-Smirnov test and the homogeneity of variance with the Levene's test. To find differences between the body length we used ANOVA variance analysis (Stanisz 2006). The level of significance for all statistical tests was accepted at $\alpha = 0.05$. Data were analyzed using MS Excel 2007, Statistica 12.0.

The juveniles and adults of *H. scabra* used in the morphological study were collected from vegetation class 8 (wet vegetated flats, beaches, slopes and river fans with some exposed *Dryas* vegetation and graminoids *Luzula* sp.) in Svalbard (Figure 1B). The ontogeny of this species is similar to that of *H. reticulata* (Seniczak *et al*. 2017), so the illustrations of *H. scabra* are limited to the body regions that show substantial differences. Illustrations were prepared from individuals temporarily mounted on slides in lactic acid. In the description of instars and figures we used the following abbreviations: prodorsal setae (*ro*, *le*, *in*, *ex*), bothridium (*bo*), bothridial seta (*bs*), notogastral or gastronotal setae (*c-*, *d-*, *l-*, *h-*, *p*-series), adanal and anal setae (*ad-*, *an*-series), aggenital seta (*ag*), epimeral setae (*1a–c*, *2a*, *3a–c*, *4a–c*), cupules or lyrifissures (*ih*, *ips*, *iad*), opisthonotal gland opening (*gla*), leg solenidia (σ, φ, ω), famulus (ϵ) and setae (*bv*, *d*, *ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl*, *v*). In *H. scabra*, the hypertrichy of epimeral setae occurs, and the hypertrichous setae were labelled as *a′* or *b′*. Terminology follows that of Grandjean (1933, 1947, 1949, 1953) and Norton and Behan-Pelletier (2009). The species nomenclature follows that of Norton and Ermilov (2014).

Vegetation and land cover types

We sampled oribatid mites in the vegetation classes and locations according to a revised vegetation map of the Svalbard (Johansen *et al.* 2012). Of the total 11 investigated vegetation classes, *H. reticulata* was absent from seven (classes 9, 10, 12, 14, 15, 17 and 18), but was present in four:

(1) Class 8 (wet vegetated flats, beaches, slopes and river fans), which is represented by Kapp Lee. This pioneer vegetation also consists of exposed *Dryas* vegetation and graminoids (*Luzula* sp.).

(2) Class 11 (moss tundra), such as Kapp Laila and occurs in areas with moderate snow cover during winter. Most often developed in the lower parts of hill slopes, on established river fans and in small depressions. The vegetation is a mixture of *Cassiope tetragona* D. Donand and moderate snowbed species, including *Salix polaris* Wahlenb., *Dryas octopetala* L., *Equisetum arvense* L., *Saxifraga oppositifolia* L. and *Silene acaulis* (L.) Jacq. The moss layer is generally moderately developed.

(3) Class 13 (Arctic meadows – rich vegetation), present in five regions (Fjortendejulibukta, Fuglehuken, Reindyrflya, Storholmen, and Signehamn). This class consists of luxuriant vegetation communities characterized by grasses and forbs with a high species diversity. These communities are associated with warm south and southwest facing slopes with available water during the growing season. To some extent the luxuriant bird cliff vegetation, established densely vegetated river fans and the drier parts of *Dupontia* meadows are included in this map unit.

(4) Class 16 (established dense *Dryas* heaths), which is exemplified by six regions (Kvadehuken, Mosselbukta, Petuniabukta, Ringhorndalen, Sørkapp and Tjuvfjord), with a more heavy snow cover dominated by *D. octopetala*. The most common variant is poor in species, while others may contain herbs, sedges and lichens. In depressions and less drained sites mosses in combination with *C. tetragona* are developed, whereas on coastal plains *S. oppositifolia* partly with lichens form the dominant cover. In mountain areas and in most of the northern and eastern regions of the archipelago *Dryas* stands with *Papaver dahlianum* (Tolm.) Elven & Nilsson are common.

RESULTS

Morphological ontogeny of *Hermannia scabra* (L. Koch, 1879)

Nothrus scaber L. Koch, 1879.
Hermannia (*Heterohermannia*) *scabra*: Woas 1992; Subías 2004, 2017.
Hermannia scabra: Woas 1978; Mehl 1979; Karppinen and Krivolutsky 1982; Golosova *et al.* 1983; Schatz 1983; Tarman 1983; Marshall *et al.* 1987; Bernini *et al.* 1995; Olszanowski *et al.* 1996.

Morphology of adult — Adult large (815 – 1,050 µm, Table 2), stocky and brown, with characters of *Hermannia* as given by Woas (1978). Our individuals smaller (815 – 945 µm, n= 30, Table 3) than those investigated by Woas (1978) (1,000 – 1,150 µm), with notogastral setae relatively longer (Figure 2A) than in Woas. In our adults, number of epimeral setae larger (3-1-4/5-6/8, most common formula 3-1-5-7, Table 4) than in Woas (3-1-5-5/6). In our adults two pairs of large aggenital setae occur (Figure 3A), whereas in Woas five pairs of small setae present. In our individuals additional anal seta rarely occurred asymmetrically on one anal plate. Leg segments as in *H. reticulata* (Seniczak *et al.* 2017) and relatively thicker than in Woas, but leg setae similar. Coupled

TABLE 2: Measurements of some morphological characters of juvenile stages of *Hermannia scabra* (mean measurements of 10 specimens in µm).

Morphological characters	Larva	Protonymph	Deutonymph	Tritonymph	Adult
Body length	340	397	559	734	880
Body width	168	191	297	416	488
Length of: seta *le*	12	24	34	52	62
seta *in*	21	22	30	44	45
seta *c* 1	14	22	46	61	62
seta *c* 3	16	27	47	58	58
seta *f* 1	26	32	48	62	82
seta *f* 2	25	31	47	61	80
seta *h* 1	23	26	43	60	69
seta *h* 2	20	23	38	57	65
genital opening	Nd	26	32	76	147
anal opening	67	81	126	162	221

Nd – not developed.

TABLE 3: Stage structure and body length of *Hermannia scabra* in vegetation classes in Svalbard.

Vegetation class, locations (samples)	Sample	Juveniles						AD	Tot	/m^2	Body length	
		L	PN	DN	TN	Tot	%				Mean	Range
Class 8. Kapp Lee (4)	a	0	0	0	0	0	0	5	5	500	868.8	848-913
	b	73	204	129	9	415	91	43	458	45800	922.6	815-897
	c	0	0	2	1	3	43	4	7	700	863.9	831-929
	d	0	0	0	0	0	0	2	2	200	920.9	897-945
	total	73	204	131	10	418	89	54	472	11800	–	–
Class 11. Kapp Laila (10)	b	0	0	1	0	1	100	0	1	100	Absent	
Class 13. Flugenhuken (6)	e	0	0	1	0	1	100	0	1	100	Absent	
Class 16. Petuniabukta (12)	a	3	78	20	32	133	89	17	150	15000	894.9	831-962
Total		76	282	153	42	553	89	71	624	–	–	–
ANOVA											F = 8.38; p = 0.007	

Vegetation classes after Johansen *et al* . (2012).

TABLE 4: Numbers setae on epimeres I–IV of adult *Hermannia scabra* in different locations of Svalbard.

Vegetation class, location	Sample	Epimere I	Epimere II	Epimere III			Epimere IV				
		3/3	1/1	4/4	4/5	5/5	6/6	6/7	7/7	7/8	8/8
Class 16, Petuniabukta	a	15	15	–	3	12	1	–	11	2	1
Class 11, Kapp Laila	a	5	5	2	–	3	–	1	4	–	–
	b	15	15	–	0	15	0	2	13	0	0
	c	4	4	–	1	3	–	–	3	1	–
	d	2	2	–	–	2	–	1	1	–	–
Total		41	41	2	4	35	1	4	32	3	1

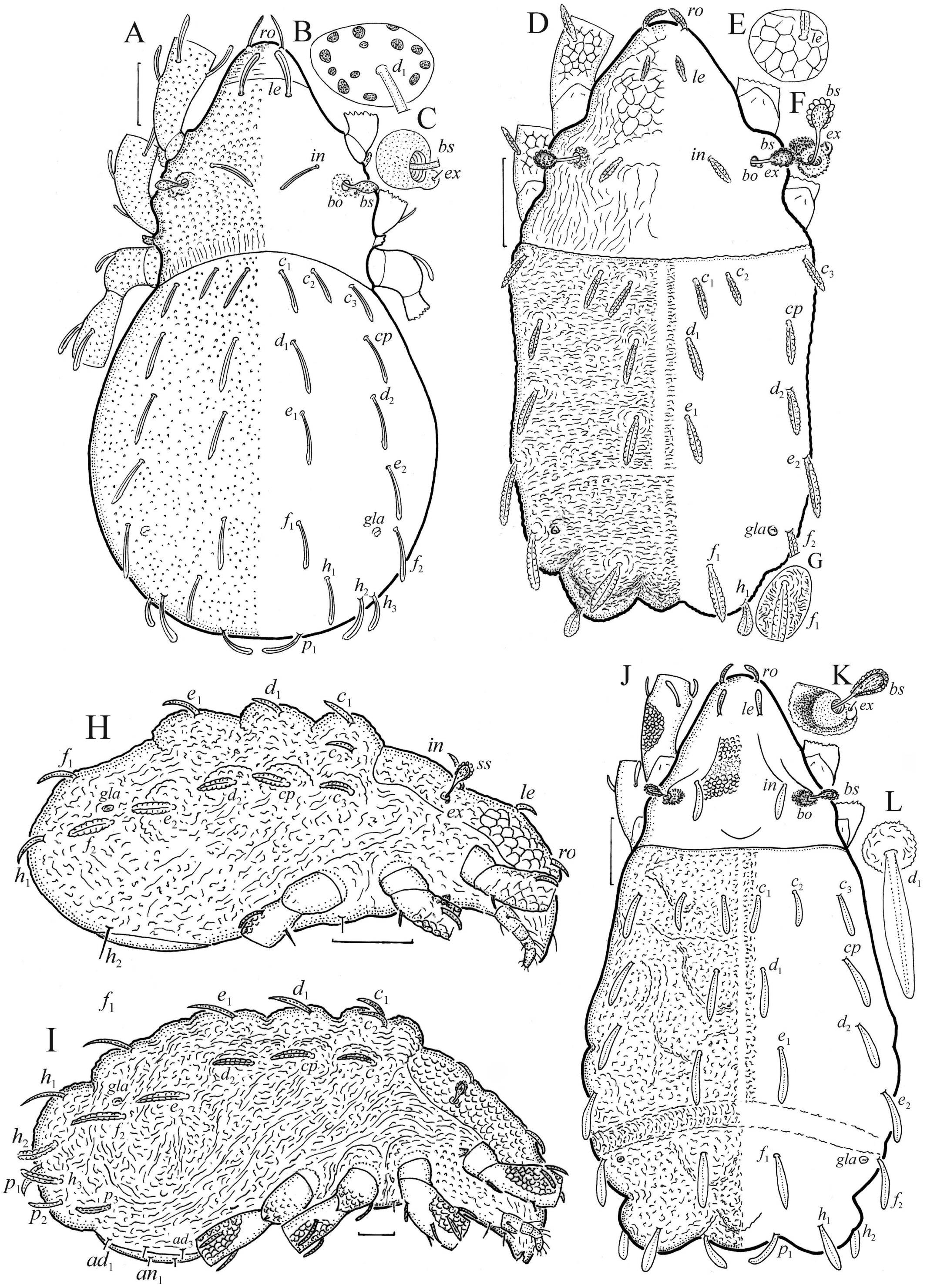

FIGURE 2: *Hermannia scabra*, legs partially drawn: A – dorsal aspect of adult, scale bar 100 µm; B – pattern of notogaster in region of seta d_1; C – bothridium and seta *ex*; B, C – enlarged; D – dorsal aspect of larva, scale bar 50 µm; E – region of seta *le*; F – bothridium and seta *ex*; G – region of seta f_1; E, F, G – enlarged; H – lateral aspect of larva, legs partially drawn, scale bars 50 µm: I – lateral aspect of tritonymph, legs partially drawn, scale bars 50 µm; J – dorsal aspect of tritonymph, legs partially drawn, scale bar 100 µm; K – bothridium and seta *ex*; L – region of seta f_1; K, L – enlarged.

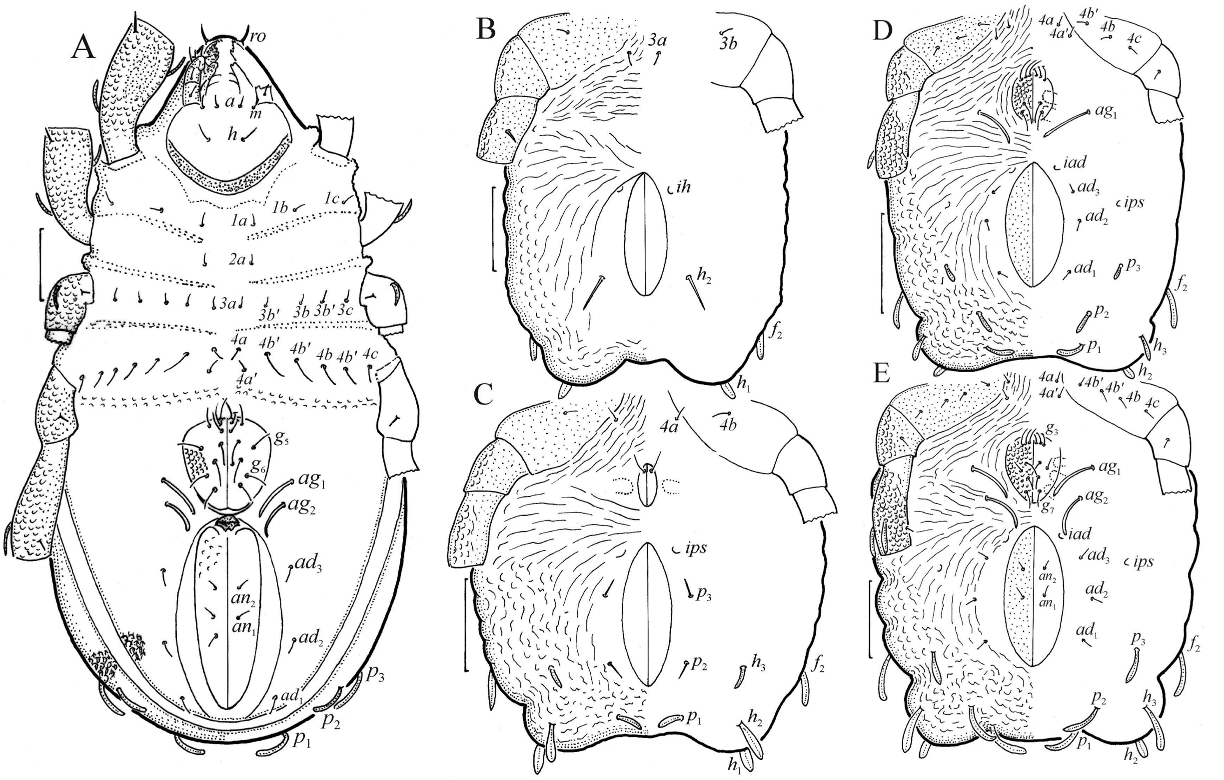

FIGURE 3: *Hermannia scabra*, ventral aspect, legs partially drawn: A – adult, scale bar 100 µm; B – opisthosoma of larva, scale bar 50 µm: C – opisthosoma of protonymph, scale bar 50 µm; D – opisthosoma of deutonymph, scale bar 50 µm; E – opisthosoma of tritonymph, scale bar 50 µm.

seta *d* present at leg solenidia σ, φ and φ_1 (Table 5). Formula of setae (+solenidia) of legs (trochanter to tarsus) of our adults: I – 1-5-(5+1)- (5+2)- (21+2), II – 1-5-(5+1)-(5+1)-(14+2); III – 2-3-(4+1)-(4+1)-13; IV – 1-3-4-(4+1)-13.

Diagnosis of juveniles — Juveniles stocky, oval in dorsal aspect and light brown, most prodorsal and gastronotal setae of medium size and phylliform. Anterior and medial part of prodorsum reticulate, bothridial seta clavate. Gastronotum uneven, most setae on apophyses. Formulae of epimeral setae: 3-1-2 (larva), 3-1-2-2 (protonymph), 3-1-3/4-4/5 (deutonymph) and 3-1-3/4-5/6 (tritonymph). Most setae on femora, genua and tibiae phylliform.

Description of juvenile stages — Larva stocky, oval in dorsal aspect and light brown, prodorsum subtriangular. Rostrum rounded (Figure 2D), prodorsal setae *ro* and *le* short, seta *in* slightly longer (Table 2), all phyliform (Figure 2G); mutual distance of pair *in* more than three times that of pairs *le* and *ro*. Opening of bothridium small, rounded (Figure 2F), with minute seta *ex* inserted close to lateral part of bothridial opening, bothridial seta short, clavate, head with short and thick barbs. Anterior part of prodorsum reticulate (Figure 2E), other parts folded (Figure 2G).

Gastronotum of larva with 12 pairs of setae, including h_2, positioned lateral to medial part of anal opening, h_3 absent (Figures 2H, 3B). All gastronotal setae of medium size (Table 2), phylliform, length slightly increasing from anterior to posterior. Gastronotum uneven, most gastronotal setae on large apophyses. Paraproctal valves (segment PS) glabrous. Cupules not evident in folded integument, except for *ih* located lateral to anterior part of anal opening (Figure 3B), opisthonotal gland opening (*gla*) anteromedial to seta f_2 (Figures 2D, H). Line of dehiscence visible in shape of inverted letter

TABLE 5: Ontogeny of leg setae (Roman letters) and solenidia (Greek letters) in *Hermannia scabra*.

Leg	Trochanter	Femur	Genu	Tibia	Tarsus
Leg I					
Larva	–	d, bv''	$(l), d\,\sigma$	$(l), v', d\,\varphi_1$	$(ft), (tc), (p), (u), (a), s, (pv), (pl), \varepsilon, \omega_1$
Protonymph	v'	$v', (l)$	–	–	ω_2
Deutonymph	–	–	v', v''	v'', φ_2	–
Tritonymph	–	–	–	–	–
Adult	–	–	–	–	$(it), (v), l''$
Leg II					
Larva	–	d, bv''	$(l), d\,\sigma$	$(l), v', d\,\varphi$	$(ft), (tc), (p), (u), (a), s, (pv), \omega_1$
Protonymph	–	$v', (l)$	–	–	–
Deutonymph	v'	–	v', v''	v''	ω_2
Tritonymph	–	–	–	–	–
Adult	–	–	–	–	l'
Leg III					
Larva	–	d, ev'	$l', d\,\sigma$	$l', v', d\,\varphi$	$(ft), (tc), (p), (u), (a), s, (pv)$
Protonymph	v'	l'	–	–	–
Deutonymph	l'	–	v'	–	–
Tritonymph	–	–	v''	v''	–
Adult	–	–	–	–	–
Leg IV					
Protonymph	–	–	–	–	$ft', (p), (u), (pv)$
Deutonymph	v'	d, l', ev'	d, l', v'	$l', v', d\,\varphi$	$ft'', (tc), (a), s$
Tritonymph	–	–	v''	v''	–
Adult	–	–	–	–	–

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.

Y. Formula of epimeral setae: 3-1-2, all setae short, except for scaliform *1c* covering Claparède's organ. Number of leg setae and solenidia as in *H. reticulata* (Seniczak *et al.* 2017), but most setae of femora, genua and tibia phylliform.

Prodorsum, prodorsal setae, bothridium and bothridial seta of protonymph as in larva, but prodorsal reticulation of cuticle denser than in larva and hysterosoma widest along 2/3 of its length. Gastronotum of protonymph uneven and with 16 pairs of setae due to appearance of setae h_3 and *p*-series (Figure 3C) that remain in other nymphs (Figures 3D, E); most setae on apophyses, setae h_1 and h_2 on large posterior apophysis. In protonymph gastronotal setae of medium size and phyliform; length of setae slightly increasing from anterior to posterior. In protonymph one pair of genital setae appears (Figure 3C), and three pairs are added in deutonymph and tritonymph each (Figures 3D, E); all of medium size and smooth. In protonymph, two pairs of setae appear on epimere IV, *4a* on unsclerotized integument with slating striae, and *4b* on sclerotized epimere IV (Figure 3C). In deutonymph and tritonymph one or two setae added on epimere III and IV each (Figures 3D, E), including *4a′* located on unsclerotized integument in deutonymph (if present unilaterally) and tritonymph; all short. Ontogeny of epimeral setae shown in Fig-

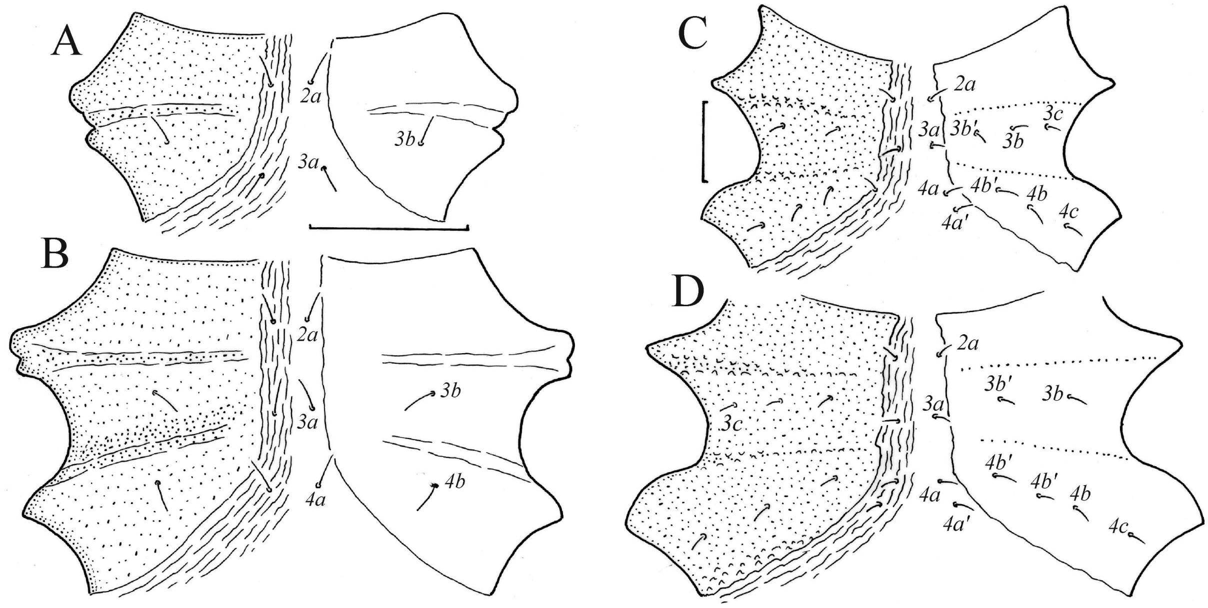

FIGURE 4: *Hermannia scabra*, epimeres, legs removed, scale bar 50 µm: A – II–III of larva; B – II–IV of protonymph; C – II–IV of deutonymph; D – II–IV of tritonymph.

ures 4A–D. In deutonymph one pair of long aggenital setae appear, and three pairs of short adanal setae, in tritonymph second pair of long aggenital setae appears and two pairs of anal setae. In deutonymph and tritonymph, setae h_2 and h_3 on large posterior apophysis (Figures 3D, E, 2J). Paraproctal valves of protonymph and deutonymph glabrous, tritonymph with two pairs of short anal setae (Figure 3E). Seta *d* present at base of leg solenidia σ, φ and φ_1, most setae on femora, genua and tibiae phyl-liform, and distribution of setae and solenidia as in *H. reticulata* (Seniczak *et al.* 2017), but ontogeny of setae differs (Tables 5, 6).

Summary of ontogenetic transformations — Prodorsal and gastronotal setae remain short or medium sized in all instars, seta *ex* is tiny, located on the lateral edge of bothridial opening, and the bothridial seta remains clavate. The larva has 12 pairs of gastronotal setae, and the nymphs and adult have 16 pairs. The epimeral formulae of *H. scabra* are: 3-1-2 (larva), 3-1-2-2 (protonymph), 3-1-3/4-4/5 (deutonymph), 3-1-3/4-5/6 (tritonymph) and 3-1-4/5-6/8 (adult). The number of epimeral setae varies in adults between locations in Svalbard, especially on epimere IV, and the most common formula is 3-1-5-7 (Table 4). Seta *4a′* occupies the posterolateral position to seta *4a* in the deutonymphs (if present), tritonymph and adult, whereas other epimeral setae are inserted in anterior row. The formula of genital setae is 1-4-7-9 (protonymph to adult), aggenital setae is 1-2-2 (deutonymph to adult), gastronotal setae is 12-16-16-16-16 and the formula of segments PS–AN is 03333-0333-022. The shape of leg solenidia and most setae remains similar in all instars, but the number of setae increases during ontogeny (Table 5), mainly in the protonymph and deutonymph.

Distribution, ecology and biology — *Hermannia scabra* has a holarctic distribution (Subías 2004, 2017; Bayartogtokh *et al.* 2011). This species is an unspecialized panphytophage (Schatz 1983; Honciuc and Lundqvist 2009) and prefers moist and wet localities (Hull 1916; Trägårdh 1931; Sellnick 1949; Hammen 1952) with moss and algae, especially on coastal rocks, in salt marshes (Gjelstrup and Solhøy 1994), and dead plant material or fungi (Brodo 2000).

Hull (1916) considers *H. scabra* common in maritime localities, semiaquatic habitat and on dead wood, whereas Trägårdh (1931) found this species under stones and on driftwood on the sea shore

TABLE 6: Ontogeny of some setae on femur, genu and tibia in the nymphs of *Hermannia gibba*, *H. reticulata* and *H. scabra*.

Leg	Femur			Genu			Tibia		
	H. gibba	*H. reticulata*	*H. scabra*	*H. gibba*	*H. reticulata*	*H. scabra*	*H. gibba*	*H. reticulata*	*H. scabra*
Leg I									
Protonymph	v', (l)	v', l''	v', (l)	–	v'	–	–	–	–
Deutonymph	–	l'	–	(v)	v''	v', v''	v''	v''	v''
Leg II									
Protonymph	–	v', l''	v', (l)	–	v'	–	–	–	–
Deutonymph	v'', (l)	l'	–	(v)	v''	v', v''	v''	v''	v''
Leg III									
Protonymph	–	l'	l'	–	–	–	–	–	–
Deutonymph	l'	–	–	(v)	v'	v'	v''	–	–
Tritonymph	–	–	–	–	v''	v''	–	v''	v''
Leg IV									
Deutonymph	d, ev'	d, l', ev'	d, l', ev'	d, l', v'	d, l', (v)	d, l', v'	l', v', d	l', (v), d	l', v', d
Tritonymph	l'	–	–	v''	–	v''	v''	–	v''

and in freshwater algae. Hammer (1969) noted *H. scabra* on lily bulbs and in soil ferns with *Sansevieria* sp. and various plants and roots, whereas Behan and Hill (1978) found this species in moss and tussock tundra. Purvis (1982) found *H. scabra* relatively abundant in undecomposed gorse needles (*Ulex europaeus* L.) in a coastal shrub of southeast Ireland, and on the earthen banks with granite boulders to a height about 1 m, whereas Żbikowska-Zdun *et al.* (2006) found this species abundant in moss and lichens covering an old 18th-century gate in the Bug River Protected Landscape Area in southern Poland. This species was also found on the feathers of black kite (*Milvus migrans* Boddaert) and sparrow hawk (*Accipiter nisus* L.) (Krivolutsky and Lebedeva 2004) and in bird collecting sites, where also the juveniles of this mite species were present (Lebedeva and Lebedev 2007).

This species was cultured by Jalil (1965) in the laboratory (20°C) on decaying skeletonized leaves collected from broadleaved woodland. The whole development of species lasted 184 days, the development time of subsequent stages increasing during the ontogeny (egg 15 days, larva 16 days, protonymph 41 days, deutonymph 42 days and tritonymph 70 days). This author also observed that the development of *H. scabra* in the field, under oak *Quercus robur* L. in Sutton Bonnington (England, Canada), required a full year. He observed oviposition of *H. scabra* from September to November with most larvae in October. The greatest total density of this species was in October, with numbers declining during the winter and was lowest from May to July when the larvae were absent.

We found *H. scabra* in four of the 11 vegetation classes, at four of the 33 locations sampled (Figure 2, Table 1), and in seven of the 174 samples. Constancy of this spe-cies in this archipelago was therefore very low (4%). If we consider only the locations occupied by *H. scabra*, the greatest constancy of this species was at Kapp Lee (100%) and the lowest was at Petuniabukta (8%). The greatest mean density of *H. scabra* (11,800 individuals per 1 m^2) was noted in vegetation class 8 at Kapp Lee (wet vegetated flats, beaches, slopes and river fans with some exposed *Dryas* vegetation and graminoids *Luzula* sp.), but the density varied here between 200 – 45800 individuals per 1 m^2. A lower density was observed in vegetation class 16 (established dense *Dryas* heaths) at Petuniabukta (15,000 individuals per 1 m^2), whereas in other vegetation classes the density was very low (Table 1).

The juveniles of *H. scabra* dominated the adults, comprising 89% of all individuals (Table 3), but the proportion of juveniles in the population varied between 88 – 100%. Among the juveniles, the

TABLE 7: Selected morphological characters of *Hermannia scabra*, *H. gibba*, *H. jesti* and *H. reticulata*.

Morphological characters	*H. scabra*	*H. gibba*[1]	*H. jesti*[2]	*H. reticulata*[3]
All instars: shape of *bs*	Clavate	Setiform	Setiform	Clavate
Adult: body size in µm	734–913	780–940	945–995	734–940
Pattern of notogastral cuticle	Punctated	Punctated	Punctated	Reticulate
Seta e_1 reaches f_2	No	Yes	No	No
Formula of epimeral setae	3-1-4/5- 6/8	3-1-3-4	3/5-4/7-7/13-11/17	3-1-3/4-4/5[4]
Nymphs: pattern of prodorsum	Reticulate	Not distinct	Not distinct	Reticulate
Transverse line of dehiscence	Wide stipe	Thin line	Absent	Thin line
Epimeral setae of: protonymph	3-1-2-2	3-1-2-1	3-3/4-6-1	3-1-2-1
deutonymph	3-1-3-5	3-1-3-3	3/-4/5-9-7/8	3-1-3-3
tritonymph	3-1-3-6	3-1-3/4-3/4	3-5-10-10	3-1-3/4-3/4
Appearance of anal setae	Tritonymph	Deutonymph	Tritonymph	Tritonymph
Larva: pattern of prodorsum	Reticulate	Not distinct	?	Not distinct
Transverse line of dehiscence	Thin line	Thin line	Absent	Thin line

[1] - according to Ermilov *et al.* (2012) and complemented with Woas (1978); [2] - according to Travé (1977a); [3] - according to Seniczak *et al.* (2017); [4] - in some individuals less or more setae were present on one side.

protonymphs dominated and the tritonymphs were least abundant. The stage structure of *H. scabra* slightly varied among samples. For example, in the most abundant population at Kapp Lee, the juveniles comprised 91% of all individuals, and the stage structure of this species was 73 larvae, 204 protonymphs, 129 deutonymphs, 9 tritonymphs and 43 adults, whereas in the less abundant population of this species at Petuniabukta, the juveniles formed 89% of all individuals and the stage structure was 3 larvae, 78 protonymphs, 20 deutonymphs, 32 tritonymphs and 17 adults.

The sex ratio of *H. scabra* was not determined because of the deep brown pigmentation and ornamentation of adults which made it impossible to determine sex by transmission light microscopy. No eggs were observed inside females. The body length of the adults in vegetation class 8 was significantly higher than in vegetation class 16, but generally it varied greatly within sampling locations, largest and smallest individuals both occurring at Kapp Lee, where the mean density of this species was the highest.

Comparison of morphological ontogeny of *Hermannia scabra* within *Hermannia*

We compare the morphological ontogeny of *H. scabra* studied here with that of *H. gibba*, *H. jesti* and *H. reticulata*, studied by Ermilov *et al.* (2012), Travé (1977a) and Seniczak *et al.* (2017) respectively. These species differ from one another by the following important morphological characters:

(1) Shape of the bothridial seta in all instars: in *H. reticulata* and *H. scabra* this seta is clavate, whereas in other species it is setiform.

(2) Pattern of cuticle on the prodorsum of larva: in *H. scabra* the cuticle is reticulate, whereas in other species the pattern is indistinct or unknown.

(3) Pattern of cuticle on the prodorsum of nymphs: in *H. reticulata* and *H. scabra* the cuticle is reticulate, whereas in other species the pattern is indistinct.

(4) These species also differ from each other by some other morphological characters and the ontogeny of epimeral setae (Table 7).

This comparison shows the great similarity of juvenile *H. reticulata* and *H. scabra*, which differ from one another mainly by the pattern of cuticle on the prodorsum and gastronotum and number of epimeral setae. These species have a clavate bothridial seta, whereas other species have it setiform. Interestingly, *H. scabra* differs from all other species by the presence of two setae on epimere IV of protonymph, instead of one in the other species. One of these setae (*4a*) is inserted on unsclerotized integument and occupies this position in deutonymphs and tritonymph. In deutonymph, one of the new setae (*4a′*) is also is inserted on unsclerotized integument, posterolateral to seta *4a*, and occupies this position in tritonymph and adult. Particularly characteristic is the ontogeny of leg setae, which differs in *H. gibba*, *H. reticulata* and *H. scabra* (Table 6). Travé (1977a) gave the numerical ontogeny of leg setae of *H. jesti*, but it differs from that of *H. gibba*, *H. reticulata* and *H. scabra*. For example, femur I of protonymph of *H. jesti* gains one seta, comparing to the larva, whereas other species gain more setae. Thus, each of four species has its own ontogeny of these setae (Table 6).

The nymphs of *H. scabra* investigated here are similar to a nymph described and illustrated by Willmann (1931); both have similar pattern of cuticle of gastronotum and a large posterior apophysis bearing setae of *h*-series. This author observed similarity of morphology of this nymph to that of *Camisia*.

The body length of the adult of *H. scabra* described by L. Koch (1879) from Novaja Zemlja (Russia) was 1,000 µm, whereas the individuals from Svalbard studied here were slightly smaller (815 – 945 µm) and similar to those studied by Willmann (1931) (length 900 µm). The maximal body lengths of this species given by Sitnikova (1975) and Woas (1978) are larger (1,550 µm and 1,150 µm, respectively), but all authors noted that the notogaster of *H. scabra* is thickly punctated as in our individuals.

We found *H. scabra* investigated here to be identical to those studied by Willmann (1931), both as adult and nymphs. In Willmann (1931) the adult of *H. scabra* has six pairs of notogastral setae in inner row (c_1, d_1, e_1, f_1, h_1 and p_1), and seta p_2 is located relatively far from p_1, as in our adults, whereas in Sitnikova (1975) and Woas (1978) seta p_2 is located close to p_1. Moreover, the adult of *H. scabra* investigated by Woas (1978) has relatively shorter notogastral setae than in our individuals and has five short pairs, whereas our adults have two pairs of long setae.

DISCUSSION

The juveniles of *H. scabra* add new morphological characters to our knowledge on the morphology of *Hermannia* species, such as a new formula of epimeral setae and new distribution of these setae on epimere IV, new pattern of ontogeny of leg setae, and the presence of a wide transverse line of dehiscence on the gastronotum of nymphs, which in other species of *Hermannia* is expressed only by a narrow line (Grandjean 1947; Ermilov *et al.* 2012; Seniczak *et al.* 2017). The line of dehiscence is also observed in the juvenile instars of *Phyllhermannia* (Colloff 2011), in the nymphs of *C. lapponica* and in all juveniles of *C. voleolata* (Seniczak 1991).

The ontogeny of epimeral setae of *H. scabra* is interesting because two pairs of setae appear on epimere IV of protonymph, instead of one pair in other *Hermannia* species, and the inner setae (*1a*, *2a*, *3a*, *4a*, *4a′*) are inserted on unsclerotized integument between epimeres, which is unique in *Hermannia*; in other species of this genus all setae are on epimeres. In this species the hypertrichy occurs on epimeres III and IV, as in *H. jesti* and *H. reticulata* (Travé 1977a; Seniczak *et al*. 2017). Grandjean (1934) observed in *Nanhermannia nana* (Nicolet, 1855) the appearance of seta *4a* in the protonymph, seta *4b* in the deutonymph (anteromedial to seta *4a*, as in most species of Brachypylina), and setae *4c* and *4d* in the tritonymph (lateral to *4a*), and all remain in the adult. However, the ontogeny of epimeral setae of *H. scabra* is different because two setae (*4a*, *4b*) appear in the protonymph, one seta (*4c*) in the deutonymph and hypertrichy in *3*- and *4*-rows occurs in the deutonymph, tritonymph and adult. In *Nothrus* species, the hypertrichy of epimeral setae appears mainly on epimere I (Seniczak 1992; Seniczak and Żelazna 1992; Seniczak and Norton 1993).

Hypertrichy makes the setal notation problematic. Probably this is why many authors omitted notation of epimeral setae in *Hermannia* (Bäumler

1970; Travé 1977a, b; Woas 1978; Olszanowski 1996; Ermilov *et al*. 2012). Colloff (2011) labelled these setae in the closely related genus *Phyllhermannia*, where hypertrichy occurs mainly on epimere IV of the tritonymph and adult. Generally, Colloff's setal labeling is positional, not indicating the homologies. The exception is *Phyllhermannia sauli* Colloff, 2011, in which his seta *4b* appears on epimere IV of protonymph, and two setae are added in the deutonymph, including his *4a* that is added medial to *4b*, as in *Nanhermannia* (Grandjean 1934). In *Ph. lemannae* Colloff, 2011, setal labeling is positional, but his seta *4a* is also added medial to *4b*, as in *Ph. sauli*.

The protonymph of *H. reticulata* also has one seta on epimere IV (*4a*), but two setae (*4b*, *4c*) are added laterally to *4a* during the ontogeny (Seniczak *et al*. 2017). In this species, the hypertrichy rarely occurs in the tritonymph, but is common in the adult. In contrast, the protonymph of *H. scabra* has two setae (*4a*, *4b*) on epimere IV, and seta *4c* is added laterally to *4b* in the deutonymph. In the latter stage the hypertrichy occurs, and develops in the tritonymph and adult. In both species, the hypertrichous setae are added in unpredictable positions and numbers on each epimere, and normal setae can also be absent, which makes labeling of epimeral setae difficult.

In the tritonymph of *H. gibba*, *H. reticulata* and *H. scabra*, the most common formula of epimeral setae of is 3-1-3-3 (Ermilov *et al*. 2012; Seniczak *et al*. 2017), which suggests that three letters (*a*, *b*, *c*) are sufficient to label the normal epimeral setae in this genus, whereas other setae (*a′*, *b′*) are hypertrichous. However, in *Nanhermannia*, a shift of the deutonymphal seta *4b* to the epimere III occurs (Grandjean 1934), whereas in *Hermannia* or *Phyllhermannia* it does not because the apodemes 3 and 4 are long, almost transverse, and the epimeral setae of *3*- and *4*-series are in their own rows.

Holotrichous setation of nymphs is not common in Crotonioidea, it occurs in *Hermannia*, *Phyllhermannia* and *Nothrus* C.L. Koch, 1836; other genera lose on the gastronotum at least seta f_1. However, the nymphs of *Hermannia* differ from those of other genera by the body form, ornamentation of the body and other morphological characters given by Seniczak *et al*. (2017).

Adult size variation in the Svalbard population was small and the largest individuals were only 16% longer than the smallest. However, the body size of *H. scabra* varies dramatically between geographically distinct populations (Willmann 1931; Sitnikova 1975; Woas 1978, 900 – 1,550 µm), which can pose the question concerning the identity of this species in this body range. Moreover, the number of aggenital setae of *H. scabra* varies greatly. For example, Woas (1978) noted five pairs of aggenital setae in the adults, but in those investigated here only two pairs are present, as in *H. reticulata* and *H. jesti* (Seniczak *et al*. 2017; Travé 1977a). In *H. gigantea* Sitnikova, 1977, there are also five pairs of aggenital setae present, and the body length (1,193 – 1,211 µm) includes that of *H. scabra*, and the notogaster is thickly punctated. All these data encourage further study of *H. scabra* from different geographical regions to determine the variability of the body length and aggenital setation of this species or define the cryptic species that may exist.

Hermannia scabra is a typical component of oribatid mite communities inhabiting the Arctic ecosystems in the Svalbard archipelago. It is not as common in this archipelago as *H. reticulata*, which has a higher constancy (12%, Seniczak *et al*. 2017) than that of *H. scabra* (4%). However, *H. scabra* forms larger agglomerations and its maximal density is greater (45,800 individuals per 1 m^2) than that of *H. reticulata* (10,300 individuals per 1 m^2), due to more abundant juvenile stages. In four vegetation classes we also observed more individuals of the former species (624 individuals) than the latter species (425 individuals).

Using the example of *H. scabra* and *H. reticulata,* it is clear how the distribution of species in the Arctic ecosystems depends on ecology of species. These species do not occur together because the former species prefers the moist and wet localities (Trägårdh 1931; Hammen 1952), such as vegetation class 8 (wet vegetated flats, beaches, slopes and river fans with some exposed *Dryas* vegetation and graminoids *Luzula* sp.) and class 16 (established dense *Dryas* heaths), where *H. reticulata* is absent (Seniczak *et al*. 2017). In contrast, *H. reticulata* prefers dry habitats, like heaths, fell field, meadows, moss and lichens (Behan and Hill 1978), the chamaephyte vegetation (Hammer 1944, 1946) and lichens (Gjel-strup 1978), and in Svalbard archipelago it mainly occupies vegetation class 12 (rich moss tundra, bird cliff vegetation) where *H. scabra* is absent. Both species occur in vegetation class 16, but *H. scabra* was abundant in one sample in Petuniabukta, where *H. reticulata* was absent, whereas *H. reticulata* occurred in one sample at Mosselbukta and in one sample at Sørkapp (Seniczak *et al*. 2014), where *H. scabra* was absent. Interestingly, the body length of the adults of *H. scabra* in vegetation class 8 significantly exceeded that in vegetation class 16, whereas in *H. reticulata* such differences were not observed (Seniczak *et al*. 2017).

Generally, the proportion of *H. scabra* juveniles was distinctly higher (89 – 100% of total mites) than that of *H. reticulata* (52 – 61%). In other Arctic oribatid species as *Mycobates sarekensis* (Trägårdh, 1910) and *Oribatella arctica* (Thor, 1930), the juveniles constituted 36% and nearly 5% of populations, respectively (Seniczak *et al*. 2015a, b). The distribution of *H. scabra* in Svalbard indicates that the abundant agglomerations of this species in vegetation classes 8 and 16 are important sources of its expansion into surrounding areas using, for example passive transport by birds (Krivolutsky and Lebedeva 2004) or other animals. In several samples in these, and other vegetation classes, the juveniles and adults of this species were present or only adults or juveniles, which may indicate the development of *H. scabra* in the adjacent habitats.

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