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A gall mite, *Aceria rhodiolae* (Acari: Eriophyidae), altering the phytochemistry of a medicinal plant, *Rhodiola rosea* (Crassulaceae), in the Canadian Arctic

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ABSTRACT

The eriophyid mite *Aceria rhodiolae* (G. Canestrini) is known to induce galls on the flowers and leaves of roseroot, *Rhodiola rosea* L., in subarctic and alpine regions of Europe. After discovering galls on the inflorescences of roseroot in Nunavik (Québec), northeastern Canada, we examined the mites extracted from the galls and compared them with specimens of *A. rhodiolae* from Europe. Through morphological analyses, we demonstrate that the mites from galls in Nunavik are conspecific with *A. rhodiolae* from Europe. We then provide a detailed redescription of the mite species based on the morphology of adult females and males from Canada and Europe, using a combination of standard light microscopy, confocal microscopy and scanning electron microscopy. Because roseroot is well-known for its medicinal properties, we tested the hypothesis that roseroot galled by the mite had altered phytochemistry, by using salidroside and rosavins as indicators. Our results show a significant reduction of almost half in salidroside content (45.8%), but not in rosavins. Moreover, because the mite sometimes affects most or all of the inflorescence of *R. rosea*, it can considerably reduce the production of seeds. We also show that *A. rhodiolae* is widespread along the Ungava Bay (Nunavik), with 31.5% of 92 sites surveyed having at least a few to numerous plants galled. Given the importance of roseroot as a crop for Inuit communities and as medicinal products used by them and other Canadians, and also in view of the commonness of *A. rhodiolae* in the Canadian Arctic and its broad distribution in Europe, the impact of the mite and its relationship with roseroot should be examined further in Nunavik and elsewhere.

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Introduction

Rhodiola rosea L. (Crassulaceae), also known as roseroot and goldenroot, is a highly valued medicinal plant species in the Old World, where it grows as a perennial plant in the Arctic and mountainous regions of Europe and Central Asia (Brown et al. 2002).

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Records of traditional and modern uses include immunostimulation, as a remedy against fatigue, stress and memory problems, as well as for its mild antidepressant properties (Fida et al. 2014; Panossian and Wikman 2014). A recent study (Cayer et al. 2013) shows that extracts have significant anxiolytic activity in animal trials.

Although sometimes considered a subspecies (*Rhodiola rosea* ssp. *rosea*) somewhat distinct from Eurasian populations, *R. rosea* also grows in the eastern subarctic and a few mountain sites of lower latitudes in North America (Cuerrier et al. 2014a, 2014b). In Canada, *R. rosea* has a sporadic distribution along the shoreline of the eastern low Arctic and the Atlantic provinces (Small and Catling 2000; Aiken et al. 2007). Nunavik roseroot is genetically close to Scandinavian populations and contains the same phytochemical markers, namely salidroside, tyrosol, rosarin, rosavin and rosin, as seen in Eurasian samples. Yet, a new compound not found in Eurasia has been discovered in Nunavik, as well as differences in a number of analytes (Filion et al. 2008; Avula et al. 2009).

Several arthropod species are known to feed on roseroot. They include at least four species of aphids (Aphididae), two of which occur in North America (Blackman and Eastop 2006; Holman 2009); a caterpillar (Papillionidae) recorded from Asia, and from the Yukon where it feeds on *Rhodiola integrifolia* (previously a subspecies of *R. rosea*) (Layberry et al. 1998); two species of leaf-mining Diptera, an Agromyzidae (Europe; and the Yukon, on *R. integrifolia*) and a Syrphidae (Europe) (Griffiths 1976; Bland 1995; Schmid 2007); and a weevil and a bark beetle species (Curculionidae) boring the roots of *R. rosea* in Russia (Kuznetsova and Krivets 1981; Smetanin 2013). Most of these insects are host-specific to *R. rosea* or restricted to crassulaceous hosts. A phytophagous mite, *Aceria rhodiolae* (G. Canestrini, 1892) (Eriophyidae), is known to induce galls on the flowers, leaves and stems of *R. rosea* in Europe (e.g. Roivainen 1950; Boczek 1961; Buhr 1965). In Canada, no plant-feeding mite has yet been recorded from *R. rosea*. Clausen (1975) noted signs of deformations of roseroot in Canada, without providing any details of a diagnosis or the causative agent.

Eriophyid mites and their close relatives in the superfamily Eriophyoidea are strictly phytophagous, feeding and developing usually on a single or a few related plant species (de Lillo and Skoracka 2010). Although inconspicuous and minute (0.1–0.5 µm long), the feeding activity of many eriophyoid species results in a deformation of the plant host's tissues. The deformations, or galls, vary in shape from enclosed, pouch-like galls protruding from the leaves, to erinea (hair-like excrescences), leaf rolling, and various deformations of buds, inflorescences and even the bark (Keifer et al. 1982). There are over 4000 species of eriophyoids currently described worldwide, but the majority of species remain to be described, including in Canada (Lindquist et al. 1979; de Lillo and Skoracka 2010; Beaulieu and Knee 2014).

Herein, we report on the presence of an eriophyid mite galling the flowers of *R. rosea* in Nunavik, eastern Canada. First, we compare its morphology with European specimens of *A. rhodiolae* to test conspecificity, and provide a description of the mite, taking into account any possible differences between Canadian and European populations; and second, we test the hypothesis that the presence of *A. rhodiolae* has an impact on the medicinal phytochemistry of roseroot by comparing levels of salidroside and rosavins in galled and ungalled plants.

Material and methods

Sampling

Populations of *R. rosea* were surveyed by V.F., A.C. and Mariannick Archambault in August 2006 and 2007 along the coastline of Ungava Bay, in Nunavik (Québec, Canada; Figure 1). Flower heads showing signs of deformation were collected and stored in 60% ethanol for future examination in the laboratory at the University of Ottawa, and the Canadian National Collection of Insects, Arachnids and Nematodes (CNC) (Ottawa, Canada). Global positioning system (GPS) points (± 5 m) were recorded for the surveyed sites. Additional samples of galled *R. rosea* were taken from Base Island, Labrador, Newfoundland, Canada. See Figure 2B and the 'Material examined' section for more collecting details. Voucher specimens of *R. rosea* have been deposited in the Marie-Victorin herbarium (MT) (Jardin botanique de Montréal) and determined by A.C.

Mite specimen preparation and examination

Some mites found among the flower buds were slide-mounted in Hoyer's medium, and the rest were preserved in a vial with 95% alcohol. Mite specimens were studied by F.B. at 400× and 1000× magnification under a compound microscope (Leica DM5500) equipped with differential interference contrast (DIC), connected to a computer and a digital camera (Leica DFC420). Images and morphological measurements were taken via Leica Application Suite software 4.2 (Basic, Live Measurements, and Interactive Measurements modules). Morphological terminology follows that of Lindquist (1996) and measurements were made according to Amrine and Manson

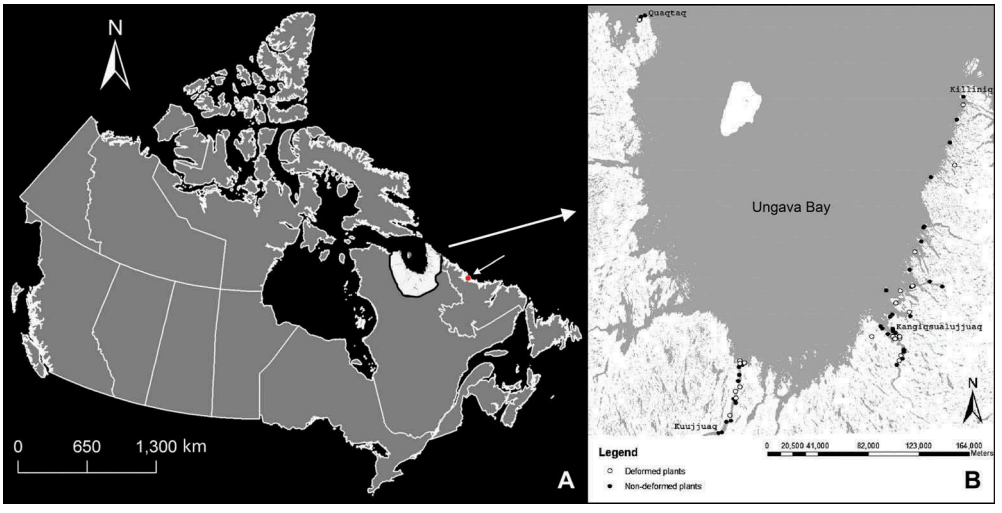

Figure 1. (A) Map of Canada, showing the area surveyed for *Rhodiola rosea* in Nunavik, Québec (in white). The small arrow indicates a site where additional samples were taken in Labrador, Newfoundland. (B) Region along the coast of Ungava Bay where populations of *R. rosea* were surveyed (geographic extremes of study sites: northwest 61.078°N, 69.632°W; northeast 60.422°N, 64.839°W; south 58.023°N). Open circles indicate sites with at least a few galled plants, whereas solid circles indicate sites with no galled plants.

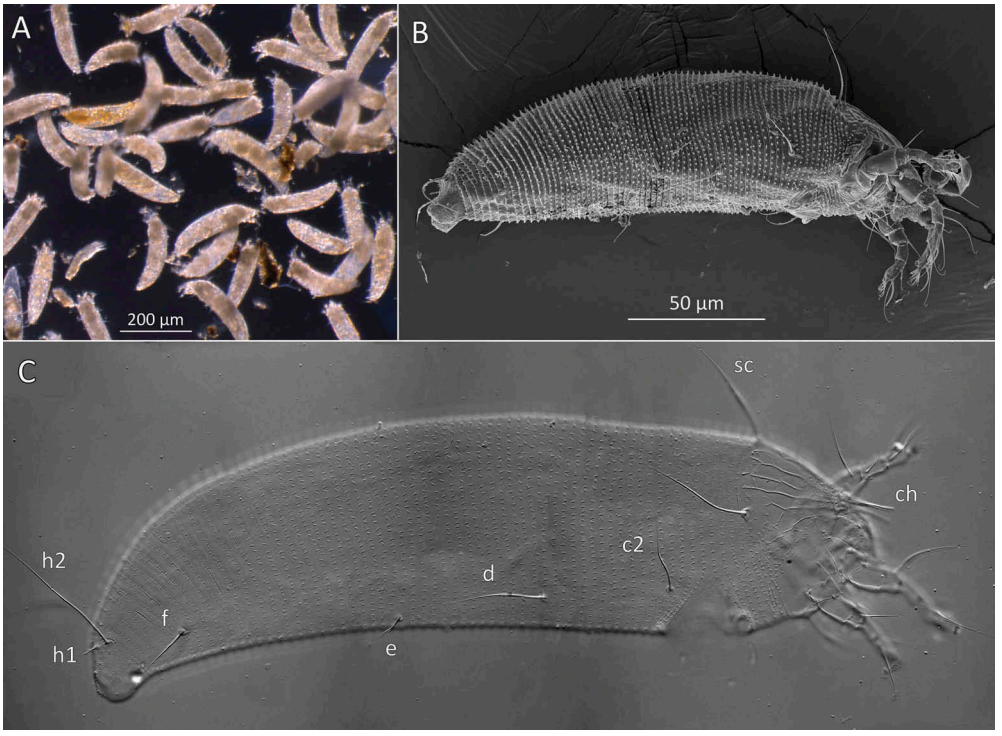

Figure 2. *Aceria rhodiolae* habitus. (A) Many (mostly adult) individuals under dissecting scope. (B) Adult female ventrolateral view (scanning electron micrograph) and (C) dorsolateral view (differential interference contrast light microscopy). Scale on (B) also applies to (C). The large size of female in (C) is in part due to some flattening of that specimen during the slide-mounting process. ch, cheliceral stylets; and other notations indicate setae of prodorsal shield and opisthosoma.

(1996), as modified by de Lillo et al. (2010), notably for the following characters: legs were measured from distal margin of tarsus to the proximal margin of trochanter; empodia were measured from distal apex to their junction with the margin of the tarsal segment. Other measurements that may need clarification are: ventral opisthosomal annuli were counted from the posterolateral corner of coxal field II; length of prodorsal shield includes the frontal lobe; the position of some leg setae (*bv, l′, l″*) were measured from the proximal margin of the segment bearing the seta; the number of microtubercles between setae *sc* are counted as the microtubercles on the first complete annulus (the first one is often incomplete) behind the prodorsal shield; the number of microtubercles between pairs of setae *c2, d, e* and *f* are counted ventrally. Internal genitalia were essentially described using the morphometrics proposed by Chetverikov et al. (2012, 2013) based on DIC light microscopy, and further interpreted using Chetverikov (2014) for females, and Chetverikov (2015) for males. Because specimens from Italy (see 'Material examined') were in poor shape (body twisted or deformed, and some setae cut or only partly discernible), the length of leg setae and the distance between opisthosomal setae for those specimens were considered unreliable and were excluded. Measurements shown in the description are ranges (in µm).

Specimens from Nunavik were compared with (1) descriptions of *A. rhodiolae* and other species associated with Crassulaceae in the literature, as well as with: (2) specimens borrowed from the Zoology Museum of the University of Padua (MZUP) (see 'Material examined' for specimen collection details); (3) specimens extracted from dried inflorescences of *R. rosea* borrowed from the Finnish Natural History Museum, University of Helsinki (MZH); and (4) specimens of *Aceria destructor* (Nalepa, 1891) collected from *Sedum* sp. (Crassulaceae). We also attempted to obtain specimens of *A. rhodiolae* previously collected by Jan Boczek in Poland (Boczek 1961) but without success (Mariusz Lewandowski pers. comm. August 2012). Mites were extracted from dried *R. rosea* (from MZH; and collected from Labrador, Canada) by removing and placing a part of the inflorescence in 95% alcohol. Mite specimens freed from plant tissues and floating in the alcohol were then picked up and slide-mounted.

External morphology was further studied using scanning electron microscopy (SEM) (Philips XL30), at the Microscopy Centre at Agriculture and Agri-Food Canada (AAFC), Science & Technology Branch (Ottawa). Specimens already stored in 95% alcohol were transferred with a pipette into a microporous capsule (30-µm pores) partly immersed in 100% alcohol in a small Petri dish, for 15 min; they were subsequently transferred to another Petri dish with 100% alcohol for another 15 min to ensure that specimens were effectively submerged in undiluted 100% alcohol before undergoing critical-point drying. Specimens were then mounted on SEM specimen stubs using a small paint brush with a few remaining hairs, and sputter-coated with gold before examination under SEM.

Additional imaging of the female prodorsal region and the male internal genitalia was obtained using a confocal light scanning microscope (CLSM) (Zeiss LSM 510) at AAFC, under 40× magnification (1.4/oil apochromatic objective), and with the following settings (Chetverikov 2012): excitation wavelength 405 nm, emission wavelength range 420–750 nm. Images were acquired at a resolution of 1024 × 1024 pixels and an electronic zoom of 3×, using ZEN lite 2012 software. In some cases, two or more images taken at different depths of a specimen were merged into a single image using Helicon Focus 5.3.14 (© Helicon Soft Ltd., 2000–2013).

Illustrations (line drawings) of morphological features were prepared using Adobe Illustrator version 15.0.0 (Adobe Systems Inc.). Selected digital photos were first imported into Adobe Illustrator, and lines were traced over the structures of interest. Other images, including from light microscopy, SEM and CLSM, were modified using Photoshop CS5 version 12.0 (Adobe Systems Inc.) to prepare plates and to improve clarity of features.

Material examined

All specimens of *A. rhodiola* from roseroot, *R. rosea*. Canada: along shore of Ungava Bay, Nunavik, Quebec: 9 adult females, 1 August 2007, coll. V. Filion; Base Island, Labrador, Newfoundland: 7 adult females, 2 adult males, 4 August 2012, 56.633°N, 61.586°W, coll. A. Cuerrier; Italy: Verona: 4 adult females and 1 male previously preserved in vials labelled as '*Phytoptus rhodiolae* Can.' themselves stored within a jar numbered CXXXIX (and # 608 in Valle 1955), coll. (probably) G. Canestrini over 100 years ago (MZUP); Russia: Pechengsky District (formerly Petsamo, Finland, and indicated as such on the

herbarium sample): 11 adult females and 1 male extracted from a single flower specimen of *R. rosea* (number: MZH 115326) mounted on a herbarium sheet, collected by I. Frosius (the surname is difficult to read and may be misspelled here), probably in the 1920s (as per communication with Juhani Terhivuo, MZH). Comparative material: 8 adult females labelled as '*Phytoptus destructor* (Nal.)', stored in jar # CXXXV (# 594 in Valle 1955), coll. from *Sedum* sp. at an unknown locality, (probably) by G. Canestrini over 100 years ago (MZUP). Kept at the CNC: slide-mounted and 95% alcohol-preserved specimens of *A. rhodiolae* and two dried, galled *R. rosea* plants, collected from Canada; slide-mounted *A. rhodiolae* specimens that were extracted from *R. rosea* flowers, and a single dried, galled flower, from Russia; and three specimens each of *A. rhodiolae* and *A. destructor* obtained from MZUP. Other material was returned to MZUP (slides, vials) and MZH (herbarium sheet).

Phytochemical analysis

The rhizomes of healthy (n = 94) and deformed (n = 60) plants were compared (by V.F. and A.S.) for salidroside and rosavins content. Each measure was made in triplicates and resulting values were averaged before statistical analysis. The rhizomes were used because their concentration of salidroside is higher than in seeds, and much higher than in leaves or stems (Filion et al. 2008). We use the same common laboratory extraction method as described in Filion et al. (2008), using 90% ethanol. Again, the high-performance liquid chromatography with diode-array detection analysis was used to decipher the variation of phytochemical contents among samples (see Filion et al. 2008; Avula et al. 2009). An unpaired t-test with Welch's correction (due to populations with possible unequal variances) was used to evaluate differences.

Results

Systematics

Comparison between specimens from Nunavik and Labrador (Canada) and those from Russia and Italy indicates that they are conspecific: quantitative characters show strong overlap between all characters measured (Table 1) and qualitative characters show high similarity, including the ornamentation of the prodorsal shield (compare Figure 3B–E with 3F,G and with 3H), coxisternal region, and of the female genital coverflap (compare Figure 5A with 5B,C,E). Morphometrics of the internal genitalia of Canadian and Russian specimens also largely overlapped. A minor difference was noted for the position of setae *2a*, which were slightly farther apart in Russian specimens (32–36 µm) than in Canadian specimens (27–33 µm); however, the ranges of values overlap and are based on few specimens, so it may represent mere variation among populations. Although many morphometric data could not be obtained for Italian specimens (e.g. lengths of coxal and leg setae), morphological traits were otherwise consistent with specimens from Canada and Russia, notably the prodorsal shield pattern, empodia with four pairs of rays, the number of opisthosomal annuli and the positions of setae on the opisthosoma. Comparison of the material examined, including Italian specimens collected by Canestrini, with description of *A. rhodiolae* by Canestrini (1892) and by other authors,

Table 1. Character measurements (range) of *Aceria rhodiolae* specimens from northeastern Canada (Nunavik and Labrador), northwestern Russia (Pechengsky district) and Italy.

		Canada	Russia	Italy	Canada+ Russia+Italy
		Female ($n \geq 5$)	Female ($n \geq 5$)	Female ($n \geq 2$)	Male ($n = 4$)
	Character	Range	Range	Range	Range
	idiosoma L	177–327*	204–283	190–258	145–259
	idiosoma W	71–88	73–83		66–85
Gnathosoma	*d*	5.4–8.3	5.5–8	5.3–7.0	5.7–6.9
	ep	2.4–3.8	2.7–3.6		2.7–3.2
	gnathosoma L	23–29	24–29	30 (n = 1)	
	chelicerae L	16–21	16–18		15–15.6
Prodorsum	shield L	37–41	37–44	40–41	36–39
	shield W	54–56	47–59		50–55
	frontal lobe L	2.5–3.1	2.5–4.8		3.0–3.6
	frontal lobe W	6.7–10.0	6.4–10.0		7.7–9.0
	sc	43–61	35–59	41–54	40–42
	sc–sc D	28–35	27–32	27 (n = 1)	30–32
Legs	leg I	41–42	38–45	37–46	36–38
	leg II	37–40	36–40	38 (n = 1)	32–34
	femur I	10.3–12.5	11.5–13.0	11.4–11.8	10.2–10.8
	femur II	10.9–13	10.3–13.4	11.2–11.5	10.9–11.4
	genu I	6.2–7.7	5.4–7.1	5.7–7.5	5.9–6.5
	genu II	5.5–6.0	4.5–6.2	5.1–5.2	4.3–4.9
	tibia I	9.0–11.0	9.0–10.5	9.7–10.9	8.1–8.7
	tibia II	7.2–8.0	8.1–8.8	7.3–7.6	6.9–7.9
	tarsus I	9.5–11.3	10.0–10.8	9.2–11.0	9.1–10
	tarsus II	9.0–11.1	9.1–10.3	9.0–10.0	8.4–8.8
	empodium I	7.9–9.0	8.2–8.8	7.7–8.7	7.2–7.6
	empodium II	7.0–9.6	8.0–10.5	7.9 (n = 1)	6.7–7.7
	ω I	10.5–11.3	10.0–11.1	9.9–10.1	9.5–11.0
	ω I	10.0–11.0	9.8–11.0	9.7–10.0	10.0–10.9
Leg setae	*bv* I	9.6–12.4	10.3–12.0		9.8–12.2
	bv II	12.4–15.0	12.4–14.5		11.9–16.8
	l″ I	27–31	27–32		20–28
	l″ II	16.2–19.0	17–21		14.8–16.9
	l′ I	9.0–10.5	9.9–12.6		7.1–10.2
	u′ I	5.6–7.5	5.6–7.2		5.2–7.4
	u′ II	5.3–7.7	5.6–7.0		6.0–6.4
	ft′ I	21–22	20–22		12–20
	ft′ II	11.9–13.0	10.8–12.0		8.4–10.9
	ft″ I	22–33	29–36		21–31
	ft″ II	32–34	29–33		26–30
Coxisternal region	*1b*	11.4–17.0	12.3–23.0		13.4–16
	1a	28–37	23–33		20–26
	2a	30–57	36–48		24–33
	1b–1b D	15–17	16–18	17–17	15–16
	1a–1a D	8.8–11.0	10.5–12.2	8.3–12.0	8.8–9.5
	2a–2a D	27–33	32–36	30–32	26–27
	1a–1b D	5.3–7.8	6.3–7.7	6.1–7.8	5.9–7.3
	1a–2a D	3.8–6.7	5.4–6.7	5.1–6.6	3.6–5.8
	No. coxigenital annuli	6–7	6–7	7 (n = 1)	6–7
Genital region	epigynal coverflap L	12–15	13–15	13–15	
	epigynal coverflap W	24–26	23–27	22–24	
	No. ridges on coverflap	8–12	10–12	10–11	
	3a	19–25	15–37	17–27	20–27
	3a–3a D	19–22	18–20	20–23	16–18

(*Continued*)

Table 1. (Continued).

		Canada	Russia	Italy	Canada+ Russia+Italy
		Female ($n \geq 5$)	Female ($n \geq 5$)	Female ($n \geq 2$)	Male ($n = 4$)
	Character	Range	Range	Range	Range
Opisthosomal setae	*c2*	37–47	36–51	30–46	44–49
	d	46–68	44–58	30–57	42–57
	e	13–21	15.0–18.0	12–19	14.2–17.4
	f	26–40	30–38	27–27	31–37
	h1	5.5–7.0	5.6–7.0	5.4–6.0	5.7–6.3
	h2	58–97	60–85	54–70	38–56
	c2–c2 D	59–67	56–69		56–66
	d–d D	40–44	41–48		37–49
	e–e D	21–26	21–26		22–29
	f–f D	30–31	28–34		27–28
	h1–h1 D	6.5–7.7	7.0–9.0		6.2–7.5
	h2–h2 D	13.1–14.5	12.5–14.5		12.3–12.4
Annuli	No. dorsal annuli	66–72	67–75	68–70	64–69
	No. ventral annuli	61–67	64–68	63–66	55–64
	c2 annulus no.	9–10	9–12	10–11	9–11
	d annulus no.	20–22	21–24	21–23	18–20
	e annulus no.	34–38	35–38	36–39	29–34
	f annulus no.	56–61	58–62	58–62	49–58
	No. annuli after *f*	5–6	6–6	5–6	6–6
No. microtubercles	between *sc–sc*	10–14	11–14		13–16
	between *c2–c2*	23–33	27–32		24–34
	between *d–d*	16–25	17–23		18–19
	between *e–e*	7–14	7–9		10–12
	between *f–f*	12–15	12–17		11–16

Minimal replication (*n*) is indicated in column heading, unless indicated in cell (when lower). D = distance.
*Labrador specimens (177–227) were shorter than Nunavik specimens (270–327). The high similarity in prodorsal shield length and the number of opisthosomal annuli between Labrador and Nunavik specimens indicate that the difference in idiosomal length is a result of differential contraction of the opisthosoma, in part due to a different preservation method.

indicates that our specimens belong to *A. rhodiolae* (see 'Taxonomic remarks' for further details). The diagnosis and description of *A. rhodiolae* below apply to all specimens studied from Canada, Russia and Italy, and values shown in the text represent the entire range of measurements.

Family **ERIOPHYIDAE**
Genus ***Aceria*** Keifer, 1944
Aceria rhodiolae (Canestrini, 1892)

Phytoptus rhodiolae Canestrini, 1892: Canestrini 1892: 722; Nalepa 1893: 294; Canestrini 1894: 803.

Phytoptus sp.: Löw 1881: 5; Löw 1885: 454; Szépligeti 1890: 20. Löw (1881, 1885) mentioned '*Phytoptus*' mites collected from 'mite galls' ('Phytoptocecidien') on *R. rosea*. Whereas Löw's illustrations of galls are only vaguely reminiscent of those induced by *A. rhodiolae*, his text seems more concordant (Löw 1881), suggesting conspecificity of the mite with *A. rhodiolae*.

Eriophyes rhodiolae (Canestrini, 1892): Nalepa 1898: 23; Nalepa 1911: 232; Nalepa 1923: 43; Ross and Hedicke 1927: 268; Nalepa 1929: 112; Kari 1932: 212; Kari 1936: 14; Julin 1936: 547; Baudyš 1938: 34; Moesz 1938: 151; Liro 1941: 4; Wahlgren 1948: 179; Liro and Roivainen 1951: 47, 125.

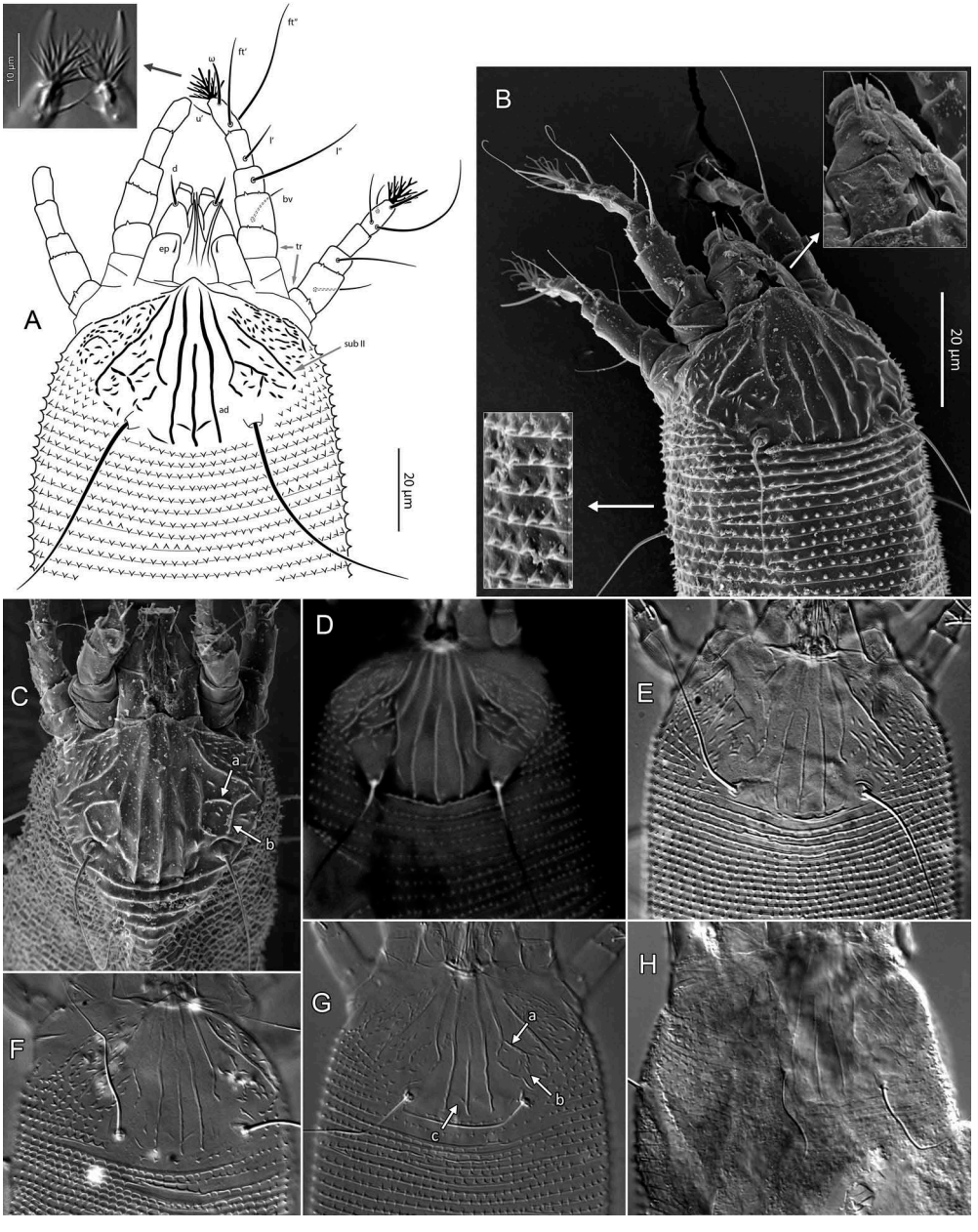

Figure 3. Prodorsal region, gnathosoma and legs of *Aceria rhodiolae* females from (B–D) Nunavik, QC (Canada); (E) Labrador, NFLD (Canada); (F,G) Russia; and (H) Italy. (A) Line drawings, (B,C) scanning electron micrographs, (D) confocal light scanning microscopy, (E–H) differential interference contrast light microscopy. Inset of (A) shows enlargement of empodia of leg I, and insets in (B) show enlargements of opisthosomal microtubercles and of dorsal gnathosoma. Notations in (A): ad, admedian line; sub II, submedian line II; tr, trochanter; so, solenidion; and others indicate setae of legs (femur to tarsus) and palp (coxal and genual setae). Arrows in (C) and (G) indicate characteristic ridges present in most (a) and some (b) specimens, respectively. The scale for images D–H is indicated on (A) and the scale for (C) is the same as that on (B).

Aceria rhodiolae (Canestrini, 1892): Roivainen 1950: 7; Leatherdale 1959: 31; Boczek 1961: 14; Buhr 1965: 1144; Farkas 1965: 23; Davis et al. 1982: 96; Amrine and Stasny 1994: 80; Bernini et al. 1995: 62; Skoracka et al. 2005: 60.

[The most of these publications merely list the species, with its host, sometimes with the type of gall it produces; a few include morphological descriptions.]

Diagnosis and similar species

Adults can be distinguished from other *Aceria* species by the following combination of characters. Only one female form is known. **Prodorsal shield** 37–44 long, including apically a small frontal lobe, pointed or narrowly rounded; Setae *sc* 27–35 apart; first pair of submedian lines reaching posterior third of shield, where they curve inwards and then outwards (curved portion sometimes interrupted into short lines); submedian I usually branching posteriorly before its curving, roughly forming a broad, reversed 'Y' facing *sc* tubercles; many short ridges or nodules scattered posterolaterad submedian I, and more densely scattered laterad submedian II. **Empodium** with four pairs of rays. **Coxal plates** with conspicuous rounded ridge(s) surrounding medially setae *1a* tubercles, and diagonal ridges laterad tubercles of setae *1b*. Prosternal apodeme strong, slightly broadened posteriorly. **Epigynial** coverflap 12–15 long × 23–27 wide with 8–12 longitudinal ridges; a pair of small, rounded lateral flaps flanking the coverflap. **Opisthosoma** covered by pointed microtubercles throughout, slightly larger dorsally than ventrally. Setae *c2* 36–51, *d* 44–68, *e* 15–21, *f* 26–40.

Aceria destructor may be a close relative, in part based on similarity in prodorsal shield pattern, particularly submedian line I and the ridge laterally branching from it (Figure 3C, 'a') (Nalepa 1891; however, illustration in Farkas (1965) differs). *Aceria rhodiolae* differs from *A. destructor* by (Table 2): generally shorter *sc* setae; fewer opisthosomal annuli, and accordingly, by setae *d–f* being inserted on different annuli number; a transversally narrower genital coverflap that bears fewer longitudinal ridges, with a few that are usually broken or abbreviated; posteromedian region of prodorsal shield, between *sc* tubercles, smooth or with few rather indistinct lineae (Figure 3) (several nodules or very short ridges present in this region in *A. destructor*; Figure 7; Nalepa 1891). In addition to the small V-shaped ridge crossing the median line near the posterior shield margin, often visible in *A. rhodiolae* (Figure 3G, 'c') and *A. destructor* (Figure 7, 'a'), another V-shaped ridge is generally present in *A. destructor*, at about 15 µm from the posterior shield margin [partly discernible on Figure 7, 'b'; clear on Figure 4 in Nalepa (1891); not in Farkas (1965)].

Aceria stinsonis (Keifer 1939) is moderately similar to *A. rhodiolae*. Based on comparison with description in the literature (Keifer 1939), *A. rhodiolae* may be primarily differentiated from *A. stinsonis* by: its longer *sc*; prodorsal shield with submedian I branched posteriorly; and coxisternal region ornamented with several nodules, and ridge(s) mesad seta *1a* and laterad *1b* (only a few scattered nodules for *A. stinsonis*; see also Table 2).

Based on the literature (Nalepa 1895; Liro and Roivainen 1951), *Aculus kochi* (Nalepa and Thomas) appears similar to *A. rhodiolae*, particularly in the ornamentation of the dorsal shield. The main difference may be the well-developed frontal lobe of the prodorsal shield, which probably was the reason why it was assigned to *Aculus* by Amrine and Stasny (1994).

Table 2. Comparative diagnosis between *Aceria rhodiolae* and similar species.

		Aceria rhodiolae	*Aceria destructor*	*Aceria stinsonis*	*'Aculus' kochi*
Prodorsal shield	Sc (µm)	43–61 (35 on a specimen)	~50–75	35	0.75× as long as prodorsal shield
	frontal lobe	small, pointed or narrowly rounded	none (or small)	none (or small)	well developed (?)
	submedian line I	branched posteriorly	branched posteriorly	simple, not branched	branched posteriorly
	posteromedian region	few or no tubercles/ ridges	many scattered tubercles or short lineae	few short lineae	few or no tubercles/ ridges
	median v-shaped ridges	often present, near base	often present: one near base, one mid-way	absent (on Figure)	present, near base
Opisthosoma	No. dorsal/ventral annuli	66–75/61–68	69–86/72–79 (Nalepa: ~80 dorsal)	~75/~75	~80 (in text); 66 ventral (illustr. in Nalepa)
	position of setae (ventral annuli #)	*c2* 9–12, *d* 20–24, *e* 34–39, *f* 56–62	*c2* 10–12, *d* 23–28, *e* 42–49, *f* 67–73	*c2* 10, *d* 24, *e* 42, *f* 67	*c2* 13, *d* 29, *e* 43, *f* 60
	genital coverflap	8–12 ridges (some broken medially); 22–27 µm wide	12–14 complete ridges; 26–29 µm wide	10–12 ridges; 25 µm wide	10 ridges; 24 µm wide
Host; distribution		Crassulaceae: *Rhodiola rosea*; Europe and Canada	Crassulaceae: *Sedum* sp.; Europe	Crassulaceae: *Dudleya caespitosa*; California (USA)	Saxifragaceae: *Saxifraga* spp.; Europe
Primary source of information		specimens	specimens; Nalepa (1891)	Keifer (1939)	Nalepa (1895), Liro and Roivainen (1951)

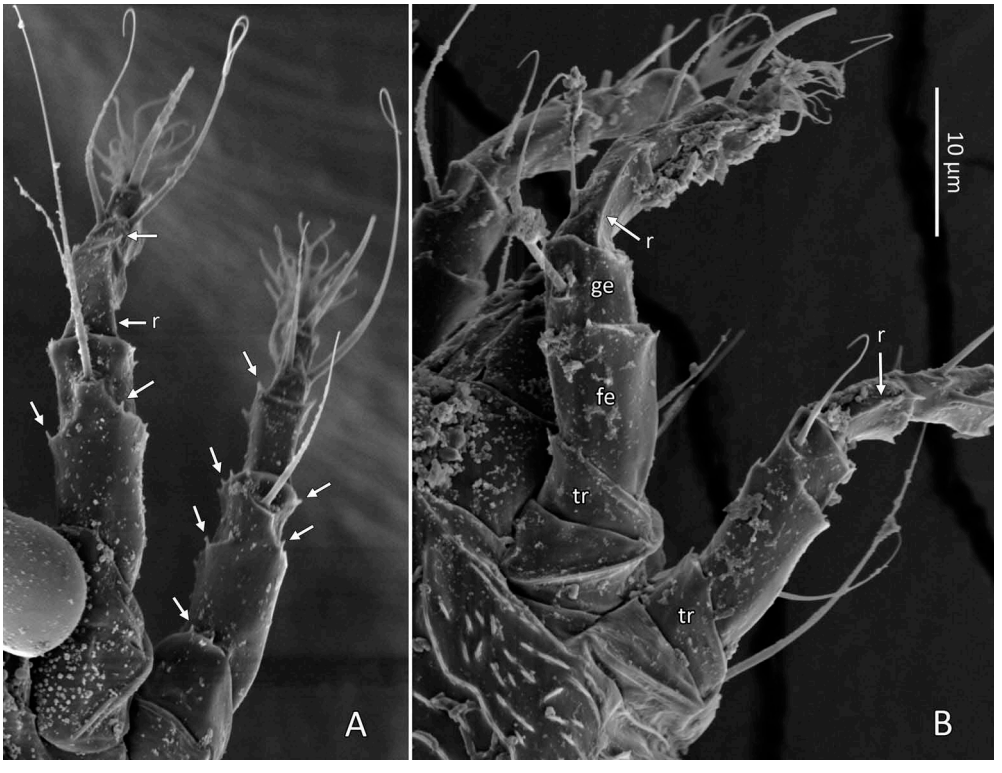

Figure 4. Legs of *Aceria rhodiolae* female (scanning electron micrographs), from Nunavik (Canada). (A) Legs I (left) and II (right); (B) legs I (left) and II (right). Arrows show ridges (r) on tibia I and II, and some of the spinules on the anterior margins of trochanter, femur, genu and tibia.

Description (Figures 2–6, Table 1)

Female (n = 22, some measurements based on fewer specimens). Beige to pale orange (in alcohol; Figure 2A). Idiosoma somewhat vermiform 177–327 long (depending on level of body contraction), 71–88 wide at level of setae *c2–d*. **Gnathosoma** (Figures 3A–C, 5C) curved downward, 23–30; palpcoxal seta *ep* 2.4–3.8, palpgenual seta *d* 5.4–8.3, palptarsal seta-like process *v* 1.7–2.8; cheliceral stylets 16–21. Cheliceral retainer a broad flap bent above cheliceral stylets; these stylets largely exposed for about the proximal half of the length of palpcoxae, and covered anteriorly by the stylet sheath (Figure 3B). **Prodorsal shield** (Figure 3) somewhat subpentagonal (or subtriangular, if not considering the region laterad submedian lines II); 37–44 long, 47–59 wide, with a small frontal lobe, narrowly rounded (Figure 3A,C,E) or pointed apically (Figure 3D,F), 2.5–4.8 long × 6.4–10 wide (may appear broadly rounded in some SEM photographs, e.g. Figure 3B, possibly due to different angle of view); lobe continuous and not clearly delineated from the rest of the shield anterior margin. Setae *sc* typically about 50 (43–61, exceptionally 35 on a single specimen), inserted at posterior margin of shield, projecting upwards and posterad in natural position (Figure 3B,C) and typically posterolaterad in slide-mounted specimens; *sc* tubercles with their basal axes transversal (hence, setae sometimes directed anteriorly on slide), setae 27–35 apart. **Shield ornamentation**: median line (ridge) conspicuous for about the posterior two-thirds of shield length, and faint or absent in anterior third; a pair of short lines (ridges) often present posteriorly on each

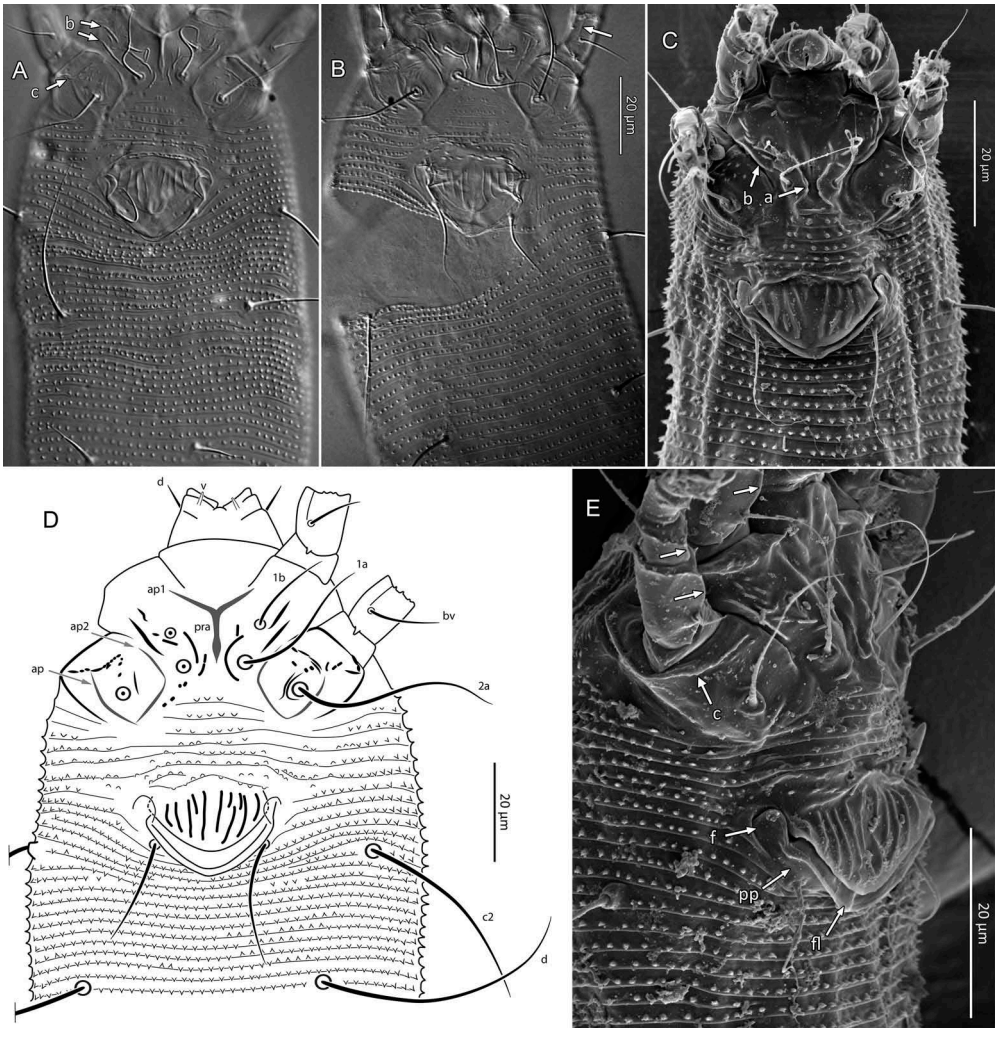

Figure 5. Coxigenital region of *Aceria rhodiolae* females from (A) Russia, and (B,C,E) Nunavik, Canada. (A,B) Differential interference contrast light microscopy, (C,E) scanning electron micrograph, (D) line drawing. Scale on (B) also applies to (A). Notations on (D) indicate palp, leg and idiosomal setae, and coxal apodemes (ap1, ap2, ap; pra, prosternal apodeme). Other arrows elsewhere indicate characteristic ridges on coxal plates (a,b,c); genital flange (fl), and underlying postgenital plate (pp), which bears setae 3a and extends anterolaterally into lateral flaps (f) that flank the genital coverflap; and ventral ridges on femur, genu, and coxal fields (E).

side of median line, directed anterolaterad, forming a broad 'V' (Figure 3A,E,F,G); admedian lines stretching from posterior margin of shield to about the base of frontal lobe, gradually converging anteriorly; submedian lines I subparallel to admedians, reaching posterior third of shield, where it curves mediad (inwards) and then laterad (outwards), approaching *sc* tubercles; curved portion of submedian lines sometimes interrupted into short ridges (Figure 3F,G). Submedian lines II running from posterolateral margins of shield to near anteromedian shield margin, at about a 90° angle from each other, and slightly curving outwards in their anterior quarter. A short ridge

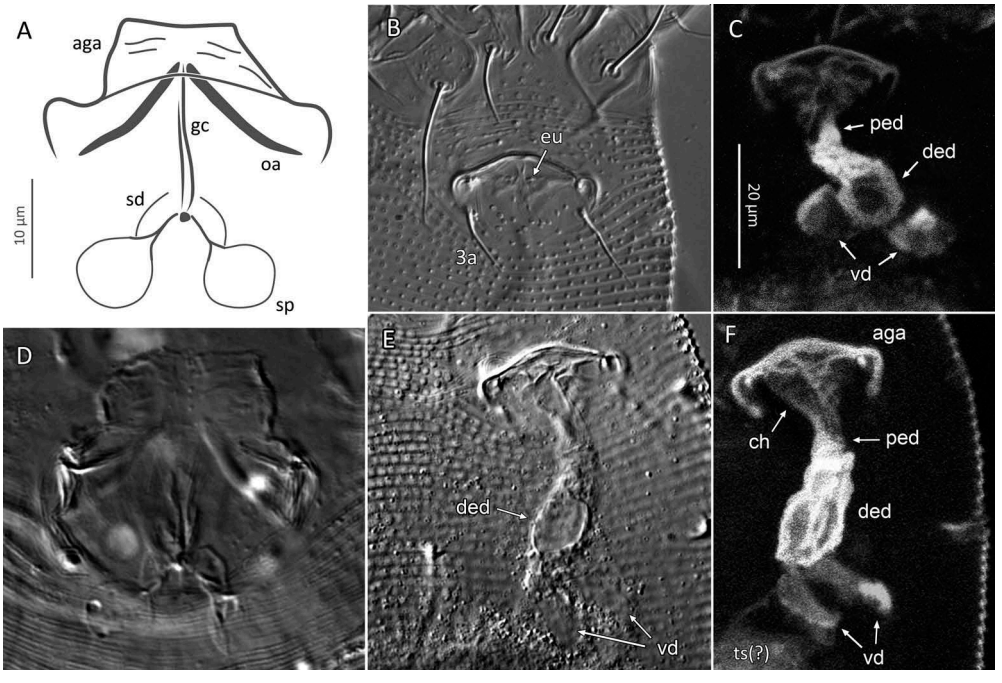

Figure 6. Internal genitalia of *Aceria rhodiolae* female (A,D) and external and internal genitalia of male (B,C,E,F). (A) Line drawing based on both Russian and Nunavik females; differential interference contrast light microscopy (B,D,E) and confocal light scanning microscopy (C,F) from a Russian female (D) and Labrador males (B,C,E,F). aga, anterior genital apodeme; ch, genital chamber; ded, distal ejaculatory duct; eu, eugenital setae; gc, walls (collapsed) of genital channel (longitudinal bridge); oa, oblique apodeme; ped, proximal ejaculatory duct; sd, spermathecal duct; sp, spermatheca; ts, putative testis; vd, vasa deferentia. Figures A and D are on the same scale, and B–C and E–F are on the same scale.

('a', Figure 3C,G) (sometimes represented by a series of about four or five shorter ridges) running posterolaterad originates from submedian line I, posteriorly forming a reversed Y-shaped bifurcation, facing *sc* tubercles (Y-shape may not be discernible, depending on other ridges present); occasionally another ridge (or series of short ridges; 'b') running perpendicular to the previously described ridge ('a'), and sometimes reaching laterally submedian line II, creating the impression of an eye-like structure (Figure 3C,G). Region between submedian lines I and II scattered with about 10–16 short ridges or nodules; region laterad submedian line II densely scattered with 30–38 ridges or nodules. **Legs** (Figures 3A,B, 4, 5) with setation normal as described for Eriophyidae (Lindquist and Amrine 1996). **Leg I** 38–45; femur 10.3–13.0, *bv* 9.6–12.4, position of *bv* 3.8–5.0; genu 5.4–7.7, *l*″ 27–32, position of *l*″ 2.7–3.6; tibia 9.0–11.0, *l*′ 9–13, position of *l*′ 1.4–2.6; tarsus 9.5–11.3, *ft*′ 20–22, *ft*″ 22–36, *u*′ 5.6–7.5; *ω* 10.0–11.3 without knob; empodium 7.9–9.0, with four pairs of rays; the two most basal pairs of rays with two (visible) secondary branches on each side, the third pair with one secondary branch, and terminal pair simple. **Leg II** 36–40; femur 10.3–13.4, *bv* 12.4–15.0, position of *bv* 3.4–4.3; genu 4.5–6.2, *l*″ 16–21, position of *l*″ 2.0–3.4; tibia 7.2–8.8; tarsus 9.0–11.1, *ft*′ 11–13, *ft*″ 29–34, *u*′ 5.3–7.7; *ω* 9.8–11.0 without knob; empodium 7.0–10.5, with four pairs of rays, with branching as that of leg I. Apical margins of trochanter, femur, genu and tibia with spinules (more easily discerned under SEM): two dorsally on trochanters I–II; two dorsally on femora I–II;

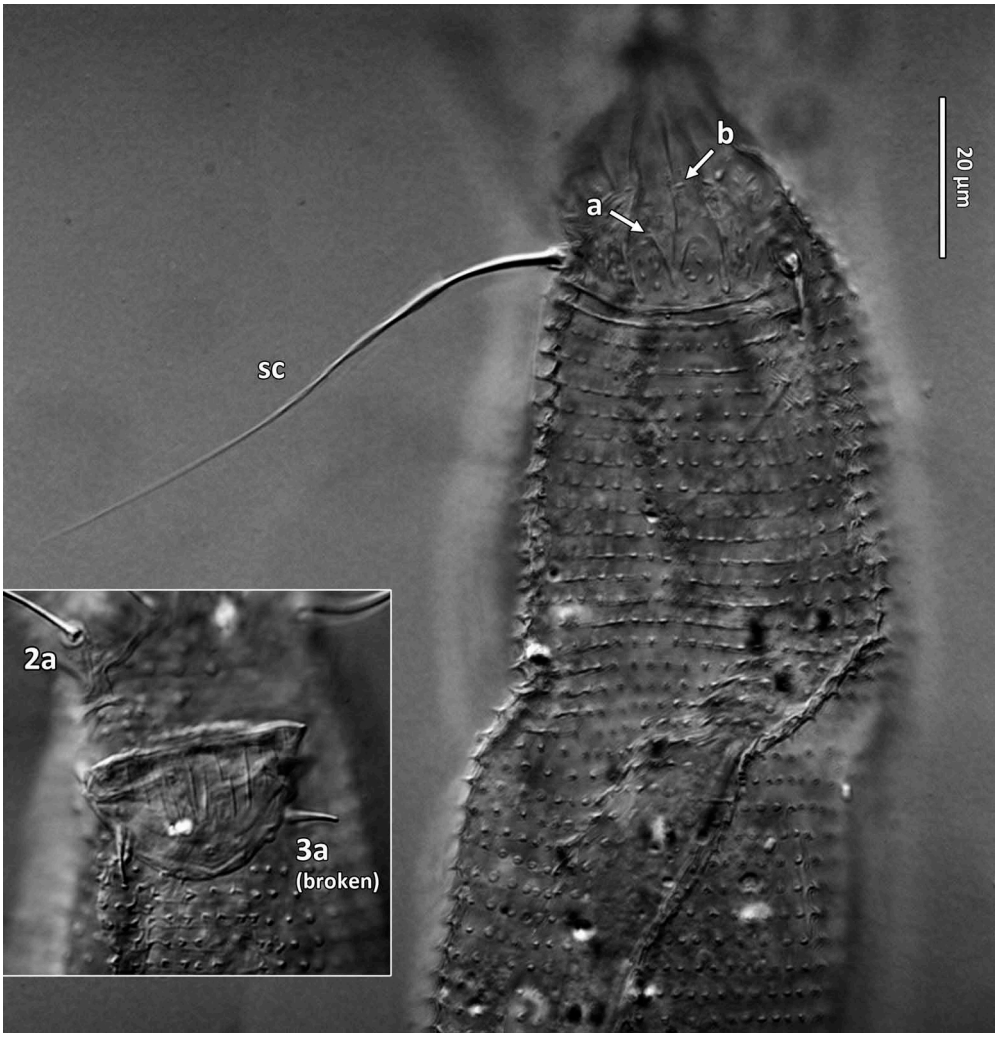

Figure 7. Prodorsal region and genital coverflap (inset) of *Aceria destructor* female (differential interference contrast light microscopy). Arrows indicate characteristic ridges discernible in most (a) and some (b) specimens, respectively.

a few spinules laterally and ventrally on femora and genua I–II; ventral spinules more tightly packed and aligned along a transversal ridge that curves medioventrally into a longitudinal ridge, which crosses genu I–II entirely, and posteriorly reaches *bv* tubercles on femora I–II; tibiae I–II each with two dorsolateral ridges and a medioventral longitudinal ridge that each end apically in a spine (Figure 4). Based on SEM, femora I–II apparently superficially fused mediodorsally with genu (between the two dorsal spinules), with apicolateral margins of femora sometimes extending dorsally on each side into a ridge that meets with the tubercle of genual setae *l″*; such ridges and fusion not apparent under light microscopy (although femoro-genual boundary may appear weak mediodorsally). Distal extension of coxal regions I and II (before connection with trochanters) with strong dorsal ridges running diagonally. **Coxal region** ornamented

with a few conspicuous ridges, in coxal field I: one or two, moderately long, curving ridges surrounding medially tubercles of setae *1a* ('a', Figure 5C); a moderately long ridge running close and parallel to coxal apodeme II, accompanied anteriorly by one or more shorter ridges laterad setae *1b* tubercles ('b', Figure 5A,C); on coxal field II: a ridge running close and parallel to trochanter II margin ('c', Figure 5A,E); all these ridges are entire or interrupted into a series of shorter ridges or nodules. A few additional short ridges or nodules, particularly anterad *2a* tubercles. Prosternal apodeme (or sternal line) strong (hardly discernible under SEM, because it is mostly internal), bifurcating anteriorly into coxal apodemes I (*sensu* Lindquist 1996), and posteriorly broadened and tapering to end at level of setae *1a*; coxal field II delimited antero- and postero-medially by a linea (may represent apodeme 2, *sensu* Lindquist 1996; Figure 5D, 'ap2'); another linea (or apodeme, 'ap') flanking posterolaterally tubercles of *2a*; the junction of these lineae posteriorly leading (more internally) to a poorly defined, inversely Y-shaped apodeme (vaguely discernible, Figure 5B). Subcapitular plate 10–14 long × 15–21 wide. Setae *1b* 11–23 long, 15–18 apart; *1a* 23–37 long, 8.8–12.2 apart; *2a* 30–57 long, 27–36 apart. About six or seven microtuberculate coxigenital annuli, of which the two to four anteriormost annuli are incomplete (i.e. segregated from lateral annuli); microtubercles on coxigenital annuli smaller, and rounder or more weakly pointed than other ventral microtubercles posterior to epigynium. **External genitalia** (Figure 5) with genital coverflap 12–15 long × 22–27 wide, more or less semicircular, anterolateral margins angled (just before meeting with anterior hinge), ornamented with 8–12 longitudinal ridges extending for most of coverflap length, except for a few abbreviated ridges (mostly medially); genital 'flange' (on which sits the coverflap at rest; see Chetverikov et al. 2013) often visible for 2–6 behind coverflap (even when coverflap 'closed'); a pair of small, rounded lateral flaps flanking coverflap (sometimes not visible on slides); setae *3a* 15–37 long, 18–23 apart. **Opisthosoma** (Figure 2) more or less parallel-sided for its anterior half (from setae *c2* to *e*); evenly rounded dorsally and ventrally, bearing 66–75 dorsal and 61–68 ventral annuli, microtuberculate throughout. First dorsal annulus behind prodorsal shield often interrupted (i.e. without microtubercles) at level of *sc* tubercles; that first dorsal annulus is three to five annuli posterad the first complete annulus behind coxal plate II. Dorsal microtubercles (Figure 3B, inset) subconical (or subtriangular if bent or flattened on slides), sharply pointed, with slightly concave sides, straight or slightly curving posteriorly in natural position (SEM); similar throughout, 1.0–1.4 long × 0.9–1.3 wide basally, except smaller on the first three to five dorsal annuli, and narrower and progressively shorter on posterior third of opisthosoma, 0.5–1.2 long × 0.5–0.8 wide (microtubercles may appear rounded if oriented upwards, especially in laterally mounted or highly contracted specimens). Laterally, microtubercles similar to dorsal ones, becoming smaller, more weakly pointed ventrally (0.7–1.2 long × 0.8–1.2 wide; Figure 5); microtubercles narrow, ridge-like on the last five ventral annuli. Setal lengths: *c2* 36–51, *d* 44–68, *e* 12–21, *f* 26–40, *h1* 5.4–7.0; *h2* 54–97. Distances between pairs of setae: *c2–c2* 56–69, *d–d* 40–48, *e–e* 21–26, *f–f* 28–34, *h1–h1* 6.5–9.0, *h2–h2* 12.5–14.5, *h1–h2* 2.3–3.4. Position of setal tubercles (the number of annuli counted from coxal plate II): *c2* 9–12, *d* 20–24, *e* 34–39, *f* 56–62; there are five or six annuli past seta *f*. **Internal genitalia** (Figure 6A,D). Anterior genital apodeme more or less flat anteriorly for 12–17 µm, with anterolateral walls bent posteriorly or posterolaterally (i.e. at a 45°–90° angle), and ending in two short curves or folds. A pair of oblique apodemes ('oa'; *sensu* Chetverikov et al. 2015), thick, 13–16 long, each slightly curved, sometimes bent midway, oriented more or less perpendicular with each other. Longitudinal bridge 13–17 long, with walls (of the genital channel; see Chetverikov 2014) sometimes discerned

apart ('gc', Figure 6A). Spermathecae spherical, usually about 6 (4.5–7.3) in diameter; spermathecal duct 3.4–4.2 long; duct connected near or at the posterior apex of longitudinal bridge, at an angle of 38–62° from bridge axis.

Male (n = 4; Figure 6B,C,E,F). Fundamentally the same as female, except for genitalia and minor quantitative differences, including shorter idiosoma, shorter leg segments, and slightly fewer dorsal and ventral annuli (Table 1). Ornamentation of prodorsal shield and coxigenital region as that of female. Epiandrium 22–24 wide, 14.5–15.3 long, including the region of irregularly scattered, rounded microtubercles between setae *3a* (Figure 6B); eugenital setae c. 1 μm long, bases 3.0–3.5 apart. Internal structures identified include anterior genital apodeme ('aga'), genital chamber ('ch'), proximal and distal ejaculatory ducts (the latter acting as a spermatophore pump), both highly sclerotized (based on their high autofluorescence under CLSM), connected posteriorly to a pair of vasa deferentia ('vd'), leading to a putative testis (Chetverikov 2015).

Taxonomic remarks

The specimens that we borrowed from the Canestrini collection had been preserved in vials (containing an alcohol-based fluid) labelled as from Verona, Italy, the presumed type locality for *A. rhodiolae* (Canestrini 1892: 'place of origin, Veronese'; note, however, that Amrine and Stasny (1994) mentioned 'woods near Trentino, Italy' as the type locality). Unfortunately, the specimens that Canestrini used to describe '*Phytoptus*' *rhodiolae* (syntypes) are probably lost, because no slides labelled as *P. rhodiolae* were retrieved from his collection (now hosted by the MZUP; Paola Nicolosi pers. comm.).

Canestrini's description (1892) of *A. rhodiolae* is the only one that includes morphological illustrations. His illustrations of the ventral habitus and prodorsal shield partly agree with our observations; they show 58 ventral opisthosomal annuli (61–68 for our specimens), 12 longitudinal ridges on the coverflap (8–12 on our specimens), and *sc* setae about two-thirds the length of the dorsal shield (his text says *sc* at least as long as the shield, which is more concordant with our observations). The text mentions 'approximately 60 annuli', which is, again, near the lower end of the range of our count of dorsal annuli (66–75). More importantly, his illustration of the prodorsal shield shows differences (no nodules or ridges other than the main median, admedian and submedian lines, and the two pairs of submedian lines show different paths) from the specimens we examined, and only three pairs of rays can be seen on all the four empodia illustrated (the text also mentions three pairs of rays only). This may in part be due to the suboptimal microscope qualities and standards of taxonomic descriptions of that period. Roivainen (1950) mentioned that *A. rhodiolae* from Sweden had more opisthosomal annuli than specimens studied by Canestrini (1892), with 70–75 opisthosomal annuli, which is more consistent with our results. The few other descriptions of *A. rhodiolae* (Nalepa 1898, 1911; Liro and Roivainen 1951; Farkas 1965) appear as a subset of, or equivalent to Canestrini's description (e.g. they all mention '60 annuli', and three-rayed featherclaws), with no additional information. We consider that three-rayed empodia is probably a mistake made by Canestrini, and which was duplicated by other authors.

Certain characters shared by *A. rhodiolae* and relatives have unclear phylogenetic significance. For instance, the ridges and spinules present on the leg segments of *A. rhodiolae* are also present in other genera of eriophyoids (Baker et al. 1996; Chetverikov et al. 2014). Second, the median, basal V-shaped ridge on the prodorsal

shield of *A. rhodiolae* and *A. destructor* occurs in other *Aceria* species, such as *Aceria anthonoma* (Nalepa), *Aceria chrysopsis* (Keifer), *Aceria lappae* (Liro), *Aceria saxifragae* (Rostrup), as well as in species in other eriophyid genera, such as *'Aculus' kochi, Aculus ligustri* (Keifer), *Aculops maculatus* (Hodgkiss) (sensu Keifer), and *Paraphytoptus mcgregori* Keifer, (see Liro and Roivainen 1951; Farkas 1965; Baker et al. 1996).

Galls

Galls were observed primarily on the female fruiting inflorescences of *R. rosea* (= Sedum rosea (L.) Scop., = *Sedum rhodiola* DC.) and occasionally on the upper leaves surrounding the infructescence (Figure 8). Galled tissues turned fleshy, wrinkled, and whitish or yellowish green (Figure 8B,C). The galled flowers were patchily distributed within inflorescences (Figure 8C,D), and sometimes comprised most or all of the inflorescence, giving a cauliflower-like appearance (Figure 8B).

Local distribution

Our survey has found galled *R. rosea* at many sites scattered along the shore of Ungava Bay, from the extreme northwest point (near Quaqtaq: 61.047°N, 69.634°W) to near the northeast extreme of the surveyed area (south of Killiniq: 60.359°N, 64.850°W) and as far south as Kuujjuaq (58.148°N, 68.336°W) (Figure 1B). From 92 sites studied in Nunavik, 29 (31.5%) had at least a few (often numerous) galled individuals of *R. rosea*, and the remaining 63 had apparently no infested individuals. In addition, we have observed galled *R. rosea* in Labrador, at multiple sites on Base island (56.633°N, 61.586°W) and in the vicinity of Saglek Fjord (58.51°N, 63.25°W), Nain (56.54°N, 61.70°W) and Rigolet (54.18°N, 58.44°W).

Impact on phytochemistry

Concentrations in rosavins did not differ between healthy (0.63 ± 0.05 mg/g) and infested (0.61 ± 0.05) plants. In contrast, salidroside concentration in galled plants (0.65 ± 0.05 mg/g) was less than half the concentration in healthy plants (1.42 ± 0.05) and this was significant ($p = 0.01$) (Figure 9).

Discussion

Our search through the literature and databases (e.g. Zoological Records; Amrine and Stasny 1994; J. Amrine and E. de Lillo unpubl. database of world eriophyoid species, pers. comm.) indicate that *A. rhodiolae* is the only current valid eriophyoid species recorded from the plant genus *Rhodiola*. An *Eriophyes* sp. (considering current concepts, this mite could actually belong to a genus other than *Eriophyes, such as Aceria*) was reported from reddish deformed flower heads of 'red orpine' (*Clementsia*) in North America, probably USA (Felt 1940). The red orpine mentioned may actually be *Rhodiola rhodantha* A. Gray (H. Jacobsen) (=*Clementsia rhodantha*), a species thriving in the western (mountainous) USA. *Rhodiola rosea* was reported as the host plant of *Phytoptus eucricotes* Nalepa, by Canestrini (1892: 706), but this was a mistake that he corrected in the same publication (1892: 721; *P. eucricotes* lives on *Lycium europaeum* L.). *Rhodiola* is a relatively small plant genus (with 90 species), and used to be considered within the larger, more broadly defined genus *Sedum* (stonecrops), which comprises 420 species (Stevens 2001 onwards). Two eriophyids are recorded from *Sedum*, in Europe: *Aceria destructor* and

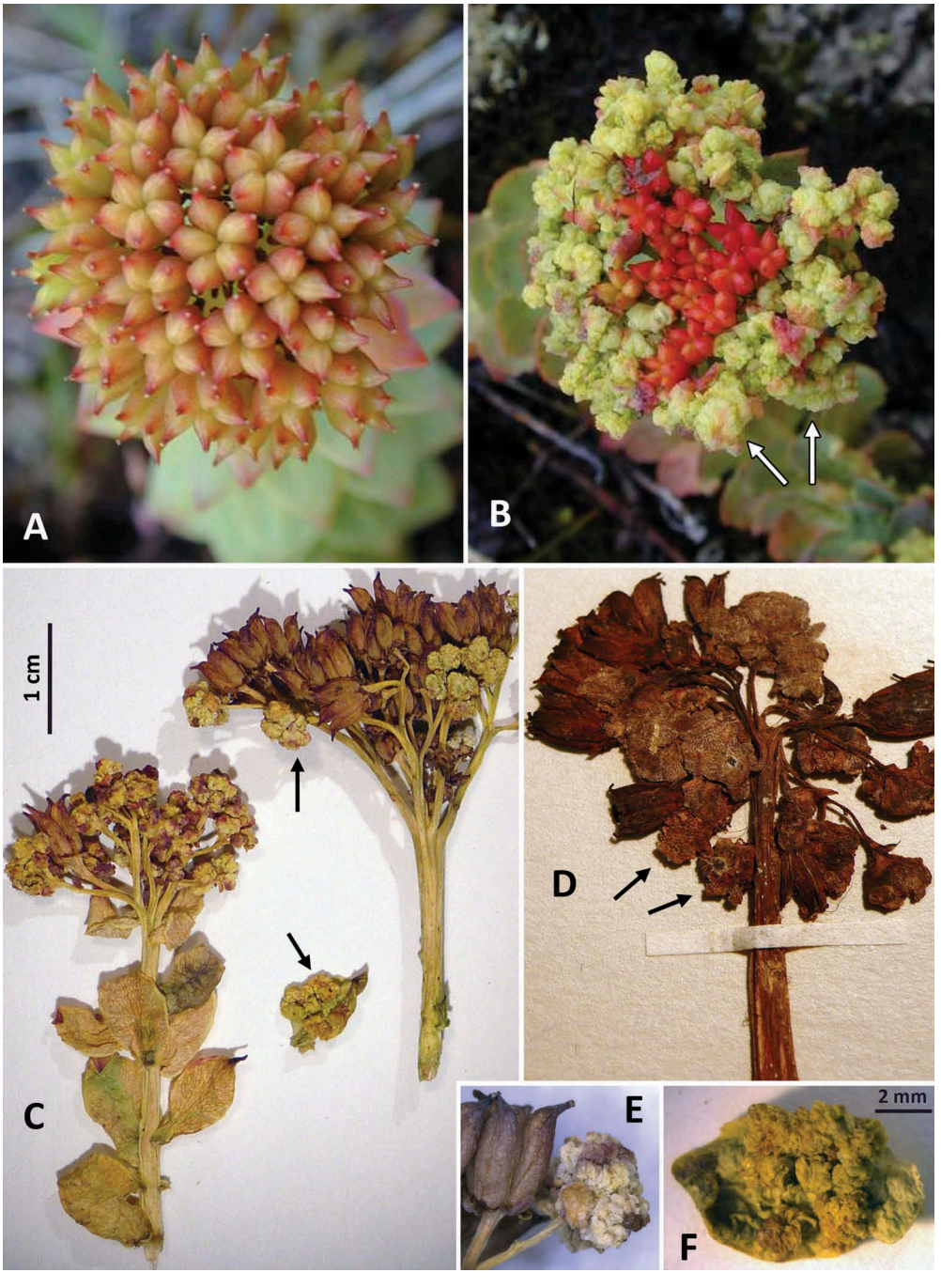

Figure 8. (A) Healthy infructescence of a *Rhodiola rosea* plant from Nunavik (Canada) versus (B) a mite-infested inflorescence (mostly pale green or yellowish) that partly (centrally) developed into fruits (yellow to red). (C) Dried inflorescences from Labrador (Canada) with a few (upper right) to most (lower left) flowers galled, and a galled leaf (isolated, in the middle). (D) Dried inflorescences from western Russia that were preserved in an herbarium for over 100 years. (E,F) Enlargement of a galled flower and galled leaf from Labrador (same scale). Arrows point at some of the galled flowers (B–D) or leaves (C). The scale on (C) also applies to (D), and is approximate for (A,B).

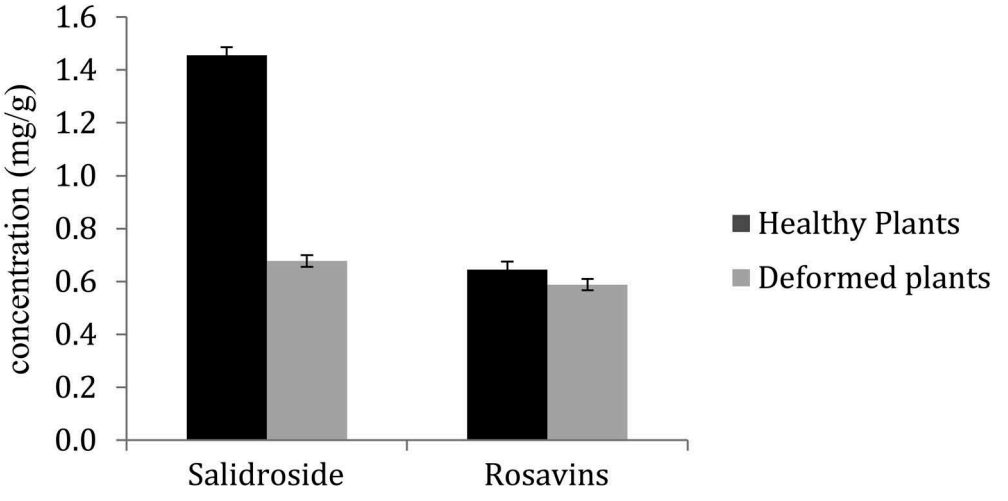

Figure 9. Salidroside and rosavins contents in *Rhodiola rosea* plants that were ungalled (healthy, n = 94) and galled (deformed, n = 60) by *Aceria rhodiolae*. Error bars on y-axis are standard deviations.

Cecidophyes glaber (Nalepa), both causing deformation of the buds and flowers of *Sedum reflexum* L. and other *Sedum* spp. (Alta and Docters van Leeuwen 1946; Petanović and Stanković 1999). Considering the entire family Crassulaceae as potential host plants, only two additional eriophyoid species are known, both collected from the leaves of sand lettuce [*Dudleya caespitosa* (Haw.) Britt. and Rose] in California: *Aceria stinsonis* and *Aculus cotyledonis* (Keifer 1939). This represents a total of five eriophyids associated with Crassulaceae worldwide – a rather humble tally considering that approximately 1400 species from 34 genera belong to that plant family (Stevens 2001 onwards).

Gall types and plant organs affected

Previous publications on *A. rhodiolae* are concordant with our observations, and describe the galls it induces as fleshy, wart-like outgrowths, with inflorescences deformed into a fleshy, frizzy ball-like mass that are reminiscent of small cauliflowers (Ross and Hedicke 1927; Liro and Roivainen 1951; Buhr 1965). Galled tissues are reported as yellowish, reddish or violet (Löw 1881; Kari 1936; Moesz 1938; Liro and Roivaninen 1951). The stems of *R. rosea* can also be galled by *A. rhodiolae* (Ross and Hedicke 1927; Wahlgren 1948; Buhr 1965), but more rarely than flowers and leaves (Kari 1936). Interestingly, the original description by Canestrini (1892) and the text of Boczek (1961) mention only leaves as the plant organ affected by galling, not the flowers. However, even Nalepa (1893, 1898, 1911), soon after the publication of Canestrini's description, mentioned both leaves and flowers as being galled. Given that galled inflorescences of *R. rosea* are conspicuous, it is difficult to conceive that both Canestrini and Boczek overlooked the galled inflorescences. Boczek (1961) made his observations on 8 August 1957, at which time healthy flowers would

have already bloomed into fruits (*R. rosea* blooms in late June to early July in Nunavik and Newfoundland; Cuerrier and Hermanutz 2012). So, it may be that flowers were not severely infested in the sites that he visited, leaving him overlooking galled inflorescences. It is also possible that the differential galling of plant organs is affected by the local climate, soil, or variations in physiology of the populations of *R. rosea* or of the mite. Boczek (1961) mentioned that *A. rhodiolae* induces galls especially along the margins of leaves. The illustration by Liro (1941), which, before our study, constituted the only adequate visual representation of galling by *A. rhodiolae*, somewhat agrees with Boczek's point, showing most of the leaf galled tissues in clusters, near or along the leaf margins, although galls often cover a large portion of the leaf.

Geographic distribution

Observations of Roivainen (1950) and Liro and Roivainen (1951) indicate that in northern Sweden and Finland, and the nearby region of Russia, roseroot plants are commonly galled by *A. rhodiolae*, and that high infestation rates (up to 60–100%) can be seen locally (Liro and Roivainen 1951), which is even higher than what we observed in Nunavik.

Aceria rhodiolae now appears Holarctic, with the Canadian Arctic as the only or main records west of the Atlantic Ocean, and numerous records east of the Atlantic, in Italy (Canestrini 1892, 1894); Germany (Nalepa 1893, 1898, 1911); Tatra mountains overlapping Poland (Boczek 1961) and Slovakia (Magas-Tátra mountains; Szépligeti 1890; Baudyš 1938; Moesz 1938); Austria (Dürrenstein mountain, near Lunz; Löw 1881); Norway (Leatherdale 1959); northern parts of Sweden (Julin 1936; Roivainen 1950) and Finland (Enontekiö (Lapland); Liro 1941), and the nearby region of Russia (formerly Finland, Petsamo region; Kari 1936; Liro and Roivaninen 1951; this study). The species therefore appears relatively widespread in Europe (Buhr 1965), and Wahlgren (1948) also mentions the species as present in Iceland, Greenland, Scotland and the Swiss Alps (although without providing references for such records). It is probable that the distribution of the mite largely follows that of its host plant, in subarctic and alpine regions, and therefore may occur as far east as the mountains of Central Asia (for instance, Tien-Shan and Himalaya; Small and Catling 2000), and as far west and south as where *R. rosea* occurs in western Nunavut and in North Carolina (Roan Mountain) in North America, respectively. However, the range of *R. rosea* is shrinking in the south and it is considered endangered or threatened in southeastern USA (Plant Industry Division 1998; Nongame and Natural Heritage Program 1999).

Impact on phytochemistry

Salidroside is a phenylethanol derivative with antidepressant properties (Brown et al. 2002; Kurkin 2003; Tolonen et al. 2004; Panossian and Wikman 2014). Therefore, the floral tissue deformation by eriophyid mites not only has a negative influence on the reproductive capability of *R. rosea* plants through the sterilization of flowers, but also significantly decreases the medicinal quality of the plants.

This may be the first time that a mite is shown to have an adverse effect on the phytochemistry of a medicinal plant. However, such findings are not surprising, given the wide range of morphological, biochemical and physiological effects of both galling and non-galling eriophyoid mites observed so far on various host plants (see reviews by Petanović and Kielkiewicz 2010a, 2010b). The distortion of plant tissues is itself linked to multiple processes affecting the directly injured epidermal cells, as well as neighbouring cells, the entire leaf and sometimes neighbouring leaves. In addition to having plant growth regulatory effects involved in the formation of galls (Royalty and Perring 1996; de Lillo and Monfreda 2004), the salivary compounds injected by the mites can also affect other hormones or enzymes involved in broader processes, including the indirect defence of plants against herbivores (Petanović and Kielkiewicz 2010a; Samsone et al. 2012). Eriophyoids, including galling and vagrant (i.e. non-galling) forms, may also substantially compromise the leaf gas exchange and photosynthesis of not only the leaf that is fed on, but also those of ungalled, neighbouring leaves (Royalty and Perring 1989; Larson 1998; Samsone et al. 2012; Patankar et al. 2013).

Several eriophyoid species are known to transmit plant viruses, some of which have a considerable impact on the plant host (e.g. Navia et al. 2013), and others enhance the establishment of fungal pathogens, and vice versa, thereby increasing disease severity (Gamliel-Atinsky et al. 2010). It is therefore not impossible that some of the changes in a plant's physiology and chemistry (e.g. overall drop in salidroside levels) may be in part due to or exacerbated by pathogens that are transmitted by eriophyoid mites.

Deutogynes and overwintering

It is unknown whether *A. rhodiolae* has an additional female form (deutogyne). A few *Aceria* species associated with herbaceous perennial plants have both protogyne and deutogyne females, such as *Aceria anthocoptes* (Nalepa) on Canada thistle (Petanović et al. 1997) and *Aceria chondrillae* (G. Canestrini) on skeleton weed (Krantz and Ehrensing 1990). Adult females of *A. rhodiolae*, regardless of the possible existence of deutogyne females (which are typically the overwintering life stage of deuterogynous species of eriophyoids), presumably overwinter within galled tissues, or more strategically, near the stem base or on rhizomes near the soil surface (Krantz and Ehrensing 1990; McClay et al. 1999) so as to easily colonize, in the spring, new shoots of *R. rosea* growing from the same rootstocks as the previous year's host.

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