

Deuterogyny and the Association of Two Vagrant Eriophyoid Mites (Acariformes, Eriophyoidea) with the Host-plant Generative Organs of Two Broad-leaved Trees in North-West Russia

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Phytoparasitic mites of the superfamily Eriophyoidea Nalepa live and feed on mature leaf surfaces, between leaf bud scales, and (though less commonly) on flowers or fruits. In this study, we focused on the seasonal associations of two eriophyoid species, *Shevtchenkella serrata* (Nalepa 1892) with the Norway maple tree (*Acer platanoides* L.), and *Brevulacus reticulatus* Manson 1984 with the common oak (*Quercus robur* L.). These species have complex life cycles with two morphologically different, seasonal female forms, the protogyne and deutogyne. In *B. reticulatus*, both forms retain all the major generic characteristics but in *S. serrata* only the protogynes conform to the diagnosis of *Shevtchenkella*, whereas the deutogynes have the typical traits of *Anthocoptes*. We confirmed the conspecificity of the protogynes and deutogynes of both eriophyoid species by sequencing a barcode fragment of the *Cox1* gene from which we obtained four pairwise identical sequences: ON920305/ON920306 (*S. serrata*) and ON920307/ON920308 (*B. reticulatus*). In addition, taxonomical studies on *Shevtchenkella* and *Brevulacus* resulted in new synonymies and combinations: (1) *Oxypleurites obtusus* Roivainen 1947 is considered a deutogyne of *S. serrata* and treated as a junior synonym of *S. serrata*; (2) two rhyncaphyoptine species from North America are transferred from the genus *Rhyncaphyoptus* to *Brevulacus*: *B. albus* (Keifer 1959) comb. nov. and *B. atlanticus* (Keifer 1959) comb. nov.; and (3) one species, *B. salicinus* Soika et al. 2017, is excluded from *Brevulacus* and transferred to *Rhyncaphyoptus*: *Rhyncaphyoptus salicinus* (Soika et al. 2017) comb. nov. Apart from distinct morphological deuterogyny in *S. serrata* and *B. reticulatus*, we observed the persistent association of *S. serrata* with the generative organs of the maple tree, *A. platanoides*, leading to transmission to the next host generation via the seed-containing winged fruits (samaras) and subsequent colonization of seedlings. In *B. reticulatus*, similar synchronization with host-plant dispersal was not detected; however, in mid-summer, temporary colonization of immature acorns and feeding was observed. Additional studies conducted in various ecosystems and including different ecological groups of plants, especially anemochorous plants, are needed to estimate the frequency of the association of eriophyoids with plant generative organs, seeds and seedlings to better understand what role in mite ecology such associations may play.

Key words: Seasonal dimorphism, Herbivore, Dispersal, Phytophagy

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BACKGROUND

The superfamily Eriophyoidea is a highly diverse, ancient lineage of phytoparasitic acariform mites (Lindquist 1996; Sidorchuk et al. 2015). They are the most difficult group of mites for taxonomists to classify due to their microscopic size (most species 200–300 μm), greatly simplified morphology and numerous undescribed species (Nuzzaci and Alberti 1996; Amrine et al. 2003). An additional complication comes from a type of seasonal dimorphism, seen in ~65 of the ~4800 total described eriophyoid species, known as *deutogyny*, a complex life cycle with two morphologically different forms of female, a *protogyne* and a *deutogyne* (Keifer 1942; Hall 1967; Manson and Oldfield 1996; Guo et al. 2015; Marini et al. 2021). Morphologically these two forms can appear nearly indistinguishable in some taxa, or so divergent that some have been assigned to different genera and even subfamilies, and only with the use of molecular data were they resolved as seasonal morphotypes of the same species (Guo et al. 2015; Druciarek et al. 2016; Chetverikov et al. 2018; Yin et al. 2020).

Most species of eriophyoid mites are obligate symbionts of plant leaves or buds, with only a small proportion of their contemporary diversity strongly associated with flowers and fruits (Oldfield 1996; Amrine et al. 2003). Chetverikov et al. (2022) showed that in the system comprising the phytoparasite, *Shevtchenkella serrata* Nalepa (Eriophyidae) on the Norway maple, *Acer platanoides* L., the association of the eriophyoid with maple fruits facilitated the eriophyoid's vertical transmission. That is, it allowed the eriophyoid to exploit the host's dispersal mechanism and colonize the next generation of hosts.

In this paper, we report advances in the same line of research by complementing our previous findings on the ecology of *S. serrata* on *A. platanoides* with new data on seasonal changes in populations of *B. reticulatus* from *Q. robur*. More specifically, we present novel data on seasonal morphological dimorphism in *Shevtchenkella* and *Brevulacus* species collected from North-West Russia, report new synonymies for several species in these two genera, and discuss the ecological role of the association of eriophyoid mite species with the plant generative organs of broad-leaved, boreal trees.

MATERIALS AND METHODS

Morphology

Eriophyoid mites were collected from *Acer*

platanoides and *Quercus robur* from 2018 to 2022 in Saint-Petersburg and Vyrizta (Leningrad Prov.) in North-West Russia. All eriophyoids were removed from separately bagged, freshly collected plant material using a fine minuten pin and a dissecting microscope, then placed in Eppendorf tubes filled with 96% ethanol. The mites were mounted in a modified Berlese medium with iodine (Amrine and Manson 1996) and cleared on a heating block at 90°C for 3–5 hours. Slide-mounted specimens were examined with a Leica DM2500 light microscope (LM) equipped with differential interference contrast (DIC) and phase contrast (PC), and photographed with a TouPCam (UCMOS09000KPB) digital camera. Images and specimens were analyzed and measured using TouPTek TouPView software. In the mite descriptions, the measurements are given as ranges in micrometers (μm) except when mentioned otherwise. Classification and terminology of external morphology follow Amrine et al. (2003) and Lindquist (1996). Drawings of mites were sketched in pencil using a video projector (Chetverikov 2016), then scanned and finalized in Adobe Illustrator CC 2014 using a Wacom Cintiq 16 (DTK1660K0B) interactive display and Wacom Pro Pen 2.

DNA extraction and sequencing

For DNA extraction, 1–3 specimens of each species were crushed with a fine pin in a 2 μl drop of distilled water on a cavity well microscope slide. The drop was then pipetted into a thin-walled PCR tube with 30 μl of 5% solution of Chelex[®] 100 Resin (Bio-Rad) before being heated three times for 5 minutes at 95°C. The DNA in the solution above the settled Chelex[®] granules was used for PCR amplification of the fragment of mitochondrial cytochrome oxidase c subunit I gene (*Cox1*). The thermocycling profiles and primers for PCR were those specified by Chetverikov et al. (2021a). After amplification, 4 μl of each reaction product was mixed with 0.5 μl of SYBR Green I (Lumiprobe) and analyzed by electrophoresis on 1% agarose gel to assess the product size and concentration. DNA sequences were obtained using BigDye Terminator v.3.1 chemistry (Applied Biosystems, Foster City, CA, USA) and a 3500xl Genetic Analyzer (Applied Biosystems). Trace files were checked and edited using GeneStudio[™] Professional 2.2.0.0.

Field observations

Every week from July 2020 to October 2021 (excluding the period from mid-December to March when night frosts were common, and the leaves and samaras (winged fruits) that had fallen on the ground

became embedded in the frozen leaf litter) (see Chetverikov et al. (2022) for the mite survey in 2020 to 2021), and every two weeks from March 2022 to August 2022, we sampled eriophyoid mites from 15 mature trees, saplings and samaras of Norway maple (*A. platanoides*) growing in a wooded area (59°23'43.5"N, 30°18'00.6"E) in the village of Vyritza in the Leningrad region of Russia. We also sampled eriophyoids from two oak trees (*Q. robur*) every 2–3 weeks during the warm seasons of 2021 and 2022, one growing in the same area in Vyritza from which the mites were collected from the maple trees, and the other (59°56'30.3"N 30°18'00.9"E) near the main building of the Zoological Museum in the center of Saint-Petersburg. We inspected both the vegetative and generative organs of the host plants, including both maple samaras and oak acorns attached to the trees as well as those found on the ground. Additionally, we partially uprooted seedlings that germinated in the springs of 2021 and 2022, and checked them for the presence of eriophyoid mites.

RESULTS

TAXONOMY

Family Eriophyidae Nalepa
Subfamily Phyllocoptinae Nalepa
Tribe Anthocoptini Amrine & Stasny
Genus *Shevtchenkella* Bagdasarian 1978

***Shevtchenkella serrata* (Nalepa 1892)**
 (Figs. 1, 2, 3)

Tegonotus serratus – Nalepa 1892: 333–335, pl. 13, figs. 7b, 8, 9.
Oxypleurites serratus – Nalepa 1898: 68; Roivainen 1947: 39, fig. 22.
Oxypleurites obtusus – Roivainen 1947: 38, fig. 21 (new synonymy).
Shevtchenkella serrata – Petanović, Stanković 1999: 67.

PROTOGYNE ($n = 10$), supplementary description (Fig. 1). Body fusiform, subtriangular, whitish or slightly yellowish, 180–207, 72–79 wide at the level of seta *c2*. Prodorsal shield semicircular, 49–56, 70–77 wide, with large apically rounded frontal lobe 10–12, 18–22 wide. Posterolateral margin of prodorsal shield with indistinct acuminate projection (Fig. 1C). Cuticle of prodorsal shield with numerous round microgranulations. Median line absent, two faint incomplete admedians and traces of putative incomplete submedians present on prodorsal shield (Fig. 1D). Epicoxal areas with microtubercles and thin striae. Scapular setae *sc* 5–8, 25–28 apart. Gnathosoma short, directed obliquely forward, 18–21, *ep* 2–3, *d* 5–7, *v* 0.5–1; chelicera 13–15. Leg I 31–34, femur 10–12, *bv*

9–11; genu 5–6, *l''* 17–22; tibia 7–8; *l'* 2–4; tarsus 5–6, *u'* 2–3, slightly angled, *ft'* 17–22, *ft''* 25–29, solenidion ω 6–7 with spherical knob apically, empodium (*em*) 6–7, 4/4-rayed, each ray except of the rays of apical pair with one subray each (Fig. 1A). Leg II 30–33, femur 10–11, *bv* 8–11; genu 5–6, *l''* 3–4; tibia 7–8; tarsus 5–6, *u'* 2–3, slightly angled, *ft'* 4–6, *ft''* 20–24, solenidion ω 6–7 with spherical knob apically, empodium (*em*) 6–7, 4/4-rayed, similar to empodium I. Infracapitular plate rounded anteriorly, microtuberculated, 11–13, 15–18 wide; sternal line distinct, 10–12. Coxal plates with numerous microtubercles and thin striae. Setae *lb* 6–8, 13–14 apart; *la* 16–19, 9–11 apart; *2a* 31–38, 27–28 apart; 2–3 incomplete and 6–8 complete coxigenital annuli before epigynium. External genitalia. Genital coverflap rounded posteriorly, 10–13, 23–25 wide, with 10–12 longitudinal ridges; setae *3a* 10–12, 16–18 apart; basal coverflap and adjacent area (homologous to the pregenital plate *sensu* Flechtmann et al. 2015) with short curved lines and microtubercles. Opisthosoma with 19–20 dorsal and 65–74 microtuberculated ventral annuli. Anterior 12–13 dorsal annuli with lateral spine-like projections; 2nd, 3rd, 4th, 5th, 7th and 9th dorsal annulus with a small subtriangular medial plate slightly overlapping next dorsal annulus. Dorsal annuli with numerous thin longitudinal ridges. Setal lengths: *c2* 23–28, *d* 60–68 very thin in distal half, *e* 8–12, *f* 20–25, *h1* about 0.5, *h2* 60–70; 11–12 annuli from the rear margin of coxa II to *c2*; 12–14 annuli between *c2* and *d*; 17–20 annuli between *d* and *e*; 18–23 annuli between *e* and *f*; 5–6 annuli between *f* and *h2*.

Male ($n = 3$): Body shaped similarly to protogynes but notably shorter, 141–152, 69–75 wide at the level of seta *c2*. Opisthosoma with 19–21 dorsal and 66–69 ventral annuli. Genital area 11–13, 20–22 wide; *3a* 9–11, 16–17 apart.

GenBank data (protogynes): ON920305 (*Cox I*).

Material examined: Numerous adults and immatures from the slide series E4701, E4702 and E4703 collected on 17 July 2021 from the lower leaf surfaces of *Acer platanoides* L. (Sapindaceae) in Russia: Leningrad Prov., Gatchina distr., vil. Vyritza, coll. P.E. Chetverikov, slide series, mites in vials with 96% ethanol. All slides and ethanol material (mites in vials filled with 96% ethanol) have been deposited in the Acarological Collection of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) in Saint-Petersburg, Russia.

Remarks: The protogyne of *S. serrata* has been frequently reported as a vagrant on the lower leaf surface of various *Acer* spp. in different European countries (Petanović and Stanković 1999; Farkas 1965; Roivainen 1947; Skoracka et al. 2005). The protogynes from our material were very similar to those from

Finland (Roivainen 1947, p. 39, fig. 22), except that our specimens had a larger number of ventral annuli (65–74 vs. 50).

DEUTOGYNE ($n = 10$, Figs. 2, 3): Body elongated, non-flattened, bright orange, 229–250, 62–67 wide at the level of seta *c2*. Prodorsal shield subtriangular 41–46, 53–58 wide, with acuminate frontal lobe 8–10, 10–12 wide. Cuticle of prodorsal shield with numerous tiny round cavities (putative pores leading to wax glands, Fig. 3A). Distinct curved

transverse line resembling a flattened letter “U” present between tubercles of *sc*. Longitudinal lines (median, admedians and submedians) absent. Epicoxal areas smooth. Scapular setae *sc* 11–15, 24–27 apart. Gnathosoma directed obliquely forward, 19–21, *ep* 2–3, *d* 6–8, *v* about 0.5; chelicera 15–17. In two specimens, the outlines of a short suboral fork (*sensu* Chetverikov and Bolton 2016) embedded in the ventral wall of the proboscis were discernible (Fig. 3F, G, H). The fork was comprised of a stalk about 3 (Fig. 3H, arrow) and two

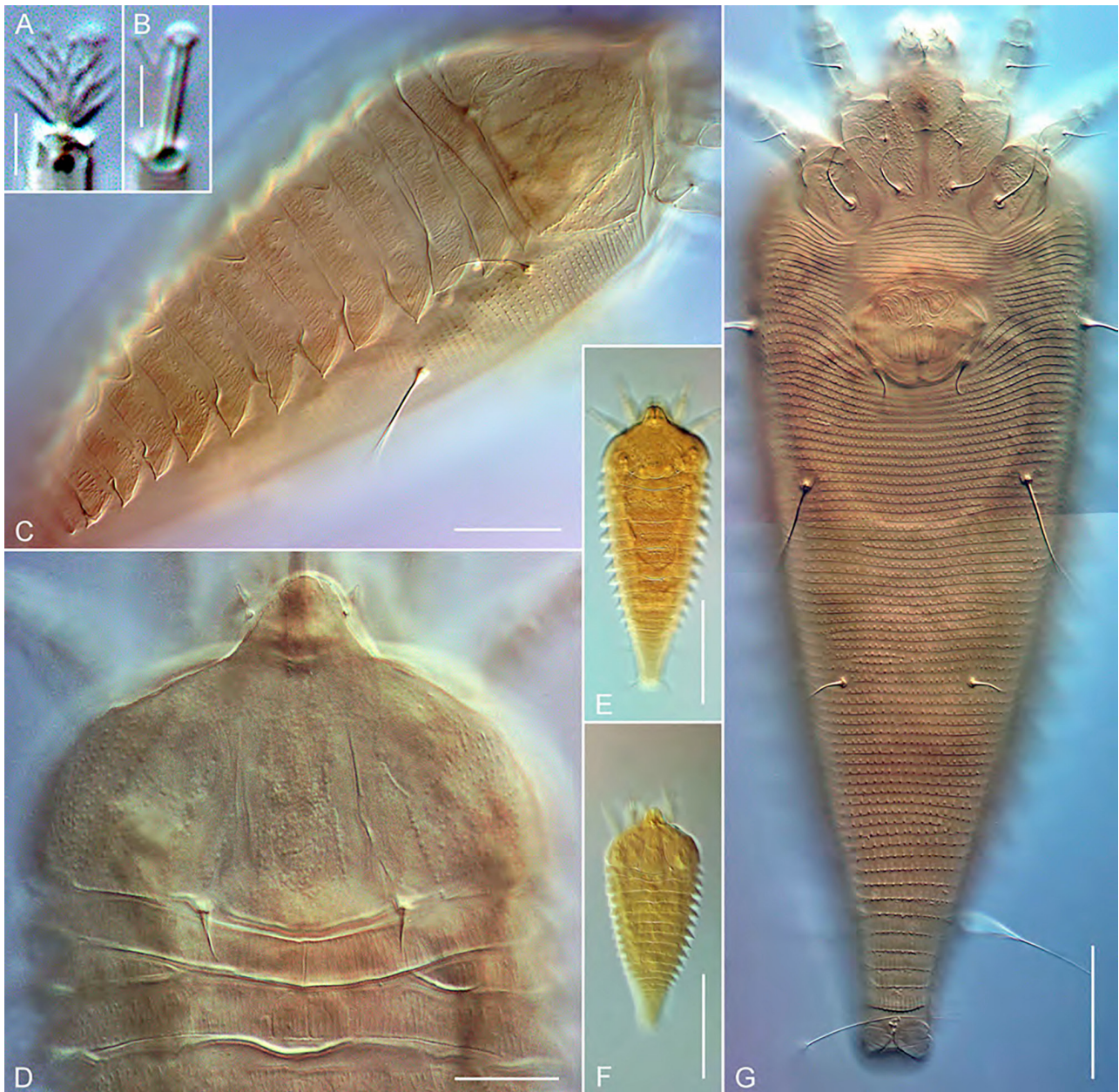


Fig. 1. DIC LM images of protogynes of *Shevtchenkella serrata*. A, empodium I. B, tarsal solenidion I. C, lateral view of opisthosoma. D, prodorsal shield. E, dorsal view of protogyne. F, dorsal view of male. G, ventral view of protogyne. Scale bars: A, B = 3 µm; C = 20 µm; D = 15 µm; E, F = 70 µm, G = 30 µm.

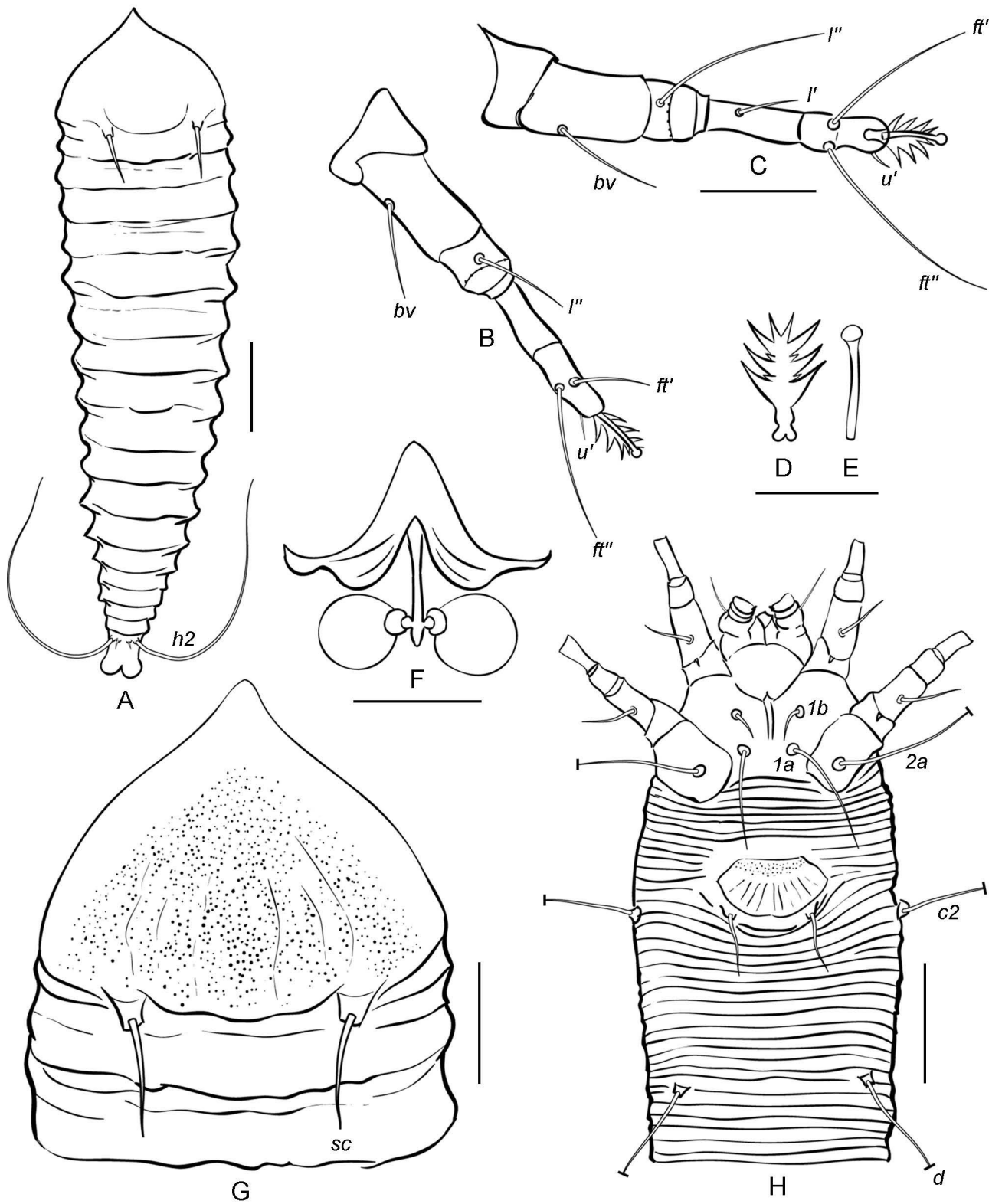


Fig. 2. Drawings of deutogyne of *Shevtchenkella serrata*. A, dorsal view of body. B, leg II. C, leg I. D, empodium I. E, tarsal solenidion I. F, internal genitalia. G, prodorsal shield. H, coxigenital area. Scale bars: A, H = 25 μ m; B, C, D, E, F = 10 μ m; G = 15 μ m.

leaf-shaped plates about $2 \times 1-1.5$ wide (Fig. 3F, G, H, arrows), and similar to suboral forks described earlier in other eriophyoids (Chetverikov and Bolton 2016).

Leg I 37–40, femur 11–12, *bv* 10–13; genu 5–6, *l''* 12–18; tibia 8–9, *l'* 4–5; tarsus 6–8, *u'* 3–5, *ft'* 19–24, *ft''* 23–28, solenidion ω 8–9 with spherical knob apically, empodium (*em*) 8–10, 4/4-rayed, rays and medial shaft of the empodium wide, flattened. Leg II 36–38, femur 10–12, *bv* 10–12; genu 5–6, *l''* 7–9; tibia 7–9; tarsus 6–7, *u'* 3–4, *ft'* 5–7, *ft''* 16–22, solenidion ω 8–9 with spherical knob apically, empodium (*em*) 8–10, 4/4-rayed, similar to empodium I. Infracapitular

plate rounded anteriorly, smooth, 12–14, 15–17 wide; sternal line distinct, 10–12. Coxal plates without distinct ornamentation. Setae *1b* 7–10, 12–14 apart; *1a* 18–24, 10–11 apart; *2a* 38–47, 26–28 apart; 2–3 incomplete and 5–6 complete coxigenital annuli before epigynium.

External genitalia: Genital coverflap oblong, 12–14, 23–25 wide, with 10–11 longitudinal ridges; setae *3a* 14–17, 14–16 apart; basal coverflap with round microtubercles. Internal genitalia ($n = 4$). Spermathecae globose, about 6–7 in diameter; spermathecal tubes short, subspherical, about 1.5–2; spermathecal process not apparent; longitudinal bridge 9–11, anterior



Fig. 3. DIC LM images of deutogyne of *Shevtchenkella serrata*. A, prodorsal shield; B, empodium I; C, tarsal solenidion I; D, dorsal view of entire mite; E, ventral view of entire mite; F, G, H, gnathosoma shown in three different planes from dorsal (F) to ventral (H). White arrows in Fig. 3. F, G, H indicate putative suboral fork. Scale bars: A = 15 μm ; B, C = 10 μm ; D, E = 60 μm ; F, G, H = 5 μm .

(transverse) genital apodeme bell-shaped, with 2–3 longitudinal ridges on each side.

Opisthosoma with 15–18 dorsal and 64–73 ventral annuli. Dorsal annuli slightly curved and smooth. Ventral annuli in anterior half of opisthosoma smooth or with traces of very faint microtubercles, ventral annuli in posterior half of opisthosoma bearing more distinct subconical microtubercles; last 3–4 ventral telosomal annuli with elongate microtubercles. Setal lengths: *c*2 20–26, *d* 58–69 very thin in distal half, *e* 10–12, *f* 29–35, *h*1 about 0.5, *h*2 85–98; 12–14 annuli from the rear margin of coxa II to *c*2; 13–15 annuli between *c*2 and *d*; 16–19 annuli between *d* and *e*; 18–22 annuli between *e* and *f*; and 4–5 annuli between *f* and *h*2.

GenBank data (deutogynes): ON920306 (*Cox 1*).

Material examined: Numerous females from the slide series E4677 and E4678, collected on 15 August 2021 from the lower leaf surface of *Acer platanoides* L. (Sapindaceae) in Russia: Leningrad Prov., Gatchina distr., vil. Vyrizta, coll. P.E. Chetverikov. All slides and ethanol material (mites in vials filled with 96% ethanol) have been deposited in the Acarological Collection of ZIN RAS (Saint-Petersburg, Russia).

Remarks: Using the morphological key of Amrine et al. (2003), rather than *Shevtchenkella*, the deutogyne conforms to *Anthocoptes*, a genus in the same subfamily, Phyllocoptinae. The tribes that *Shevtchenkella* and *Anthocoptes* belong to (Tegonotini and Anthocoptini, respectively) are primarily differentiated by the presence or absence of lateral lobes or spine-like projections, as shown in the protogyne of *S. serrata* (Fig. 1C, E, F), but absent in the deutogyne (Fig. 3). In contrast to the protogynes, the deutogynes have smooth dorsal annuli without lateral projections and medial plates, smooth prodorsal shield, flat paddle-like empodia, and more elongated body proportions. The deutogynes from our material very closely approximate *Oxypleurites obtusus* Roivainen 1947 which was described in sympatry with *S. serrata* from the lower leaf surface of *A. platanoides* in Finland, except that they were notably larger (229–250 vs. 160–175) and had an acuminate vs. blunt frontal lobe. We consider *Oxypleurites obtusus* Roivainen 1947 to be the deutogyne of *S. serrata* and treat it as a junior synonym of *S. serrata* (Nalepa 1892).

Family Diptilomiopidae Keifer
Subfamily Rhyncaphytoptinae Keifer
Genus *Brevulacus* Manson 1984

Diagnosis: Mites of this genus have a complete set of all common opisthosomal, prodorsal, leg and gnathosomal setae, dorso-ventrally differentiated opisthosomal annuli, large anteriorly notched frontal lobe of prodorsal shield, and bushy undivided empodia

with 3–7 well-developed secondary rays on all primary empodial rays, except the terminal pair.

Remarks: Manson (1984) reported that the tarsal solenidia ω are displaced laterally in the type species, *B. reticulatus*. However, considering the artifact positions of setae *u'* and empodium in the drawings from the original description (Manson 1984, fig. 36F, 43F), and the fact that different authors observed normal positioning of ω in this species (Pye 2012, this paper), we do not consider this trait to be either a true characteristic of *B. reticulatus* or a differentiating character of the genus *Brevulacus*.

Species included: *Brevulacus reticulatus* Manson 1984 (type species) from *Quercus* sp. in New Zealand, *B. jilinensis* Xue et al. 2009a from *Quercus* sp. in China, *B. carpathicus* Ripka 2011 from *Quercus petraea* (Matt.) Liebl. in Hungary, *B. extensus* Pye 2012 from *Quercus robur* L. in Great Britain, *B. albus* (Keifer 1959) n. comb. from *Quercus alba* L. in USA, and *B. atlanticus* (Keifer 1959) n. comb. from *Ulmus americana* L. in USA.

Remarks: Twenty five years before Manson (1984) erected the genus *Brevulacus* and described the type species, *B. reticulatus*, from *Quercus* sp., Keifer (1959) described two *Rhyncaphytoptus* species from the northern USA, *R. albus* from *Quercus alba* L. (Fagaceae) and *R. atlanticus* from *Ulmus americana* L. (Ulmaceae). These two *Rhyncaphytoptus* species are very close morphologically to *B. reticulatus*, having almost identical net-like ornamentation of the prodorsal shield (Fig. 4 A, B, E, F), and possessing large bushy empodia and a broad notched frontal lobe. We transfer these two species from g. *Rhyncaphytoptus* to g. *Brevulacus* because we consider them members of the same putatively monophyletic group of rhyncaphytoptines with a notched frontal lobe defined by Manson (1984) as the genus *Brevulacus*. Another *Brevulacus* species (*B. salicinus*) was described from *Salix* sp. (Salicaceae) from Iran (Soika et al. 2017). However, this species does not conform to the generic diagnosis of *Brevulacus* because it has an acuminate frontal lobe of the prodorsal shield (Fig. 4D). Additionally, it lives on *Salix* sp. (Salicaceae), in contrast to most other *Brevulacus* spp. that are associated with oaks (Fagaceae). Morphologically, this species fits the diagnosis of the genus *Rhyncaphytoptus* Keifer. Therefore, we propose a new combination, *Rhyncaphytoptus salicinus* (Soika et al. 2017) comb. nov. Seven *Rhyncaphytoptus* species are known from willows (*Salix* spp.) worldwide, including *R. acilius* Keifer 1939, *R. alsasuensis* Roivainen 1953, *R. capreae* Liro 1942, *R. funali* Xue et al. 2009a, *R. salicifoliae* Keifer 1939, *R. salicis-glaucuae* Roivainen 1950 and *R. tibetisalis* Song, Xue & Hong 2009. Future comparison is needed to determine if “*salicinus*”

is a junior synonym of one of these species or a true species.

Hosts: Oaks (Fagaceae: *Quercus*) and elm (Ulmaceae: *Ulmus*).

Relation to hosts: All known species of *Brevulacus* are vagrant and cause no visible damage to their hosts.

***Brevulacus reticulatus* Manson 1984**

Brevulacus reticulatus Manson 1984: 87–88, fig. 32–39 (protogyne), fig. 40–46 (deutogyne).

B. reticulatus Skoracka et al. 2005: 25; Xue et al. 2009b: 33; Ripka 2011: 133; Pye 2012: 61.

Remarks: Manson (1984) found the type species, *B. reticulatus*, on *Quercus* sp. in three cities of New Zealand (Levin, Upper Hutt and Christchurch) and reported on its seasonal dimorphism. Since then this species has been recorded many times on *Quercus* spp. in different European countries and in China. According to Breitwieser et al. (2010), all oak species currently known from New Zealand are non-indigenous. Colonists introduced them, presumably from Europe most likely along with different associated symbionts, including *B. reticulatus*. Below we give supplementary data on the protogyne and deutogyne of *B. reticulatus*, based on material collected from *Q. robur* in North-West Russia.

PROTOGYNE (*n* = 10), supplementary description (Figs. 4B, 5, 6I, M–T). Body fusiform,

yellowish, 238–255, 83–89 wide at the level of seta *c*2. Prodorsal shield subtriangular, 42–47, 63–70 wide, with large apically notched smooth frontal lobe 10–12, 15–19 wide. Prodorsal shield ornamentation net-like with distinct cells between median, admedian and submedian lines. Median line complete, entire (Figs. 4B, 5A, C). Scapular setae *sc* 25–29, 33–37 apart, directed up and forward. Gnathosoma large, directed obliquely downward, 41–50, *ep* 3–4, *d* 10–13, *v* 5–7, angled. Leg I 43–46, femur 11–13, *bv* 12–16; genu 5–7, *l''* 33–40; tibia 9–10, *l'* 9–12; tarsus 7–8, *u'* 4–6, *ft'* 24–30, *ft''* 26–32, solenidion ω 9–10 with small knob apically, empodium (*em*), 7–9, 8-rayed, each ray, except of the rays of apical pair, with 3 to 7 subrays (Fig. 6M–T). Leg II 40–43, femur 10–12, *bv* 10–14; genu 5–6, *l''* 17–22; tibia 8–10; tarsus 7–8, *u'* 4–6, *ft'* 9–13, *ft''* 27–31, solenidion ω 9–11 with small knob apically, empodium (*em*) 7–9, 7-rayed, similar to empodium I. Infracapitular plate rounded anteriorly, smooth, 11–12, 22–25 wide; sternal line distinct 9–11. Coxal plates striated. Setae *Ib* 14–18, 11–13 apart; *Ia* 26–33, 10–12 apart; *2a* 58–70, 27–31 apart; 12–17 incomplete coxigenital annuli bearing microtubercles before epigynium. External genitalia. Genital coverflap subtriangular, smooth, 9–11, 31–35 wide, preceded by distinct ribbon-shaped pregenital plate (*sensu* Flechtmann et al. 2015; Fig. 5D, arrow); setae *3a* 34–45, 23–25 apart. Opisthosoma with 49–57 microtuberculated dorsal annuli forming three faint longitudinal ridges and 87–107 microtuberculated

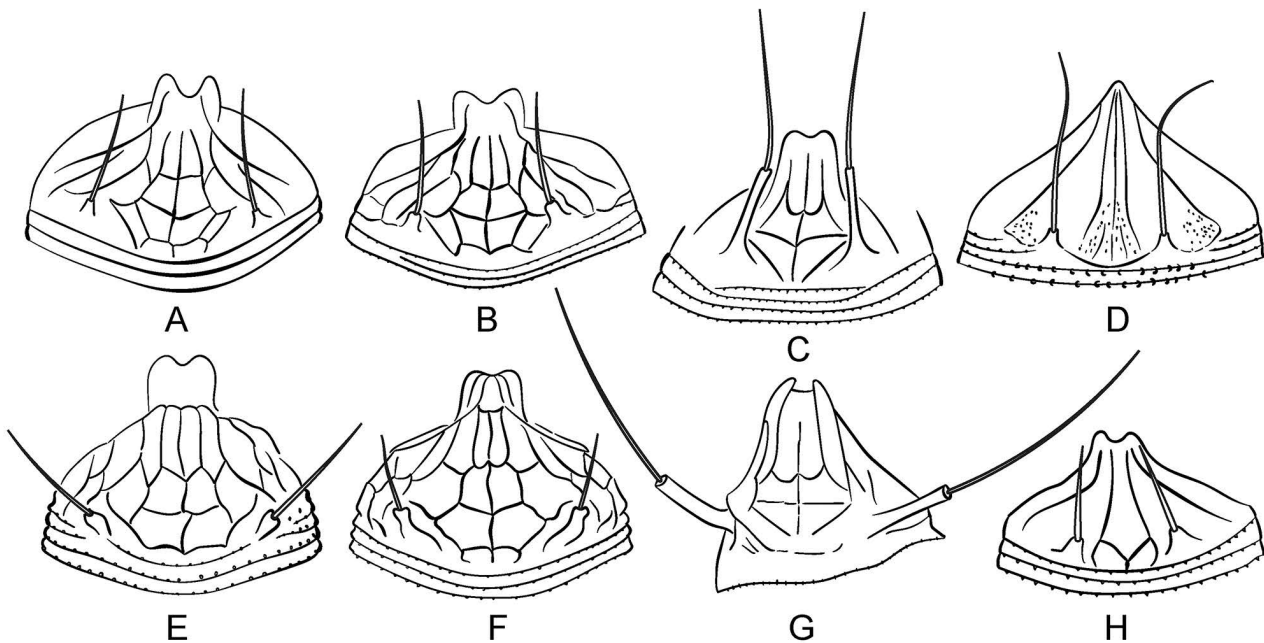


Fig. 4. Prodorsal shields in females of *Brevulacus reticulatus* Manson 1984 (protogyne, A, from original description. B, this paper), *B. extensus* Pye 2012 (C), *Rhyncaphytoptus salicinus* (Soika et al. 2017) n. comb. (D), *B. albus* (Keifer 1959) n. comb. (E), *B. atlanticus* (Keifer 1959) n. comb. (F), *B. carpathicus* Ripka 2011 (G), and *B. jilinensis* Xue, Song & Hong 2009 (H). All except figure 4B redrawn from original descriptions.

ventral annuli. Setal lengths: *c2* 36–43, *d* 46–52, *e* 29–34, *f* 46–52, *h1* 4–5, *h2* 70–85, all opisthosomal setae, except *c2* and *h1*, very thin in distal half; 18–22 annuli from the rear margin of coxa II to *c2*; 16–22 annuli between *c2* and *d*; 13–16 annuli between *d* and *e*; 35–41 annuli between *e* and *f*; 5–6 annuli between *f* and *h2*. Paired cuticular tubes associated with rectum (the elements of anal secretory apparatus, *sensu* Chetverikov et al. 2019) were clearly visible under the telosomal cuticle in all studied protogynes (not shown).

Male (*n* = 6): Body shape similar to protogynes but notably shorter, 178–202, 70–73 wide at the level of seta *c2*. Prodorsal shield ornamentation similar to those in protogynes. Opisthosoma with 51–56 dorsal and 81–87 ventral annuli. Genital area 12–15, 20–24 wide; *3a* 22–26, 17–19 apart; *eu* 0.5–1. Paired cuticular tubes associated with rectum (the elements of anal secretory

apparatus *sensu* Chetverikov et al. 2019) were observed in all studied males (not shown).

GenBank data (protogynes): ON920307 (*Cox 1*).

Material examined: Numerous adults collected on 10 June 2022 from the lower surfaces of leaves of *Quercus robur* L. (Fagaceae) in RUSSIA: Leningrad Prov., Gatchina distr., vil. Vyritza, coll. P.E. Chetverikov, slide series, mites in vials with 96% ethanol. All slides and ethanol material have been deposited in the Acarological Collection of ZIN RAS (Saint-Petersburg, Russia).

Remarks: The protogynes in our study are very similar to those described by Manson (1984) from New Zealand, except that our specimens have a larger number of ventral annuli (87–107 vs. 70–76, respectively) and longer prodorsal shield (42–47 vs. 31–39, respectively); the difference between the

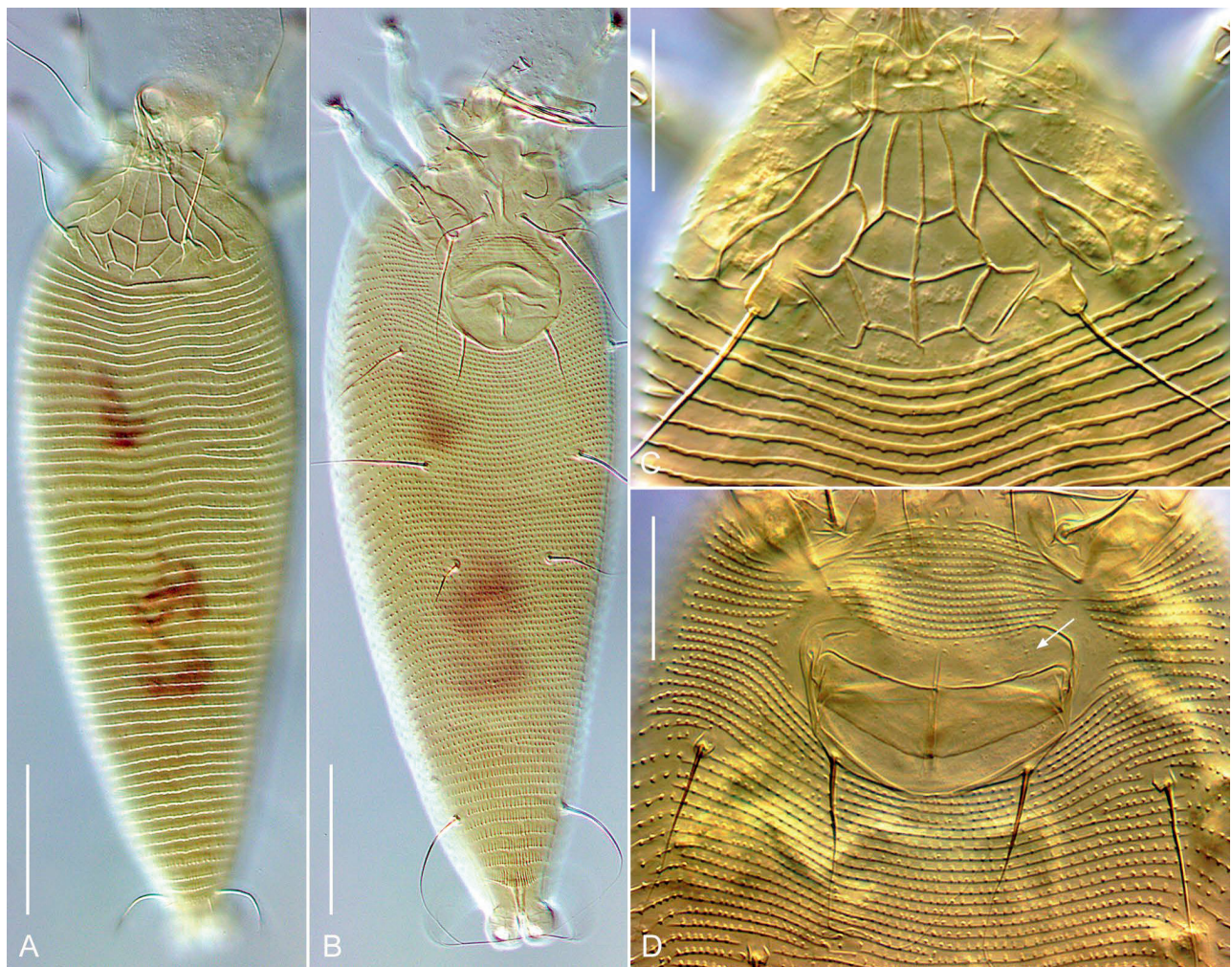


Fig. 5. DIC microphotographs of protogyne of *Brevulacus reticulatus* Manson 1984. A, dorsal view of body. B, ventral view of body. C, prodorsal shield. D, genital area (arrow indicates pregenital plate). Note: setae *sc* in live mites are directed anterior (Fig. 5A), in contrast to many slide-mounted mites with artifact backward directed *sc* (Fig. 5C). Scale bars: A, B = 40 µm; C, D = 15 µm.

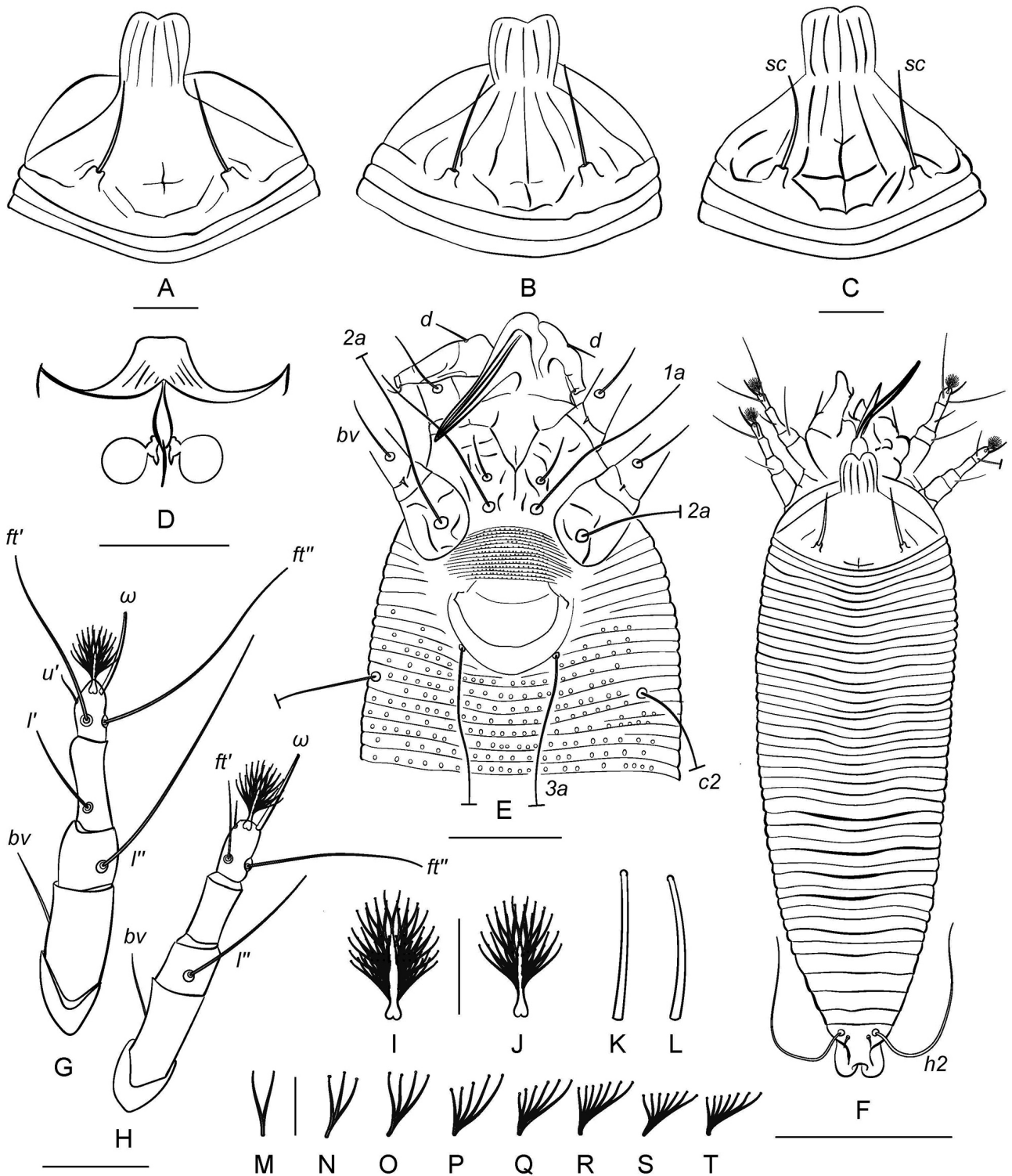


Fig. 6. Drawings of deutogyne (A–H, J–L) and protogyne (I, M–T) of *Brevulacus reticulatus*. A–C, prodorsal shield ornamentation. D, internal genitalia (deutogyne). E, coxigenital area. F, dorsal view of entire deutogyne. G and H, legs I & II. I, empodium I (protogyne). J, empodium I (deutogyne). K and L, tarsal solenidia II & I (deutogyne). M–T, terminal (M) and lateral (N–T, from distal to proximal) empodial rays (protogyne). Scale bars: A–D = 15 μ m; E = 30 μ m; F = 60 μ m; G, H = 10 μ m; I–L = 5 μ m; M–T = 2 μ m.

prodorsal shield measurements is possibly because our measurements include the length of the frontal lobe but Manson's measurements do not.

DEUTOGYNE ($n = 8$, Figs. 6A–H, J–L, 7). Body elongated in comparison to protogynes, dark orange or brownish, 250–268, 73–80 wide at the level of seta *c2*. Prodorsal shield subtriangular, 40–46 (including frontal lobe), 53–59 wide, with large apically notched ribbed frontal lobe 12–14, 12–15 wide. Ornamentation of prodorsal shield varies (Fig. 6A, B, C, Fig. 7A, B): in some deutogynes it is almost smooth, in others indistinct traces of longitudinal lines and cells between them can be seen; however, in all cases the ornamentation notably less developed than in protogynes. Scapular setae *sc* 14–18, 28–32 apart. Gnathosoma large, directed obliquely downward, 39–44, *ep* 4–5, *d* 10–13, *v* 5–7. Leg I 38–42, femur 11–12, *bv* 15–18; genu 6–7, *l''* 25–31; tibia 9–10, *l'* 7–12, tarsus 6–7, *u'* 3–4, *ft'* 17–23, *ft''* 25–33, solenidion ω 8–9 with indistinct knob apically, empodium (*em*) 7–8, 6-rayed, each ray, except for the rays of apical pair, with 3 to 7 subrays. Leg II 35–38, femur 10–12, *bv* 14–18; genu 5–6, *l''* 12–16; tibia 8–9; tarsus 6–7, *u'* 3–4, *ft'* 6–9, *ft''* 23–30, solenidion ω 8–10 with indistinct knob apically, empodium (*em*) 7–8, similar to empodium I. Infracapitular plate rounded anteriorly, smooth, 14–16, 21–25 wide; sternal line distinct 10–12. Coxal plates striated, setae *1b* 8–11, 9–11 apart; *1a* 28–35, 9–11 apart; *2a* 38–47, 29–32 apart; 18–23 incomplete coxigenital annuli bearing microtubercles before epigynium. External genitalia. Genital coverflap subtriangular, smooth, 10–13, 26–29 wide, preceded by indistinct ribbon-shaped pregenital plate (*sensu* Flechtmann et al. 2015); setae *3a* 34–48, 23–26 apart. Opisthosoma with 42–50 smooth dorsal annuli forming faint longitudinal median ridge and 56–71 ventral annuli bearing round microtubercles that are notably larger than those on coxigenital annuli (Fig. 7E). Every second dorsal annulus thickened in posterior half or in almost whole opisthosoma (Fig. 7C, D). Setal lengths: *c2* 29–36, *d* 47–58, *e* 24–37, *f* 33–38, *h1* 4–5, *h2* 50–60; all opisthosomal setae except *f* and *h1* very thin in distal half; 9–12 annuli from the rear margin of coxa II to *c2*; 10–14 annuli between *c2* and *d*; 11–14 annuli between *d* and *e*; 22–26 annuli between *e* and *f*; 4–6 annuli between *f* and *h2*. Paired tubes associated with rectum (the elements of anal secretory apparatus *sensu* Chetverikov et al. 2019) were clearly seen in all studied deutogynes (Fig. 7F).

GenBank data (deutogynes): ON920308 (*Cox I*).

Material examined: Sparse females collected on 6 June 2022 from the lower leaf surface of *Quercus robur* L. (Fagaceae) in RUSSIA: Leningrad Prov., Gatchina distr., vil. Vyritza, coll. P.E. Chetverikov, slide series, mites in vials with 96% ethanol. All slides and ethanol

material have been deposited in the Acarological Collection of ZIN RAS (Saint-Petersburg, Russia).

Remarks: The deutogynes from our material were very similar to those described by Manson (1984) from New Zealand, except that our specimens were notably longer (250–268 vs. 159–216).

Barcode data, blast search results and sequence comparison

The *Cox1* sequences of protogynes (collected in July 2021, ON920305, 648 bp, $n = 2$) and deutogynes of *S. serrata* (collected in April 2022, ON920306, 657 bp, $n = 1$) from *A. platanoides* were identical. Also, the *Cox1* sequences of protogynes (collected in June 2022, ON920307, 619 bp, $n = 3$) and deutogynes (collected in May 2022, ON920308, 631 bp, $n = 3$) of *B. reticulatus* collected from *Q. robur* contained the same four degenerated sites (Y) and were identical in all other nucleotide positions.

Nucleotide blast (BLASTN) search for our *S. serrata* sequences (ON920305 and ON920306) revealed the sequence OK489799 (*S. serrata*) and series of sequences MZ482237–MZ482243 (*Aculops* sp.) to be the closest, with the highest values for percent identity (98.4–99.5%) and coverage (96–99%). Also, a protein blast (BLASTX) search for *S. serrata* returned 100% identical sequences UOK10252 and UOK10253 (*Aculops* sp.) and UCS82605 (*S. serrata*). Considering our data on seasonal morphological dimorphism (see above) and BLAST results, *Aculops* sp. could be a deutogyne of *S. serrata*.

Nucleotide blast (BLASTN) search for our *B. reticulatus* sequences (ON920307 and ON920308) revealed a large group of moderately similar (79–87% identity) sequences of rhyncaphytoplines of the genera, *Rhyncaphytoplus*, *Diptilomiopus* and *Brevulacus*, from China, with the highest value for percent identity being 87.54% for sequence MZ483311 of *R. albus*, and the lowest value of 79.11% for sequence MZ482490 of *B. reticulatus*. Protein blast (BLASTX) search for our *B. reticulatus* sequences revealed largely the same group of similar sequences, with highest amino acid composition identity ranging from 98.56% to 99.52% in sequences of *R. albus* (UOK11311), *Diptilomiopus hexogonus* (UOK10706) and *B. reticulatus* (QVU25232).

Remarks: The pairwise identity of the *Cox1* sequences confirmed the conspecificity of morphologically different seasonal forms of both *S. serrata* and *B. reticulatus*. In addition, molecular based identification of *B. reticulatus* produced unexpected results, in that sequences of conspecifics from GenBank were less similar to our sequences than sequences of a non-conspecific, *Rhyncaphytoplus albus*.



Fig. 7. DIC microphotographs of deutogynes of *Brevulacus reticulatus* Manson 1984. A and B, prodorsal shield in two deutogynes. C and D, dorsal view of two deutogynes differing in the appearance of dorsal opisthosomal annuli. E, genital area, F, paired tubes (arrows) of anal secretory apparatus. Scale bars: A, B, E = 15 μ m; C, D = 40 μ m; F = 10 μ m.

Morphologically, *B. reticulatus* and *R. albus* clearly differ in ornamentation of the female genital coverflap: smooth in *B. reticulatus* and with about 18 longitudinal ribs in *R. albus* (Keifer 1959, p. 17, fig. 13). Since our

specimens were clearly closer to *B. reticulatus* than to *R. albus*, it is necessary to verify the identifications of the rhyncaphytopine mites from GenBank prior to drawing further conclusions.



Fig. 8. Locations (arrows) of overwintered females of *Shevtchenkella serrata* collected on 18 April 2021 (A, B) and on 16 May 2021 (C, D, E) from seedlings (A, B, C) and saplings (D, E) of *Acer platanoides* from North-West Russia.

Field observations

Shevtchenkella serrata from *Acer platanoides*

Detailed 2020–2021 seasonal data on *S. serrata* was presented by Chetverikov et al. (2022). Here we complement it with confirmatory observations performed in 2022. In brief, both morphotypes of *S. serrata* (protogynes and deutogynes) were found feeding on the epidermal tissue on the lower leaf surfaces of *A. platanoides*, as well as on the epidermis of the pericarp of immature samaras still attached to the parent trees in August 2020. In autumn 2020 and up to early December 2020, they were observed near terminal buds and in crevices on young stems and on the fallen maple samaras. Motionless deutogynes were detected on the samaras on the ground at the end of March 2021. In April 2021, solitary deutogynes were observed near the soil level on the hypocotyls of young seedlings, and in the space between unseparated juvenile leaves (Fig. 8A, B arrows). In the middle of May 2021, actively moving deutogynes were found on the lower surface of cotyledons and on the petiole bases and leaves of seedlings, saplings (Fig. 8C, D, E arrows) and large maple trees growing nearby. In the middle of June 2021, numerous protogynes, males and immatures suddenly appeared on the same branches of the maple trees that had been sampled earlier in spring 2021 and on seedlings and small saplings, together with deutogynes. During July 2021, only protogynes (maximum 480 per leaf) were present in the samples. However, in August 2021, we detected both deutogynes and protogynes on maple leaves. They were both present on leaves and samaras from mid-August 2021 until the leaves began to fall in autumn, after which they were again detected on the samaras on the ground. Similar to the 2021 observations, in April and May 2022, solitary deutogynes were found on maple seedlings; in early June 2022 the first protogynes appeared and coexisted with deutogynes; in July 2022, protogynes were present but deutogynes were absent; and in early August 2022, both morphotypes were again found in sympatry on leaves and immature samaras.

Brevulacus reticulatus from *Quercus robur*

At the end of May 2021, 1–4 brownish deutogynes of *B. reticulatus* were found on the lower surface of leaves of the two model *Q. robur* trees. At the beginning of June 2021, the first protogynes were recorded and deutogynes were still present on leaves, although some of them were not moving and considered to be likely dead. In late June 2021, only protogynes, males and immatures were found on *Q. robur* leaves. In July 2021,

deutogynes were not recorded and appeared again on leaves at the beginning of August 2021 only. Solitary protogynes were observed feeding on green, immature acorns in mid-July and early August, 2021. However, by the time the acorns hardened in autumn, no mites were found on them or on the acorns on the ground. Also, we did not find any eriophyoids on the numerous oak seedlings that were around the two model *Q. robur* trees. Up to the end of September 2021, deutogynes and protogynes were present together on the leaves. During September 2021, the number of protogynes gradually decreased. In October and December 2021, groups of 3–12 motionless deutogynes were observed overwintering near buds. The first overwintered deutogynes were detected slowly moving near buds at the beginning of May 2022. At the end of May 2022, they were observed laying eggs on young *Q. robur* leaves, and at the beginning of June 2022, mixed colonies containing the first generation of protogynes and very sparse deutogynes were observed on *Q. robur* leaves.

DISCUSSION

Seasonal dimorphism in *S. serrata* and *B. reticulatus*

In this study, we presented full taxonomic descriptions of two morphotypes of morphologically different females, the protogyne and deutogyne, of *S. serrata* and showed that the protogyne of this species conforms to the diagnosis of *Shevtchenkella* and the deutogyne conforms to *Anthocoptes*. According to Keifer (1975, p. 458), two other New World *Shevtchenkella* species found on maples have deutogynes that are so morphologically different from the protogynes that they were initially identified as separate species: *S. dentatus* (Hodgkiss 1913) (deutogyne = *S. trilobis* (Hodgkiss 1913)) from *A. platanoides*, and *S. dentilobus* (Hodgkiss 1913) (deutogyne = *S. variabilis* (Hodgkiss 1913)) from *Acer saccharum* Marsh. We hypothesize that such pronounced deuterogyny could be characteristic to many members of the genus *Shevtchenkella* and perhaps to the whole genus. *Shevtchenkella* comprises ~80 species living on various Holarctic host plants, mainly in the families Sapindaceae, Hippocastanaceae and Oleaceae, including 14 species associated with *Acer* spp. Many hosts of *Shevtchenkella* are also registered as hosts of various phyllocoptine species, some of which may be deutogynes of *Shevtchenkella* spp., similar to *S. serrata*, *S. dentata* and *S. dentilobis* from maples. A careful search for deuterogyny in all members of

Shevtchenkella is needed to clarify these uncertainties.

Deuterogyny in *B. reticulatus* is not as confusing as in *S. serrata* because the slide-mounted protogynes and deutogynes had all the generic traits of *Brevulacus* and could be assigned to the same genus, despite looking like non-conspecifics at first glance (Fig. 5A, B vs. Fig. 7C, D). *Brevulacus reticulatus* is the only member of the genus with demonstrated female seasonal dimorphism (Manson 1984); however, future seasonal observations may reveal deuterogyny in other *Brevulacus* spp. In both the investigated species, *S. serrata* and *B. reticulatus*, the deutogynes and protogynes differed in the appearance of dorsal opisthosomal annuli, empodial morphology and ornamentation of prodorsal shield which were the same differences reported for other deutogynous species (Manson and Oldfield 1996; Guo et al. 2015; Yin et al. 2020). The determination of the functional role of these morphological differences, which remains poorly understood, provides an interesting research opportunity.

The factors explaining the presence of morphologically different protogyne and deutogyne in the eriophyoid life cycles are not clear. Sukhareva and Chetverikov (2013) summarized the data on morphological transformations during the transition from protogyne to deutogyne in the life cycles of Eriophyoidea. They (1) concluded that in different suprageneric taxa such transformations go in opposite directions, (2) hypothesized that these patterns of transformation could be phylogenetically significant, and (3) pointed out that establishing eriophyoid taxa on the basis of the homoplastic characters that change their states during protogyne/ deutogyne transformation may lead to artificial classification.

Several hypotheses propose the adaptive nature of deuterogyny and seek to explain it as either a result of a putatively complex life cycle in the ancestors of Eriophyoidea, or as a consequence of climate change influencing ancestral populations (Keifer 1942; Manson and Oldfield 1996; Guo et al. 2015; Cvrković et al. 2016; Chetverikov et al. 2018). It is also possible that in different eriophyoid lineages, different combinations of these factors resulted in the occurrence of deuterogyny. A related and interesting question concerns the genetic mechanisms regulating seasonal changes in the morphology and metabolism of deutogynous eriophyoid species, a problem that could be targeted using contemporary omics technologies. The deuterogyny phenomenon seriously affects the taxonomy of Eriophyoidea because different forms of the same species can be described under different names, which then persist in the literature for decades and even longer. Investigations of life cycles is a very laborious and

time-consuming but reliable way to reveal deuterogyny (Putman 1939; Keifer 1942; Ozman 2001); however, modern molecular techniques can solve this problem easier and faster through the sequencing of marker genes (Guo et al. 2015; Yin et al. 2020; Chetverikov et al. 2022). For instance, in this study the pronounced seasonal dimorphism in two eriophyoid species was confirmed via the sequencing of a fragment of the *CoxI* gene that showed identical sequences in conspecific protogynes and deutogynes. This represents a strong argument for avoiding descriptions of new eriophyoid taxa without barcode data, especially when dimorphism is suspected.

Association of *S. serrata* with maple (*A. platanoides*) generative organs: ecological and evolutionary notes

In addition to the common eriophyoid life style on leaves and hibernating near buds on twigs, the deutogynous species *S. serrata* infest immature maple samaras, feed on the pericarpal epidermis until the ripe samaras fall on the ground, overwinter in the crevices of the winged pericarp, and migrate in spring to seedlings where they start feeding and reproducing (Chetverikov et al. 2022). As a result, a new young host is infested at the very start of its life, a phenomenon known as vertical transmission in various parasitic systems (Poulin 2011). According to Ponomareva (1978, p. 29), sympatric populations of vagrant eriophyids of two different habitus (*Shevtchenkella*-like and *Anthocoptes*-like), possibly conspecific seasonal forms, were common on the leaves of maples at the end of summer in Kyrgyz Republic. Ponomareva (1978) also reported that one of the unnamed anthocoptine species (highly likely the deutogyne of *Shevtchenkella*) was twice as numerous on samaras of *Acer tataricum* L. subsp. *semenovii* as on leaves and formed colonies (~30 mites) in micro-cavities of the pericarp. The author did not check the samaras on the ground but reported that in winter the same mites were found hibernating in the bases of buds and in bark crevices. These data suggest that association with generative organs may be common for eriophyoids on *Acer* spp. and may be an important aspect of their ecology.

Seeds of different maples, including *A. platanoides*, require cold stratification to break dormancy, but some, such as *A. saccharinum*, germinate immediately (Hong and Ellis 1990; Gleiser et al. 2004). Specialists of the private arboretum “Sad lesa” situated in the village of Krasniy Partisan of the Altai Krai in Russia (sad-lesa.ru/spravka/acer/) reported that 6 of the 14 *Acer* spp. tested in the arboretum germinated in the second or third year (*A.*

mandshuricum Maxim., *A. campestre* L., *A. barbinerve* Maxim., *A. palmatum* Thunb., *A. tegmentosum* Maxim., *A. pseudosieboldianum* (Pax) Kom.) and the other eight germinated in the spring of the first year (*A. pseudoplatanus* L., *A. mono* Maxim. ex Rupr., *A. platanoides* L., *A. ginnala* Maxim., *A. saccharum* Marshall, *A. semenovii* Regel & Herder, *A. tataricum* L., *A. rubrum* L.). The 14 tested maple species also differed in the proportion of successfully overwintered seeds, with the minimum values for seed germination about 50% in *A. saccharum* and *A. rubrum*. Apparently the host plant species with a single season dormancy period and a high germination rate are the most likely to support the development of overwintering associations of eriophyoids with seeds in regions with a cold climate. Besides maples, various deciduous broadleaf trees of the genera, *Fraxinus*, *Tilia* and *Ulmus*, possess samaras, and taxa with rapidly germinating seeds could have similar “mite-samara” associations to that we observed on *A. platanoides*.

In *S. serrata*, the hibernation of deutogynes on seeds fallen on the ground is an additional diapause mode because typically eriophyoids on this host overwinter on the young twigs. Interestingly, hibernation on seeds implies a long period of survival in leaf litter on the soil and spring migration from the germinating samara to the developing seedling. Data from literature suggest that many eriophyoid species have a period in their life cycle when they are closely associated with soil or even live on the plant parts at the soil level. Although eriophyoids have not been reported as feeding on roots, they have been found feeding and overwintering on below-ground buds of stems and leaves on a rhizomatous perennial, or on modified leaves such as bulb scales (Krantz and Ehrensing 1990; Petanović et al. 1997; Asadi et al. 2014; Chetverikov et al. 2021b). These reports may indicate an underestimated role of the soil in the ecology of eriophyoid mites. Association with soil in extant eriophyoids could be some kind of an ecological throwback to when nematolytic-like ancestors of the eriophyoids started developing associations with the above-ground organs of plants (Bolton et al. 2017 2018; Klimov et al. 2018 2022). A search for eriophyoids in soil and leaf litter samples and careful investigations of the invertebrates associated with plant roots and mycorrhizae, especially in ancient intact biomes like the forests of Amazonia, Kalimantan and Australia, may result in the finding of unusual forms of eriophyoids or eriophyoid-like mites that could help clarify the evolutionary relationship between the ancestral soil mites and contemporary phytophagous eriophyoids.

CONCLUSIONS

The correct identification of phytophagous mites and fundamental knowledge about their life cycles are critical for pest management in agricultural crops. The eriophyoid mites (Acariformes, Eriophyoidea) are among the smallest known herbivores. They are highly host specific and include numerous economically important pests of both annual and perennial crop plants. Seasonal changes in populations of some eriophyoid species involve the co-occurrence of morphologically different, conspecific seasonal forms, the deutogyne and protogyne, a phenomenon termed deutogyny. Although only a small proportion of currently known eriophyoids are proven to be deutergynous, this phenomenon might be more common than currently understood and may have created a situation in which the same taxon could have been described under different names by different authors. DNA barcoding is the most effective tool for testing the conspecificity of eriophyoids collected from mixed populations. Therefore, the inclusion of barcode data in future descriptions of new taxa of eriophyoids is essential, especially when deutogyny is suspected. In this study, we reported on seasonal dimorphism in eriophyoid mites of the genera *Shevtchenkella* and *Brevulacus*. Although the two studied species, *S. serrata* and *B. reticulatus*, both fed on the generative organs of their hosts in late summer, only one of them (*S. serrata*) dispersed with seed-containing winged fruits in autumn, overwintered on them in leaf litter and colonized the new seedlings emerging in spring. Various uninvestigated plant species could be appropriate hosts for eriophyoids adapted to exploit the seed dispersal abilities of their hosts in a similar way to *S. serrata*. Additional studies conducted in various ecosystems and including different ecological groups of plants, especially anemochorous plants, are needed in order to estimate the frequency of the association of eriophyoids with plant generative organs and to better understand the role of such associations in their ecology.

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Authors' contributions: Chetverikov PE and Sukhareva SI designed the study, collected mites, analysed the DNA data, drafted the manuscript and submitted the manuscript. Chetverikov PE and Romanovich AE performed slide-mounting, PCR and DNA sequencing. Desnitskiy AG, Klimov PB and Ozman-Sullivan SK helped to revise the drafts of the manuscript. All authors are in agreement with the content of the manuscript.

Competing interests: All authors declare that they have no competing interests.

Availability of data and materials: Slide-mounted mites and ethanol material have been deposited at Acarological Collection of the Zoological Institute of the Russian Academy of Sciences. The DNA sequences have been uploaded to the GenBank database.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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