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New phytoptids (Eriophyoidea, Phytoptidae) from southern African endemic dicotyledons: description of two new species of *Solenocristus* n. g. and updated key to world genera of the tribe Sierraphytoptini

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Abstract

A new phytoptid genus and two new species, *Solenocristus karooensis* n. g. & n. sp. and *S. searsius* n. sp. (Phytoptidae, Sierraphytoptinae, Sierraphytoptini), were collected in the Eastern and Western Cape provinces of South Africa, from southern African endemic dicotyledonous trees *Schotia afra* (Fabaceae) and *Searsia lucida* (Anacardiaceae) respectively. They are described and illustrated with the aid of conventional light microscopy and low temperature scanning electron microscopy. Females of both new species possess a distinct pregenital plate divided into two parts by a subcuticular medial ridge. Additionally, in *S. karooensis* n. sp. the movable digit of the male chelicerae varies in length: among six observed males, three males had a movable digit (md) twice shorter than the fixed digit (fd), in one male it was slightly shorter than fd and in the remaining two males md and fd were of the same length. An updated key to the world genera of the tribe Sierraphytoptini is given. The key incorporates data on seven sierraphytoptine genera including three genera (*Neoprothrix* Reis & Navia, *Solenoplalobus* Chetverikov & Craemer and *Solenocristus* n. g.) which were described since the last generic key of Eriophyoidea by Amrine *et al.* (2003) was published.

Key words: African endemics, LT-SEM, *Searsia*, *Schotia*, eriophyoid mites, fixed digit, movable digit

Introduction

The paraphyletic family Phytoptidae *sensu* Amrine *et al.* (2003) comprises five subfamilies (*sensu* Amrine *et al.* 2003) of which monophyly is questionable. Chetverikov *et al.* (2015a) inferred the basal phylogeny of Eriophyoidea based on two markers (COI and D1–2 rRNA), and found two monophyletic lineages of phytoptids differing in genital anatomy, prodorsal shield setation and host-plant associations: Phytoptidae-1 (corresponds to Phytoptidae *sensu* Boczek *et al.* 1989 from angiosperms) and Phytoptidae-2 (corresponds to Nalepellidae *sensu* Boczek *et al.* 1989 from gymnosperms). They also proposed to exclude the tribe Pentasetacini Amrine *et al.* 2003 (includes genera *Pentasetacus* Schliesske and *Loboquintus* Chetverikov *et al.*) from phytoptids. Later Chetverikov & Petanović (2016) accepted the family Pentasetacidae Shevchenko *et al.* 1991 and argued that the tribe Pentasetacini Amrine *et al.* 2003 should be treated as a family.

The subfamily Sierraphytoptinae Keifer 1944 includes all representatives of the clade Phytoptidae-1 with dorso-ventrally differentiated annuli. In the generic key by Amrine *et al.* (2003) this subfamily is divided into the tribes Sierraphytoptini and Mackiellini based on the presence/absence of opisthosomal seta *c1* and the association with different groups of angiosperms: dicotyledons (sierraphytoptines) and monocotyledons (mackiellines). This division implies that (1) evolution of Sierraphytoptinae might have followed basal divergence of angiosperms into “monocots” and “eudicots”, the two large clades of Magnoliophyta revealed by Byng *et al.* (2016) or (2) one of the tribes originated from the other as a result of a host shift. One of these hypotheses might be true, however, monophyly of the sierraphytoptine tribes has never been tested, therefore the scheme proposed in Amrine *et al.* (2003) remains non-verified.

In the most recent generic key of Eriophyoidea (Amrine *et al.* 2003) the tribe Sierraphytoptini is represented by four genera (*Neopropilus* Huang, *Austracus* Keifer, *Fragariocoptes* Roivainen, and *Sierraphytoptus* Keifer). Since 2003 several new sierraphytoptine genera have been described, however a series of curious mistakes were published making the literature on Sierraphytoptini slightly confusing. Chetverikov & Sukhareva (2009) reported that two sierraphytoptine genera, *Fragariocoptes* Roivainen and *Sierraphytoptus* Keifer, should be synonymized. However, after recollecting the type species of *Sierraphytoptus* in North America and comparing it with European members of *Fragariocoptes*, Chetverikov (2016a) concluded that these are two different genera. Chetverikov & Sukhareva (2009) revealed that contrary to the drawings from the original descriptions, *Sierraphytoptus taiwanensus* Huang possesses tibial solenidion I (which does not fit the diagnosis of *Sierraphytoptus* Keifer) and transferred it to the genus *Austracus* Keifer. However, later, investigating the same type material, Chetverikov & Craemer (2016) decided that “*taiwanensus*” Huang should be placed in a new genus, *Solenoplatilobus*, based on the presence of a broad based translucent frontal lobe of the prodorsal shield as well as the absence of overlapping dorsal opisthosomal plates, which are characteristic of *Austracus*. Reis *et al.* (2014) described a new genus *Neoprothrix* Reis & Navia and assigned it to the phytoptid subfamily Prothricinae Amrine based on the presence of tiny paired setae *vi*. However, one year later it was demonstrated that the structures originally interpreted as setae *vi* are two internal rod-like apodemes (Chetverikov *et al.* 2015b) and the genus *Neoprothrix* was transferred to the tribe Sierraphytoptini of the subfamily Sierraphytoptinae.

In this paper we describe a new sierraphytoptine genus *Solenocristus* **n. g.** and two new species (*Solenocristus karoensis* **n. sp.** and *S. searsius* **n. sp.**) collected in South Africa from endemic arboreal dicotyledons. We also provide an updated key to the world genera of the tribe Sierraphytoptini, which incorporates data on all known sierraphytoptine genera including the three genera (*Neoprothrix* Reis & Navia, *Solenoplatilobus* Chetverikov & Craemer and *Solenocristus* **n. g.**) which are absent in the last published generic key of Eriophyoidea (Amrine *et al.* 2003).

Material and methods

Collection and morphological measurements. Mite specimens were studied using different light microscopy (LM) techniques (phase contrast – PC LM, and differential interference contrast – DIC LM), and low-temperature scanning electron microscopy (LT-SEM). The mites were collected in South Africa from leaves and entire shoots using a minuten pin, examined under a stereo microscope, and stored in Eppendorf tubes with 96% ethanol and in a drop of “sorbitol fluid” in Eppendorf tubes following the methodology proposed by C. Craemer and S. Nesar (see de Lillo *et al.* 2010, p. 289). All other steps including transfer of the specimens, slide-mounting in modified Berlese medium with Iodine (Amrine & Manson 1996) and clearing were conducted the same as those described in Chetverikov *et al.* (2017b).

Adults of the new species were described based on DIC LM and PC LM observations of slide-mounted specimens. All measurements in the descriptions are given in micrometers (μm), and are lengths except when stated otherwise. In the descriptions the measurements of females are based on the holotype, whereas the ranges (in brackets) are based on measurements of the paratypes and holotype. In the descriptions of males and immatures, only ranges are given. Terminology of eriophyoid morphology and classification of Phytoptidae follow Lindquist (1996) and Amrine *et al.* (2003), respectively. Terminology of internal genitalia follows Chetverikov *et al.* (2012) and Chetverikov (2014). The drawings of the mites were made based on PC LM with the aid of a video projector as described by Chetverikov (2016b). Images of male chelicerae of *S. karooensis* **n. sp.** were obtained in ImageJ® with four different algorithms (Minimum, Average, Sum Slices, Maximum, all embedded in ImageJ®) based on DIC LM microphotographs with gradually increasing depth of focus.

LT-SEM technique. For LT-SEM, the live mites *S. searsius* **n. sp.** were placed on double-sided carbon tape with the aid of a minuten pin tool under a stereo-microscope. The piece of tape with the mites was pasted onto a sample holder and plunge frozen in liquid nitrogen and immediately prepared for and studied with SEM. All other steps (transferring under vacuum, etching, coating and studying with the aid of LT-SEM) follow those described in Chetverikov *et al.* (2017a), except the specimens were coated with an average of 10 nm thick iridium. SEM observations of *S. searsius* **n. sp.** are presented in a separate section below the formal description based on LM of slide-mounted specimens.

Comparative material. Paratype female of *Solenoplatilobus taiwanensus* (Huang 2006) from *Trochodendron aralioides* Siebold & Zucc., (Trochodendraceae), vagrant on lower leaf surface, no visible damage, TAIWAN: Nantou Renai, 16 April 2003, coll. K.W. Huang, slide #030416–01. Females of *Sierraphytoptus alnivagrans* Keifer 1944 from *Alnus incana* subsp. *tenuifolia* (Nuttall) Breitung (Betulaceae), vagrant on lower leaf surface, no visible damage, USA: California, Shasta County, Hat Creek; 40°50'56"N, 121°31'54"W; 6 June 2014, coll. P.E. Chetverikov and J.W. Amrine, slides #54–14, #55–14, #56–14. Paratype females of *Fragariocoptes ambulans* (Chetverikov & Sukhareva 2009) from *Fragaria vesca* L. (Rosaceae), lower leaf surface, no visible damage, RUSSIA: Leningrad Province, Gatchina district, fir-forest on the right bank of the river Oredezh near the village Vyritza; 59°23.6'N, 30°18.3'E; 21 September 2008, coll. P.E. Chetverikov, slide # 53–08. Females of *Neoprothrix hibiscus* (Reis & Navia in Reis *et al.* 2014) from *Hibiscus rosa-sinensis* L. (Malvaceae), lower leaf surface, no visible damage, BRAZIL: Recife, Pernambuco, February 2014, coll. D. Navia, slides #6–14 and #9–14. Two females of *Austracus havrylenkonis* Keifer 1944 accidentally collected from extracts of swamp monocotyledonous herbs *Carex magellanica* (Cyperaceae) and *Rostkovia magellanica* (Juncaceae), CHILE: Laguna Parrillar National Reserve, 53°24'01.5"S; 71°13'31.9"W; 15 November 2015, coll. A. Przhiboro, slides #1–16 and #2–16.

Results

Family Phytoptidae Murray 1877

Subfamily Sierraphytoptinae Keifer 1944

Diagnosis. Phytoptid mites *sensu* Amrine *et al.* (2003) with four (paired *ve* and *sc*) or two (when *sc* is absent) prodorsal shield setae and dorso-ventrally differentiated opisthosomal annuli; associated with angiosperms.

Tribe Sierraphytoptini Keifer 1944

Diagnosis. Opisthosomal seta *c1* present; tibial solenidion φ I present or absent; prodorsal shield setae *ve* present, *sc* present or absent; associated with dicotyledons.

Genus *Solenocristus* n. g.

Diagnosis. Four setae present on prodorsal shield: paired *ve* and *sc*. Tubercles of *ve* situated below anterolateral margin of prodorsal shield; *ve* directed up and anterolaterad. Tubercles of *sc* situated ahead of rear margin of prodorsal shield; *sc* directed up and diverging anteriad. Frontal lobe of prodorsal shield present. Opisthosomal annuli dorso-ventrally differentiated into broader, smooth dorsal annuli and narrower microtuberculate ventral annuli. Dorsal opisthosomal annuli form three longitudinal ridges: distinct median ridge and one lateral ridge on each side. All usual leg, gnathosomal and opisthosomal setae present. Opisthosomal setae *c1* and tibial solenidion φ I present. Empodium undivided.

Differential diagnosis. Among the six genera of the tribe Sierraphytoptini currently recognized, the new genus is most similar to *Solenoplatilobus* Chetverikov & Craemer 2016. Both genera possess four prodorsal shield setae (paired *ve* and *sc*), tubercles of *ve* displaced below anterolateral margin of prodorsal shield, tibial solenidion φ I present. However, in *Solenocristus* n. g. dorsal opisthosomal annuli are notably fewer, broader, devoid of microtubercles and forming three longitudinal ridges. In *Solenoplatilobus* dorsal opisthosomal annuli are narrower and microtuberculate; opisthosomal ridges absent.

Type species: *Solenocristus karoensis* n. sp.

Species included: *S. karoensis* n. sp., *S. searsius* n. sp.

Host plants and distribution. Up to now, mites of the genus *Solenocristus* n. g. have been recorded only twice, as vagrants on leaves and petioles of *Schotia afra* (Fabaceae) and *Searsia lucida* (Anacardiaceae) in the Eastern and Western Cape Province of South Africa respectively.

Etymology. The generic name, *Solenocristus*, is derived from two words: “solenidion”, indicating the presence of tibial solenidion φ I, and “crista”, indicating the presence of well-developed medial opisthosomal ridge in mites of this genus; gender masculine.

Solenocristus karoensis n. sp.—Figures 1,2,3,4,5 and Table 1.

FEMALE (n=12). Live mites orange and covered with wax¹; body comma-shaped, difficult to slide-mount dorso-ventrally, 228 (210–242), 65 (60–70) wide at the level of setae *c2*. Prodorsal shield covered with tiny, rounded indentations, less on dorsal annuli. **Prodorsal shield** subtriangular, with rounded sides, 52 (50–56), 64 (62–69) wide; frontal lobe consists of dorsoproximal central elevation² and ventrodistal marginal plate; central elevation 11 (10–12) long, subtriangular; marginal plate 14 (12–15) long, semi-oval, rounded anteriorly, thin and translucent. Prodorsal shield smooth except indistinct arc-shaped line or fold between tubercles of *sc*; prodorsal shield cuticle with numerous tiny indentations; large cleft between posterior margin of prodorsal shield and first dorsal opisthosomal annulus in laterally oriented slide-mounted mites. Prodorsal shield setae: *ve* 14 (12–15), directed up

1. Many eriophyoid species are capable for producing wax-like secretions, however it has never been proved chemically that the secretions really are wax. In this paper, for brevity, we call the wax-like secretions “wax”.

2. In laterally oriented slide-mounted specimens the central elevation of the frontal lobe was not apparent, however in those mites oriented dorsoventrally the elevation and the marginal plate were clearly seen.

and anterolaterad, tubercles of *ve* situated below anterolateral margin of prodorsal shield, 35 (34–39) apart; *sc* 21 (20–24), 19 (15–20) apart, directed up and anterolaterad. **Gnathosoma** large, directed down, obliquely down and back or obliquely down and forward (Fig. 2 A,C,D). Palps 50 (48–55); chelicerae 32 (29–34), cheliceral digits (n=12) of equal length; outer infracapitular stylets 36 (32–37); oral stylet (n=5) angled, 16 (15–17); suboral fork (*sensu* Chetverikov & Bolton 2016) thick, distinct, 8–11 (n=3). Gnathosomal setae: seta *v* 1 (0.5–1); pedipalp genual seta *d* non-bifurcate, 6 (4–6); pedipalp coxal seta *ep* 3 (2–3); cheliceral retainer absent. Suboral plate rounded, with indistinct faint microtubercles.

Leg I 31 (30–33), tarsus 5 (4–5), *u'* 2 (2–3), *ft'* 14 (13–18), *ft''* 17 (16–21), *ω* 8 (7–9) knobbed; empodium 6 (6–7), symmetrical, 7–8-rayed; tibia 7 (6–7), *l'* 5 (5–6); *φ* 12 (11–12), knobbed; genu 5 (4–5), *l''* 19 (18–25), situated on dorsal surface of genu near tibio-genual articulation; femur 10 (10–12), *bv* 13 (12–16). **Leg II** 27 (25–29), tarsus 5 (4–5), *u'* 2 (2–3), *ft'* 5 (5–7), *ft''* 15 (15–17), *ω* 10 (9–12) knobbed; empodium 6 (6–7), symmetrical, 7–8-rayed; tibia 5 (5–6); genu 5 (4–5), *l''* 16 (15–18), situated on lateral surface of genu near femoro-genual articulation; femur 9 (8–9), *bv* 9 (8–10). **Coxal plates** with sparse indistinct ridges and rounded microtubercles. Setae *lb* 13 (12–17), 11 (11–13) apart; *la* 32 (32–40), 12 (12–14) apart; *2a* 46 (42–48), 20 (19–22) apart; 8 (7–8) coxigenital annuli before epigynium. Prosternal apodeme faint, indistinctly forked posteriorly, approximately 10. **External genitalia.** Genital coverflap rounded, smooth, 9 (9–11), 15 (15–17), wide; setae *3a* 9 (9–13), 16 (15–16) apart; pregenital plate (*sensu* Flechtmann *et al.* 2015) distinct, with medial subcuticular ridge³ symmetrically dividing pregenital plate into two parts. Internal genitalia damaged or not visible in all studied females.

Opisthosoma dorsally with 22 (21–23) smooth annuli forming distinct medial ridge and two faint lateral ridges, ventrally with 42 (41–46) microtuberculate annuli between the epigynium and caudal lobes. Each dorsal annulus (except last 5–6 annuli) with small medial subrhomboid or subrectangular thickening slightly protruding above the next annulus; in some specimens one or two annuli adjacent to tubercles of *c1* and several pretelosomal annuli with a thin ribbon-like plate instead of subrhomboid thickening (Fig. 5); last 5–6 annuli with a narrow translucent rounded plate overlapping next annulus. Setal lengths: *c1* 20 (19–21), *c2* 8 (8–12), *d* 19 (18–23), *e* 7 (7–10), *f* 11 (10–15); *h1* 2 (1–2); *h2* 65 (62–77); 2 annuli from rear shield margin to *c1* in all studied females; 7 (7–9) annuli from rear shield margin to *c2*; 13 (12–14) annuli between *c2*–*d*; 10 (10–12) annuli between *d* and *e*; 14 (13–15) annuli between *e* and *f*; and 4 (4–5) annuli between *f* and *h2*.

MALE (n=6). Most qualitative characters of males (ornamentation of prodorsal shield and coxae; shape of leg appendages and directions of setae; distribution and shape of microtubercles and ridges) are similar to those of females. Only morphometric traits are given below. Body 200–228, 61–68 wide at the level of setae *c2*. **Prodorsal shield** 50–57, 62–67 wide; frontal lobe 11–12; *ve* 13–15, 34–36 apart; *sc* 20–22, 16–20. **Gnathosoma** directed down or obliquely down; palps 50–54. Chelicerae 31–34; in three males movable digit (md) was twice shorter⁴ than fixed digit (fd) (Fig. 3B), in one male md was slightly shorter than fd, and in two males md and fd were of the same length. Outer infracapitular stylets 35–37; oral stylet (n=4) angled, 15–16. Gnathosomal setae: seta *v* about 1; pedipalp genual seta *d* 4–5; pedipalp coxal seta *ep* 2–3. **Leg I** 30–32, tarsus 4–5, *u'* 2–3, *ft'* 14–17, *ft''* 15–20, *ω* 7–8 knobbed; empodium 5–7, 7-rayed; tibia 6–7, *l'* 5–6; *φ* 10–12, knobbed; genu 4–5, *l''* 18–22; femur 10–11, *bv* 11–15. **Leg II** 24–28, tarsus 4–5, *u'* 2–3, *ft'* 4–7, *ft''* 12–18, *ω* 9–11 knobbed; empodium 5–7, 7-rayed; tibia 5–6; genu 4–5, *l''* 15–16; femur 8–9, *bv* 8–11. **Coxal setae:** *lb* 11–16, 10–12 apart; *la* 30–36, 11–14 apart; *2a* 40–46, 20–21 apart; 6–8 coxigenital annuli before

3. In the slide-mounted specimens this ridge was observed in another focal plane (deeper inside the mite's body) than on the surface of the ventral cuticle. This observation led us to an assumption that this ridge is subcuticular.

4. Careful LM investigation of these movable digits showed that they were not broken.

external genitalia. **External genitalia** 10–13, 14–17 wide; setae *3a* 8–12, 16–17 apart. **Opisthosoma** dorsally with 20–22 smooth annuli forming distinct medial ridge and two faint lateral ridges, ventrally with 40–45 microtuberculate annuli between external genitalia and caudal lobes. Setal lengths: *c1* 20–22, *c2* 9–10, *d* 18–22, *e* 7–10, *f* 12–14; *h1* 1–2; *h2* 50–62; 2 annuli from rear shield margin to *c1* in all studied males; 8–9 annuli from rear shield margin to *c2*; 11–14 annuli between *c2*–*d*; 10–13 annuli between *d* and *e*; 14–16 annuli between *e* and *f*; and 4–5 annuli between *f* and *h2*.

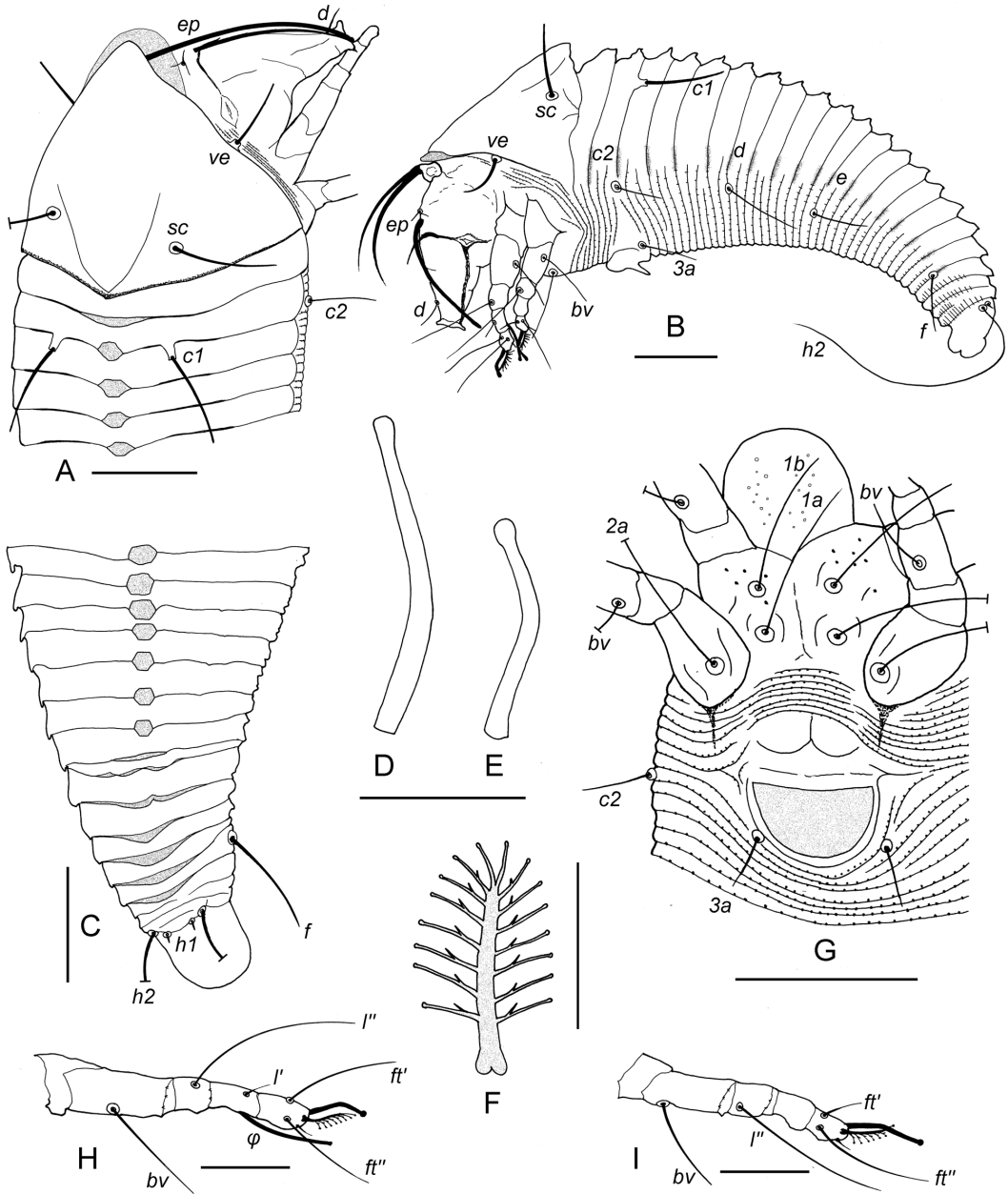


FIGURE 1. Drawings of *Solenocristus karoensis* n. sp. (female, based on PC LM). A—dorsal view of anterior part of body (leg setation not shown); B—lateral view of entire mite; C—dorsal view of posterior part of body; D—tarsal solenidion II; E—tarsal solenidion I; F—empodium I; G—coxigenital area; H—leg I; I—leg II. Scale bar: A,B,C = 20 μ m; D,E,F = 5 μ m; G = 20 μ m; H,I = 10 μ m.

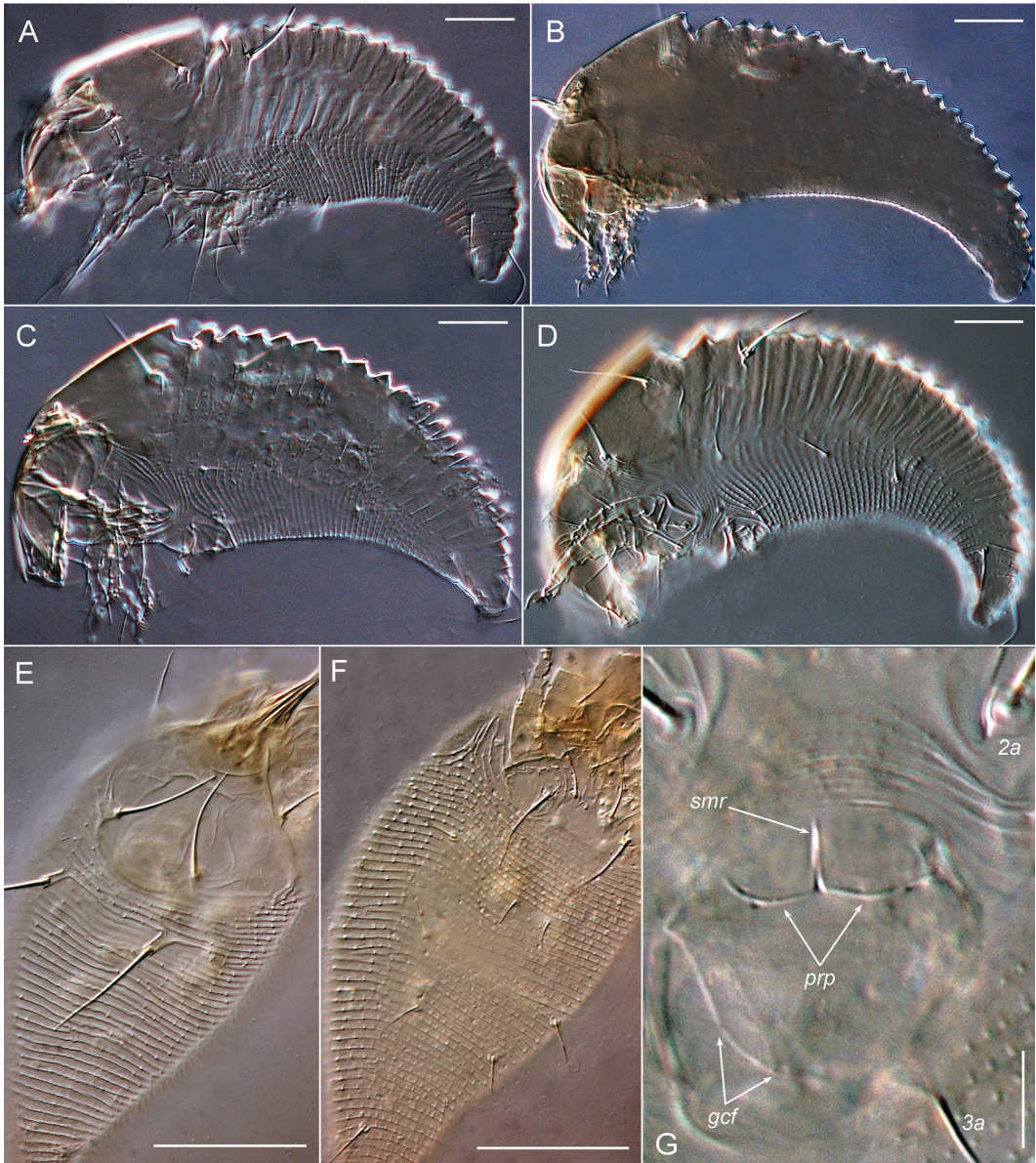


FIGURE 2. DIC LM images of females (A,C,D,G), male (B), and nymph (E,F) of *Solenocristus karoensis* n. sp. A,B,C,D—lateral view of four mites with differently oriented gnathosoma relative to longitudinal body axis; E—dorsal view of nymph; F—ventral view of nymph; G—female genital area. Scale bar: A,B,C,D = 20 μ m; E,F = 30 μ m; G = 5 μ m. Notations: *gcf*—genital coverflap; *prp*—pregenital plate; *smr*—subcuticular medial ridge of pregenital plate.

NYMPH (n=2, Fig. 2E,F). Body orange, 111–115, 51–56 wide at the level of setae *c2*. **Prodorsal shield** subrhomboid, 40–43, 50–55 wide; frontal lobe 11–12. Prodorsal shield with several indistinct lines in lateral field and faint U-shaped line between tubercles of *sc*; posterior margin of prodorsal shield hanging over first 2–3 dorsal annuli. Prodorsal shield setae: *ve* 14–17, directed up and anterolaterad, tubercles of *ve* situated below anterolateral margin of prodorsal shield, 28–30 apart; *sc* 18–20, 18–21 apart, directed up and anterolaterad. **Gnathosoma** large, directed obliquely down and slightly backward. Palps 32–35; chelicerae 27–28; outer infracapitular stylets

32–33. Gnathosomal setae: seta *v* about 1; pedipalp genual seta *d* non-bifurcate, 4–5; pedipalp coxal seta *ep* 2–3. Suboral plate rounded, smooth.

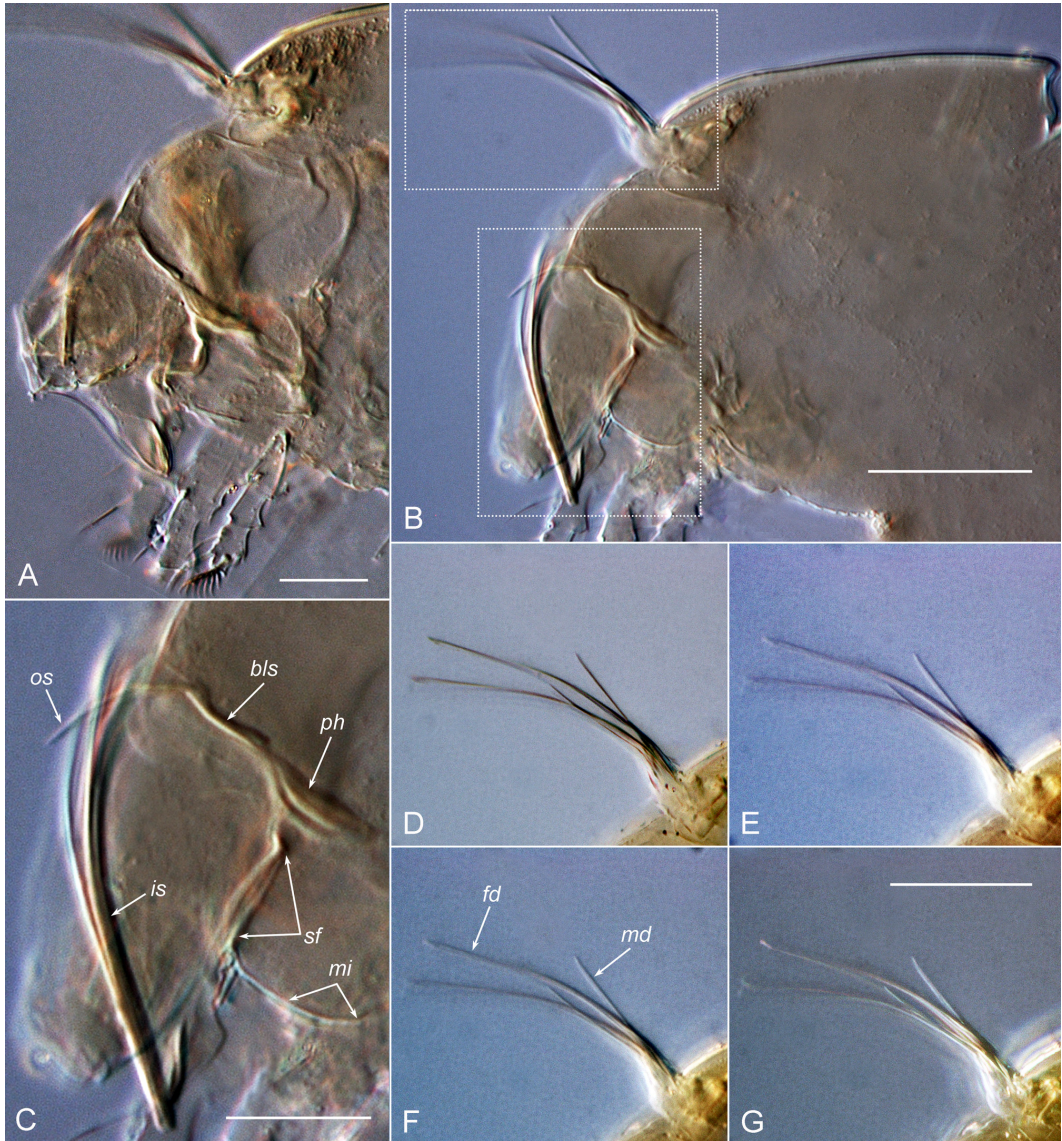


FIGURE 3. DIC LM images showing gnathosomal morphology in female (A, slightly deformed) and male (B–G) of *Solenocristus karoensis* n. sp. Note: Fig. 3C is enlarged lower rectangular fragment of Fig. 3B; figures 3D, 3E, 3F, and 3G are four combined images of the same area as upper rectangular fragment of Fig. 3B obtained with four different algorithms embedded in ImageJ® (*Minimum*—Fig. 3D, *Average*—Fig. 3E, *Sum Slices*—Fig. 3F, and *Maximum*—Fig. 3G) based on five DIC LM microphotographs with gradually increasing depth of focus. Notations: *bls*—basal labral segment, *fd*—fixed digit, *is*—infracapitular stylets, *md*—movable digit, *mi*—mentum infracapituli, *os*—oral stylet, *ph*—pharynx, *sf*—suboral fork. Scale bar: A, C = 10 μ m; B, D, E, F, G = 15 μ m.

Leg I 27–28, tarsus 3–4, *u'* 2–3, *ft'* 12–15, *ft''* 15–18, ω 5–6 with tiny knob, empodium 5–6, symmetrical, 7-rayed; tibia 5–6, *l'* 3–4; ϕ 7–8 with tiny knob; genu 3–4, *l''* 15–17; femur 8–10, *bv* 9–12. **Leg II** 23–25, tarsus 3–4, *u'* 2–3, *ft'* 4–5, *ft''* 10–11, ω 7–8 with tiny knob; empodium 5–6, symmetrical, 7-rayed; tibia 4–5; genu 3–4, *l''* 12–16; femur 7–8, *bv* 7–10. **Coxal plates** with sparse

indistinct ridges. Setae *1b* 6–8, 6–7 apart; *1a* 15–18, 7–8 apart; *2a* 23–27, 16–17 apart; prosternal apodeme indistinct; 12–13 coxigenital annuli before tubercles of *3a*; seta *3a* 7–8, 6–7 apart.



FIGURE 4. PC LM images showing structure of frontal lobe of prodorsal shield in three females of *Solenocristus karoensis* n. sp. Notations: *CEL*—central elevation of frontal lobe; *MP*—marginal plate of frontal lobe. Scale bars: A = 15 μ m, B = 10 μ m, C = 20 μ m.

Opisthosoma without ridges and furrows; dorsally with 42–44 annuli bearing sparsely distributed microtubercles; ventrally with 50–53 microtuberculate annuli between coxae II and caudal lobes. Setal lengths: *c1* 22–23, tubercles of *c1* elongate, 4–5; *c2* 7–8, *d* 7–8, *e* 8–10, *f* 18–20; *h1* 0.5–1; *h2* 30–35; 4–5 annuli from rear shield margin to *c1*; 8–9 annuli from rear shield margin to *c2*; 12–13 annuli between *c2*–*d*; 7–8 annuli between *d* and *e*; 12–14 annuli between *e* and *f*; and 4–4 annuli between *f* and *h2*.

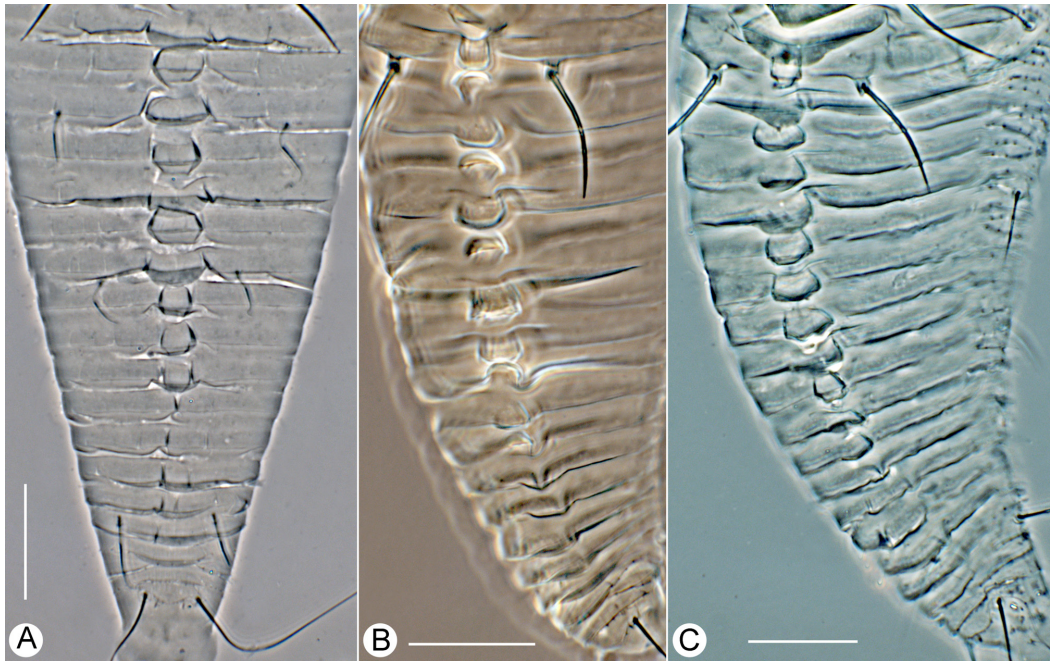


FIGURE 5. PC LM images showing the variation in midsomal ridge in three females of *Solenocristus karoensis* n. sp. Scale bar = 20 μ m.

Host plant. *Schotia afra* (L.) Thunb. (Fabaceae), southern African endemic.

Remark. This endemic tree comprises of two geographically isolated subspecies: (1) *S. afra* var. *afra* occurring in the coastal districts of the Eastern Cape (mainly along the banks of dry streams and small rivers in the Little Karoo) and the southern Western Cape, and (2) *S. afra* var. *angustifolia* occurring inland in Namaqualand and Namibia (Codd 1956, Coates Palgrave 2002). Contrary to *S. afra* var. *angustifolia* which is considered rare and protected by law, *S. afra* var. *afra* has a large distribution range and does not appear to be threatened (IUCN 2018). It is highly possible that both varieties of *S. afra* are infested by mites of the genus *Solenocristus* n. g. Further collections from *Schotia* in Namaqualand and Namibia are needed to test this hypothesis. If *Solenocristus* n. g. mites are found on the Namibian variety (*S. afra* var. *angustifolia*), it would be interesting to compare them morphologically and genetically with *S. karoensis* n. sp. from *S. afra* var. *afra* in order to estimate the influence of geographical isolation on the evolution of *Solenocristus* n. g.

Relation to the host. Vagrant on lower surface of leaves, causing no visible damage.

Type locality. South Africa, Eastern Cape, about 4km North of Steytlerville, Noorspoort Guest Farm, roadside near folded rocks, 33°16'54.8"S, 24°22'45.5"E.

Type material. Holotype female in slide #E4340, 28 paratypes on 25 slides (##E4265–E4274, E4313–E4319, and E4338–E4345), collected 5 November 2016 in South Africa, Eastern Cape, Noorspoort Guest Farm, 33°16'54.8"S, 24°22'45.5"E, coll. P. Chetverikov, C. Craemer, S. Neser. Holotype and some paratypes are deposited in South African National Collection of Arachnida (NCA)—Acari at ARC-PPRI, Pretoria, some paratypes deposited in Acarological collection in ZIN RAS.

Etymology. The species epithet “*karoensis*”, gender masculine, is a Latin adjective derived from Karoo, the dry area in South Africa where the host plant of *S. karoensis* n. sp. is distributed.

Differential diagnosis. The new species is very similar to *Solenocristus searsius* **n. sp.** (described below). The main characters separating these two species are listed in Table 1 after the description of *S. searsius* **n. sp.**

***Solenocristus searsius* n. sp.—Figures 6,7,8; Table 1.**

FEMALE (n=9). Live mites pale orange and covered with wax; body flattened, 187 (182–204), 67 (64–71) wide at the level of setae *c2*. Dorsal body cuticle with tiny round indentations, which are especially numerous on prodorsal shield and medial plates of dorsal annuli. **Prodorsal shield** subtriangular with rounded sides, 43 (42–46), 61 (60–67) wide; anterior part of prodorsal shield forms complex frontal lobe extending over basal gnathosoma. Frontal lobe consists of dorsoproximal central elevation and ventrodiscal marginal plate forming together a double structure (Fig. 7 A,B,D); central elevation 5 (4–6) long, subtriangular, lateral sides of this elevation continues backwards forming a ridge-like lateral edge of prodorsal shield; marginal plate 10 (8–11) long, subtriangular, rounded anteriorly, thin and translucent, covering basal part of gnathosoma. Prodorsal shield smooth except an arc-shaped fold between tubercles of *sc*; posterior shield margin indistinct with no border between prodorsal shield and first dorsal opisthosomal annulus observed in the slide-mounted specimens. Prodorsal shield setae *ve* and *sc* thick and stout, approximately 1 µm thick: *ve* 12 (12–15), directed up and anterolaterad, tubercles of *ve* situated slightly below anterolateral margin of prodorsal shield, 33 (31–36) apart; *sc* 15 (14–17), 24 (22–25) apart, directed up and anterolaterad. **Gnathosoma** directed obliquely down and forward. Palps 34 (34–39); chelicerae 28 (27–29); outer infracapitular stylets 22 (21–25); oral stylet (n=3) angled, 8–10. Gnathosomal setae: seta *v* 3 (2–3); pedipalp genual seta *d* non-bifurcate, 6 (6–7); pedipalp coxal seta *ep* 3 (2–3); cheliceral retainer absent. Suboral plate rounded, with sparse microtubercles and two indistinct longitudinal ridges.

Leg I 31 (30–32), tarsus 5 (5–6), *u'* 4 (2–4), *ft'* 12 (10–13), *ft''* 20 (18–23), *ω* 7 (7–9) knobbed; empodium 6 (5–6), symmetrical, 5-rayed; tibia 6 (6–7), *l'* 2 (2–4); *φ* 10 (9–11) knobbed; genu 5 (5–6), *l''* 23 (22–26); femur 9 (8–10), *bv* 11 (10–14). **Leg II** 28 (26–29), tarsus 5 (4–5), *u'* 2 (2–3), *ft'* 6 (6–7), *ft''* 19 (16–20), *ω* 8 (8–9) knobbed; empodium 6 (5–6), symmetrical, 5-rayed; tibia 6 (5–6); genu 5 (4–5), *l''* 5 (5–8), situated on lateral surface of genu close to femorogenual articulation; femur 10 (8–10), *bv* 11 (9–11). **Coxal plates** with irregular short cuticular ridges; prosternal apodeme forked posteriorly, about 9 (9–10). Setae *lb* 12 (10–13), 9 (9–11) apart; *la* 30 (29–38), 10 (10–13) apart; *2a* 36 (33–45), 20 (19–21) apart; 10 (9–10) coxigenital annuli before epigynium. **External genitalia.** Genital coverflap rounded, smooth, 10 (9–11), 19 (17–20), wide; setae *3a* 12 (10–12), 15 (15–16) apart; pregenital plate (*sensu* Flechtmann *et al.* 2015) distinct, divided by a short longitudinal ridge into two cell-shaped areas. **Internal genitalia (n=4).** Spermathecae pyriform, 8–10 long, 4–6 wide; spermathecal tubes sausage-like, 7–9 long, 2–3 wide, directed anteriorly; spermathecal process (*sensu* Duarte *et al.* 2016) absent; longitudinal bridge 12–17 with rudimentary postspermathecal part; anterior genital apodeme trapezoidal; oblique apodeme (*sensu* Chetverikov *et al.* 2015a) absent.

Opisthosoma dorsally with 14 (13–15) annuli forming distinct medial ridge and two lateral ridges, ventrally with 44 (43–48) microtuberculate annuli between epigynium and caudal lobes, microtubercles small and pointed, becoming more elongated and ridge-like on ventral annuli beyond setae *f*. Dorsal annuli overlap each other medially so that in slide-mounted specimens overlapping parts of dorsal annuli look like translucent subtriangular medial plates with rounded posterior margins; in some specimens plates with central folds or ridges (possibly an artifact of slide-mounting); medial plate of first dorsal annulus as wide as body, whereas other plates notably narrower. In all partially cleared specimens remnants of serial putative wax producing structures

represented by dark subcuticular spots⁵ about 3–4 µm in diameter observed between dorsal annuli (Fig. 7C) and near tubercles of *sc* (not shown). Setal lengths: *c1* 16 (16–19), about 1 µm thick (notably thicker than other opisthosomal setae), *c2* 17 (15–18), *d* 23 (19–24), *e* 9 (9–10), *f* 16 (15–17); *h1* 3 (2–3); *h2* 33 (30–37); 2 (2–3) annuli from rear shield margin to *c1*; 8 (7–9) annuli from rear shield margin to *c2*; 10 (10–13) annuli between *c2*–*d*; 10 (10–14) annuli between *d* and *e*; 14 (13–15) annuli between *e* and *f*; and 4 (4–5) annuli between *f* and *h2*.

MALE (n=5). Males slightly smaller than females and generally similar to them. Body 176–180, 60–63 wide. Prodorsal shield smooth except for an arc-shaped fold between tubercles of *sc*; 39–42, 54–55 wide; *ve* 13 (12–14), 30 (30–33) apart; *sc* 19 (14–19), 23 (22–24) apart. Leg I 29–32, leg II 25–27. Opisthosoma dorsally with 13–14 medially overlapping smooth annuli and ventrally with 45–48 microtuberculate annuli between external genitalia and caudal lobes. Genital area subtriangular, 17–20 wide, flanked laterally by short longitudinal microtuberculate ridge and anteriorly by a transverse slightly curved cuticular fold. Gonopore indistinct, situated in the middle of a narrow semicircular genital slit. Postgenital region situated between tubercles of *3a*, limited anteriorly by the genital slit and posteriorly by an arc-shaped microtuberculate semi-annulus and sparsely covered by microtubercles and tiny irregular ridges. Eugenital setae seemingly absent. Setae *3a* 13–14, 17–20 apart. Lengths of opisthosomal setae: *c1* 13–14, about 1 µm thick (notably thicker than other opisthosomal setae), *c2* 16–18, *d* 9–14, *e* 9–12, *f* 10–16; *h1* 1–2; *h2* 20–28.

Host plant. *Searsia lucida* (L.) F. A. Barkley (Anacardiaceae), southern African endemic.

Remark. The genus *Searsia* has remarkable Afro-Asian disjunctive distribution: about 100 *Searsia* species occur widely in the tropics and subtropics in continental Africa (about 90 of them are distributed mainly in South Africa) whereas three species (*S. paniculata* (Wall. Ex G.Don), *S. parviflora* (Roxb.) F.A. Barkley, and *S. mysorensis* (G.Don) Moffett) are restricted to eastern Asia (eastern Himalayas, southern India and Sri Lanka) (Coates Palgrave 2002, Moffett 2007, Yang *et al.* 2016). This disjunction was interpreted by Yang *et al.* (2016) based on the results of phylogenetic analyses of nuclear (*ETS* and *ITS*) and chloroplast (*trnL-F* and *ndhF*) sequences. According to their results (1) the Asian taxa of *Searsia* form a monophyletic lineage; (2) the divergence time of the genus *Searsia* between eastern Asia and Africa is dated to 23.36 Ma; (3) expansion of the *Searsia* lineage between Africa and Asia most likely happened in the late Oligocene to early Miocene via Gomphotherium landbridge. This landbridge was formed as a result of the tectonic collision between the Arabian plate and the Eurasia closing the Tethys Sea and connecting Africa and western Asia (van Hinsbergen *et al.* 2009). These paleotectonic changes resulted in overland migration between Africa and Asia via the expanded tropical forests associated with the Miocene warming trend (Zhou *et al.* 2012). Different scientists, e.g. Zhou *et al.* (2012), Yang *et al.* (2016), stressed that, similar to *Searsia*, multiple angiosperm taxa (e.g. palaeotropical families Annonaceae, Burseraceae, Malpighiaceae, Meliaceae and others) exhibit Afro-Asian disjunctive distributions which could have arisen from the same paleogeographic events (Africa–Arabia–Eurasia collision and formation of Gomphotherium landbridge). These interesting observations by botanists can be an important contribution elucidating our recent data on the links between eriophyoid faunas of Asian and African angiosperms (Chetverikov & Craemer 2017; Chetverikov *et al.* 2017a, 2018). Along with palms and tropical arboreal dicotyledons mentioned by Chetverikov *et al.* (2018), plants of the genus *Searsia* represent a perspective model for reconstruction of the history of host-plant associations of

5. These structures were observed only in specimens which were kept in “sorbitol fluid” before slide-mounting; in the specimens mounted after about five months in 96% ethanol these structures were not observed, possibly dissolved. Similar subcuticular spots have been recently described in mites of the genera *Pseudotagmus* Chetverikov *et al.* 2017a and *Tumescoptella* Chetverikov *et al.* 2018 which were similar to *S. searsius* n. sp. heavily covered with wax. It is possible that such structures could be also found in *S. karoensis* n. sp. (and other eriophyoids which were reported to produce wax) if the mites are slide-mounted live or after preserving in isopropanol instead of ethanol.

Eriophyoidea. Further collections of eriophyoid mites from *Searsia* in southern Africa and eastern Asia are of special interest because it may result in new findings of sierraphytoptines similar to African genus *Solenocristus* n. g. and Asian genera *Solenoplatilobus* Chetverikov & Craemer and *Neopropilus* Huang which in turn would be an important step in our attempts to understand the evolution of phytoptids on angiosperms.

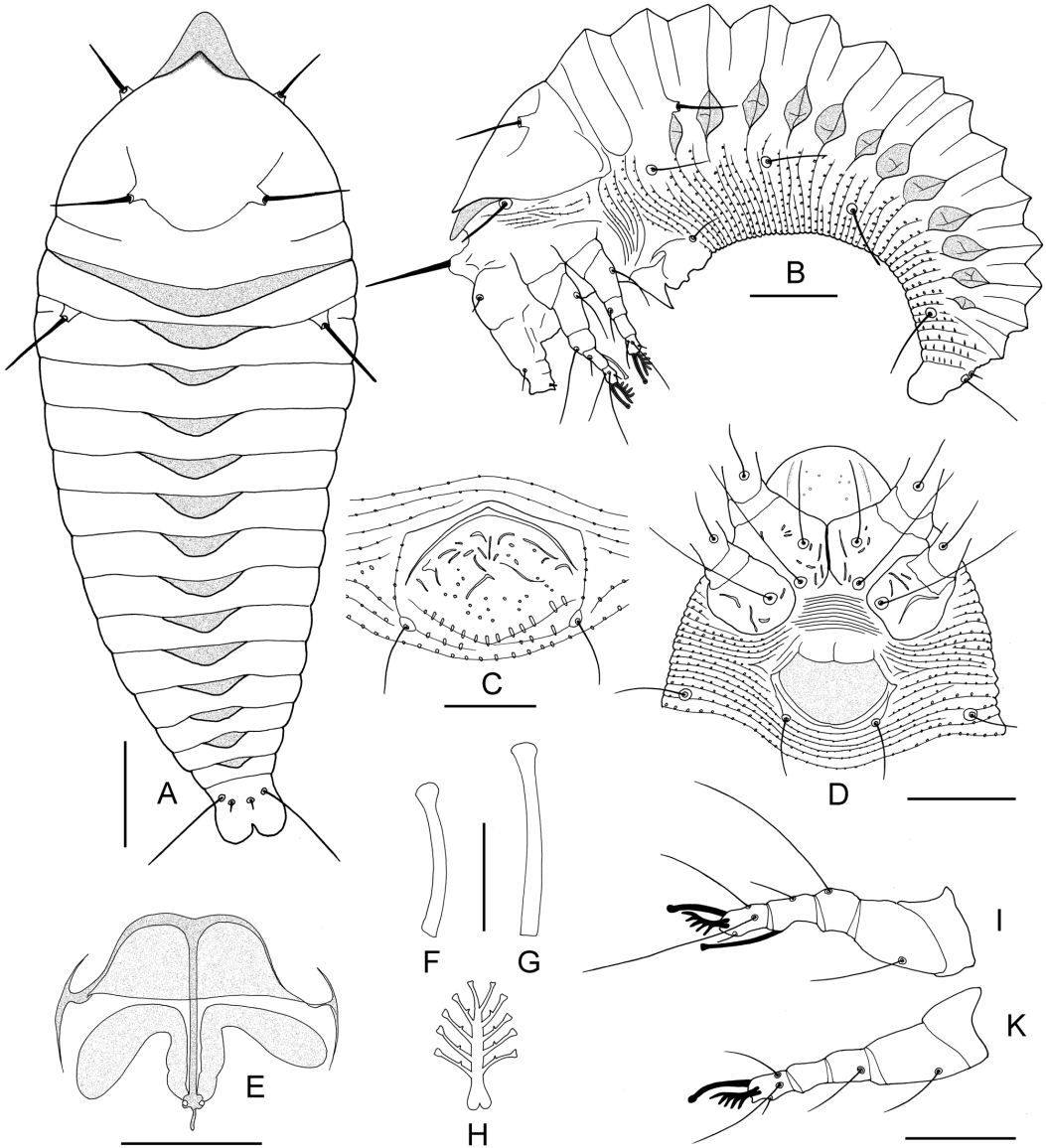


FIGURE 6. Drawings of *Solenocristus searsius* n. sp. (based on PC LM). All drawings except Fig. 6C are of females. A—dorsal view of entire mite; B—lateral view of entire mite; C—male external genitalia; D—coxigenital area; E—internal genitalia; F—tarsal solenidion I; G—tarsal solenidion II; H—empodium I; I—leg I; K—leg II. Scale bar: A,B,D = 20 µm; C,E,I,K = 10 µm; F,G,H = 5 µm.



FIGURE 7. DIC LM images of *Solenocristus searsius* n. sp. (females). A—dorsal view of entire mite, B—prodorsal shield and anterior part of opisthosoma, C—internal genitalia with putative sperm cells (white arrows) within spermathecae, D—lateral view of entire mite. Scale bar: A,B = 20 μ m; C = 10 μ m; D = 40 μ m.

Relation to the host. Vagrant on hairy young stems and leaf petioles, causing no visible damage.

Type locality. South Africa, Western Cape, about 5km West of Kleinmond, Lower Palmiet River, road side, 34°19'42.2"S 18°58'47.1"E.

Type material. Holotype female in slide #E4355, 14 paratypes on 12 slides, collected 5 November 2016 in South Africa, Western Cape, 34°19'42.2"S 18°58'47.1"E, coll. C. Craemer, P.E. Chetverikov and S. Nesor. Holotype and some paratypes are deposited in South African National

Collection of Arachnida (NCA)—Acari at ARC-PPRI, Pretoria, some paratypes deposited in Acarological collection in ZIN RAS.

Etymology. The species epithet “*searsius*”, gender masculine, is an Latin adjective derived from the generic name of the host plant (*Searsia*).

Differential diagnosis. This new species is very similar to above described *Solenocristus karoensis* n. sp. The two species can be easily separated based on the characters listed in Table 1. Additionally, these two species inhabit different host plants (*Schotia afra* vs *Searsia lucida*).

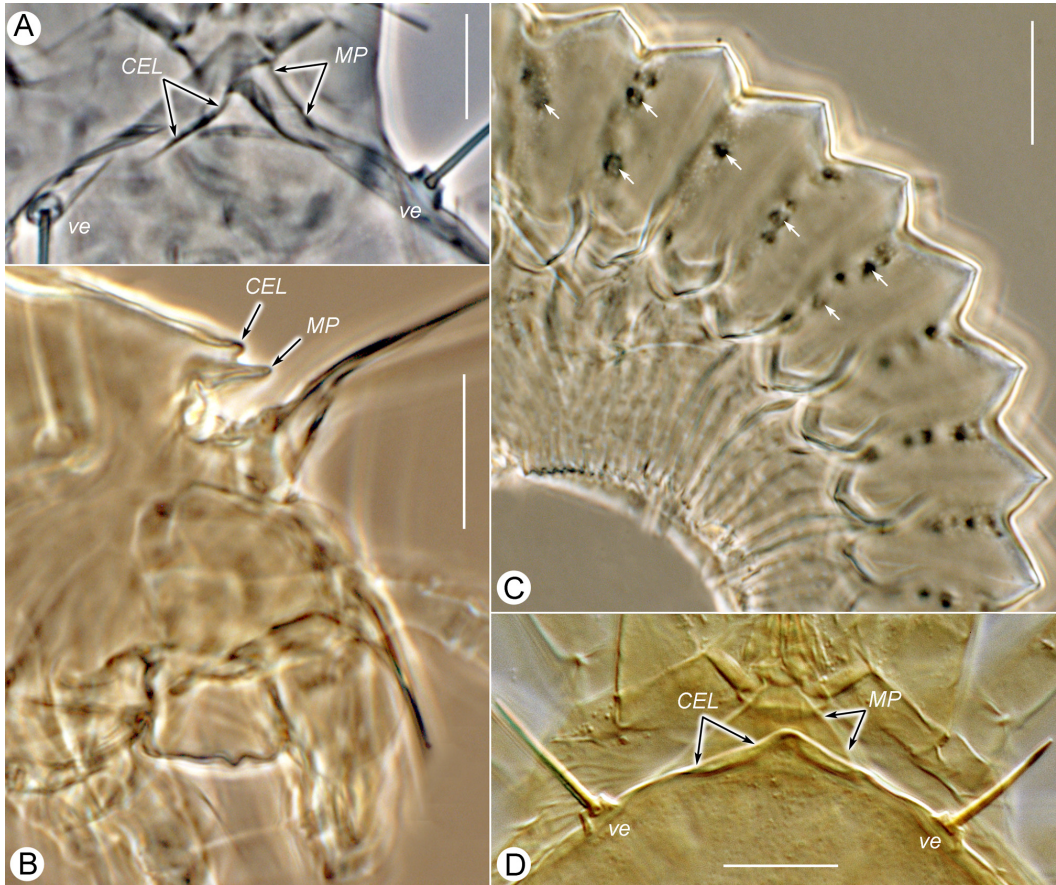


FIGURE 8. PC LM (A,B,C) and DIC LM (D) images of *Solenocristus searsius* n. sp. (females) showing topography of anterior extension of prodorsal shield (A,B,D) and putative subcuticular wax-producing structures (C, white arrows). Notations: *CEL*—central elevation of frontal lobe; *MP*—marginal plate of frontal lobe. Scale bars: A,D = 10 μ m, B,C = 20 μ m.

LT-SEM observations on *Solenocristus searsius* n. sp. (n=10)—Figs. 9, 10, 11, 12.

The main differences between the mites observed under LT-SEM and those investigated with the aid of light microscopy are in the shape and topography of prodorsal shield and opisthosomal annuli. In our opinion, these differences appeared mainly as a result of the artificial flattening of the mites during slide-mounting.

Topography of anterior part of prodorsal shield. Anteriorly, prodorsal shield forms a delicate rounded acute-angled subtriangular plate-shaped structure (corresponds to the “marginal plate” in

the description above) protruding above the basal gnathosoma. This plate is ventrodistal continuation of the cuticle situated below the subtriangular anterior ledge (corresponds to the “central elevation” in the description above). The ledge is formed by two well-developed converging ridges representing anterolateral margin of prodorsal shield. In lateral view of one specimen the ledge seems to be separated from the plate, but this could not be ascertained in the other SEM images and might be an artifact.

TABLE 1. Morphological differences between females of *Solenocristus karoensis* n. sp. and *S. searsius* n. sp.

Characters	Species	
	<i>Solenocristus karoensis</i> n. sp.	<i>S. searsius</i> n. sp.
Cleft between rear prodorsal margin and first opisthosomal dorsal annulus in laterally oriented specimens	Distinct	Posterior shield margin indistinct so that no distinct border between prodorsal shield and first dorsal opisthosomal annulus observed
Medial ridge and thickenings of dorsal opisthosomal annuli	Each dorsal annulus (except last 5–6 annuli) with small medial rhomboid thickening slightly protruding above next annulus; last 5–6 annuli with narrow translucent plate overlapping next annulus	Each dorsal annulus with translucent subtriangular rounded medial plate overlapping next annulus; medial plate of first dorsal annulus as wide as body, other plates are notably narrower
Lateral opisthosomal ridges	Weak	Distinct
Length of palps	48–55	34–39
Length of outer infracapitular stylets	32–37	21–25
Number of empodial rays	7–8	5
Number of dorsal annuli	21–23	13–15

Ornamentation and setation of prodorsal shield. Prodorsal shield is covered with roughly structured wax. In contrast with the seemingly smooth prodorsal shield observed with LM, LT-SEM revealed several distinct depressions and raised areas between and around tubercles of *sc*. The area between *sc* is raised and rounded posteriorly (this creates the artificial arc-shaped fold between tubercles of *sc* under LM, observed in Fig. 7A,B). Three shallow rounded depressions in a row are present between and slightly forward to setae *sc* anterior to the raised central area. Two elongate deeper depressions situated along the ridge-shaped antero-lateral shield margin followed more posteriorly with two depressions on the outer side of setae *sc*. One short partial annulus is visible on the latero-posterior corners of the shield. Setae *ve* and *sc* are directed up and diverging anteriorly, less diverging than in flattened slide-mounted specimens.

Gnathosoma is without obvious ornamentation except for tiny conical protuberance on the lateral surface of each palp slightly posterior to the level of palp setae *d*; this protuberance possibly marks the border between the palptibia and the palp trochantero-femoro-genu. Cheliceral retainer absent, details of the interlocking apparatus (*sensu* Chetverikov & Craemer 2015) were not observable. Seta *ep* is situated right next to the medial margin of the palpcoxa which forms a rounded flap pressed against the basal part of the chelicerae. Suboral plate with some microtubercles and a faint cuticular ridge on each side.

Legs. Segments with tiny spines on mostly the distal margins of tibiae and genua. Seta *u'* I and II is broadly angled, with small curved knob-like protuberance next to it, this protuberance might be homologous to the “ventral leaf-like process of tarsus” discussed and illustrated by Chetverikov *et*

al. (2013 fig. 3 colored violet; p. 26); genual seta *l''* of leg II is clearly displaced laterally to the antiaxial side of and close to the basal margin of the genu. Empodia 5-rayed.

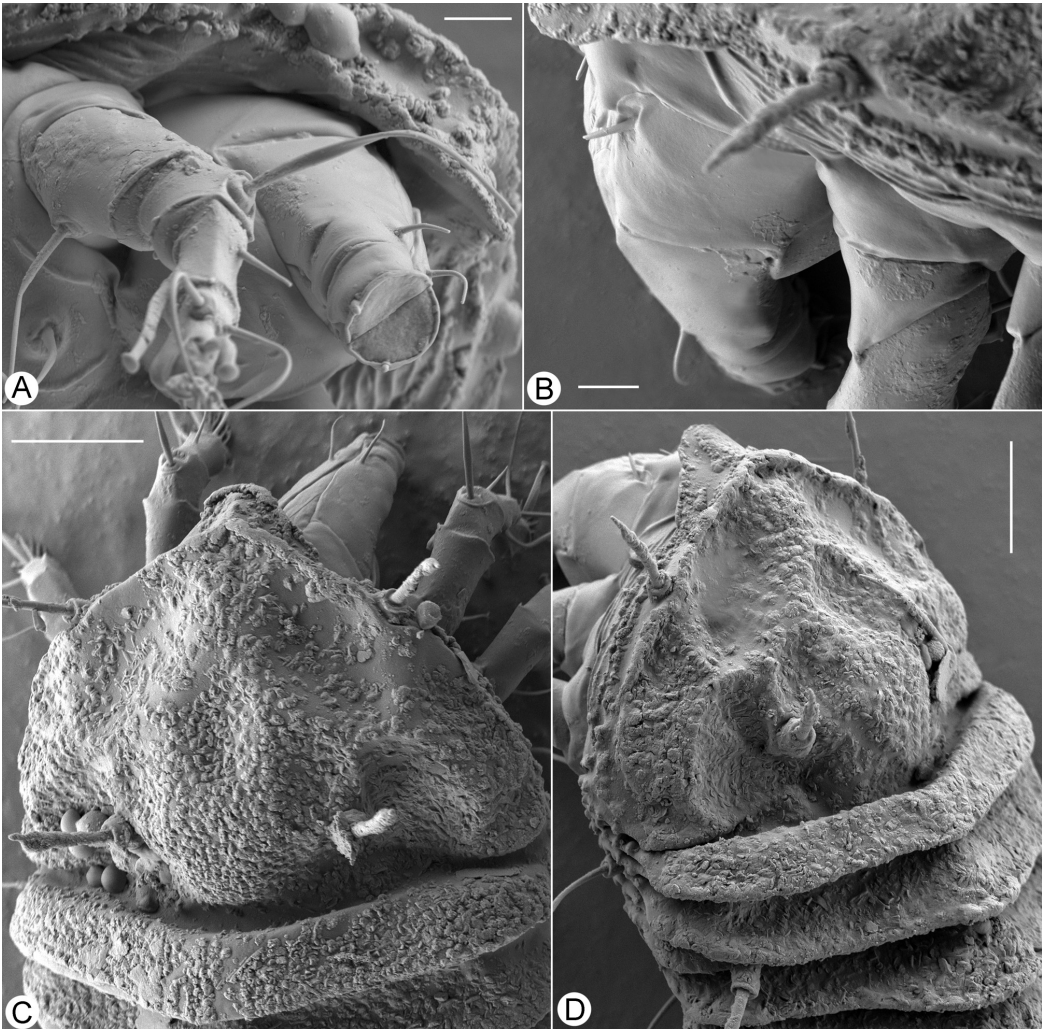


FIGURE 9. LT-SEM images showing gnathosoma (A, B) and prodorsal shield and anterior dorsal annuli (C, D) of *Solenocristus searsius* **n. sp.** Scale bars: A = 4 µm; B = 3 µm; C,D = 10 µm.

External genitalia. Genital flap smooth, with shallow central notch in the rear margin; pregenital plate (*sensu* Flechtmann *et al.* 2016) similar to that in *S. karoensis* **n. sp.**, consisting broadly of two cell like areas and a medial ridge separating them.

Opisthosoma. Dorsally opisthosoma is entirely covered with an uneven rough wax layer similar to that on prodorsal shield; no wax on the ventral body surface. SEM indicates that microtubercles on the ventral annuli are pointed, slightly elongated and situated on the rear annuli margins, microtubercles on the telosomal annuli are more elongated and rib-like. Pretelosomal dorsal annuli extend above the body surface, broadly overlapping each other medially and laterally; overlapping parts of dorsal annuli form a distinct middorsal ridge (represented by “translucent medial plates” as interpreted in the species description above) and one lateral ridge on each side on the border between the dorsal and ventral annuli. The first entire dorsal annulus behind the prodorsal shield is more or

less the same width throughout causing this annulus to be interpreted as “medial plate of first dorsal annulus as wide as body” in the description above. The middorsal ridge is of approximately constant width along entire body. Telosomal annuli are non-differentiated dorsoventrally, narrow, and bearing elongate sparse microtubercles; anterior most telosomal annulus dorsally fused with the preceding broad dorsal pretelosomal annulus.

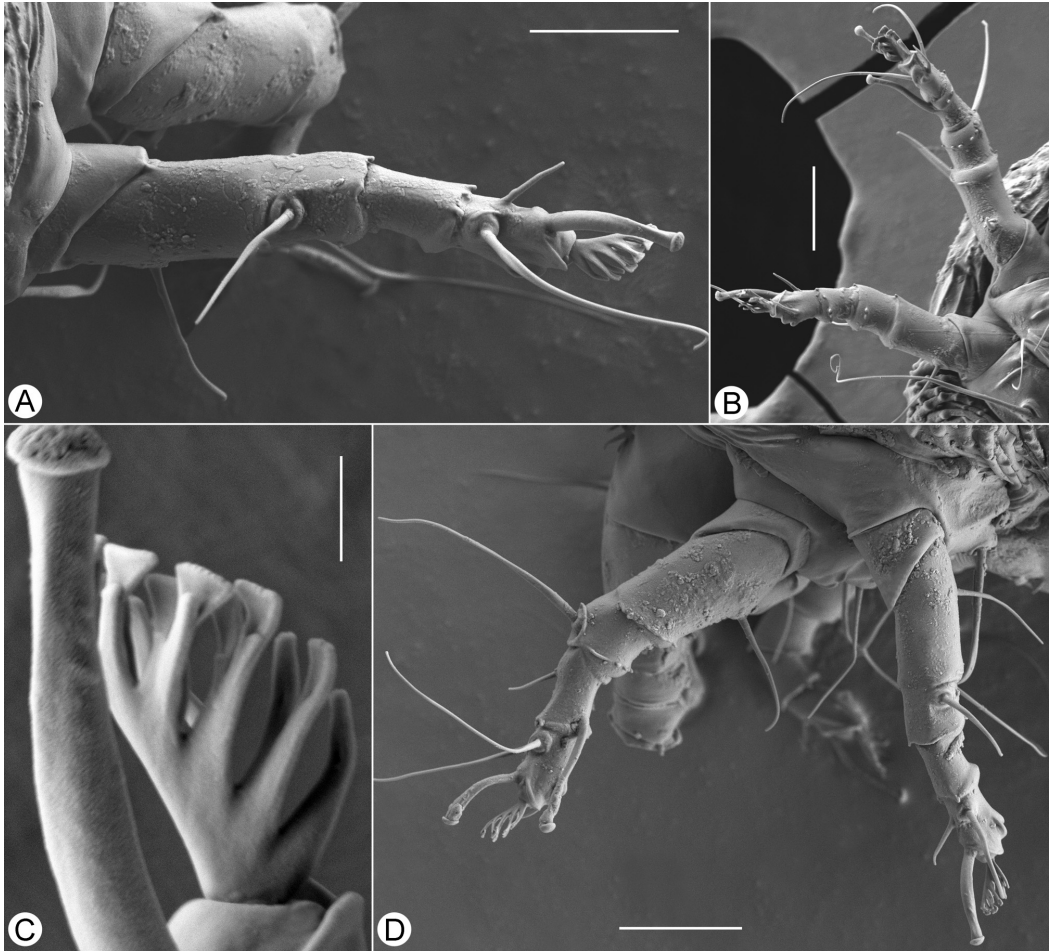


FIGURE 10. LT-SEM images showing legs and terminal tarsal appendages of *Solenocristus searsius* n. sp. A—leg II; B—ventral view of legs I and II; C—empodium II and tarsal solenidion II; D—dorsal view of legs I and II. Scale bars: A,D = 10 μm; B = 3 μm; C = 1 μm.

Updated key to world genera of Sierraphytoptini Keifer 1944

- 1. Tibial solenidion ϕ I present 2
- Tibial solenidion ϕ I absent 6
- 2. Prodorsal shield setae *sc* and opisthosomal setae *d* and *e* present 3
- Prodorsal shield setae *sc* and opisthosomal setae *d* and *e* absent 5
- 3. Dorsal opisthosomal annuli forming distinct medial ridge and two more or less developed lateral ridges; frontal lobe thick and triangular *Solenocristus* n. g.
- Dorsal opisthosoma without longitudinal ridges, frontal lobe absent or it is thin, broad and rounded 4

4. Prodorsal shield with thin broad frontal lobe covering basal chelicerae; tubercles of *ve* displaced below the anterior prodorsal shield margin. *Solenoplatilobus* Chetverikov & Craemer 2016
- Frontal lobe of prodorsal shield absent; tubercles of *ve* not displaced below the anterior prodorsal shield margin. *Austracus* Keifer 1944
5. Opisthosomal setae *c2* present *Neoprothrix* (Reis & Navia 2014 in Reis *et al.* 2014)
- Opisthosomal setae *c2* absent *Neopropilus* Huang 1992
6. Opisthosoma with two lateral longitudinal ridges and concave furrow between them; rear prodorsal shield margin distinct; tubercles of *sc* situated in deep indentation of posterior edge of prodorsal shield *Sierraphytoptus* Keifer 1939
- Opisthosoma without ridges and furrows; rear prodorsal shield margin indistinct; tubercles of *sc* situated almost in middle of prodorsal shield. Live on rosaceous plants of genera *Fragaria* and *Potentilla* *Fragariocoptes* Roivainen 1951

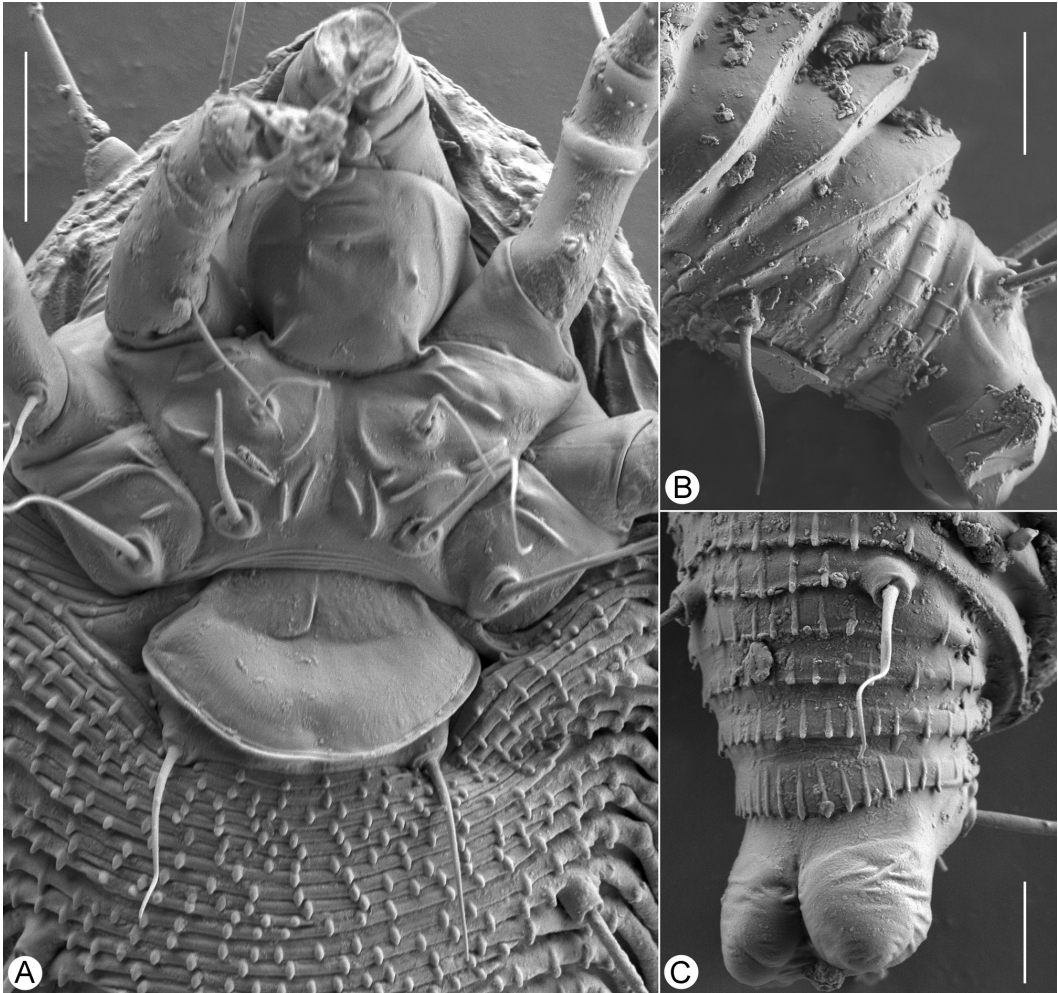


FIGURE 11. LT-SEM images showing coxigenital area (A) and telosoma (B—lateral view, C—ventral view) of *Solenocristus searsius* n. sp. Scale bars: A,B = 10 µm; C = 5 µm.

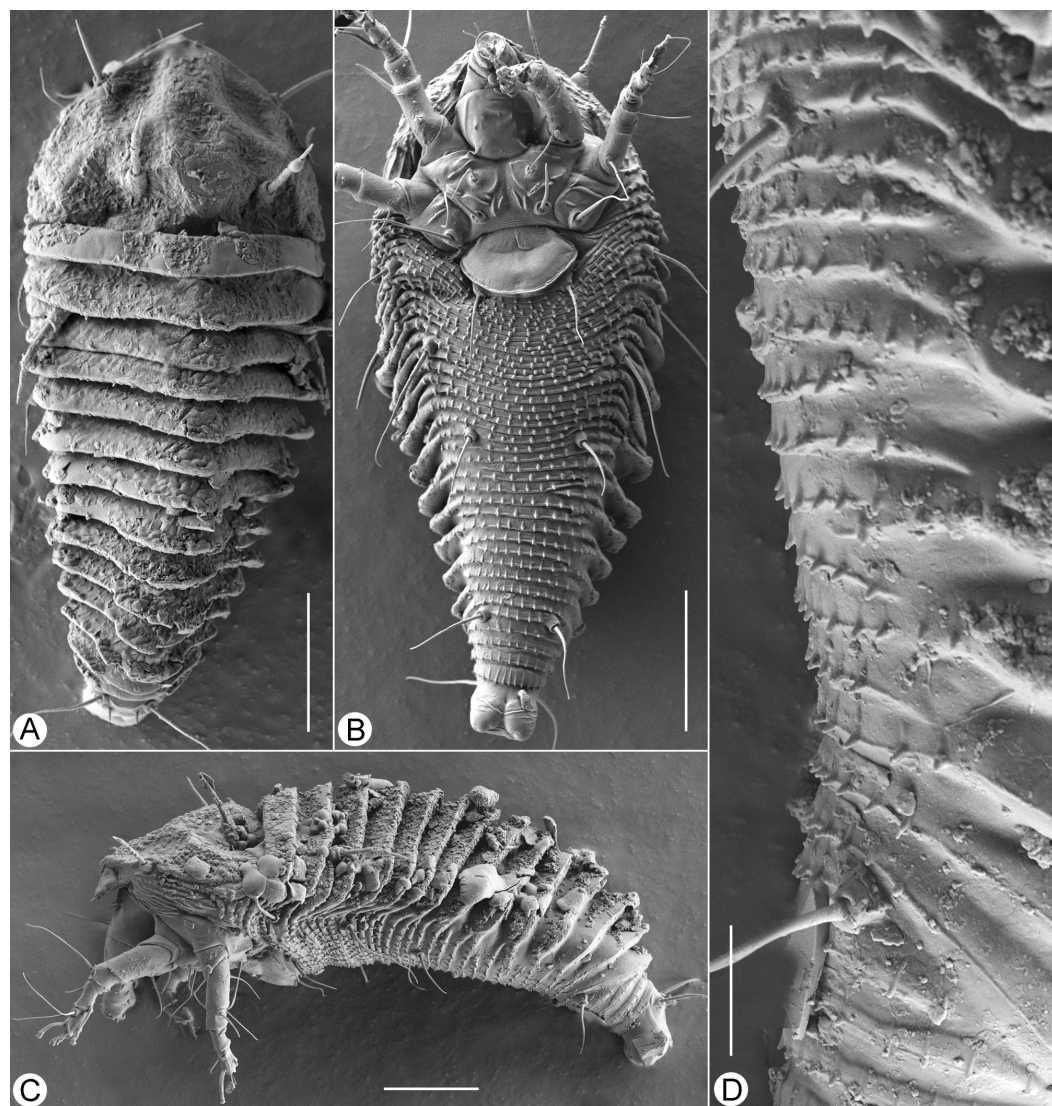


FIGURE 12. LT-SEM images showing body topography of *Solenocristus searsius* n. sp. A—dorsal view of entire mite; B—ventral view of entire mite; C—lateral view of entire mite; D—fragment of lateral cuticle showing lateral opisthosomal ridge and border between ventral and dorsal annuli. Scale bars: A,B,C = 20 μ m; D = 3 μ m.

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