

# New pseudotagmic genus of acaricaline mites (Eriophyidae, Acaricalini) from a South African palm *Hyphaene coriacea* and remarks on lateral opisthosomal spines and morphology of deutogyne in Eriophyoidea

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## Abstract

A new genus, *Tumescoptella* **n. g.**, with two new sympatric species *Tumescoptella aculeata* **n. sp.** and *T. rotundiscuta* **n. sp.**, was found on the indigenous South African palm *Hyphaene coriacea*, Lala palm. Both species are described and illustrated with the aid of conventional light microscopy, confocal laser scanning microscopy and low temperature scanning electron microscopy. Additionally, a new record of *Tumescoptes dicrus* Meyer collected from *Phoenix reclinata* (Arecaceae), near Kirstenbosch Gardens (Cape Town, South Africa), is reported. Morphologically the *Tumescoptella* **n. g.** is most similar to *Tumescoptes* Keifer, but possesses a more reduced chaetome and more derived pseudotagmosis. Pseudotagmosis is one type of body consolidation in vagrant eriophyoids, realized through the formation of dorsal opisthosomal plates, pseudotagmata. Along with previously described pseudotagmata (prodorsum, cervix, postprodorsum, superpostprodorsum, pretelosoma, and telosoma), a new term, anteroscutum, is proposed for the complex pseudotagma formed as a fusion of the three anterior pseudotagmata (prodorsum+cervix+postprodorsum) in several phyllocoptine mites from palms. An anteroscutum is present in monotypic *Scolocenus* Keifer from coconut and in the new genus *Tumescoptella* **n. g.** Protogyne females of *Tumescoptella* **n. g.** have uncommonly large lateral opisthosomal spines. Along with tiny spinules, triangular cuticular plates, band-shaped processes, and areas of thickened cuticle, the lateral spines belong to a common group of serial derivatives of dorsal opisthosomal annuli. We give a brief review on variation of spine-like structures across taxa of Eriophyoidea and their morpho-functional evaluation. Contrary to protogyne females, deutogyne females of *T. aculeata* **n. sp.** lack lateral spines, and they possess a smoother topography of the anteroscutum. Morphological similarity of these deutogyne with mites of the less transformed genus *Tumescoptes* is in accordance with a previous hypothesis on the possible correspondence of deutogyne morphology to that of an ancestral taxon. Two hypotheses on the origin of the presumably monophyletic group of *Tumescoptes*-like phyllocoptines (TP) from palms, comprising genera *Scolocenus*, *Tumescoptella* **n. g.**, *Tumescoptes*, and *Pseudotagmus*, are proposed based on morphological similarity with two groups of eriophyoid genera: (a) pseudotagmic genera associated

with aboriginal Asian dicotyledonous tropical trees, and (b) South American phyllocoptines from arecoid palms.

**Key words:** pseudotagma, palm mites, wax, arthropod structure, LT-SEM, CLSM, Arecaceae

## Introduction

The Arecaceae (palms) is an economically important group of predominantly arboreal or shrub-like plants with large evergreen leaves widely distributed throughout moist tropical and subtropical regions worldwide (Nayar 2017). It is an ancient monocotyledonous clade with a rich fossil record dating back to the Late Cretaceous (about 90 Mya), although molecular dating analyses suggest that the lineage is substantially older (Baker *et al.* 2009). Molecular biogeography indicates that five palm subfamilies (Calamoideae, Nypoideae, Coryphoideae, Ceroxyloideae, Arecoideae) started diverging during the mid-Cretaceous period about 100 Mya at northern latitudes within Laurasian regions (Couvreur *et al.* 2011; Faurby *et al.* 2016). According to the data by botanists, palms appear to have undergone an early period of adaptive radiation so that by about 60–50 Mya, many of the modern, specialized genera of palms appeared and became widespread and common, much more widespread than their range today (Baker & Couvreur 2013; Meerow *et al.* 2015).

According to our estimates, the large complex of described eriophyoid mite species associated with palms comprises 81 species from 38 genera of three families: Phytoptidae (6 genera/20 species), Eriophyidae (27/56) and Diptilomiopidae (5/5). Several palm inhabiting phytoptid and eriophyid species of the genera *Aceria*, *Acathrix*, *Mackiella*, *Colomerus*, and *Retracrus* have been listed as economically important, although only *Aceria guerreronis* Keifer and *Retracrus* spp. are considered to be serious pests of palms (Lindquist & Amrine 1996; Moore & Howard 1996). Due to intensive studies in Brazil (Navia *et al.* 2007, Reis *et al.* 2014 and papers cited) and the high diversity of Arecaceae in that region, the eriophyoid fauna of South American palms is best known. Numerous new findings of eriophyoids could be expected in the future from the poorly explored regions with rich palm diversity, e.g. from equatorial Africa, Madagascar, South Asia, and Oceania.

Southern Africa is rich in endemic flora, but possibly due to very dry and hot summers in most areas, only seven indigenous palm species occur in this region: four species from subfamily Coryphoidea (*Borassus aethiopicum*, *Hyphaene coriacea*, *H. petersiana*, *Phoenix reclinata*), one from Arecoidea (*Jubaeopsis caffra*), and two from Calamoidea (*Raphia australis* and *R. farinifera*) (Coates Palgrave *et al.* 2002). Currently, six eriophyoid mite species inhabiting coryphoid palms (*Phoenix* and *Hyphaene*) are known from southern Africa: *Afrodialox dimorphopalpalis* Chetverikov & Craemer, *Borassia borassis* (Mohanasundaram), *Mackiella reclinata* Chetverikov *et al.*, *Pseudotagmus africanus* Chetverikov *et al.*, *Tumescoptes dicrus* Meyer, and *T. phoenixi* Meyer. In our previous paper (Chetverikov *et al.* 2017) we discussed the phenomenon of pseudotagmatisation in Eriophyoidea and described a genus *Pseudotagmus* characterized by unusually shaped pseudotagmata and large lateral opisthosomal spines from the indigenous southern African palm *Hyphaene coriacea*. In this paper we describe two new “spiny” phyllocoptine species of a new pseudotagmic genus *Tumescoptella* n. g. which were found on the same palm species. We also compare these bizarre mites with some other members of subfamily Phyllocoptinae Nalepa and analyze data on their host association and biogeography in order to hypothesize a possible origin of these new palm mites. Finally, we discuss the variety of spine-like opisthosomal structures across Eriophyoidea and do a morpho-functional evaluation.

## Material and Methods

**Collection and morphological measurements.** Mite specimens were studied using different light microscopy (LM) techniques (phase contrast (PC LM), differential interference contrast (DIC LM), confocal laser scanning microscopy (CLSM)), and low-temperature scanning electron microscopy (LT-SEM). The mites were collected in South Africa using a minuten pin while being examined under a stereo microscope. All other equipment and steps (preserving mites in a drop of “sorbitol fluid”, transferring the samples to Russia, recovering mites from “sorbitol fluid” and slide-mounting) were in accordance with Chetverikov & Craemer (2017) except that for CLSM investigation some mites were mounted in Hoyer’s medium (Amrine & Manson 1996).

Females and males of the new species are described based on DIC LM, PC LM and CLSM observations of slide-mounted specimens. All measurements in the descriptions are given in micrometers ( $\mu\text{m}$ ), and are lengths except when stated otherwise. In the description of protogyne females, the measurements 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 deutogynes, only ranges are given. Terminology of eriophyoid morphology and classification 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 (2016).

**CLSM technique.** CLSM acquisition was carried out using a Spectral confocal & multiphoton system Leica TCS SP2 with objective 63x N.A. 1.4-0.60 Oil IBL HCX PL APO at an excitation wavelength of 405 nm (blue laser) at 12% intensity. Acquisition resolution was 1024x1024 pixels, level of gain 430–560, and zoom range of 1.1–4.0 times. Stacks of 18 to 42 optical slices were recorded digitally from each of the 12 studied specimens of *Tumescoptella* mites. The obtained CLSM stacks were processed using Amira®5.3.2 software. The CLSM images were recorded using the “Snapshot” command in Amira®; they are Volume Rendering images obtained via a combination of Voltex and Orthoslice modules of Amira® with different transparency adjustments.

**LT-SEM technique.** For LT-SEM, the live mites were placed on double-sided carbon tape with the aid of a minute pin tool under a stereo-microscope. Thereafter the various pieces of tape with mites were pasted onto sample holders, plunge frozen, and stored in liquid nitrogen for two to three months. Later, the holders with mounted specimens were transferred under vacuum with the aid of a Leica EM VCT-100 shuttle (Leica Microsystems, Vienna, Austria) to the Leica EM ACE 600 coater. The samples were then etched for 40 minutes at  $-80\text{ }^{\circ}\text{C}$  and some samples were coated with platinum and others in e-beam mode with iridium. The samples were then transferred to a Zeiss Crossbeam 540 FEG SEM (Zeiss, Oberkochen, Germany) with the shuttle system and studied with the stage cooled to  $-160\text{ }^{\circ}\text{C}$ . SEM allows morphological characters to be readily observed that are invisible or indistinct in slide-mounted specimens. Moreover, slide-mounting causes some structures of the mites to become severely distorted, so that their real shapes could be detected only under SEM. Therefore, we report on our SEM observations of the new species in a separate section below the formal descriptions based on LM and CLSM investigation of slide-mounted specimens.

**Comparative material.** Females and males of *Tumescoptes dicrus*<sup>1</sup> Meyer 1992 collected from upper leaf surface of planted *Phoenix reclinata* Jacq. (Arecaceae), 12 October 2016, SOUTH AFRICA, Cape Town, Kirstenbosch Gardens, left bank of Liesbeek River, 33°59'11.7"S 18°26'04.0"E, coll. P. Chetverikov, slides #E4277 and #E4276 kept in Acarology collection of ZIN RAS. Slide-mounted mites of different eriophyoid genera from the Acarology collection of Zoological Institute of Russian Academy of Science and South African National Collection of

1. New distribution record

Arachnida—Mites at ARC-PPRI, images from original descriptions, catalogs (Baker *et al.* 1996, Chandrapatya *et al.* 2017) and a generic key by Amrine *et al.* (2003) were used for comparisons between taxa and illustrating the variation of opisthosomal spine-like structures among supraspecific taxa of Eriophyoidea.

## Results

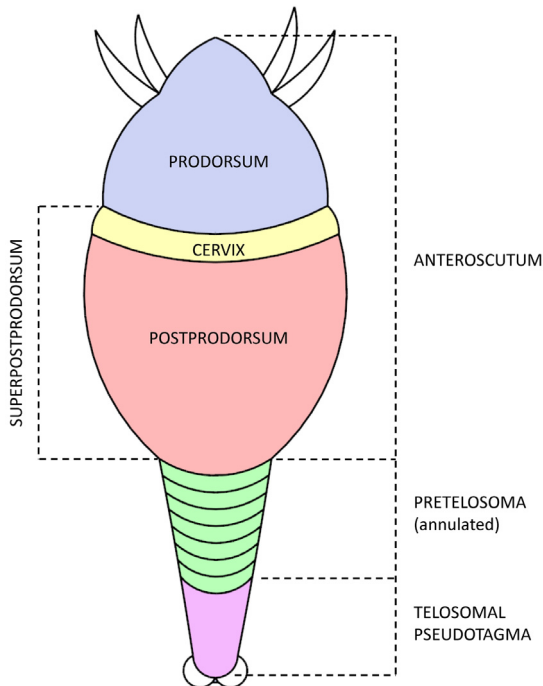
### Family Eriophyidae Nalepa

#### Subfamily Phyllooptinae Nalepa

#### Tribe Acaricalini Amrine & Stasny

#### Genus *Tumescoptella* n. g.

**Diagnosis.** Body flattened dorso-ventrally, and dorsally subdivided into three distinct pseudotagmata: anteroscutum (formed by fused pseudotagmata prodorsum, cervix and postprodorsum), pretelosoma and telosoma; two of them (anteroscutum and telosoma) plate-like, pretelosoma annulate (Fig. 1). In protogynes, anteroscutum and pretelosoma with large lateral spines; anteroscutum in protogynes with symmetrically distributed rounded spots of subcuticular thickening. Scapular setae *sc* situated anterior to rear shield margin, directed convergently mediad (in slide-mounted specimens) or up (under SEM). Prodorsal shield frontal lobe extending over gnathosoma, completely hiding palps. Empodia I & II divided. Gnathosomal seta *d* bifurcate; leg seta *u'* angled; opisthosomal setae *d*, *e*, *h1* and leg setae *bv* I, *bv* II, *l''* II and *1b* absent. Dorsal cuticle with numerous tiny rounded indentations or putative micropores, and with intensive wax secretion.



**FIGURE 1.** Pseudotagmata in *Tumescoptella* n. g. Terminology and colorization of pseudotagmata (except *anteroscutum*, proposed in this paper) correspond to those from Chetverikov *et al.* 2017 (fig. 15 & 16).

**Differential diagnosis.** Among currently described genera of Eriophyoidea, the new palm-inhabiting genus is closest to *Tumescoptes* Keifer, *Scolocenus* Keifer, and *Pseudotagmus* Chetverikov *et al.*, which also live on palms. The new genus and these three genera lack leg setae *bv* I & II, and opisthosomal setae *d* and *h1*. They also have well developed dorsal opisthosomal plates (pseudotagmata), but the plates have different shapes and locations (Tab. 1). Apart from this, these genera differ in: (a) direction of *sc*; (b) shape of pedipalp seta *d*, empodia, and tubercles of *sc*; and (c) presence/absence of setae *l'*, *l''* II, *1b*, *e*, lateral opisthosomal spines and a groove anterior to *sc* (Tab. 1).

**TABLE 1.** Morphological differences between genera *Tumescoptella* n. g., *Scolocenus*, *Tumescoptes* and *Pseudotagmus*.

Characters	Genera			
	<i>Tumescoptella</i> n. g.	<i>Scolocenus</i>	<i>Tumescoptes</i>	<i>Pseudotagmus</i>
Dorsal pseudotagmata	plate-like anteroscutum and telosoma, annulated pretelosoma	plate-like anteroscutum and telosoma, annulated pretelosoma	plate-like prodorsum and incompletely developed postprodorsum, annulated cervix, pretelosoma and telosoma	plate-like prodorsum, postprodorsum and telosoma, annulated cervix and pretelosoma
Lateral opisthosomal spines	present along entire lateral margin of body except several posterior-most pretelosomal annuli and telosoma	present only along postprodorsum (posterior half of anteroscutum)	absent	present along pretelosoma
Direction of <i>sc</i>	directed up or convergently mediad	directed up or convergently mediad	directed up or convergently mediad	directed transversely laterad
Tubercles of <i>sc</i>	common or tiny	tiny	tiny	large, directed transversely laterad
Groove anterior to tubercles of <i>sc</i>	absent	absent	absent	present
<i>l'</i>	present	present	present	absent
<i>l''</i> II	absent	present	absent	present
<i>1b</i>	absent	absent	present	absent
<i>e</i>	absent	present	absent	absent
Empodium	clearly divided, central pair of rays absent	undivided, central pair of rays present	clearly divided, central pair of rays absent	undivided, central pair of rays present
Pedipalp <i>d</i>	clearly bifurcate	?	angled, not bifurcate	angled, not bifurcate

**Type species:** *Tumescoptella aculeata* n. sp.

**Host plant and distribution.** Mites of this genus have been recorded only as vagrants on young leaves of Lala palm (*Hyphaene coriacea* Gaertn., Arecaceae) in South Africa.

**Etymology.** The generic name, *Tumescoptella*, is a combination of “Tumes” (reduced version of “*Tumescoptes*”, the name of the previously described genus which morphologically is close to the new genus), “coptes” (κόπτης, Greek)—cutter, cutting machine, slicer, and “-ella”—diminutive suffix; gender feminine.

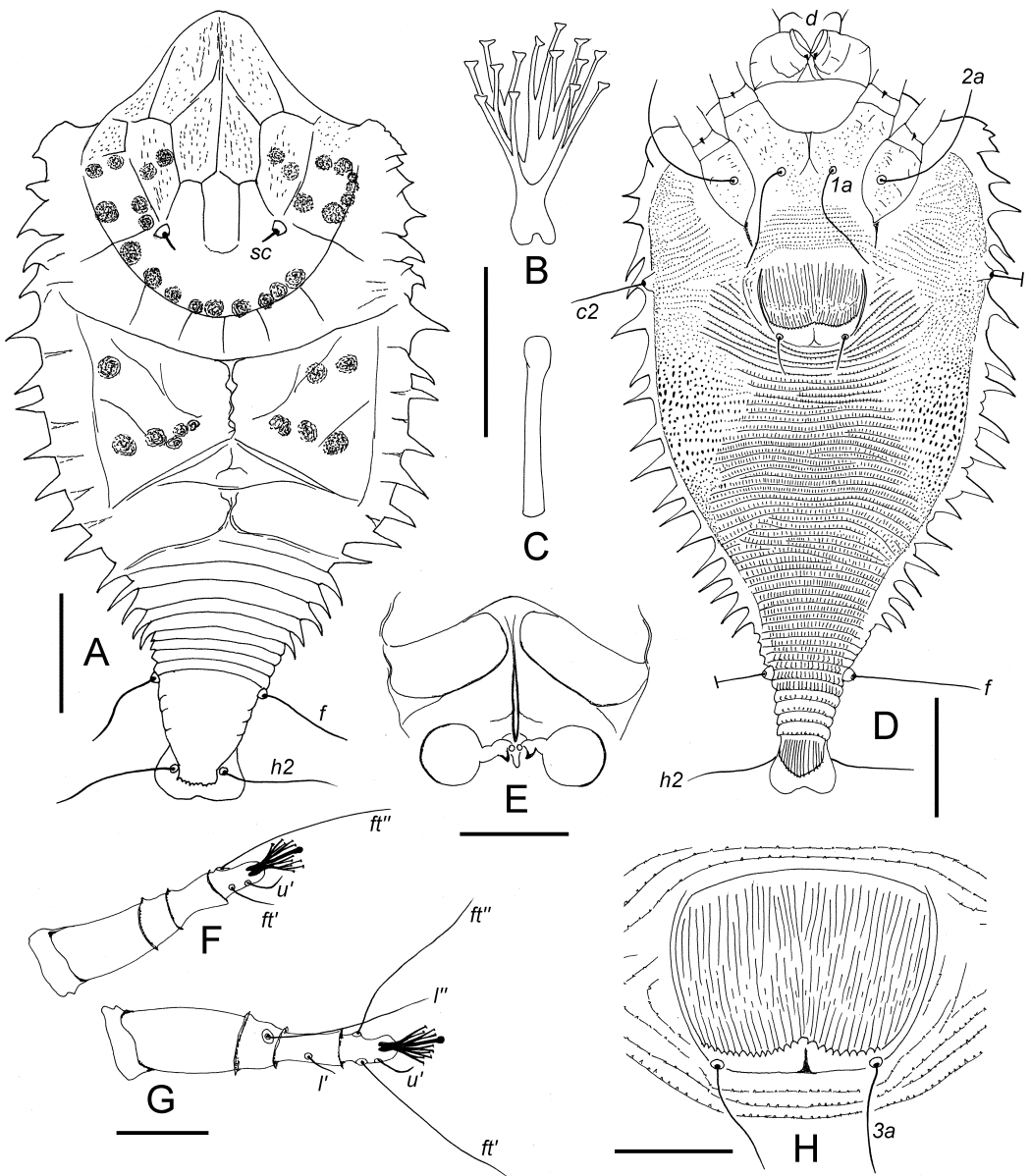
**Remark.** Etymology of the generic name *Tumescoptes* Keifer 1939 was not stated by the describer. It could be a combination of English “tumescence” or Greek “τομέας” (sector) and a Latinized Greek word “κόπτης” (coptes)—cutter.

*Tumescoptella aculeata* n. sp.—Fig. 2,3,4,5,6,10.

**PROTOGYNE FEMALE (n=11).** Body flattened dorso-ventrally, 186 (170–202), 77 (62–81) wide at the level of setae *c2*. Some parts of body covered with wax, washed off in slide-mounting process, but detectable in live specimens, and captured in SEM images (see below). **Prodorsal shield** suboval, 60 (58–63), 56 (50–59) wide; anterior extremity of prodorsal shield forms a large frontal lobe protruding over gnathosoma by 15 (12–16)  $\mu\text{m}$ ; posteriorly prodorsal shield separated from cervix by arc-shaped groove. Prodorsal shield ornamentation with several large cells separated by cuticular ridges. Prodorsal shield as well as cervix and postprodorsum with tiny, round indentations (putative micropores for wax secretion) and round spots of subcuticular thickenings (dark under LM and brightly autofluorescing under CLSM). Scapular setae *sc 3* (2–4), 19 (15–20) apart, directed up or convergently mediad. **Gnathosoma** short, directed down or obliquely down. Palps 20 (18–21); chelicerae 15 (15–17), outer infracapitular stylets 18 (15–18), oral stylet indistinct. Gnathosomal setae: seta *v 1* (0.5–1); pedipalp genual seta *d* bifurcate, basal part 5 (4–6), medial branch 5 (5–6); lateral branch 2 (2–3); pedipalp coxal seta *ep 1* (1–2); cheliceral retainer triangular-shaped, about 2–3. Suboral plate rounded, smooth in slide-mounted specimens.

**Leg I** 33 (30–34), tarsus 5 (4–5), *u'* 5 (4–6) notably curved, *ft'* 17 (16–23), *ft''* 21 (19–25), *o* 5 (4–6) knobbed; empodium 5 (5–6), in most slide-mounted specimens empodium seems to be divided into two 4–6 rayed branches, although the true empodial structure could only be determined with SEM (see below); tibia 7 (6–7), *l' 1* (1–2); genu 5 (4–5), *l''* 22 (18–24); femur 11 (11–14), *bv* absent. **Leg II** 24 (23–28), tarsus 4 (4–5), *u'* 5 (4–5) notably curved, *ft'* 4 (3–6), *ft''* 22 (18–23), *o* 5 (4–5) knobbed; empodium 5 (5–6), similar to empodium I; tibia 5 (4–5); genu 4 (4–5), *l''* absent; femur 10 (9–12), *bv* II absent. **Coxal plates** with numerous tiny microtubercles and sparse striae largely covering coxisternal plates I and II. Setae *1b* absent; *1a* 22 (20–29), 9 (9–12) apart; *2a* 35 (32–41), 32 (30–36) apart; 10 (9–11) coxigenital annuli before epigynium. Prosternal apodeme faint, deeply forked posteriorly, 10 (9–12). **External genitalia.** Genital coverflap subrectangular, bilobed posteriorly, with delicate striations, 16 (15–18), 23 (22–25) wide; setae *3a* 11 (10–14), 14 (13–16) apart; pregenital plate (*sensu* Flechtmann *et al.* 2015) absent. **Internal genitalia (n=4).** Spermatheca spherical, 4–5 in diameter; spermathecal process (*sensu* Duarte *et al.* 2016) minute, directed divergently posteriad, about 1–2; spermathecal tube short, 2–3, 1–2 wide; prespermathecal part of longitudinal bridge 14–17, postspermathecal part rudimentary; oblique apodeme (*sensu* Chetverikov *et al.* 2015) distinct and anteriorly recurved; anterior genital apodeme short subtrapezoid, half-length 14–16.

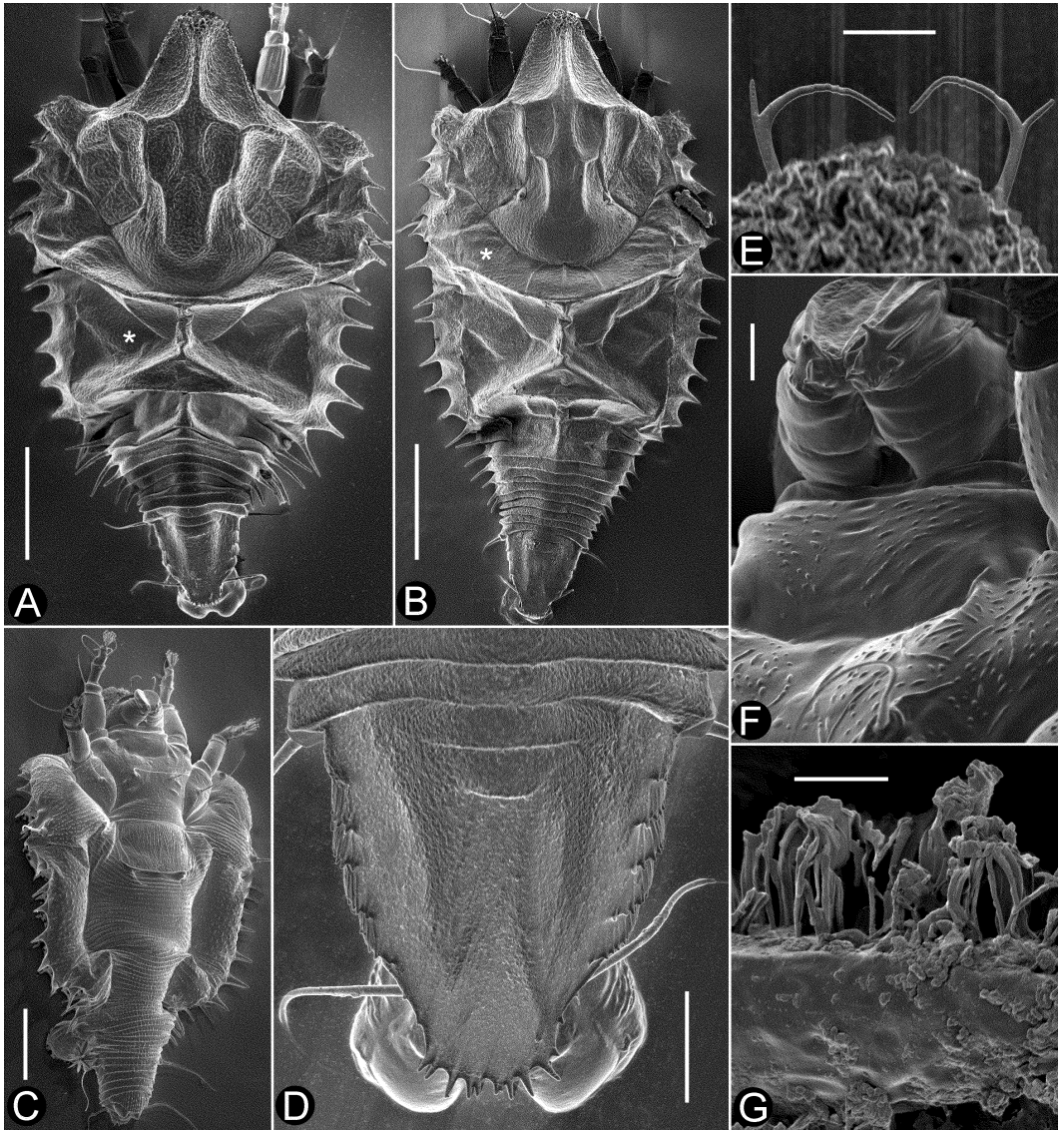
**Pseudotagmata.** Dorsally, mite body subdivided into three distinct pseudotagmata: anteroscutum (formed by fused plate-like prodorsum, cervix and postprodorsum), annulated pretelosoma and plate-like telosoma with delicate denticles or spinules on rear margin. Anteroscutum and pretelosoma with 19 (16–20) large lateral spines presumably corresponding to fused dorsal opisthosomal annuli, anterior most spine along prodorsum broader and more rounded than remainder of spines; anteroscutum with symmetrically distributed rounded spots of subcuticular thickening mainly situated along posterior margin of prodorsal shield and in lateral fields of postprodorsum. Cervix (Fig. 3B, asterisk) with 5–7 short longitudinal ridges dividing cervix into several indistinct cells. Postprodorsum (Fig. 3A, asterisk) with sinuous medial ridge followed by two diverging oblique ridges and a transverse ridge delimiting a triangular field. One shorter sinuous medial ridge and two oblique ridges forming posterior margin of anteroscutum behind triangular plate. Pretelosoma with 9 (9–11) smooth, dorsal annuli, posterior most four or five of them without lateral spines. **Opisthosoma** (herein the part of body behind prodorsum) ventrally with 41 (38–49) microtuberculate annuli between epigynium and caudal lobes. Except the posterior-most 3–4 annuli, all ventral opisthosomal annuli narrow and uniform with numerous tiny microtubercles; posterior-most 3–4 ventral annuli notably broadened and bearing less numerous rib-like microtubercles; last ventral annulus plate-shaped, with about 20 longitudinal ridges. Ventro-lateral opisthosomal cuticle at the level of postprodorsum devoid of annuli, forming wide band-like area covered with numerous round and oval microtubercles. Setae *c2* 23 (19–26), their tubercles situated on the lateral wall of the opisthosoma below lateral spines; setae *d* and *e* absent; *f* 27 (24–30); *h1* absent; *h2* 25 (23–35).



**FIGURE 2.** *Tumescoptella aculeata* n. sp. (protogyne female, drawings based on PC LM). A—dorsal view; B—empodium I; C—tarsal solenidion I; D—ventral view; E—internal genitalia; F—leg II (dorsal aspect); G—leg I (dorsal aspect); H—external genitalia. Scale bar: A, D = 25  $\mu$ m; B, C = 5  $\mu$ m; E, F, G, H = 10  $\mu$ m.

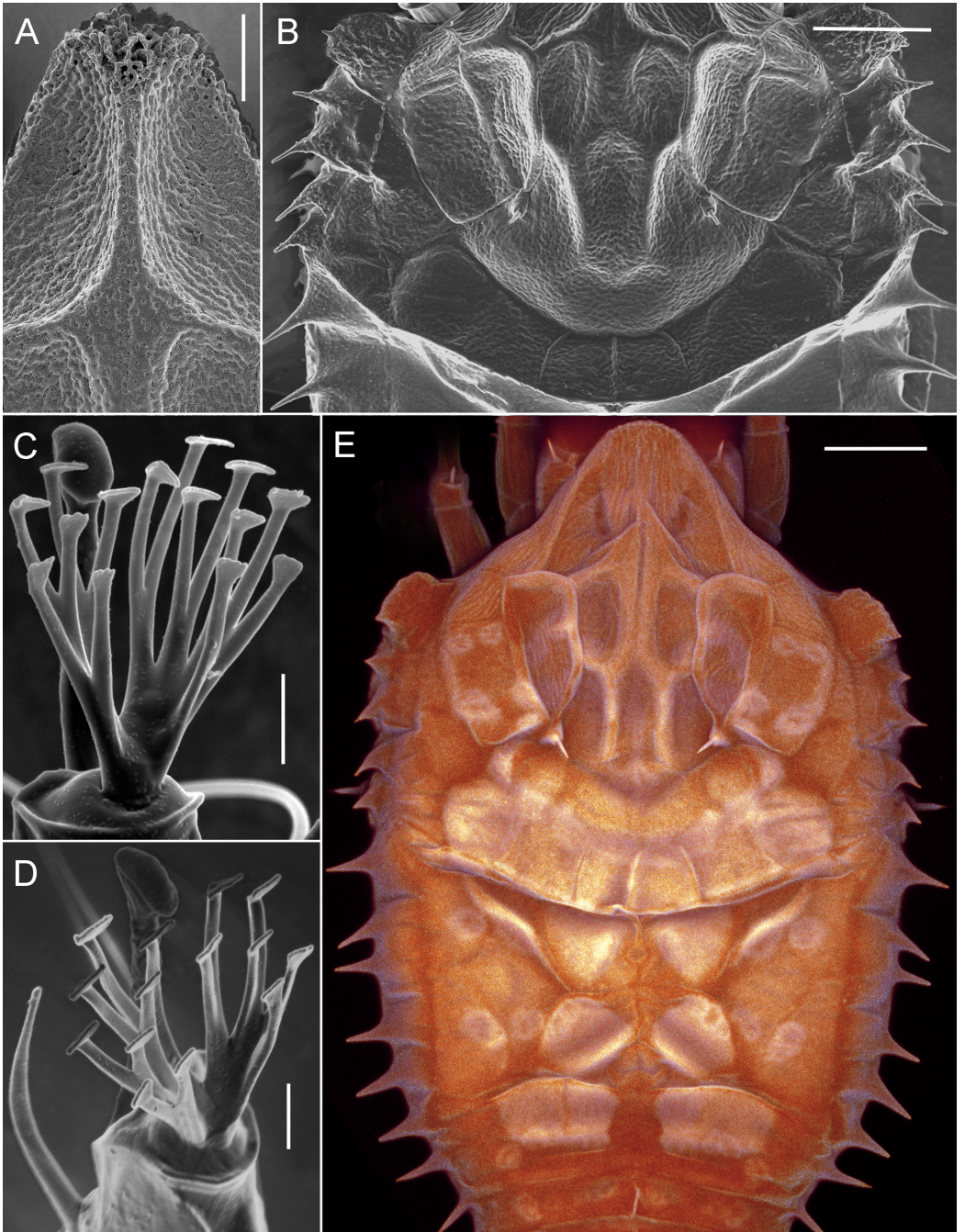
**MALE (n=6).** Most qualitative characters of males (opisthosomal pseudotagmata and their shapes and topographies; ornamentation of prodorsal shield and coxae; shape of leg appendages and directions of setae; distribution and shape of microtubercles and ridges) are similar to those of females. Only morphometric traits and descriptions of the genital area are given below. Body, 165–180, 70–74 wide at the level of seta *c2*. **Prodorsal shield** 56–60, 52–54 wide; frontal lobe 14–17. Scapular setae *sc* 2–3, 16–18 apart. **Gnathosoma.** Palps 18–20; gnathosomal setae: seta *v* 0.5–1; pedipalp genual seta *d* bifurcate, basal part 4–5, medial branch 4–5; lateral branch 1–3; pedipalp coxal seta *ep* 1–2. **Leg I** 30–33, tarsus 4–5, *u'* 5–6 curved, *ft'* 18–24, *ft''* 20–23, *w* 4–5 knobbed; empodium 4–6, divided into two 4–6 rayed branches;

tibia 5–6, *l'* 1–2; genu 4–5, *l''* 19–25; femur 10–12, *bv* absent. **Leg II** 26–29, tarsus 4–5, *u'* 4–5 curved, *ft'* 3–7, *ft''* 21–27, *ω* 4–5 knobbed; empodium 4–5, similar to empodium I; tibia 4–5; genu 4–5, *l''* absent; femur 10–11, *bv* II absent. **Coxal setae:** *lb* absent; *la* 21–26, 11–12 apart; *2a* 31–38, 32–34 apart; 10–11 coxigenital annuli before epiandrium. Prosternal apodeme indistinct, forked, 7–8. **Epiandrium** 15–17, 18–20 wide; two arc-shaped cuticular folds precede forked genital lip, delimiting gonopore anteriorly (Fig. 5C); *3a* 10–13, 13–16 apart, cuticle between tubercles of *3a* (postgenital region *sensu* Chetverikov & Petanovic 2016) with thin diagonal ridges; *eu* 0.5–1. **Pseudotagmata.** Anteroscutum and pretelosoma bear 18–19 lateral spines. Pretelosoma with 10–11 smooth dorsal annuli, posterior most four or five of them without lateral spines. **Opisthosoma** ventrally with 43–45 microtuberculate annuli between epiandrium and caudal lobes. Setal lengths: *c2* 21–27, *f* 22–27, *h2* 26–38.

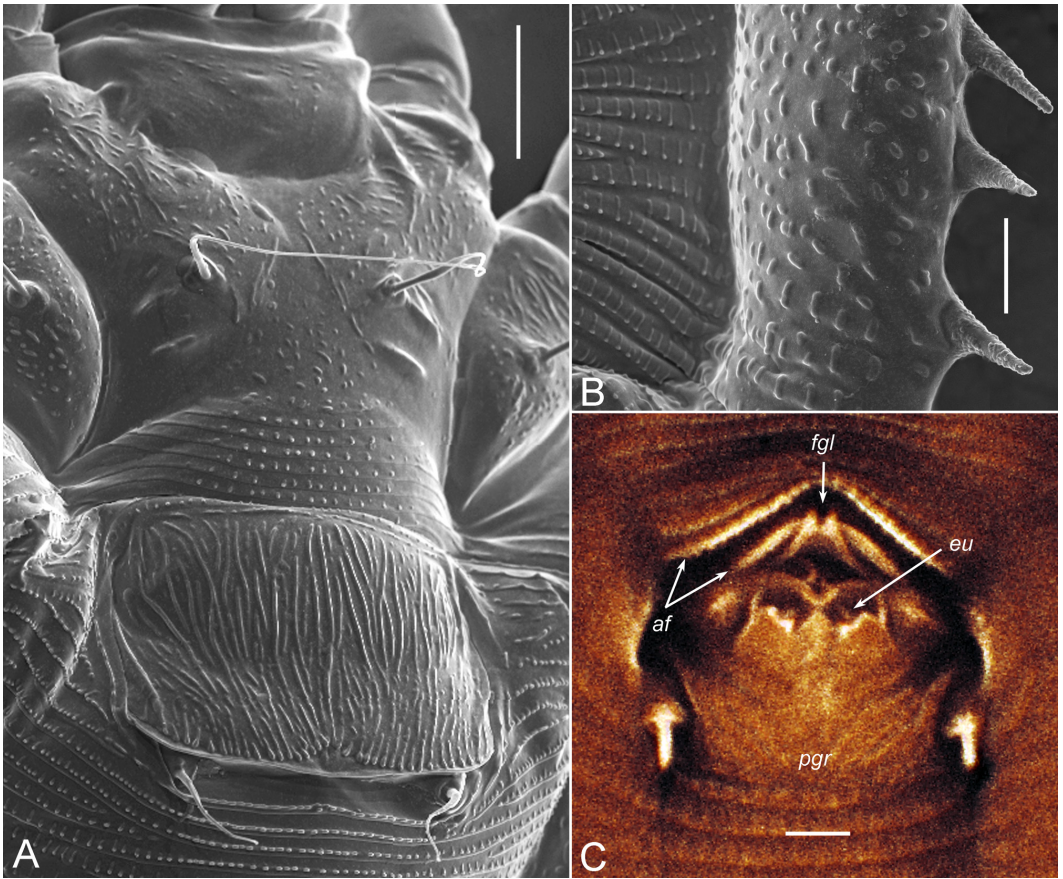


**FIGURE 3.** LT-SEM images of protogyne females of *Tumescoptella aculeata* n. sp. (A–F) and *T. rotundiscuta* n. sp. (G). A,B—dorsal view; C—ventral view; D—dorsal telosomal pseudotagma; E—bifurcate gnathosomal setae; F—infracapitulum and palps, ventral aspect; G—wax. Scale bar: A,B,C = 30  $\mu$ m; D = 10  $\mu$ m; E,F = 2  $\mu$ m; G = 1  $\mu$ m. Note: asterisk in Fig. 3A indicates postprodorsum, asterisk in Fig. 3B indicates cervix.





**FIGURE 4.** LT-SEM (A,B,C,D) and CLSM (E) images of *Tumescoptella aculeata* n. sp. (protogyne females). A—anterior extremity of prodorsal shield; B—main part of prodorsal shield; C,D—empodium and tarsal solenidium; E—prodorsum and superpostprodorsum. Scale bar: A = 5  $\mu\text{m}$ ; B,E = 15  $\mu\text{m}$ ; C,D = 1  $\mu\text{m}$ .



**FIGURE 5.** LT-SEM (A,B) and CLSM (C) images of *Tumescoptella aculeata* n. sp. (protogyne). A—female coxigenital area; B—magnified fragment of ventrolateral opisthosomal annuli with lateral spines; C—male external genitalia. Scale bar: A = 10 μm; B = 3 μm; C = 3 μm. Notations: *af*—arc-shaped cuticular folds, *eu*—eugenital seta, *fgl*—forked genital lip, *pgr*—postgenital region.

**Remark.** Except protogyne females and males described above, several atypical females were registered. Three of them were found among slide-mounted specimens and two among specimens studied under SEM (Fig. 6A,B,C). These rare females were present in mite colonies along with typical females and males. Morphologically, atypical females are very similar to the typical ones. The largest differences between these two types of females pertain to: (1) the topography of the dorsal cuticle; (2) presence/absence of lateral opisthosomal spines and spots of subcuticular thickenings. We consider the atypical females to be the deutogyne form of the same species, *T. aculeata* n. sp.

**DEUTOGYNE FEMALE (n=3).** Body flattened dorso-ventrally, 185–191, 75–80 wide at the level of seta *c*<sub>2</sub>. No wax in slide-mounted specimens; under SEM, wax present on anterior margin of frontal lobe. **Prodorsal shield** and cervix almost fused, forming together a common plate 72–76, 75–80 wide; frontal lobe 15–16. Prodorsal shield ornamentation considerably less distinct than in protogyne; two sinuous admedian lines divide prodorsal shield into three large areas (two lateral and one medial), cells and ridges in medial area absent. Prodorsal shield, cervix and postprodorsum with tiny, round indentations (putative micropores for wax secretion); round spots of subcuticular thickenings absent under LM and CLSM. Scapular setae *sc* 3–4, 18–20 apart, directed up or

convergently mediad. **Gnathosoma** short, directed down or obliquely down. Palps 20–21; chelicerae 16–17, outer infracapitular stylets 17–18, oral stylet indistinct. Gnathosomal setae: seta *v* 0.5–1; pedipalp genual seta *d* bifurcate, basal part 4–5, medial branch 5–6; lateral branch 2–3; pedipalp coxal seta *ep* 2–3; cheliceral retainer triangular-shaped, about 2–3.

**Leg I** 31–33, tarsus 4–5, *u'* 4–5 notably curved, *ft'* 15–21, *ft''* 20–24, *ω* 4–5 knobbed; empodium 5–6, divided into two 4–6 rayed branches; tibia 6–7, *l'* 1–2; genu 4–5, *l''* 19–23; femur 11–13, *bv* absent. **Leg II** 26–27, tarsus 4–5, *u'* 4–5 notably curved, *ft'* 4–5, *ft''* 19–24, *ω* 4–5 knobbed; empodium 5–6, similar to empodium I; tibia 4–5; genu 4–5, *l''* absent; femur 10–11, *bv* II absent. **Coxal plates** with numerous tiny microtubercles and sparse striae largely covering coxisternal plates I and II. Setae *Ib* absent; *Ia* 21–26, 10–11 apart; *2a* 34–40, 31–33 apart; 9–10 coxigenital annuli before epigynium. Prosternal apodeme faint, indistinctly forked posteriorly, 9–10. **External genitalia.** Genital coverflap similar to that of protogynes, 18–19, 22–24 wide; setae *3a* 7–10, 15–16 apart. Internal genitalia similar to that of protogynes.

**Pseudotagmata.** Anterostutum with less distinct topography than in protogynes; furrow separating cervix and prodorsum absent so that cervix seems to be fused with prodorsum. Lateral spines and rounded spots of subcuticular thickening absent. Wax secretion not apparent in live and slide-mounted specimens except on anterior edge of frontal lobe. Postprodorsum with 3–4 transverse sinuous ridges and one faint sinuous medial ridge. Pretelosoma with 9–10 smooth dorsal annuli. **Opisthosoma** ventrally with 45–48 microtuberculate annuli between epigynium and caudal lobes; posterior-most 3–4 ventral annuli broadened and with fewer minute microtubercles; last ventral annulus plate-shaped, with about 15 longitudinal ridges. Ventro-lateral opisthosomal cuticle at the level of postprodorsum devoid of annuli, forming wide band-like area covered with numerous round and oval microtubercles. Setae *c2* 24–28; setae *d* and *e* absent; *f* 26–29; *h1* absent; *h2* 32–36.

**Host plant.** *Hyphaene coriacea* Gaertn. (Arecaceae: Coryphoidea: Borasseae: Hypheninae).

**Relation to the host.** Vagrant, sparsely distributed on young leaves, causing no visible damage.

**Type locality.** South Africa, KwaZulu-Natal, R22 road from Mbazwana to Hluhluwe, 27°29'356"S 32°34'106"E.

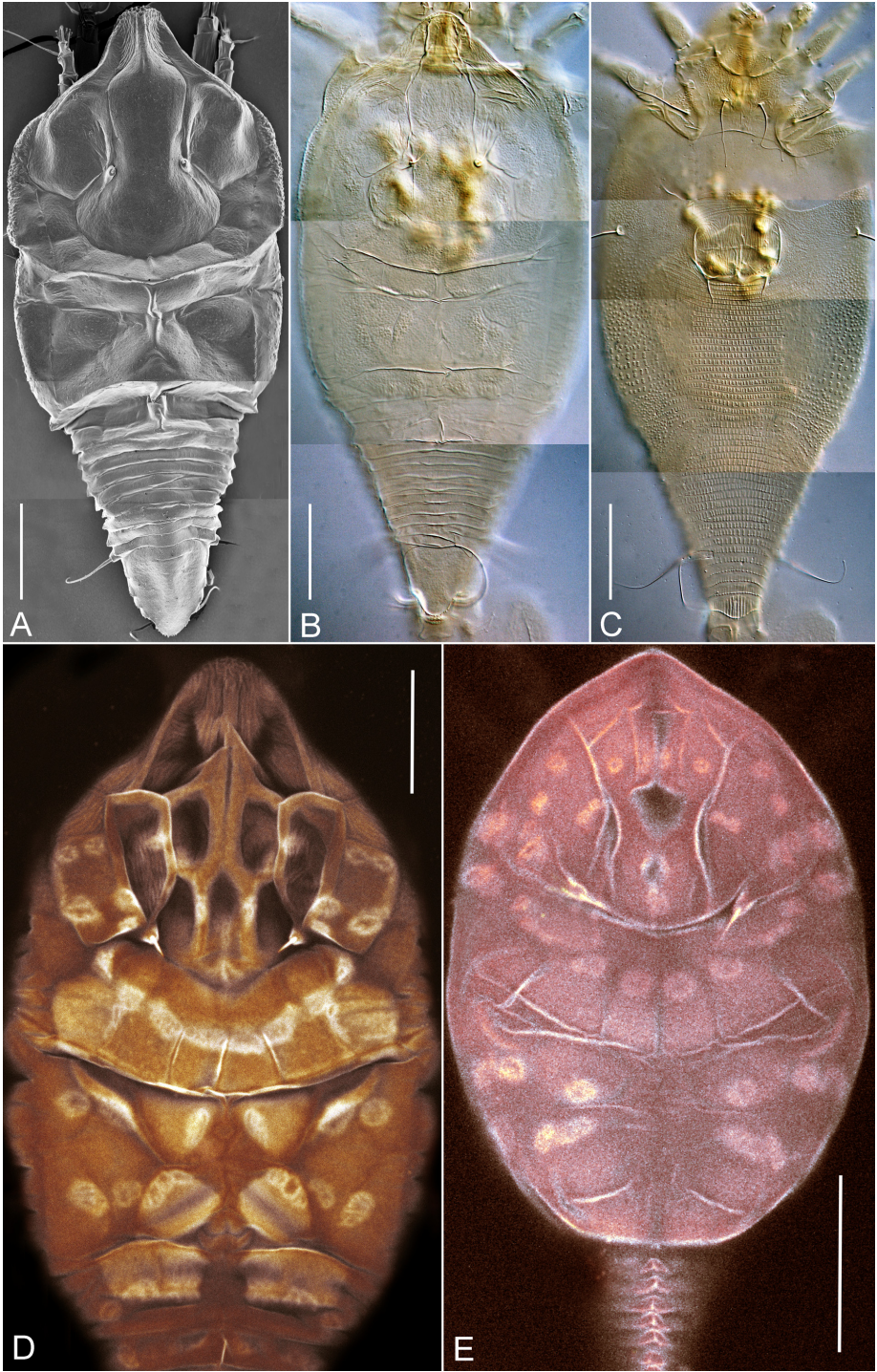
**Type material.** Holotype female in slide #E4013, 22 paratypes on 14 slides, collected 24 February 2016 in South Africa, KwaZulu-Natal, R22 from Mbazwana to Hluhluwe, 27°29'356"S 32°34'106"E; coll. C. Craemer. Holotype and some paratypes are deposited in South African National Collection of Arachnida (NCA)—Acari at ARC-PPRI, Pretoria, some paratypes deposited in Acarological collection in ZIN RAS.

**Additional material.** Two females in slides #E2455 and #E2454 collected 10 March 2013 in South Africa, KwaZulu-Natal, 28°41'686"S 32°00'543"E; coll. P. Chetverikov and S. Nesor.

**Remark.** In some samples from type locality mites *T. aculeata* n. sp. and *T. rotundiscuta* n. sp. were found together forming mixed colonies on the same palm leaf.

**Etymology.** The species epithet “*aculeata*”, gender feminine, is a Latin adjective meaning “sharp”, referring to the large lateral opisthosomal spines of the new species.

**Differential diagnosis.** The new species is very similar to the species *Scolocenus spiniferus* Keifer 1962. These two species can be easily separated based on the generic characters, mentioned in Table 1. Additionally, the new species has a large number of lateral opisthosomal spines (16–20) in comparison to *S. spiniferus* (three). The new species is close to *Tumescoptella rotundiscuta* n. sp., the most contrasting differences between *T. aculeata* n. sp. and *T. rotundiscuta* n. sp. are given in the section “Differential diagnosis” of *T. rotundiscuta* n. sp. and in Table 2.



**FIGURE 6.** LT-SEM (A), DIC LM (B,C) and CLSM (D,E) images of females of *Tumescoptella aculeata* n. sp. (A,B,C,D) and *Tumescoptella rotundiscuta* n. sp. (E). A, B—dorsal view of a deutogyne; C—ventral view of deutogyne; D—distribution of subcuticular dorsal thickenings (brightly autofluorescing spots) in anteroscutum of deutogyne of *T. aculeata* n. sp.; E—distribution of subcuticular dorsal thickenings in anteroscutum of *T. rotundiscuta* n. sp. Scale bar: A,B,C,D = 20  $\mu$ m; E = 15  $\mu$ m. *Note:* in Fig. 6D & 6E lateral opisthosomal spines are out of focus.

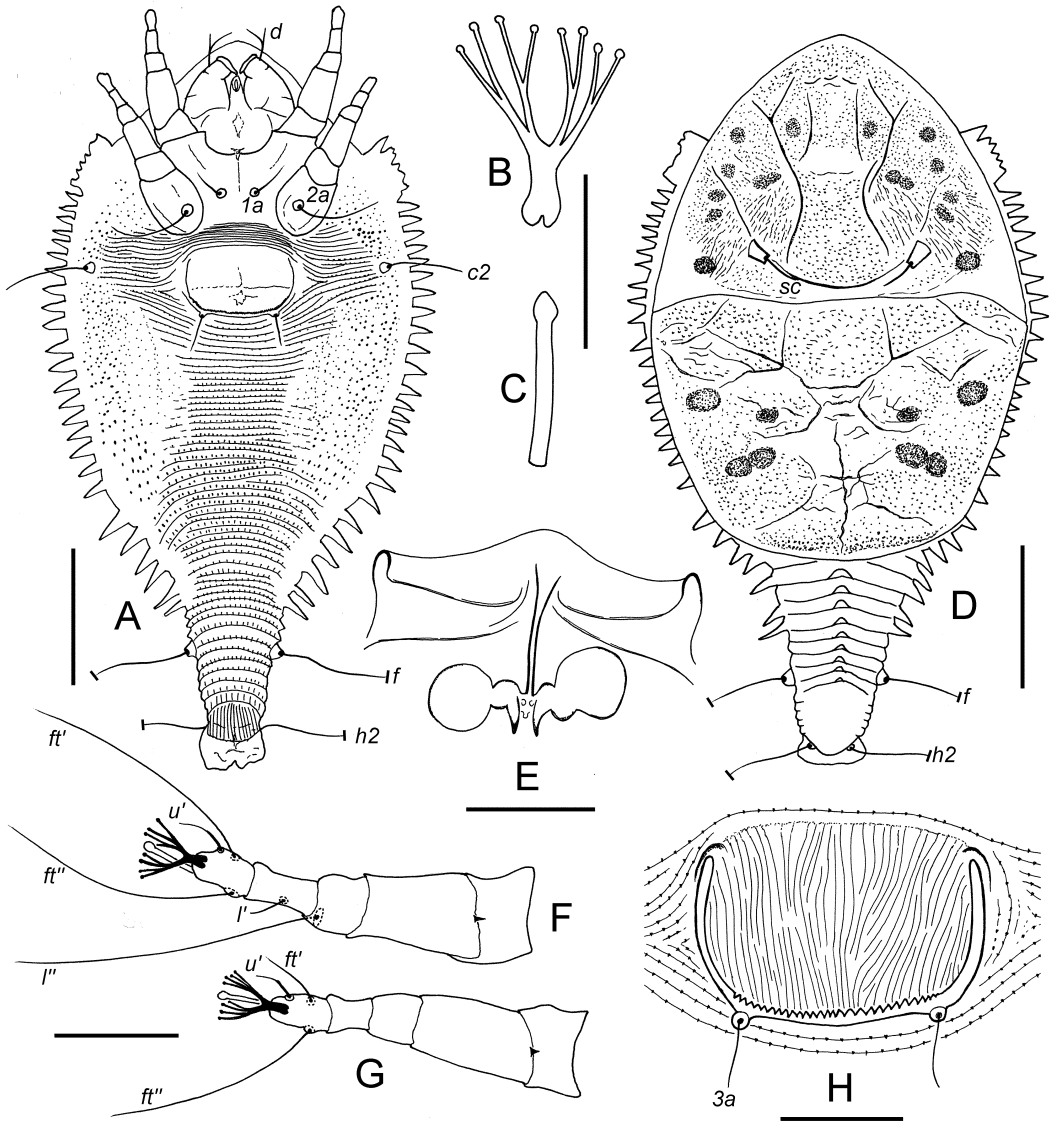
*Tumescoptella rotundiscuta* n. sp.—Fig. 6,7,8,9,10.

**FEMALE (n=11).** Body flattened dorso-ventrally, 164 (159–170), 80 (76–82) wide at the level of seta *c2*. Some parts of body covered with wax, washed off in slide-mounting process, but detectable in live specimens, and captured in SEM images (see below). **Prodorsal shield** subtriangular, 58 (57–61), 77 (74–80) wide; frontal lobe 9 (9–10); prodorsal shield separated posteriorly from superpostprodorsum (fusion product of cervix and postprodorsum) by distinct transverse cuticular fold or ridge. Prodorsal shield ornamentation with two widely spaced sinuous admedian lines and large arc-shaped ridge bearing tubercles of *sc*. Anteriorly, admedians forked, two short longitudinal ridges between admedians in anterior part of shield. Prodorsal shield as well as superpostprodorsum with tiny, round indentations, microridges, cuticular wrinkles and round spots of subcuticular thickenings (dark under LM and brightly autofluorescing under CLSM). Scapular setae *sc* 8 (6–8), 30 (29–32) apart, directed up or convergently posteromedial in slide-mounted specimens (Fig. 8 A,B,E), but divergently laterad under LTSEM (Fig. 9A,B). **Gnathosoma** short, directed down or obliquely down. Palps 13 (12–14); gnathosomal stylets very short and difficult to measure, chelicerae (n=1) about 6, outer infracapitular stylets (n=1) about 7, oral stylet indistinct. Gnathosomal setae: seta *v* indistinct; pedipalp genual seta *d* bifurcate, basal part 5 (4–5), medial branch 7 (6–7); lateral branch 3 (3–4); pedipalp coxal seta *ep* and cheliceral retainer not observable. Suboral plate rounded, smooth in slide-mounted specimens, 11 (10–12); 17 (17–18) wide.

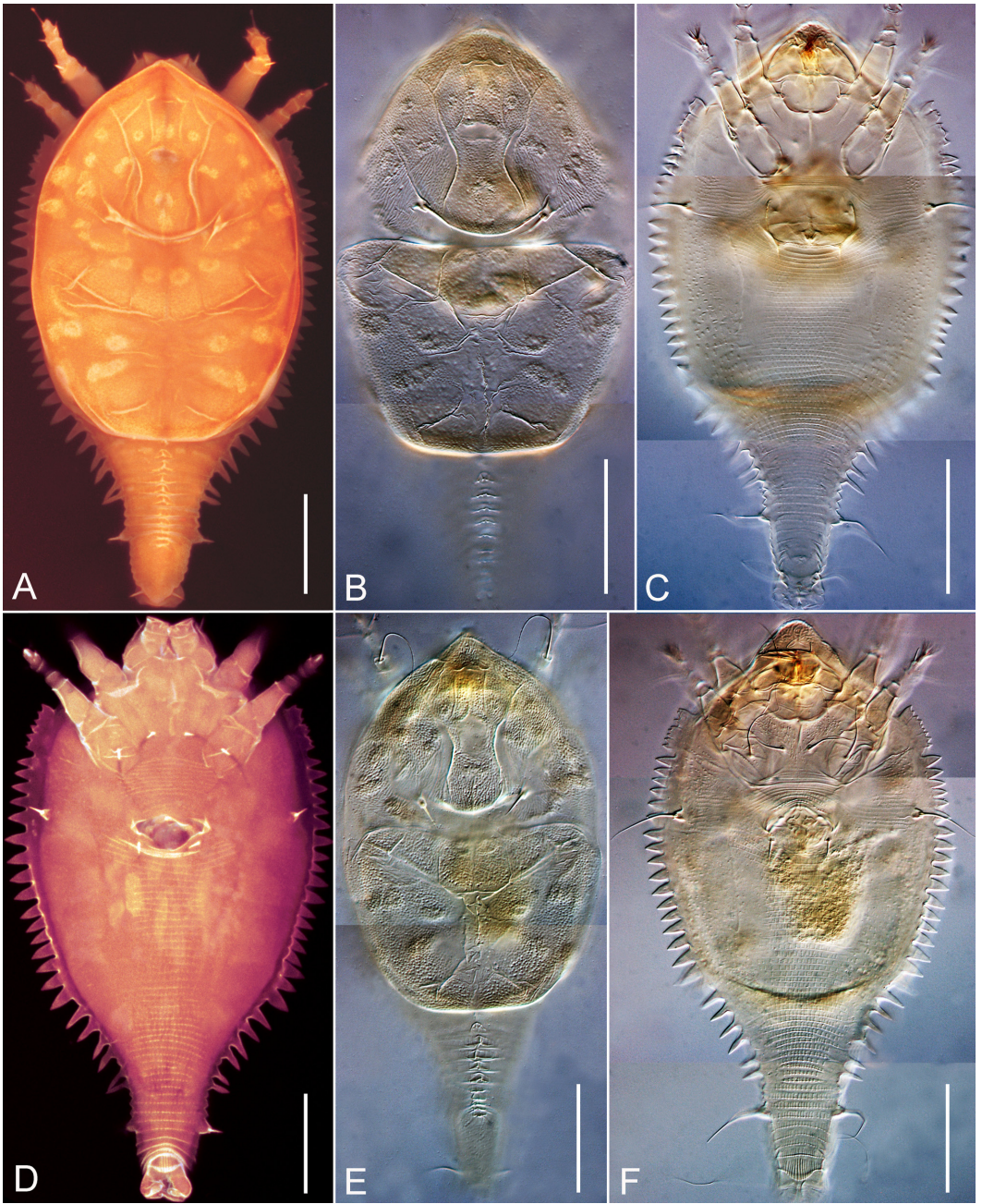
**Leg I** 34 (31–34), tarsus 6 (5–6), *u'* 4 (4–5) notably curved, *ft'* 22 (20–26), *ft''* 23 (21–26), *ω* 5 (4–5) knobbed; empodium 6 (6–7), in most slide-mounted specimens empodium seems to be divided into two 4–5 rayed branches, although the true number of empodial rays and their topography is not clear; tibia 6 (6–7), *l'* 2 (2–3); genu 4 (4–5), *l''* 30 (29–33); femur 11 (11–12), *bv* absent. **Leg II** 26 (25–29), tarsus 5 (4–5), *u'* 4 (3–4) notably curved, *ft'* 5 (4–6), *ft''* 22 (20–25), *ω* 5 (4–5) knobbed; empodium 6 (5–7), similar to empodium I; tibia 4 (4–5); genu 4 (4–5), *l''* absent; femur 10 (9–11), *bv* II absent. **Coxal plates** with indistinct striae largely covering coxisternal plates I and II. Setae *lb* absent; *la* 20 (18–27), 6 (6–7) apart; *2a* 10 (8–14), 24 (23–26) apart; 8 (8–10) coxigenital annuli before epigynium. Prosternal apodeme faint, indistinctly forked posteriorly, 10 (9–10). **External genitalia.** Genital coverflap subrectangular, with delicate striations, tiny denticles posteriorly, 16 (15–17), 24 (23–25) wide; setae *3a* 7 (7–9), 16 (15–17) apart; pregenital plate (sensu Flechtmann *et al.* 2015) absent. **Internal genitalia (n=3).** Spermatheca spherical, 4–5 in diameter; spermathecal process (sensu Duarte *et al.* 2016) minute, directed posteriad, about 1–2; spermathecal tube short, 2–3, 2–3 wide; prespermathecal part of longitudinal bridge 11–14, postspermathecal part rudimentary; oblique apodeme (sensu Chetverikov *et al.* 2015) distinct laterally and indistinct medially; anterior genital apodeme short subtrapezoid, half-length 15–19.

**Pseudotagmata.** Dorsally mite body subdivided into three distinct pseudotagmata: anteroscutum, pretelosoma and telosoma. Anteroscutum plate-like, suboval or rounded, subdivided by transverse cuticular ridge (or fold) into two large parts: prodorsum and superpostprodorsum, the latter consisting of fused cervix and postprodorsum. Cervix subtriangular, with several short longitudinal lines subdividing cervix into five sectors. Postprodorsum with sinuous medial ridge and several symmetrical, indistinct arc-like wrinkles delimiting 3–4 laterally open cells. Pretelosoma with medial ridge and 9 (9–10) smooth dorsal annuli, posterior most four or five of them without lateral spines. Telosoma plate-like, with indistinct traces of fused dorsal annuli; indistinct tiny spinules from posterior margin of dorsal telosomal plate (smaller than those of *T. aculeata*), better seen under SEM. Anteroscutum and pretelosoma with 26 (24–27) large lateral spines, first lateral spine wide, plate-like; anteroscutum with symmetrically distributed rounded spots of subcuticular thickening.

**Opisthosoma** (herein the part of body behind prodorsum) ventrally with 51 (48–54) microtuberculate annuli between epigynum and caudal lobes; last ventral annulus plate-shaped, with about 15 longitudinal ridges. Ventro-lateral opisthosomal cuticle devoid of annuli, forming wide band-like area covered with numerous round microtubercles. Setae *c2* 23 (20–25), their tubercles situated on lateral wall of opisthosoma below lateral spines; setae *d* and *e* absent; *f25* (24–27); *h1* absent; *h2* 45 (40–48).



**FIGURE 7.** *Tumescoptella rotundiscuta* n. sp. (female, drawings based on PC LM). A—ventral view; B—empodium I; C—tarsal solenidion I; D—dorsal view; E—internal genitalia; F—leg I (ventral aspect); G—leg II (ventral aspect); H—external genitalia. Scale bar: A, D = 30  $\mu$ m; B, C = 5  $\mu$ m; E, F, G, H = 10  $\mu$ m.



**FIGURE 8.** CLSM (A,D) and DIC LM (B,C,E,F) images of females (B,C) and males (A,D,E,F) of *Tumescoptella rotundiscuta* n. sp. A,B,E—dorsal aspect; C,D,F—ventral aspect. Scale bar = 15  $\mu$ m.

**MALE (n=4).** Most qualitative characters of males (opisthosomal pseudotagmata, including their shapes and topographies; 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 and description of the genital area are given below. Body, 149–155, 73–76 wide at the level of seta *c2*. **Prodorsal shield** 53–56, 70–75 wide; frontal lobe 8–9. Scapular setae *sc* 5–6, 24–26 apart. **Gnathosoma.** Palps 13–15; setae *v* and *ep* indistinct; pedipalp

genual seta *d* bifurcate, basal part 3–4, medial branch 4–5; lateral branch 2–3. **Leg I** 30–32, tarsus 4–5, *u'* 3–5 curved, *ft'* 21–24, *ft''* 20–23,  $\omega$  4–5 knobbed; empodium 4–6, divided into two 4–5 rayed branches; tibia 4–5, *l'* 1–2; genu 4–5, *l''* 21–27; femur 11–12, *bv* absent. **Leg II** 24–26, tarsus 4–5, *u'* 3–5 curved, *ft'* 4–7, *ft''* 21–25,  $\omega$  4–5 knobbed; empodium 4–5, similar to empodium I; tibia 4–5; genu 3–4, *l''* absent; femur 10–11, *bv* II absent. **Coxal setae:** *1b* absent; *1a* 17–23, 7–8 apart; *2a* 25–34, 24–26 apart; 10–12 coxigenital annuli before epiandrium. **Epiandrium** 10–11, 18–20 wide; *3a* 8–9, 14–15 apart, cuticle between tubercles of *3a* with indistinct thin ridges; *eu* about 1. **Pseudotagmata.** Anteroscutum and pretelosoma with 23–25 lateral spines; first spine wide, plate like. Pretelosoma with 10–11 smooth dorsal annuli, posterior-most four or five pretelosomal annuli without lateral spines. **Opisthosoma** ventrally with 46–48 microtuberculate annuli between epiandrium and caudal lobes, posterior-most ventral annulus plate like, with 15–18 ridges. Setal lengths: *c*2 17–18, *f* 16–19, *h*2 27–32.

**Host plant.** *Hyphaene coriacea* Gaertn. (Arecaceae: Coryphoidea: Borasseae: Hypheninae).

**Relation to the host.** Vagrant on young leaves causing no visible damage.

**Type locality.** South Africa, KwaZulu-Natal, R22 road from Mbazwana to Hluhluwe, 27°29'356"S 32°34'106"E.

**Type material.** Holotype female in slide #E4025, 19 paratypes on 12 slides, collected 24 February 2016 in South Africa, KwaZulu-Natal, R22 from Mbazwana to Hluhluwe, 27°29'356"S 32°34'106"E; coll. C. Craemer. 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.

**Remark.** In some samples from type locality mites *T. rotundiscuta* n. sp. and *T. aculeata* n. sp. were found to be sympatric on the same palm leaf.

**Etymology.** The species epithet “*rotundiscuta*”, adjective gender feminine, is a combination of Latin “*rotundus*” (round) and “*scutum*” (shield) referring to suboval and rounded anteroscutum of the new species.

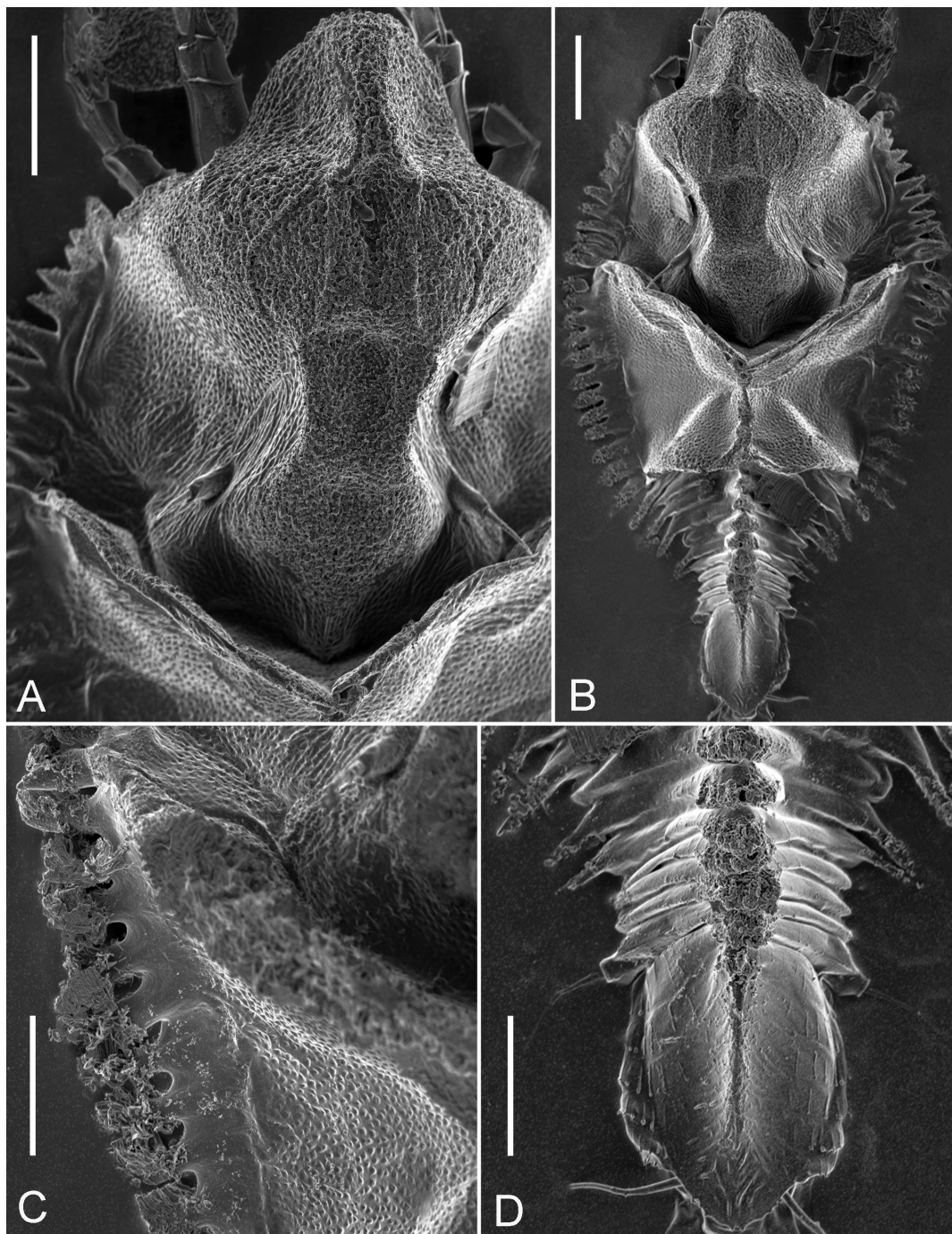
**Differential diagnosis.** The new species is very close to the species *Tumescoptella aculeata* n. sp. These two species can be easily separated based on the shape of anteroscutum, telosomal plate and lateral opisthosomal spines, and length of palps (Table 2).

#### LT-SEM observations on *Tumescoptella aculeata* n. sp. and *T. rotundiscuta* n. sp.

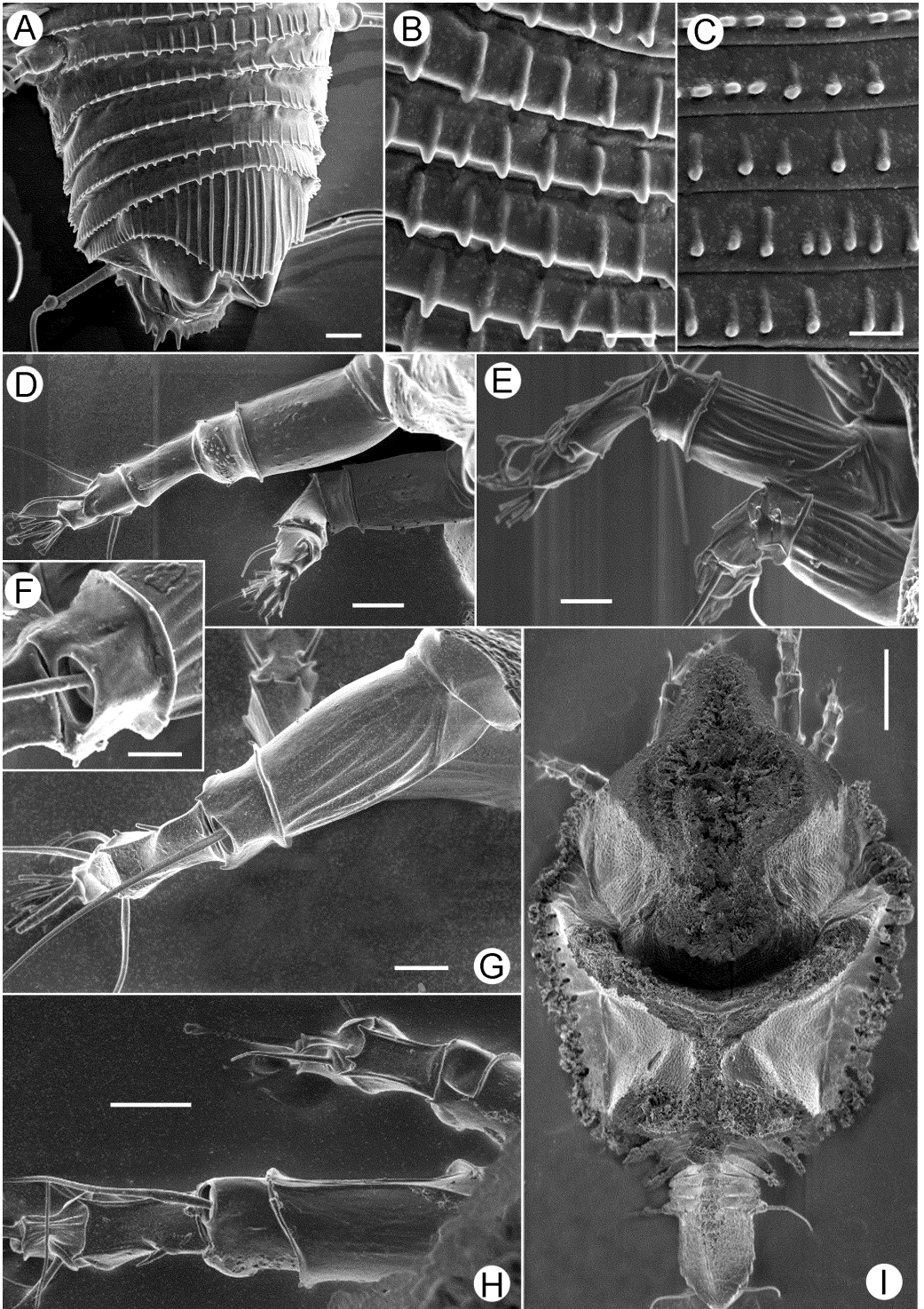
***Tumescoptella aculeata* n. sp.** The topography of exoskeleton (Fig. 3A,B), including orientation of the cervix, the groove between the cervix and prodorsal shield, shapes of ventro-lateral and ventro-medial areas of the body forming a longitudinal shallow groove between them, more detailed true topography of the prodorsal shield and two partial annuli on dorsal, proximal area of the plate-like telosoma were clearly visible under SEM contrary to LM. SEM revealed that in protogynes the entire dorsal body surface, including bases of lateral opisthosomal spines, is covered with an uneven rough wax layer (Figs 3D; 4B); wax extensions protrude from the anterior margin of the frontal lobe (Fig. 4A) and less so in the deutogyne (Fig. 6A). No obvious wax occurs on the ventral body surface (Figs 3C,F; 5A) except on spines of protogynes (Fig. 5B).

Orientation, shape and insertion site of some setae were more accurately seen with SEM than with LM, although it could sometimes be detected in LM. Scapular setae *sc* project up (Fig. 4B), while seemingly directed convergently mediad in slide-mounted specimens (Fig. 2A). Presence of palp setae *v* were hard to observe with LM, but their presence and position could be confirmed with SEM (Fig. 3F). Tarsal setae *u'* broadly angled (Fig. 10E,G). Genual seta *l''* I strong, inserted in a cup-like cavity (Fig. 10D,F,G) rendering it broadly similar to a trichobothrial seta.





**FIGURE 9.** LT-SEM images showing dorsal topography of *Tumescoptella rotundiscuta* n. sp. A—prodorsal shield; B—dorsal aspect of a mite; C—dorsolateral margin of postprodorsum; D—pretelosomal dorsal annuli and telosomal pseudotagma. Scale bar: A,B = 10  $\mu$ m; C,D = 5  $\mu$ m.



**FIGURE 10.** LT-SEM images of adults of *Tumescoptella aculeata* n. sp. (A–G) and *T. rotundiscuta* n. sp. (H,I). A,B,C—enlargement of ventral opisthosomal microtubercles, caudal (A), just anterior to seta *f* (B), just posterior to genitalia (C); D, F, G, H—dorsal aspects of legs; E—ventral aspect of legs; I—dorsal view of entire mite. Scale bar: A,F = 2 µm; B,C = 1 µm; D,E,H = 4 µm; G = 3 µm; I = 20 µm.

**TABLE 2.** Morphological differences between *Tumescoptella aculeata* n. sp. and *T. rotundiscuta* n. sp.

Characters	Mite species	
	<i>T. aculeata</i> n. sp. (protogyne)	<i>T. rotundiscuta</i> n. sp.
Shape of anteroscutum	subrectangular	suboval, rounded
Shape of posterior margin of dorsal telosomal plate	with delicate spinules from posterior margin of telosomal plate	with spinules from posterior margin of telosomal plate, but much fewer and smaller than those in <i>T. aculeata</i> n. sp.
Shape and number of lateral opisthosomal spines	19 (16–20) long sharp spines; first spine larger and more rounded	26 (24–27) shorter and more blunt spines; first spine plate-like
Length of palps	20 (18–21)	13 (12–14)

Palptarsus ventro-distally with two subtriangular structures, one of them larger than the other (Fig. 3F). A transverse cuticular ridge proximal of  $v$  (Fig. 3F). Tiny, round microtubercles present on suboral plate (Figs 3F; 5A) were undetectable in slide-mounted specimens. Legs I and II with fine ventral and dorsal ornamentation, which was unclear under LM. Ventrally—small rounded and pointed microtubercles on femora, and tiny rounded microtubercles on genu, mostly at the base, where the genu articulates with the tibia (Fig. 10E). Dorsally—femora with somewhat irregular longitudinal cuticular ridges, with a diagonal ridge at the base and a ridge on the margin between the femur and genu (Fig. 10D,G). Sharp spinules present on some distal leg segment margins, especially on genu and tibia (Fig. 10D,G). Empodia divided and asymmetrical. The two stems of the empodium are somewhat expanded, with all of the bifurcate rays stemming from them. One stem has three rays and the other has four rays; each ray on both stems with well-developed subray (Fig. 4C,D).

*Tumescoptella rotundiscuta* n. sp. Only dorsal aspect of *T. rotundiscuta* n. sp. was available for SEM observation. The 3D body shape of *T. rotundiscuta* n. sp. revealed by SEM is notably different from the LM observations of flattened slide-mounted specimens. Obvious differences include the shape and ornamentation of prodorsal shield and telosoma, and the orientation and fusion of the cervix and postprodorsum (Fig. 9).

The pretelosomal annuli form the middorsal ridge, with fine longitudinal ridges extending virtually from anterior to posterior annulus margin, ending in tiny spinules extending from rear annulus margin, in some specimens fading laterally until absent. The dorsal telosoma is plate-like with partially fused and indistinctly indicated annuli; in some specimens the proximal two annuli are clearly separated centrally. Telosomal annuli bear elongate striae-like microtubercles laterally and form a narrow middorsal ridge which is a continuation of the middorsal pretelosomal ridge. Caudally the ridge ends in a few short converging cuticular ridges. These ridges go up to the telosomal plate rear margin, which has tiny spinules (Fig. 9D).

The entire dorsal body surface is not covered by a wax layer as in protogyne of *T. aculeata* n. sp., but some body areas are profusely covered with dense filament-like wax strands extending from the body surface (Fig. 9A,C,D). Some wax structures were apparently lost from various parts of SEM studied specimens, but areas that are covered largely include: (1) a central raised area of the prodorsal shield, including frontal lobe, cervix and raised parts of the postprodorsum; (2) the narrow middorsal ridge extending from the postprodorsum across the pretelosoma and telosoma; (3) the lateral body spines (Fig. 9).

Scapular setae *sc* directed divergently laterad (Fig. 9A,B), while seemingly directed up or convergently posteromedial in slide-mounted specimens (Fig. 8A,B,E). In *T. rotundiscuta* n. sp. femora dorsally without cuticular ridges found in *T. aculeata* n. sp.; a cuticular ridge present on the margin between femur and genu; spines present on some distal leg segment margins, especially on distal margins of genu and tibia (Fig. 10H). Like *T. aculeata* n. sp., genual seta *l*' I is strong and inserted in a large cup-like cavity (Fig. 10H).

## Discussion

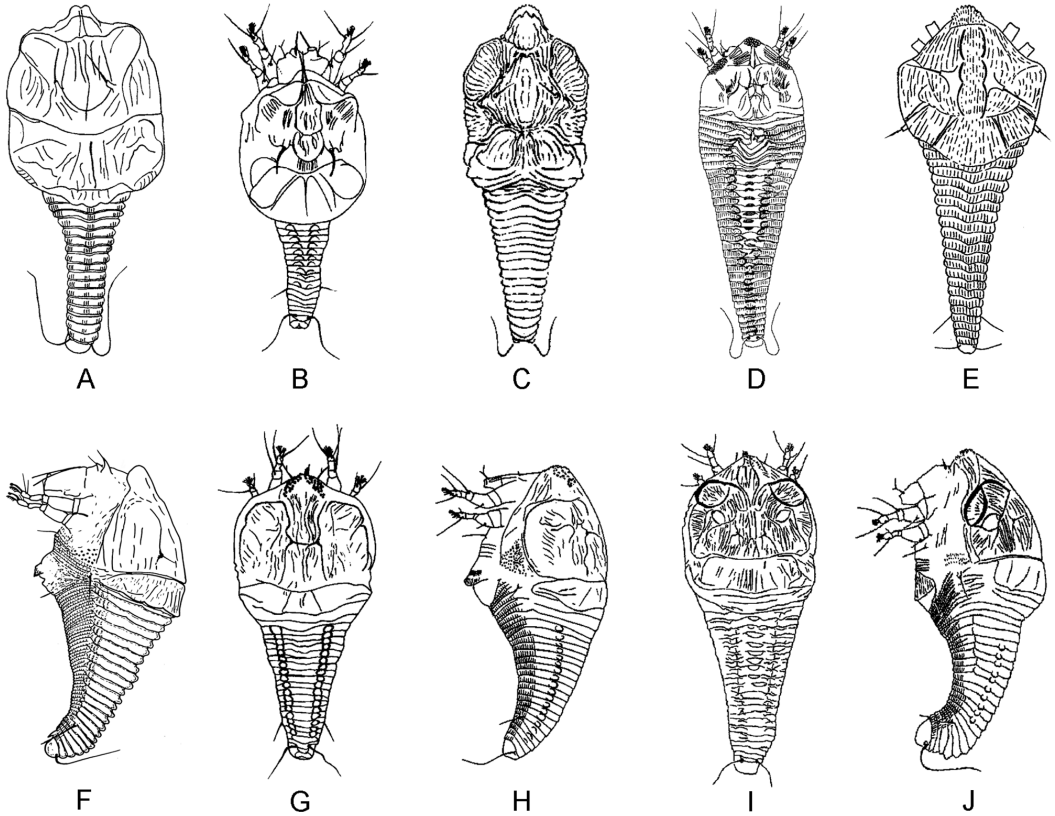
**Hypotheses on the origin of *Tumescoptes*-like phyllocoptines (TP) from palms.** In this paper we describe a new genus *Tumescoptella* n. g. from South African indigenous coryphoid palm *Hyphaene coriacea*. This palm species belongs to the tribe Borasseae which originated about 38 Mya from a Eurasian ancestor in the Indian Ocean, where it later diverged and spread to Africa, India, Eurasia and the Pacific (Baker & Couvreur 2012). *Hyphaene* is one of the largest and most widely distributed borassoid genera, growing naturally in arid and semiarid environments in Africa, Madagascar and India (Palmweb 2017). Based on the Oligocene (27–28 Mya) fossil of *Hyphaene* from Ethiopia, Pan *et al.* (2006) hypothesized that this genus might have been present continuously in Africa since the Oligocene.

Our present and previous (Chetverikov & Craemer 2017; Chetverikov *et al.* 2017) data indicate that *Hyphaene* palms house very diverse fauna of morphologically uncommon eriophyoid mites including three bizarre pseudotagmic genera of the subfamily Phyllocoptinae—*Tumescoptes* Keifer, *Tumescoptella* n. g. and *Pseudotagmus* Chetverikov *et al.* Along with genus *Scolocenus*, which is associated with coconut and possesses the well-developed pseudotagma, *anteroscutum* (a term proposed in this paper), these four genera form a presumably monophyletic group of *Tumescoptes*-like phyllocoptines (TP) which share the following traits: (a) femoral setae *bv* I & II absent; (b) opisthosomal setae *h1* and *d* absent; (c) gnathosomal seta *d* and tarsal seta *u'* distinctly angled or bifurcate; (d) body flattened with differently developed dorsal pseudotagmata; (e) unusual shape of empodia, and (f) association with one plant family—Arecaceae. Genera *Scolocenus*, *Pseudotagmus* and *Tumescoptella* n. g. have large lateral opisthosomal spines, an advanced morphological trait which is absent in *Tumescoptes*. Remarkably, genus *Scolocenus* possesses the most complete chaetome of the legs and opisthosoma. However, it is the genus *Tumescoptes* which has the least developed pseudotagmata. In our opinion the formation of pseudotagmata is a much slower evolutionary process than the reduction of the chaetome. Based on this assumption we consider *Tumescoptes* to be basal in the TP clade, although a final conclusion requires a formal cladistic analysis, which is beyond the scope of this paper.

Current data on the diversity, distribution and host plant association of eriophyoids are highly incomplete, fragmented and correlated with the historical centers of eriophyoid studies (de Lillo & Skoracka 2010). At the same time, the phylogenetic relations within large clades of Eriophyoidea are still poorly understood (Lindquist & Amrine 1996; Li *et al.* 2014, 2016). However, there are two morphologically distinct groups of eriophyoid genera (here named groups I and II) associated with different lineages of host-plants and demonstrating remarkable morphological similarity with TP-mites, which could be considered their possible relatives.

The first group (Fig. 11) comprises several small genera (e.g. *Asetidicrothrix* Wei *et al.*, *Bangphracarus* Chandraparya *et al.*, *Dicrothrix* Keifer, *Hemiscolocenus* Mohanasundaram, *Kosacarus* Chandraparya *et al.*, *Kraducarus* Chandraparya *et al.*, *Neodicrothrix* Mohanasundaram, *Proneotegonotus* Mohanasundaram, *Protumescoptes* Pandit & Chakrabarti, *Soleula* Huang) associated with tropical dicotyledonous trees of the families Anacardiaceae, Apocynaceae, Dipterocarpaceae, Euphorbiaceae, Fabaceae, Fagaceae, Meliaceae, Menispermaceae, Piperaceae, Rosaceae, Rubiaceae, Sterculiaceae, and Ulmaceae. Most of these mites were described from China, Thailand and India, where they mainly inhabit plant species restricted to South-East Asia. Some exceptions are: *Neodicrothrix piperae* Mohanasundaram found not on a tree, but on liana (*Piper nigrum*, native to India); *Dicrothrix* Keifer mites found not in Asia, but in South America (Venezuela) on *Anacardium occidentale*, a tree native to Brazil and cultivated in Asia (Archak *et al.* 2009); *Kraducarus suregadi* Chandrapatya *et al.* found on the plants of the euphorbiacean genus *Suregada*, which has a wide native distribution and grows on all continents delimiting the Indian

ocean (Fell 2007). Morphologically, group I is characterized by the presence of more or less developed anterior pseudotagmata (prodorsum, cervix and postprodorsum). Additionally, similar to TP, some of the members of group I have a remarkably reduced chaetome, bifurcate gnathosomal *d*, and divided empodia. However, contrary to TP, members of group I are not so flattened and none of them inhabit monocots.

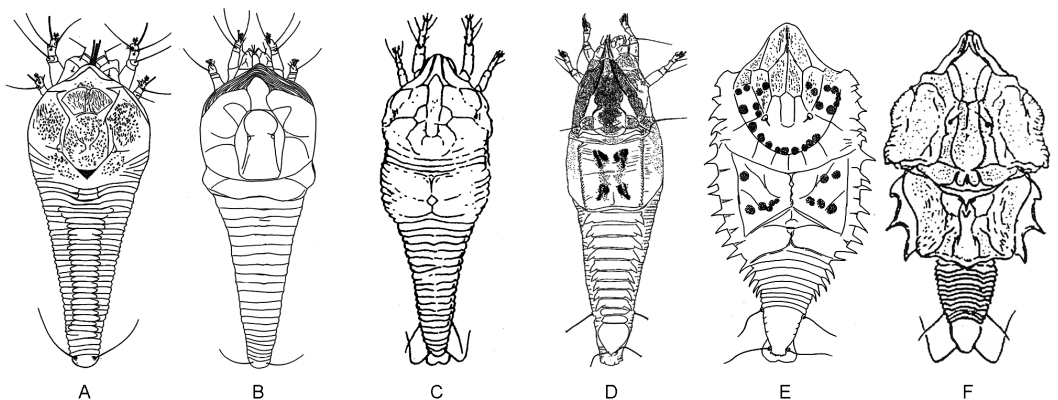


**FIGURE 11.** Mites of the group I from dicotyledonous trees. A—*Asetidicrothrix*, B—*Bangphracarus*, C—*Dicrothrix*, D—*Kraducarus*, E—*Hemiscolocenus*, F—*Proneotegonotus*, G & H—*Kosacarus*, I & J - *Protumescoptes*.

The second group (Fig. 12) comprises genera *Navia* Nemesio and *Glabrisceles* Navia & Flechtmann, described from Brazil and associated with indigenous South American arecoid palms of the genera *Geonoma* (Arecoideae: Geonomeae) and *Euterpe* (Arecoideae: Areceae). Although in these mites pseudotagmatisation is weakly expressed, they share two important characters with TP-mites: angled or bifurcate tarsal seta *u'* and a notably flattened body with a distinct lateral margin. Additionally, similar to TP, *Navia* and *Glabrisceles* live on palms. In our recent study on a group of *Dialox*-like diptilomiopines (DD) from Areceae (Chetverikov & Craemer 2017), we considered data on paleogeography of palms and concluded, following the paleohistories of their hosts, that DD could have originated in South America on attaleine palms (Areceae: Cocoseae) in the Paleocene, migrated to the Indian Ocean through Antarctica, shifted to borassoid palms (Coryphoideae: Borasseae), and diverged in India and Africa during the Eocene. Assuming the same evolutionary scenario for TP, the similarity between TP and South American mites of group II is not so surprising. Interestingly, there are several much less modified vagrant mites associated with South American palms (e.g. mites from genera *Amrineus* Flechtmann, *Epitrimerus* Nalepa, *Nasuchus* Navia &

Flechtmann, *Tegonotus* Nalepa), suggesting that some of them belong to the same lineage of palm-inhabiting phyllocoptine mites, the most derived members of which had evolved in Africa and acquired pseudotagmata.

Although South American origin of TP seems to be quite realistic, the less plausible, alternative hypothesis might be that TP had originated in an Asian region. Unfortunately, except sparse faunistic papers by Keifer (1962a,b; 1963, 1969, 1979), Huang (2001), Wei & Feng (2002), Xue & Zhang (2008), Das & Chakrabarti (1985), Mohanasundaram (1981, 1982, 1983, 1994), and Al-Atawi *et al.* (2014) from Philippines, New Zealand, China, India and Saudi-Arabia, no other data are available on the eriophyoids from palms native to Asia; palms in Thailand have never been inspected for eriophyoids (A. Chandrapatya, pers. comm. September 2017). According to these publications, about 13 eriophyoid species are known from Asian palms and only one of them, *Scolocenus spiniferus* Keifer, belong to TP. The following facts are consistent with the hypothesis on the Asian origin of TP. First, one specimen of *Pseudotagmus* was recorded from an unidentified palm near Bangalore in India in 2002 (Dr. Hashem Kamali, pers. comm. 9 December 2017); the occurrence of this mite in India as well as previous finding of *Scolocenus* on *Cocos* in the Philippines by Keifer (1962) could be explained by a close relation of TP to Asian genera of the group I. Second, the palm genus *Trachycarpus*, the host of one of the three known *Tumescoptes* species (*T. trachycarpi* Keifer, 1939) and the entire palm tribe Borasseae (to which host plants of genera *Pseudotagmus* and *Tumescoptella* n. g. belong) have an Asian origin (Baker & Couvreur 2012). Third, *Bangphracarus* and *Kosacarus* have very similar morphologies to TP mites, although they do not have dorsal telosomal pseudotagma and lateral opisthosomal spines. Finally, some of the hosts of the mites from group I (e.g. *Suregada*) have a very broad distribution in Africa, Asia and Australia, or belong to plant families with pantropical distributions (e.g. Dipterocarpaceae), creating the right conditions for host shifts in geographically remote regions. Overall, much more work remains to be done to resolve the problem of the origin of TP mites. And, apart from precise comparative analyses, additional collections of eriophyoids from Asian and African palms as well as from other tropical trees are needed. The Eriophyoidea of the following botanical groups are of special interest: Arecaceae (particularly the primitive taxa), *Suregada*, Dipterocarpaceae in Borneo and the Amazon basin, and Nothofagaceae in New Zealand and Chile.



**FIGURE 12.** Mites of the group II (A,B) and *Tumescoptes*-like phyllocoptines (C,D,E,F) from palms. A—*Navia*, B—*Glabrisceles*, C—*Tumescoptes*, D—*Pseudotagmus*, E—*Tumescoptella* n. g., F—*Scolocenus*.

**Remarks on morphology of deutogynes in Eriophyoidea.** Many eriophyoid species have two different forms of females (and rarely males) in their life cycle. Seasonal dimorphism of females was reported first by Putman (1939). Later this phenomenon was described by Keifer (1942) in the course of his observations on the North American mite *Shevtschenkella aesculifoliae* (Keifer), and he called

it *deuterogeny* (Manson & Oldfield 1996). Morphological differences between deutogyne (D) and protogyne (P) females usually are not very prominent. They largely pertain to body size and color, number of opisthosomal annuli, and setal lengths. However, there are examples of very strong morphological differences between the D and P forms of the same species, resulting in the description of the distinct forms as different species or even different genera (Amrine *et al.* 2003; Britto *et al.* 2008). Currently, the aberrant morphology of D forms is believed to increase survival under unfavorable conditions, and is largely interpreted as an adaptation to adverse climatic seasons, although some other (“atypical”) forms of deuterogeny associated with migration and dispersal have also been reported (Manson & Oldfield 1996).

Recently, Sukhareva & Chetverikov (2014) undertook a statistical analysis of the morphological differences between P and D females across taxa of Eriophyoidea. They concluded that morphological transformation (P→D) in different phylogenetic lineages of Eriophyoidea may happen in opposite directions, and therefore should not be considered exclusively as a consequence of adaptive evolution. They also hypothesized that the aberrant morphology of deutogynes might reflect changes in life style or occupied ecological niches relating to ancestral conditions (e.g. transition from living inside natural shelters to vagrant life style or vice versa, transition from living in one part of a plant to another). In this case, D is a form in the life cycle of a modern species that has retained similarities with the ancestral taxon.

In this study we report on a new remarkable example of deuterogeny: in deutogyne females of *Tumescoptella aculeata* **n. sp.** the large spines, situated along the lateral margin of opisthosoma in protogynes, are absent. As far as we know, this is the first indication that presence/absence of lateral opisthosomal spines could be associated with deuterogeny in Eriophyoidea. Due to the absence of the spines and smoother anteroscutum, deutogynes of *T. aculeata* **n. sp.** resemble the members of the genus *Tumescoptes* much more than the protogynes. The genera *Tumescoptes* and *Tumescoptella* **n. g.** are so morphologically similar that they might be sister taxa. However, *Tumescoptella* **n. g.** is morphologically much more derived in comparison to *Tumescoptes*. The higher similarity of deutogynes of *T. aculeata* **n. sp.** with *Tumescoptes* mites is in accordance with the hypothesis that morphologically, the D form may be a reminiscent of an ancestral taxon (MCR of *Tumescoptes* and *Tumescoptella* **n. g.** in this particular case). In a recent study by Guo *et al.* (2015), it was demonstrated that a comparison of partial sequences of 18S and 28S genes is an efficient tool to show whether morphologically different eriophyoids represent different forms of one species or belong to different taxa. Applying the same approach, it would be possible to check the hypothesis by Sukhareva & Chetverikov (2014) on the nature of D forms in Eriophyoidea. The group of *Tumescoptes*-like mites might be a prospective model for such a study due to their distinct morphology and possible monophyly.

**Variation of lateral opisthosomal spines across taxa of Eriophyoidea (Fig. 13).** One of the most distinctive features of *Tumescoptella* **n. g.** is the presence of large cuticular spines situated along the lateral margin of the opisthosoma. Similar spine-like structures (SS) can be found in some other genera of Eriophyoidea. However, their variation, origin and function have never been a subject of a special discussion. Below we give an overview of the variation of SS among supraspecific taxa of Eriophyoidea and perform morpho-functional evaluation of these structures.

**Triasacaridae Lindquist & Sidorchuk and Pentasetacidae Boczek *et al.*** Among four monotypic extinct triasacarid genera described from Triassic amber (*Ampezzoia*, *Cheirolepidoptus*, *Minyacarus* and *Triasacarus*.) and two extant pentasetacid genera (*Loboquintus* and *Pentasetacus*), spine-shaped lateral structures are known in *Ampezzoia* only (Fig. 13H). These structures are associated with a transparent film-like substance (interpreted as wax filaments) and described as “wax-secreting lateral lobes” in the original description (Schmidt *et al.* 2012). Additionally, according to the revised

description of this taxon, each of the broad dorsal annuli of *Ampezzo* might be a composite of four fused narrower annuli, a state considered derived (Sidorchuk *et al.* 2015).

**Phytoptidae s.l. sensu Chetverikov *et al.* 2015.** Among phytoptids, true lateral spines have been recorded only in the genus *Propilus* (Fig. 13 I) from palms. In Phytoptidae s.str (phytoptids from angiosperms), the lateral margins of dorsal opisthosomal annuli are serrate in dorsal view, and resemble small spines in the palm inhabiting genus *Retracrus* Keifer, and *Neopropilus* Huang and *Neoprothrix* Reis *et al.* from dicotyledons; these three genera, which contain only one or a few species, include small vagrant mites with highly flattened and consolidated bodies. In Nalepellidae Boczek *et al.* (phytoptids from gymnosperms), one monotypic genus *Phantacrus* Keifer (Fig. 13 P), possesses several longitudinal rows of large dorsal lobes, which could be homologous to the discussed opisthosomal spines.

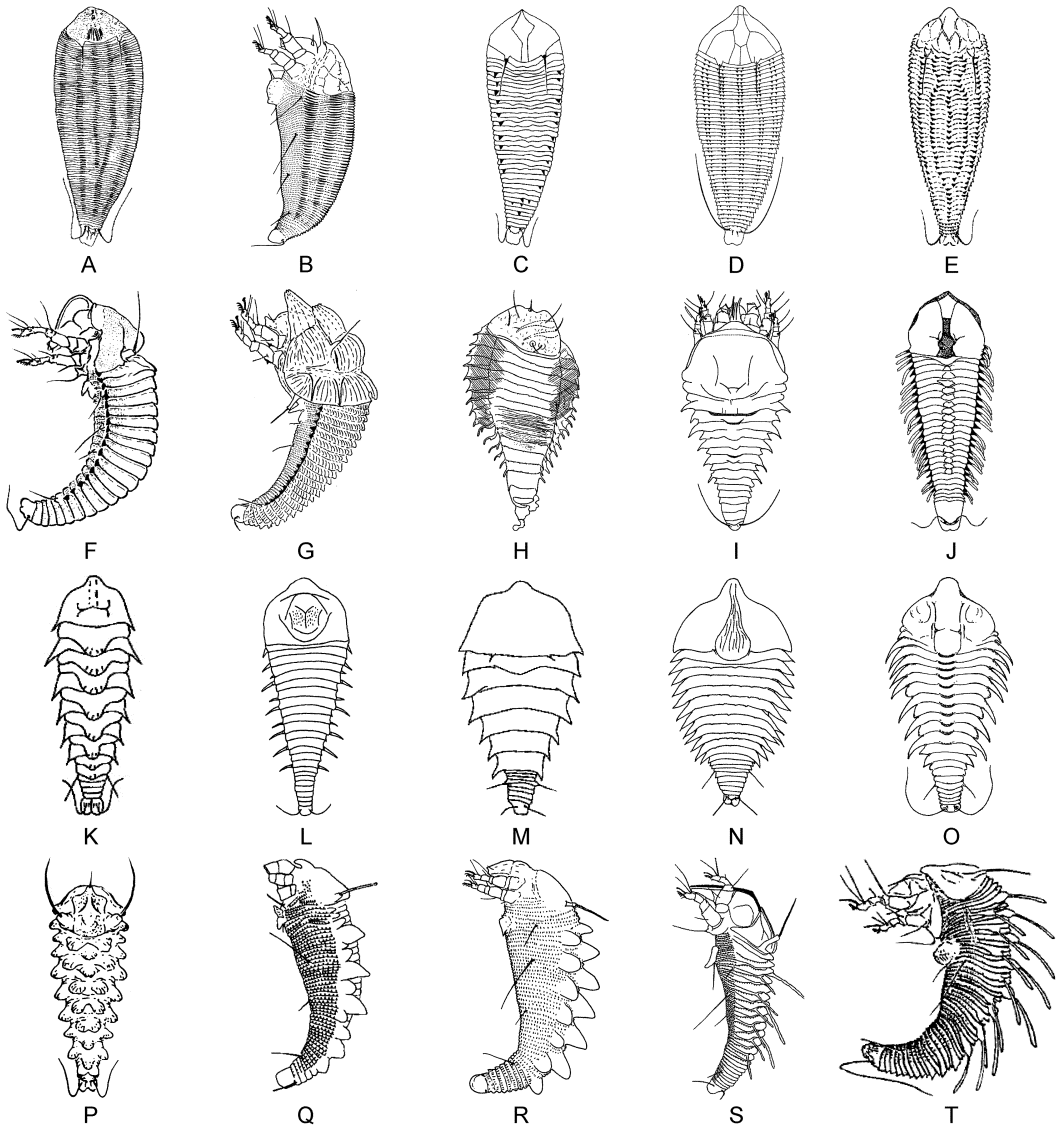
**Diptilomiopidae Keifer.** In this family only two monotypic genera, *Peralox* Keifer (Fig. 13F) and *Scoliquadracus* Wei *et al.* (Fig. 13S), have distinct SS. On the lateral wall of the opisthosoma of *Peralox*, each dorsal annulus bears a small spine-like triangular plate directed backward. Similar tiny spines are present in the tegonotine genera *Hemiscolocenus* Mohanasundaram (Fig. 13) and *Gongella* Kuang & Luo (Eriophyidae: Phyllocoptinae: Tegenotini). The second aforementioned diptilomiopid genus, *Scoliquadracus*, possesses three longitudinal rows of unique ribbon-shaped cuticular processes situated on the posterior margin of notably overlapping tile-shaped dorsal annuli. Similar processes are currently known in only one more genus, *Neodactylus* Umapathy (Eriophyidae: Phyllocoptinae: Anthocoptini; Fig. 13 T). Genera *Scoliquadracus* and *Neodactylus* belong to the “pangolin” morphotype, one of the two previously described morphotypes of vagrant mites with consolidated opisthosomata (Chetverikov *et al.* 2017).

**Eriophyidae Nalepa.** Among eriophyid subfamilies, in Aberoptinae, Cecidophyinae and Eriophyinae, SS are absent. In Nothopodinae only the monotypic genus *Nonthaburinus* Chandrapatya has well developed lateral spines associated with thin, presumably wax, filaments (Fig. 13J). Most eriophyid mites possessing SS belong to the subfamily Phyllocoptinae. About 30 phyllocoptine genera have a series of one of the following SS usually associated with longitudinal opisthosomal ridges: (a) broad lobes, (b) spinules or small triangular plates and (c) large lateral spines. Mites of two anthocoptine genera (*Neophantacrus* Mohanasundaram and *Meyerella* Amrine *et al.*) possess a series of large dorsal lobes projecting from the dorsal annuli (Fig. 13 Q,R), similar to those of the nalepellid genus *Phantacrus*. In several genera (e.g. *Costarectus* Meyer & Ueckermann, *Dipentamerus* Wang & Wei, *Notacaphylla* Mohanasundaram & Singh, *Pentamerus* Roivainen, *Lamyacarus* Chandrapatya *et al.* and *Callyntrotus* Nalepa), there are 2 to 6 longitudinal rows of tiny triangular plates or spinules, usually bearing wax secretions present on dorsal opisthosomal annuli (Fig. 13C,D,E). Remarkably, in some phyllocoptines, e.g. *Echinacarus psophocarpi* (Chandrapatya) and calacarines, e. g. in *Calacarus palmae* Mohanasundaram or *Procalacarus aliyarensis* Mohanasundaram, distinct areas of thickened cuticle, producing wax, are situated on the opisthosomal ridges instead of spines (Fig. 13A,B). Finally, mites of the genera *Spinacarus* Xue *et al.*, *Spinaetergum* Hong & Kuang, *Wanleelagus* Boczek, *Scolocenus* Keifer, *Pseudotagmus* Chetverikov *et al.*, *Tumescoptella* n. g. and some *Shevtchenkella* spp. (e.g. *S. acer* Wei *et al.*) and *Tegenotus* spp. (e.g. *T. heptacanthus* Nalepa) possess long lateral opisthosomal spines (Fig. 13K,L,M,N,O).

**Morpho-functional evaluation of lateral opisthosomal spines in Eriophyoidea.** Along with tiny spinules, triangular cuticular plates, band-shaped processes and areas of thickened cuticle, large lateral spines belong to a common group of serial derivatives of dorsal opisthosomal annuli, named here “spine-like structures” (SS). The brief review above indicates that such large spines are present only in vagrant eriophyoids with flattened and highly consolidated opisthosomata, where they provide additional strengthening of the lateral wall of the body anterior to opisthosomal seta *f.* As a



rule, SS are situated on longitudinal opisthosomal ridges and along the lateral margin of the opisthosoma. Usually SS (especially large lateral spines) are associated with wax production and provide support for wax secretions.



**FIGURE 13.** Examples of spine-like structures in Eriophyoidea. A—*Procalacarus aliyarensis* Mohanasundaram, B—*Echinacarus psophocarpus* (Chandrapatya), C—*Lamyacarus longani* Chandrapatya *et al.*, D—*Costarectus zeyheri* Meyer & Ueckermann, E—*Pentamerus rhamnicroceae* (Keifer), F—*Peralox insolita* Keifer, G—*Hemiscolocenus raris* Mohanasundaram, H—*Ampezzoa triassica* Lindquist & Grimaldi, I—*Propilus alternatus* Navia & Flechtmann, J—*Nonthaburinus litchi* Chandrapatya, K—*Spinaetergum adinae* Hong & Kuang, L—*Spinacarus guniujiangensis* Xue *et al.*, M—*Wanleelagus cerberus* Boczek, N—*Shevchenkella acer* Wei *et al.*, O—*Tegonotus heptacanthus* (Nalepa), P—*Phantacrus lobatus* Keifer, Q—*Meyerella bicristata* (Meyer), R—*Neophantacrus mallotus* Mohanasundaram, S—*Scoliquadracus longipetiolatus* Wei *et al.*, T—*Neodactylus mohanasundarami* Umopathy.

Large lateral spines are a rare trait in Eriophyoidea. They are typical for a very limited number of genera that contain one or a few species<sup>2</sup>. Such genera could be true small clades or represent aberrant morphotypes within larger monophyletic groups. In both cases, the lateral spines appear to

be attributes of evolutionarily isolated representatives of eriophyoids, which might be “long branches” on the DNA tree of Eriophyoidea when it is reconstructed. Definitely, mites with less transformed opisthosomata, probably morphologically similar to genera *Epitrimerus* Nalepa or *Phyllocoptes* Nalepa, were ancestors of the modern forms bearing lateral opisthosomal spines. The data at hand suggest that the development of such spines is a protective adaptation; moreover presence of large lateral spines seems to be a homoplasy within Eriophyoidea. Although mites with such spines presumably do not form a clade, at the lower taxonomic level their presence can be used for phenotypically grouping similar forms together, like it was done in Amrine *et al.* (2003). Further, within a particular phylogenetic lineage, such spines are presumed to be present in the most derived forms. In this assumption we are in accordance with Lindquist (in Sidorchuk *et al.* 2015), who interpreted *Ampezzoa*, possessing transformed opisthosoma with large lateral spines, to be the most derived form in comparison to other triasacaroids, which are devoid of such structures.

Finally, our data on *Tumescoptella aculeata* n. sp. indicate that in an eriophyoid life cycle, different forms of females with and without lateral spines may be present. This hypothesis opens two important questions. (1) Could some triasacaroid and eriophyoid taxa that are devoid of spines be deutogynes of other taxa, which were described based on “spiny” holotypes? This rhetorical question points out the significance of further reexamination of previously described type specimens and careful seasonal observations on extant eriophyoid mites prior to creating a new taxon. (2) What is the true role of deutogynes in *Tumescoptella* mites associated with palms? Addressing this question, it is reasonable to reference Couvreur *et al.* (2011), who demonstrated that the earliest palm lineages were primarily restricted to tropical rain forests (TRF) and stressed that adaptation to dry non-TRF biomes did not arise until the Paleocene, within the fan palm subfamily Coryphoideae. These observations by botanists tentatively suggest that (a) the discussed deutogynes might be the forms adapted for dry summer periods, e.g. for estivation, and that (b) the dry climate in the new areas invaded by the evolving coryphoid palms, about 50 Mya, could be the main evolutionary factor influencing morphological transformation of TP on palms. These assumptions provide an important rough date on the origin of the TP lineage, no earlier than the beginning of Paleocene.

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2. except large genera *Shevtchenkella* and *Tegonotus* which we consider to be paraphyletic

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