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Two Eocene species of peacock mites (Acari: Tetranychoidae: Tuckerellidae)

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ABSTRACT

Tuckerellidae are suctorial plant feeders with a wide host range, exploiting both above-ground and underground plant parts. A new species, *Tuckerella weiterschani* n. sp., is described from Eocene (ca. 40 mya) Baltic amber, and *Tuckerella fossilibus* Khaustov, Sergeyenko & Perkovsky, 2014 from Eocene Rovno (Ukrainian) amber is redescribed, each based on single holotype specimens. The two mites are morphologically distinct, with most striking differences concerning posterior, H-row of idiosomal setae. *Tuckerella fossilibus* has unusually large, obovate setae h_1 , while the other setae in H-row are robust and flagellate with three different lengths. The new species, *T. weiterschani*, has small, narrowly lanceolate setae h_1 , while flagellate h_2 – h_8 are fine, filiform and similar in length. Setae h_1 – h_8 in the holotype of *T. weiterschani* are held erect and directed forward over the mite's body, in a position reminiscent of the apparently defensive posture displayed by recent *Tuckerella* species. Tarsal setations of the two fossils and comparison with those of the recent Tuckerellidae advances discussion on the evolutionary significance of setal variation in acariform mites.

Keywords fossil, plant-feeding mites, new species, fluctuating asymmetry, vertitions, regressive evolution, leg chaetotaxy

Zoobank <http://zoobank.org/086E8B1E-6B45-4250-B67F-9A6C470BFA09>

Introduction

Plant-feeding trombidiform mites – gall and rust mites, tetranychoid, some tydeoid, eupodoid and heterostigmatic mites – are presently ubiquitous on higher plants. Phytophagy was repeatedly acquired by different lineages of Trombidiformes, and some of these acquisitions might have happened as early as in the Mesozoic (Lindquist 1998). There is, however, very little direct evidence of this evolution, for the fossil record of phytophagous mites is extremely scant. The oldest Tetrapodili, four species of Triasacaroidea, are described from the Triassic (ca 230 mya) amber of South Dolomites in Italy (Schmidt *et al.* 2012; Sidorchuk *et al.* 2014). A middle/late Eocene (ca 35 mya) Eriophyidae specimen from Maslin fossil beds in South Australia is described as a species in a Recent genus, *Aculops* Keifer, 1966 (Southcott and Lange 1971). Two possible spider mite species are described from Eocene (56 to 33 mya) Baltic amber by C.L. Koch in Koch and Berendt (1854): *Panonychus gibbus* (C.L. Koch, 1854) and *Schizotetranychus? brevipes* (C.L. Koch, 1854), but their morphology is only partly known (Oudemans 1937). One species of a peacock mite (Tetranychoidae: Tuckerellidae), *Tuckerella fossilibus* Khaustov, Sergeyenko, Perkovsky, 2014, is known from Eocene Ukrainian (Rovno) amber. It was described from a single poorly preserved specimen. A close preparation was not undertaken due to the risks involved, and although this resulted in its description being incomplete, there was not doubt as to the species identity. Recently, a new peacock mite fossil was found in Eocene Baltic amber by Thomas Weiterschan, who has kindly lent the specimen for our study. The mite, fossilized in a defensive posture characteristic for extant tuckerellids, appeared to represent a distinct species, new to science.

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By this contribution, we aim to describe the new species, *Tuckerella weiterschani* n. sp., and augment the description of *T. fossilibus* after closer examination of its holotype.

Materials and methods

Material

The Baltic amber piece with a single inclusion, representing a new species of *Tuckerella*, originally in the collection of Thomas Weiterschan (TW), collection identification number TW 1288. The piece is transferred to the collection of the Geological-Paleontological Museum and University of Hamburg (GPIH), and assigned a new collection number GPIH 4598. The piece is translucent, light yellow in colour. The fragment measuring 1x0.7x0.7 mm, containing the mite, was extracted and polished on six sides. For a review, and further data on the geology, of Baltic amber, see Weitschat and Wichard (2002). The Holotype of *Tuckerella fossilibus* is a Rovno amber piece, found in Klesov (Fedorovka) locality in Ukraine. The geology and fauna of this locality is reviewed by Perkovsky *et al.* (2010). The specimen is deposited in I.I. Schmalhausen Institute of Zoology, National Academy of Science, Kiev (SIZK), collection number KF-2237. A fragment, sized 2x1x0.5 mm, of the piece was mounted in the Buehler EpoThin epoxy resin between two 1 cm round coverslips. The fragment has a fracture that runs through the anterior part of the mite specimen. The preparation is labeled and glued with a hot-melt adhesive to a 1.5 mm-thick transparent plastic frame with a round aperture, allowing for observation from dorsal and ventral sides. The frame was also labeled.

Amber preparation

Amber pieces were cut and polished following protocols of Sidorchuk (2013), with tools described by Sidorchuk and Vorontsov (2016).

Imaging

All observations were done with light microscopy. Image stacks were obtained with Zeiss AxioImager A2 compound microscope with dry lenses and differential interference contrast (DIC) illumination with AxioCam 506 color digital camera. Bright field and polarized light micrographs were obtained with Nikon Eclipse 800 microscopes with 60x water immersion lens, Nikon DS-Fi1 and Nikon D7000 digital cameras. All images were corrected for light, color, noise and sharpness using Adobe Lightroom, then processed with Helicon Focus algorithm A, always with some detail manually transferred from the individual focal planes to the resulting images. These images are further referred to as “layered”. Original image stacks are available through Figshare, doi:10.6084/m9.figshare.c.3743399.

Drawings are made in Adobe Photoshop with stacks of the light micrographs as a background or in InkScape with a live capture from the Amscope MU900 camera mounted on Nikon Eclipse 800 microscope as a background (Sidorchuk and Vorontsov 2014).

Terminology

The terminology is that developed by F. Grandjean for acariform mites (see Trávě and Vachon 1975 for review and bibliography, and Lindquist 1985 for application to Tetranychoidae); shapes of setae are described using botanical glossary by Beentje (2010). Idiosomal setae designations follow Beard *et al.* (2013), *i.e.* prodorsal setae are named sc_1 , sc_2 , v_1 , v_2 , setal row D contains 6 setae and row E contains 3 setae. There are three versions of the homologization of tuckerellid tarsal setae to those of the other acariform mites: (1) Quiros and Baker 1984, (2) Lindquist 1985, reproduced in Servin and Otero 1989, and (3) Bochkov *et al.* 2009. We accept here Lindquist’s version, in which the primilateral setal pair (pl) is considered present in the larva of Tetranychoidae (including Tuckerellidae), the tectal setal pair (tc) and seta l_1 ”

are added in postlarval stages, dorsal seta *d* and antelateral setal pair (*a*) are absent. Leg setal counts are written from trochanter to tarsus as the number of tactile/eupathidial setae followed by the number of solenidia in parentheses. Leg setation formulae represent the cumulative data from both legs. For example, when on the right tibia III the setae *l'* and *v'* are visible, while on the left these are *d* and *v'*, observed setal count is $d+l'+v'=3$ setae.

Comparative data on the leg setation was obtained from the following species and works: *T. pavoniformis* Ewing, 1922 and *T. ornata* Tucker, 1926 – from Baker and Pritchard 1953; *T. litoralis* Collyer, 1969, *T. japonica* Ehara, 1975, *T. anommata* Smith Meyer and Ueckermann, 1997, *T. channabasavannai* Mallik and Kumar 1992, *T. revelata* Beard and Walter, 2005 – from the original descriptions of these species. Hypotheses on the setal homologies are ours, but for the latter species Jennifer Beard has generously supplied additional sketches with her setal homologies, confirming our hypotheses. In addition, Evert E. Lindquist (EEL) has kindly examined and sketched for us tarsi I and tarsus II of a male *T. flabellifera* Miller, 1964 and tarsus I of female *T. ornata*, kept at the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa); for these, setal homologies are by EEL.

Measurements

The measurements were taken from edge to edge of a sclerite or seta in its widest part, choosing where possible the structures oriented perpendicularly to the optical axis of the microscope. As the orientations were non-ideal, all measurements are to be treated as the minimal estimates, and are rounded to closest 5 if over 50. The unit is micrometer (μm).

Systematic paleontology

Class Arachnida Cuvier, 1812

Order Trombidiformes Reuter, 1909

Family Tuckerellidae Baker & Pritchard, 1953

Genus *Tuckerella* Womersley, 1940

Type species: *Tenuipalpus ornatus* Tucker, 1926, by original designation

Tuckerella weiterschani n. sp. (Figs 1–4)

Zoobank: [AB714EE7-5602-4792-A9A0-B42618B1E983](https://doi.org/10.24349/AB714EE7-5602-4792-A9A0-B42618B1E983)

Description — Tritonymph or adult, gender unknown. Length of idiosoma – 275, width – 155, height – 55; body length including gnathosoma – 310.

Gnathosoma (Figs 1, 2, 4) — Only right palp clearly visible. Palpgenu dorsally with seta *d*, reaching just beyond tip of tibia. Palptibia with large, hooked tibial claw and three setae: *d*, slightly longer than palpgenu; short *l''*, reaching to tip of tibial claw; medium-sized *l'*, about as long as palptibia+tibial claw. Palptarsus completely covered by tibial claw in dorsal view, and elongate, roughly necktie-shaped as visible in lateral view, 14 long, phaneres not visible. Subcapitulum long and narrow, with alveolus of seta *m* visible basally and one pair of small peg-like adoral setae visible apically (Fig. 2, arrow). Peritremes prominent and emergent (Figs 1H, 4A). Stylophore and cheliceral stylets not visible.

Idiosomal dorsum (Figs 1, 3, 4A) — Visible ornamentation reticulate (Fig. 1D–F). Prodorsum with 4 pairs of setae (vertical *v*₁, *v*₂, scapular *sc*₁, *sc*₂). Setae *v*₂, *sc*₁ and *sc*₂ fan-like (Figs 1D, 4A); setae *v*₁ broadly lanceolate, with tapered tip (Fig. 1H). Two pairs of eyes located anterolaterally to bases of setae *sc*₁ (Figs 1F, 4A, oc); posterior eye distinctly larger than anterior. Hysterosoma with 7 setae in C-row, 6 in D-row, 3 in E-row, 2 in F-row, 8 in H-row. All setae in rows C–F broadly obovate to orbicular. Setae *c*₁–*c*₃ and *d*₁–*d*₃ of medium size (12x20), subequal. Setae *e*₁ and *e*₂ slightly smaller than *c*₁–*c*₃ and *d*₁–*d*₃. Setae *f*₁ and

Figure 1 *Tuckerella weiterschani* n. sp. holotype. Layered DIC micrographs: A – dorsal view, inserts show two aspects of amber piece containing holotype and its package, not to scale; B – ventral; C – posterior; D, E, details of idiosomal setae, ventral view; F, eyes; G, posterior idiosomal setae laterally; H, detail of prodorsal seta v_1 and peritreme; J, lateral aspect. Rectangles in A, B, J show positions of Figs D-G. Abbreviations: an, anal area; ge, genital area; oc, eyes; per, peritreme; plp, palp; sub, subcapitulum; I–IV, legs.

Figure 2 *Tuckerella weiterschani* n. sp. holotype. Layered POL micrograph. Gnathosoma laterally, arrow points to adoral seta. Abbreviations: palp segments: Fe, femur; Ge, genu; Ta, tarsus; Ti, tibia; ti.cl, palptibial claw.

f_2 (8x14) distinctly smaller than e_1 and e_2 ; f_2 situated anterolaterally to bases of f_1 . Setae c_4 (20x30) distinctly larger than c_1 – c_3 ; c_5 (20x40) more elongate and narrow than c_4 ; setae c_6 and c_7 similar to c_5 , but with stronger tapered tips, especially well visible on left side of body (Figs 1D, 3). Setae d_4 – d_6 and e_3 similar in shape to c_4 – c_7 , but clearly larger (d_6 30x60). Distinct apophyses of h -series setae situated close to each other in one transverse line. Setae h_1 short, narrowly lanceolate, barbed, 30 long (Fig. 1G), much shorter than filiform and weakly barbed setae h_2 – h_8 . Setae h_2 – h_8 longer than body (h_2 440) and directed dorsad and antieriad (Fig 1A, C, G, J). Only shield margins visible are anterior margins of dorsal shields C and D (Figs 1A, 3).

Idiosomal venter (Fig. 1B) — Somewhat collapsed, mostly obscured by legs. Cuticle lightly striate, setation not discernible. As far as visible, typical for females of Recent *Tuckerella* species (see for example Fig. 2 in Beard and Walter 2005). Genital and anal openings discernible, but no setae visible with certainty.

Legs (Figs 1B, J; 4) — Leg I (Fig. 4A, A'). Femur with 3 large, fan-like dorsal and lateral setae (d , l' , l''), and 2 small, setiform ventral setae visible (probably ventral v'' and v_1''). Genu with 5 large, fan-like dorsal and lateral setae (d , l' , l_1' , l'' , l_1'') and one visible setiform seta v'' . Tibia with large, fan-like setae l'' , l_1'' , l' ; and more narrow d ; solenidion ϕ baculiform, situated on short protuberance; single visible seta v'' small, setiform. Tarsus with two claws and empodium with tenent hairs (Figs 1A, 4A, A'); two solenidia present, ω_1 about 1.5 times longer than ω_2 ; unguinal setae (u) poorly visible, only on left leg, modified, comb-like; other setae on tubercles: abaxial members ($'$) of fastigial (ft) and primilateral (pl) pairs long, distinctly longer than tarsus, their adaxial members ft' and pl' about half as long; pl' weakly barbed; tectal (tc) smooth, tapered; proral p'' blunt, thick, probably eupathidial, possible alveolus of p' visible on right leg; simple primiventral seta p_v visible on left tarsus; on right tarsus, alveolus in position l_1'' visible and what may be seta l_1'' discernible. Leg II (Fig. 4B) setation partly visible, tip of tarsus and trochanter hidden in deformed venter. Femur with 3 fan-like – d and (l) – and one poorly visible simple seta, possibly basiventral bv'' . Genu with 4 fan-like setae (d , (l), l_1'), tibia

Figure 3 *Tuckerella weiterschani* n. sp. holotype dorsally.

with 3 fan-like setae – *d*, (*l*) – visible. Tarsus with one blunt phanere on prominent tubercle (probably solenidion ω) and 7 simple setae or their alveoli visible: *pv'*, pairs (*p*) and (*tc*) on low tubercles, seta *pl''* and possible alveolus of *ft''*. Legs III and IV (Fig. 4C, D, D') visible almost entirely, with paired claws, paired empodia and at least 4 pairs of tenent hairs each. Setation: leg III trochanter with single thick, heavily barbed seta *l'* visible, femur with 2 setae: simple euventral *ev'* and short, narrow, barbed *d*; genu with single short, narrow, barbed seta *d* visible, tibia with 3 setae: short, narrow, barbed *d*, fan-like *l'*, simple *v'*; tarsus with two setae and three alveoli visible, setal pair (*p*) and solenidion apparently absent. Leg IV trochanter and femur without visible setae; genu with setiform *v'* and short, narrow, barbed *d*, tibia with single short, narrow, barbed seta *d* visible. Tarsus with 7 setae: pairs (*ft*), (*tc*) and (*u*) visible dorsally (in ventral aspect of mite, Fig. 4D'), seta *pv'* – in lateral aspect (Fig. 4D). Observed leg setation formulas: leg I: ?-5-6-5(1)-12(2); leg II: ?-4-4-3-7(1); leg III: 1-2-1-3-5; leg IV: ?-?-2-1-7.

Holotype and type repository — Originally from private collection of Thomas Weiterschan, coll. # TW 1288, housed in the Geological-Paleontological Museum and University Hamburg (GPIH), collection number GPIH 4598. The holotype is the only inclusion in a rectangular

Figure 4 *Tuckerella weiterschani* n. sp. holotype details. A', right tarsus I adaxially; A, left leg I abaxially, gnathosoma and anterior idiosoma dorsally; B, leg II abaxially; C, leg III abaxially; D, leg IV abaxially; D', tarsus and tibia IV dorsally. Abbreviations: oc, eyes; per, peritreme; plp, left (poorly visible) palp; sub, subcapitulum; ti.cl, palptibial claw. Gray lines represent poorly discernible structures.

light yellow amber piece measuring 1x0.7x0.7 mm, polished on six sides, stored in plastic O-ring-capped vial with water and preservative Thymol (Fig. 1A).

Type locality, occurrence and geological age — Type locality is Baltic Sea Coast, amber in Blue Earth fossil beds, dated late Eocene. Only known from the type specimen and locality.

Etymology — The new species is named in honor of Thomas Weigershan, who discovered the specimen, promoted its study and assured its holotype deposition in a public repository.

Remark — The holotype and only known specimen of *T. weiterschani* has emergent peritremata, leg I tarsal setae l_1'' and leg I genual and tibial setae (l_1) present. These features

suggest that the specimen is at least tritonymphal (Servin and Otero 1989, Beard and Walter 2005). In the presence of the tapered setae v_1 and lateral idiosomal setae and in the absence of clear view on the genital area, however, we cannot distinguish between an adult and a tritonymphal stage. Emergent peritremes in immature tuckerellid mites, not mentioned in the literature to our best knowledge, do occur at least in four Recent species starting from the deutonymphal stage (J. Beard, pers. comm.), and are thus inconclusive. The Diagnosis below is hence preliminary, and only uses those characters known to be relatively stable through the last two stages of the tuckerellid ontogeny.

Differential diagnosis — By the presence of seven pairs of subequal filiform setae h_2 – h_8 the new species is similar to five Recent species: *T. coleogynis* Jorgensen, 1967, *T. elegans* Rossi de Simons, 1972, *T. eloisae* Servin and Otero, 1989, *T. hypoterra* McDaniel and Morihara in McDaniel *et al.* 1975 and *T. spechtae* Womersley, 1957. The new species differs from *T. spechtae* and *T. hypoterra* by the relative positions of setal pairs f_1 and f_2 , f_1 being inserted clearly posterior to f_2 in *T. weiterschani*, as opposed to slightly anterior in these two species; in addition, *T. spechtae* has setae h_6 shorter than the other flagellate setae. From *T. eloisae* the new species differs by its much smaller size (total body length – including gnathosoma – 310 in *T. weiterschani* vs. 480 in tritonymph, 473 – 566 in adults of *T. eloisae*). *T. elegans*, only slightly larger than *T. weiterschani* (adult idiosomal length 342 – 370 in *T. elegans* vs. 275 in *T. weiterschani*), and *T. coleogynis* differs from the new species by its setae v_1 having a smooth edge and uneven reticulation vs. these setae widely lancetiform, with tapered tips in *T. weiterschani* (the validity of this character is only certain if *T. weiterchani* holotype is an adult female), and having setae h_2 – h_8 as long as body, vs. at least 1.5 times body length in *T. weiterschani*. *T. coleogynis*, whose size is unknown, is the most similar to *T. weiterschani*, differing in the shape of dorsolateral idiosomal setae (only significant if *T. weiterchani* holotype is an adult female) and distribution of setulae on the setae h_2 – h_8 : present only in basal part in *T. coleogynis*, evenly distributed throughout the length in *T. weiterschani*.

***Tuckerella fossilibus* Khaustov, Sergeyenko & Perkovsky, 2014. (Figs 5–7)**

Tuckerella fossilibus Khaustov, Sergeyenko & Perkovsky, 2014, p. 367, Figures 1–5.

Redescription — Deutonymph. Length of idiosoma – 245, width – 165.

Gnathosoma (Figs 5D, 7B, C) — Left palp covers main part of right palp dorsally, both palps preserved in a way to cover infracapitulum dorsally. Palpgenu dorsally with seta d slightly not reaching base of tibial claw. Palptibia with large, hooked tibial claw and three pairs of setae: d slightly longer than length of palpgenu; short l'' , reaching to tip of tibial claw; medium-sized l' , about length of palptibia+tibial claw. Inner margin of tibial claw transversely striate. Palptarsus with 5 visible phaneres: 3 terminal, blunt-ended (probably palpal eupathidia), one short dorsal and one short ventral. Subcapitulum long and narrow with visible stylet protruding apically (Figs 5D, 7B, st); ventrally with one pair of long subcapitular setae m . Peritremes not evident. Oval stylophore, ca 100x40, visible inside body (Figs 5A, 6, sty).

Idiosomal dorsum (Figs 5, 6, 7B) — Cuticular ornamentation, where visible anterodorsally, irregularly reticulate (Fig. 5A). Number of dorsal idiosomal setae as in *T. weiterschani* n. sp. Setae v_2 , sc_1 and sc_2 fan-like (Fig. 5C, D); v_1 considerably different from other prodorsal setae, with smooth margins and weakly tapered tip (Figs. 5D, 7). Two pairs of eyes located anterolaterally to bases of setae sc_1 ; posterior eye distinctly larger than anterior (Fig. 7B, oc). All setae of C, D, E and F-rows broad, flat, ovate to obovate in shape: c_1 – c_3 , d_1 – d_3 and e_1 , e_2 of medium size, subequal (16 – 18 x 24 – 28); f_1 and f_2 slightly smaller than e_1 and e_2 ; f_2 situated on same transverse level as f_1 . Lateral setae c_5 – c_7 , d_4 – d_6 and e_3 distinctly larger than central, more elongate, with rounded tips, largest d_6 28 x 60. Setae h_1 large, flat, obovate (27 x 55), setae h_2 – h_8 flagellate: h_2 , h_4 , h_5 , h_7 long, barbed, tapered (180, 270, 180, 220 respectively),

Figure 5 *Tuckerella fossilibus* Khaustov, Sergeyenko & Perkovsky, 2014 holotype deutonymph. Layered DIC micrographs: A – dorsal view, rectangles show positions of figures C, D, insert shows container with holotype; B – ventral; C – detail of idiosomal setae; D – left leg I and anterior proterosoma dorsally. Abbreviations: st, cheliceral stylets; sty, stylophore; ta, palptarsus; ti.cl, palptibial claw.

Figure 6 *Tuckerella fossilibus* Khaustov, Sergeyenko & Perkovsky, 2014 holotype deutonymph dorsally. Abbreviation: sty, stylophore.

h_6 short, thick, heavily barbed, blunt (40); h_3 , h_8 intermediate in length and thickness, barbed, tapered (80). Only anterior margins of dorsal shields C and D clearly visible (Fig. 6).

Idiosomal venter (Figs 5B, 7A, D, E, F) — Dark and collapsed, obscured by legs. Only coxal setae are partly discernible: $1a-c$ and $2b$ smooth, fine, $1a$ longest; $2c$ long, thick, heavily barbed. Genital and anal openings indiscernible.

Legs (Fig. 7) — Dark and curled, mostly visible in ventral aspect, with some setae poorly discernible. Leg I (Fig. 7A, B): trochanter without visible setae; femur with three large obovate setae (d , l' , l'') and setiform bv'' , other ventral setae not visible. Genu with three large obovate setae (d , l' , l'') and setiform v'' , other ventral setae not visible. Tibia with large, obovate seta l'' and narrower d , l' ; ventral setae not visible; solenidion ϕ baculiform, situated on short tubercle. Tarsus with two claws and empodium, each with clearly visible tenent hairs; two solenidia present, ω_1 about 2 times longer than ω_2 ; setae: (u) simple and short, abaxial (') members of pairs (ft) and (pl) long, distinctly longer than tarsus, pl' about half shorter on right leg, absent

Figure 7 *Tuckerella fossilibus* Khaustov, Sergeyenko & Perkovsky, 2014 holotype deutonymph detail: A – right tarsus I in ventral view of mite; B – leg I, gnathosoma and anterior proterosoma, dorsal view; C–J, legs in ventral view of mite: C – right leg II; D – left leg II and seta 3a; E – right leg III; F – left leg III; H – right leg IV; J – left leg IV. Abbreviations: oc, eyes; st, cheliceral stylets; ta, palptarsus; ti.cl, palptibial claw. Gray lines represent poorly discernible structures.

on left leg; (*tc*) situated on tubercles, fine, tapered, (*p*) blunt, short, apparently eupathial, difficult to discern where hidden behind ambulacrum; *pv'* setiform. Leg II (Fig. 7C, D): trochanter not discernible; femur with long, thick, heavily barbed seta *bv''* and 3 obovate large setae *d* and (*l*) (*d* and *l''* artificially split on left leg); genu with 3 obovate setae visible; tibia with 3 obovate and one or two long simple seta visible ((*v*) on left, only *v''* on right leg); tarsus with ambulacrum as in leg I (well visible on right leg), one solenidion, and 10 smooth setae: long *ft''*, shorter *ft'*, (*pl*), (*tc*), (*u*) (one member of pair visible on each leg), *p''* and *pv'*. Leg III (Fig. 7E, F): trochanter with single visible seta *l'* thick, long, heavily barbed; femur with small obovate seta *d* and smooth simple *ev'*; genu with single visible small obovate seta *l'*; tibia with 2 clearly visible setae, simple *v'* and small obovate *l'* (visible transversally on right leg), and one spot that may be alveolus of seta *d*; tarsus with ambulacrum like in leg II and 7 simple setae (only 4 clearly visible on right leg): (*ft*), (*tc*), (*u*) and *pv'*. Leg IV (Fig. 7H, J): poorly visible, dark, trochanter and setation of femur indiscernible; genu with one well visible narrowly obovate seta *d* on left leg, no visible setae on right; tibia with 2 ventral setae well visible, two discernible on right leg, one well visible seta and one discernible on left; tarsus with two claws discernible, 3 setae visible on left and one on right leg. See figure for possible setal homologies. Observed setation (trochanter to tarsus, solenidia in parentheses): leg I: ?-5-3-4(1)-11(2); leg II: ?-4-3-5-10(1); leg III: 1-2-1-2/3?-7; leg IV: ?-?-1-2?/4?-?

Remarks — Khaustov *et al.* (2014) in original description of *T. fossilibus* were not able to identify its life stage. Now, after more detailed description we can suggest that it is probably a deutonymph. Our opinion is based on the setation of leg I, which shows: (1) two tarsal solenidia, (2) absence of the tarsal seta l_1 , (3) three obovate setae on each genu and tibia. According to observations by Quiros-Gonzalez and Baker (1984), Lindquist (1985), Beard and Walter (2005) and Beard *et al.* 2013, although there is some interspecific variation, the second tarsal solenidion is deutonymphal, tarsal seta l_1 is tritonymphal, and three obovate setae on first genu and tibia are only present in deutonymphs: known protonymphs are found to have 1–2 obovate setae per segment, while tritonymphs and adults have five.

Addition to the differential diagnosis — Certain caution is necessary when using this comparison, for the immature specimen is being compared to adults. Based on the available descriptions (Quiros-Gonzalez and Baker 1984, Lindquist 1985, Beard and Walter 2005, Beard *et al.* 2013), ontogenetic changes of the opisthonotal setation may affect setae v_1 (in *T. revelata* they are obovate, with rough edge, in larva, with outline smoothing out in the subsequent stages), leaf-shaped C-H-row setae (relatively narrower and more tapered in the immatures) and flagellate H-row setae (becoming relatively shorter during ontogeny). *T. fossilibus* is so far unique tuckerellid species known to have obovate setae h_1 similar in size to the lateral setae of C-, D- and E rows. By the shape of proterosomal setae v_1 and the relative shortness of setae h_1 and h_6 , deutonymphal *T. fossilibus* is similar to adults of *T. pavoniformis* (Ewing, 1922), *T. indica* Prasad, 1973 and *T. channabasavannai* Malik and Kumar, 1992. It differs from them by much larger setae h_1 and by the differentiated shapes of the other H-row setae (*T. pavoniformis* has setae h_2 – h_5 , h_7 and h_8 all similar, whip-like (Baker and Pritchard 1953), as do *T. indica* and *T. channabasavannai*). By the shape of setae v_1 *T. fossilibus* is also similar to *T. japonica* Ehara, 1975 and to *T. kumaonensis* Gupta, 1979, but these species have three pairs of comparatively small leaf-like setae in *h*-series.

Holotype container — Amber fragment with holotype, sized 2x1x0.5 mm, is mounted in the Buehler EpoThin epoxy resin between two 1 cm coverslips. The preparation is glued with a low-temperature hot-melt adhesive to a 1.5 mm-thick transparent plastic frame (Fig. 5A).

Discussion

With the restricted number of known fossils of the phytophagous mites, the discovery of a tuckerellid specimen in Baltic amber appears lucky. Unlike saprophagous mites, whose recently redescribed species are the same for the two amber deposits (Sidorchuk and Norton 2010; 2011a, b; Sidorchuk and Klimov 2011), the tuckerellids from Rovno and Baltic ambers are not conspecific. Their dissimilarity is indicative of a morphological diversity in Eocene (ca 40 mya) tuckerellids comparable to that found among Recent species. It is difficult, though, to discuss the groups of species in Tuckerellidae, for the family is in much need of a thorough revision, as most species are only cursorily illustrated. We can only attempt some general implications based on the morphological similarities discussed in Remarks, as follows.

Ethological implication: the defensive posture. Holotype of *T. weiterschani* is captured in the posture, first described as defensive by Ochoa (1989) in *Tuckerella knorri* Baker and Tuttle, 1975. When disturbed, a tuckerellid mite makes a few quick movements, alternately raising and lowering its ‘tail’ of the *h*-setae. The whip-like setae of the H-row are often long enough to cover the whole body, legs and gnathosoma of the mite, possibly disturbing an intruder. Our finding shows (Figs 1A–C) the defensive adaptation of a peacock mite dates back at least to the Eocene.

Ecological and geographical implications. Tuckerellidae are suctorial plant feeders, like other tetranychoid mites. Recent species are known to exploit both aboveground and

underground parts of the plants, including bark and roots (Jorgensen 1967, McDaniel *et al.* 1975, Beard *et al.* 2013). The host range of even an individual species may include multiple plant species, not necessarily closely related: for example, *T. japonica* is known from Ulmaceae, Theaceae, Actinidiaceae, Ebenaceae, Ericaceae, Rhamnaceae and even coniferous Juniperaceae (Beard *et al.* 2013). Tuckerellidae are found in climes from humid tropical through Mediterranean and hot desert, but also in cold arid areas. Their presence in amber, therefore, is not informative with regard to the amber forest composition or climate.

Evolutionary implications: setal variation. Our specimens appear to have asymmetrical setation at least on tarsi I (Figs 4, 7, 8): KF-2237 (deutonymph) does not show seta *pl'* on the left (Figs 7B, 8C), while this seta is present on the right (Figs 7A, 8D), and GPIH 4598 (tritonymph or adult) has at least an alveolus in *l₁'* position on the right leg (Figs 4A', 8A), while there is no such seta or alveolus on the left (Figs 4A, 8B). This encouraged us to review what is known on the tuckerellid tarsi (see Material and Methods). Below, we only consider tarsi I, and only the setae (*pl*), (*ft*) and *l₁'*, for they are the best visible and the least likely overlooked. It appeared that these setae vary within modern tuckerellid species. In *T. ornata*, seta *l₁'* is present in the specimen examined by E. Lindquist, absent in Baker and Pritchard 1953 Fig. 6b. In *T. revelata*, variable setae appear to be *ft'* (absent in female, Fig. 4A by Beard and Walter 2005, present in all other illustrated immature and adult legs) and *pl'* (absent in protonymph, Fig. 12A by Beard and Walter 2005). Note that although Beard and Walter 2005 give setal formulae 14(2) for adult and tritonymph and 13(2) for deutonymph tarsus I in the text, they illustrate 12 setae plus 2 solenidia for the adults and tritonymph and 11(2) for the deutonymph, which is in accordance with the otherwise known maximum complement in this family. The discrepancy is due to the authors' counting for the solenidia twice: (1) in the total count of phaneres and (2) in parentheses (J. Beard, pers. comm., June 2017). Seta *pl'* also is variable in *T. anommata*: present according to the counts, illustrated for the male, but lacking in the illustrated female left tarsus, where the remaining seta *pl'* has an almost dorsal position (Smith Meyer and Ueckermann 1997, Figs. 89 and 85, respectively).

Each of them being admittedly questionable, these observations considered together evoke a long-standing discussion on the possible link between the variation and evolution of leg setae in mites. There are two notions on this link. Based on his 46-year studies on Acariformes, including rearing experiments on parthenogenetic oribatid mite *Platynothrus peltifer*, Grandjean (1974) formulated the hypothesis of the RVA – regressive evolution (of a seta in the simple row within a lineage) by the alternating vertitions. Unilateral absence of a seta, according to this hypothesis, is an indication of its future disappearance, and the frequency of such absences should grow, albeit very slowly, in a lineage of many generations. Wauthy *et al.* (1991) brought to acarology another notion, that of the fluctuating asymmetry (Ludwig 1932, Van Valen 1962) – the phenomenon common for bilateral organisms, variation resulting from the random developmental accidents and having no evolutionary implications. In this model, the frequency of absence of a particular seta is not indicative of its future loss, and this parameter for a particular seta is not inheritable. The latter notion is developed and substantiated with new observations and statistical analysis (see Wauthy *et al.* 1998, Laponce *et al.* 2001), studying three strains of the haplodiploid prostigmatan *Tetranychus urticae*, although each with two generations (mothers and sons) only. Although their results were statistically significant, this evolutionary experiment was very far from analyzing ‘hundreds, maybe hundreds of thousands of generations’ that Grandjean (1974) considered necessary for a seta to become lost by alternating vertitions. He (Grandjean, 1974: 779) has actually predicted that no notable change of the vertition frequency would be statistically observable within ten or twenty generations of a parthenogenetic lineage – thus, he indicated that the RVA hypothesis cannot be rejected by a feasibly long artificial experiment.

Paleontological evidence somehow shows us the result of an unfeasibly long evolutionary experiment. Although they are not linked by a direct lineage from mother to daughter, the two fossils described here on one hand and the modern tuckerellids described in the literature on the other hand are random specimens within the same genus, separated by at least 40 million

Figure 8 Leg I setation of two Eocene *Tuckerella* specimens (layered DIC micrographs). A–B, *T. weiterschani* holotype: A – right leg abaxially, note at least alveolus of tarsal seta l_1'' present; B – left leg I abaxially, note setae visible but l_1'' apparently absent; C–D, *T. fossilibus* holotype deutonymph: C – left leg ventrally, note setation well visible but tarsal pl' apparently absent; C', part of C – individual focal plane showing tibial solenidion and seta l'' ; D – right leg, tarsus dorsally, note seta pl' present.

generations. These specimens seem to show variations of the same, eustatic, setae, which may mean that the frequency of their absences, or vertitions, is high in Recent tuckerellids and was already high in the Eocene ones. In the light of RVA, suggesting a slow but steadily augmenting growth of the frequency of vertitions in the course of evolutionary time, presence in the Recent *Tuckerella* of the setae commonly hit by vertitions 40 million generations ago in the same genus would be extraordinary. In the light of the fluctuating asymmetry notion, such presence does not seem overly surprising: high frequency of the asymmetrical expression of some leg setae may be part of the stability of the tuckerellid habitus itself. Fossils show us that the body plan of *Tuckerella* was already fully formed forty million years ago, and it apparently kept existing without notable change since that time. This remarkable stasis possibly included the degree of imperfection of the mite body's symmetry. To learn whether this is true or not, and whether this is widespread in Acari, careful studies of leg setations in Recent and fossil mites are necessary.

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