

New fossil stilt-legged mites of *Neophyllobius* Berlese, 1886 (Acariformes, Camerobiidae) from Eocene Baltic amber

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Abstract.—The fossil record of the family Camerobiidae has been represented by only one species, *Neophyllobius succineus* Bolland and Magowski, 1990, described from Eocene Baltic amber. These prostigmatan mites are distinguishable by their distinctly long and slender stilt-like legs, and they are associated with aboveground vegetation where they hunt for other small invertebrates. This paper enhances the knowledge of fossil stilt-legged mites. Two new fossil species, *N. electrus* new species and *N. glaesus* new species, are described from samples of Baltic amber, and remarks on their morphology and taphonomy are provided. The discovery is complemented with a discussion on morphological singularities (the shape of the prodorsum, the location of setae *h1* and *h2* in living specimens, and lengths of genital setae), an anomaly of hypertrophied seta (found in the *N. glaesus* holotype), and some biogeographical issues.

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Introduction

Mites of the family Camerobiidae (Acariformes, Prostigmata, Raphignathoidea) are recognizable by an almost round (especially when it comes to specimens mounted on microscope slides), dorsoventrally flattened idiosoma that is suspended on long, slender, stilt-like legs, mostly with long setae, which yield a characteristic appearance (Bolland, 1986, 1991). Camerobiids are free-living predators of small invertebrates (e.g., plant-associated mites and crawlers of scale insects [Hemiptera, Coccoidea]). Camerobiids hunt their prey on aboveground vegetation (including tree bark) but have also been found in the litter (Gerson et al., 2003; Walter et al., 2009). In the literature, more than 160 extant species have been described in seven genera: *Acamerobia* Fan and Walter, 2011; *Bisetulobius* du Toit, Theron, and Ueckermann, 1998; *Camerobia* Southcott, 1957; *Decaphyllobius* Bolland, 1986; *Neophyllobius* Berlese, 1886; *Tillandsobius* Bolland, 1986; and *Tycherobius* Bolland, 1986. Most species are monotypic, and the reason for this is the single, rare occurrence of these mites, which probably do not occur in larger aggregations as adults (Bolland, 1986, 2001). The historical aspect of the developing systematics hypotheses of the family and its constituent genera was summarized by Fan and Walter (2011).

Baltic amber is one of the richest sources of animal remains, which are exceptionally well preserved in the form of three-dimensional inclusions. Despite the long history of research on fossil organisms (Koch and Berendt, 1854 published the first study that included mites), new information is continually provided on the structure of the so-called Eocene Amber Forests (Weitschat and Wichard, 2002; Seyfullah et al., 2018). In addition, because of a diverse paleocarofauna including the presence of minute and weakly sclerotized mites, this Lagerstätte

is essential for further paleocarological studies (Sidorchuk, 2018).

The fossil record of the superfamily Raphignathoidea is scarce and consists of only two described species: *Mediolata eocenia* Kuznetsov, Khaustov, and Perkovsky, 2010 (Stigmaeidae) from Rovno amber and *Neophyllobius succineus* Bolland and Magowski, 1990 from Baltic amber (Dunlop et al., 2019). None of the studied inclusions was subjected to appropriate grinding techniques (which were developed later) helpful for studying microarthropods (Sidorchuk, 2013; Sidorchuk and Vorontsov, 2018), and quality pictures of the specimens were not taken (there is only one black-and-white photograph in Kuznetsov et al., 2010).

This work presents descriptions of two new fossil species, *Neophyllobius electrus* n. sp. and *N. glaesus* n. sp., which were found in samples of Baltic amber (Fig. 1). These descriptions are accompanied by detailed images, line drawing interpretations, and reconstructions of their habitus. Thus, the paper expands the knowledge about the Camerobiidae mites inhabiting the extinct Eocene ecosystem where resin originated.

Materials and methods

Materials.—1. Baltic amber sample with two inclusions determined by Ekaterina Sidorchuk as postlarval Camerobiidae and adult Phthiracaroida from the Senckenberg Museum of Natural History Görlitz, Am Museum 1, 02826 Görlitz, Germany, under the collection (Sammlung Oribatida) number SMNG 07/36290-78.

2. Baltic amber with a representative of Camerobiidae from the private collection of the author and subsequently donated and deposited in the Geological–Paleontological



Figure 1. Habitus of studied inclusions: (1) *Neophyllobius glaesus* n. sp. (SMNG 07/36290-78a); (2) *Neophyllobius electrus* n. sp. (GPIH 4995a). Scale bars = 100 μm .

Institute and Museum of the University of Hamburg, now CeNak—Centrum für Naturkunde, ‘Geomatikum,’ Bundesstraße 55, 20146 Hamburg, Germany, under the collection number GPIH 4995; this institution is its final deposition after preparation and study.

Amber preparation.—Amber samples were cut using a handheld cutting tool (Proxxon Micromot 60/E), and then obtained pieces were polished according to methods of preparation described by Sidorchuk (2013), using the tools introduced by Sidorchuk and Vorontsov (2016, 2018). Because of cracks along a natural amber fissure and the small size of the preparation, some fragments were embedded in Buehler EpoThin 2 epoxy resin between two round glass coverslips. One sample that had not been embedded in the resin was placed in a test tube filled with aqueous thymol solution. All preparations are labeled following the information given in this paper.

Observations and imaging.—Observations were done with a light compound microscope Nikon Eclipse Ni-U equipped with differential interference contrast (DIC) optics, 10 \times plan apochromatic dry, and 40 \times and 60 \times apochromatic water-immersion lens objectives. Image stacks were obtained with a Nikon DS-Ri2 microscope camera using Nikon NIS-Elements D imaging software (Nikon Corporation). All images were corrected for light, tone, noise, and sharpness using Adobe Photoshop Lightroom (Adobe Systems). Layered images were obtained by processing the focal planes with Helicon Focus

Pro (Helicon Soft Ltd) rendering method A; minor retouch of the final image has been conducted to make some morphological structures visible. Drawings are interpretations of studied inclusions and were made with Adobe Photoshop (Adobe Systems) with the aid of a graphic tablet Wacom Intuos Pro on the basis of obtained pictures. Reconstructions of the species’ habitus are based on the studied material, data from the literature, and pictures of living specimens. Original images are available through Figshare data-set collections (see details provided in the Material sections of individual descriptions of species).

Measurements.—All measurements are made and given herein in micrometers (μm), and they are rounded to the nearest integer. Measurements have been made with the aid of Nikon NIS-Elements D (Nikon Corporation) calibrated for used objectives. Due to the nature of preservation, measurements of organs and body parts that are oriented in three-dimensional space should be considered as minimum estimates.

Repositories and institutional abbreviations.—Type specimens examined in this study are deposited in the following institutions: Senckenberg Museum of Natural History Görlitz (SMNG), Görlitz, Germany, and Geological–Paleontological Institute and Museum of the University of Hamburg (GPIH), now CeNak—Centrum für Naturkunde, Hamburg, Germany.

Systematic paleontology

- Class Arachnida Cuvier, 1812
 Superorder Acariformes Zakhvatkin, 1952
 Order Trombidiformes Reuter, 1909
 Suborder Prostigmata Kramer, 1877
 Supercohort Eleutherengonides Oudemans, 1909
 Cohort Raphignathina Kethley, 1982
 Superfamily Raphignathoidea Kramer, 1877
 Family Camerobiidae Southcott, 1957
 Genus *Neophyllobius* Berlese, 1886

Type species.—*Neophyllobius elegans* Berlese, 1886 by original designation from material collected in Italy.

Terminology.—Terminology used here follows that developed in works by F. Grandjean (reviewed by Travé and Vachon, 1975; general terminology combined by van der Hammen, 1980). Its application to Camerobiidae follows Kethley (1990) and Fan and Walter (2011). The left and right sides of the body and its structures correspond to those of the dorsal view. Symbols and abbreviations used in the text are explained in the legends of the corresponding figures. Leg setae were designated with diligence on the basis of three-dimensional specimens. However, the nature of the appendages (long, slender, stilt-like) may cause difficulty in the correct determination of lateral and ventral setae; hence, the chaetotaxy of setae *l* and *v* on tibiae should be considered a simplification. Application of Grandjean's system for leg phanerotaxy has been already applied in the recent literature (e.g., Fan and Walter, 2011; Paredes-Leon et al., 2016; Khaustov and Abramov, 2017).

Neophyllobius electrus new species
 Figures 1.2, 2–6; Table 1

Holotype.—Adult female (Fig. 1.2) in two preparations that consist of polished amber embedded in epoxy resin between two round glass coverslips. One preparation (SMNG 07/36290-78a) contains most of the specimen's body. Another (SMNG 07/36290-78b) contains some parts of the ventral cuticle (Fig. 5.1) and partial tarsi I and II (Fig. 3.3, 3.8, 3.11). Type material is deposited in SMNG, Sammlung Oribatida, under the collection number 07/36290-78. Data from the label: Baltischer Bernstein, coll. Wunderlich, Ankauf 2007. Camerobiidae (postlarv) Phthiracaroida (ad) det. Sidorchuk. See Zmudzinski (2020a) for original series of pictures of the specimen.

Diagnosis.—Peritremes with at least one loop. Fourteen pairs of barbed idiosomal setae present. Setae *vi* and *ve* on anterior margin of prodorsum directed forward; together with *c2*, *d1*, *e1*, and *fl* longer than other idiosomal setae; ratio *c1*:*c2*:*d1* = 1:2:2.8. Setae *d* on genua I–IV barbed and relatively short (I, 51–60 µm; II, 77 µm; III, 25–42 µm; IV, 47 µm). Each of tarsi I–IV with only one midventral seta vs. Leg phanerotaxy formulae (trochanter to tarsus, tarsal setae estimated, κ setae not counted): (I) 1–4–1–9(φ)–9(ω); (II) 1–3–1–8(φ)–9(ω); (III) 1–3–1–8(φ)–7; (IV) 1–2–1–7(φ)–7.

Occurrence.—Single inclusion within the sample of Baltic amber, middle Eocene 48–38 Ma (Weitschat and Wichard, 2002).

Description of inclusion.—Gnathosoma (Fig. 5.2) situated ventroterminally on the idiosoma, partially covered from above by the anterior part of the idiosomal prodorsum, 61 µm long (measured from its base to the tip of the infracapitulum) and 62 µm wide basally, cuticle striated only on palps. Stylophore stumpy, partially visible from dorsal view. Peritremes present but hardly visible. Cheliceral stylets retracted, visible inside the stylophore, each 17 µm long. Subcapitulum smooth, without any ornamentation, with simple subcapitular setae: medial *m* (10–13 µm long; distance *m*–*m* 9 µm) situated on its middle third, and short oral *or1* (5–6 µm) and *or2* (4 µm; visible only on the left side), almost on the tip of the infracapitulum. Palps directed anteriad, their total length 52–63 µm. Palptrochanters without any setae. Palpfemora, each with lateral setae *l'* 8–10 µm long and dorsal setae *d* 25–29 µm. Palpigenua with dorsal setae *d* 14–17 µm. Each palptibia with a longitudinal sclerotized structure (most likely a complex of palptibial setae and claw + palptarsus).

Idiosoma (Fig. 2) oval, 310 µm long and 183 µm wide (measured at the level of the bases of setae *c2*). Cuticle partially striated, except prodorsum, midlateral dorsum, around the setae *d1*, *e1*, and *fl*, and epimeral (coxal) fields. Dorsal idiosoma with fourteen pairs of barbed, relatively thick setae set on cuticular tubercles. Each tubercle single (not coupled). Setae *vi* (63–73 µm long; distance *vi*–*vi* 26 µm) and *ve* (53–56 µm; *ve*–*ve* 69 µm) directed forward and set on the largest protuberances situated on the anterior margin of prodorsum. Setae *sci* (22–38 µm; *sci*–*sci* 112 µm) and *sce* (26–27 µm; *sce*–*sce* 170 µm) on the lateral margins of prodorsum. Between them, just above the level of *sce* on each side, two eyes present, anterior one (8.5 µm in diameter) a little smaller than the posterior one (10.5 µm). Four pairs of setae in the central part: *c1* the smallest (24 µm long; distance *c1*–*c1* 12 µm) with distinctly marked barbs and *d1* (66 µm; *d1*–*d1* 19 µm), *e1* (68 µm; *e1*–*e1* 16 µm), and *fl* (51–64 µm; *fl*–*fl* 18 µm) much longer, gently bent backward, and similar in length. Setae *c2* (50 µm; *c2*–*c2* 192 µm), *d2* (35–36 µm; *d2*–*d2* 159 µm), *e2* (44–45 µm; *e2*–*e2* 141 µm), and *f2* (34–35 µm; *f2*–*f2* 100 µm) situated on the lateral margins. Setae *h1* (39–40 µm, *h1*–*h1* 17 µm), and *h2* (28–31 µm; *h2*–*h2* 66 µm) terminate the idiosoma. Extremities of epimera visible from the dorsal side; the dorsolateral cuticle passes between second and third epimera. Supplementary distances: *vi*–*ve* 22–25 µm; *ve*–*sci* 50–52 µm; *sci*–*sce* 55 µm; *c1*–*c2* 92–95 µm; *d1*–*d2* 73–79 µm; *e1*–*e2* 71–72 µm; *fl*–*f2* 43–52 µm; *h1*–*h2* 18–25 µm; *c1*–*d1* 55–62 µm; *d1*–*e1* 46–50 µm; *e1*–*fl* 66 µm; *f2*–*h2* 32 µm; *e2*–*f2* 59 µm; *d2*–*e2* 53 µm; *c2*–*d2* 58 µm; *sce*–*c2* 32–34 µm. Coxal fields grouped into two areas: I partially fused with II, and coxal field III partially fused with IV. Epimeral setae slightly barbed and set on cuticular protuberances: *1b* 25–58 µm long; *1c* 18–25 µm; *2c* 21–30 µm; *3b* 35–46 µm; *3c* 26–33 µm; *4b* 11–17 µm; *4c* 20–22 µm. The anogenital area (Fig. 5.3) visible, but difficult to discern its details. A pair of short, simple, smooth aggenital setae *ag* situated just above its anterior margin. Genital valves with one pair of short, simple,

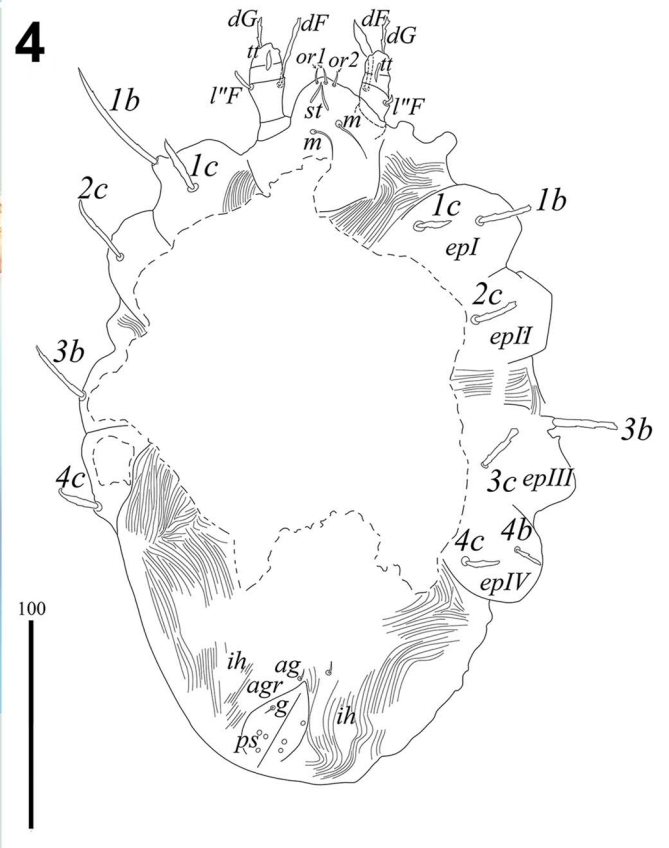
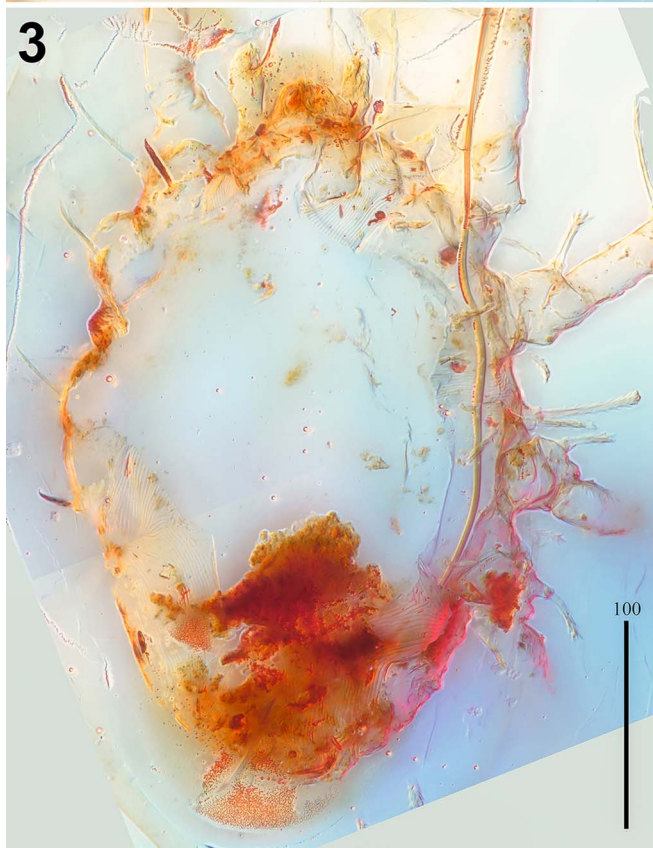
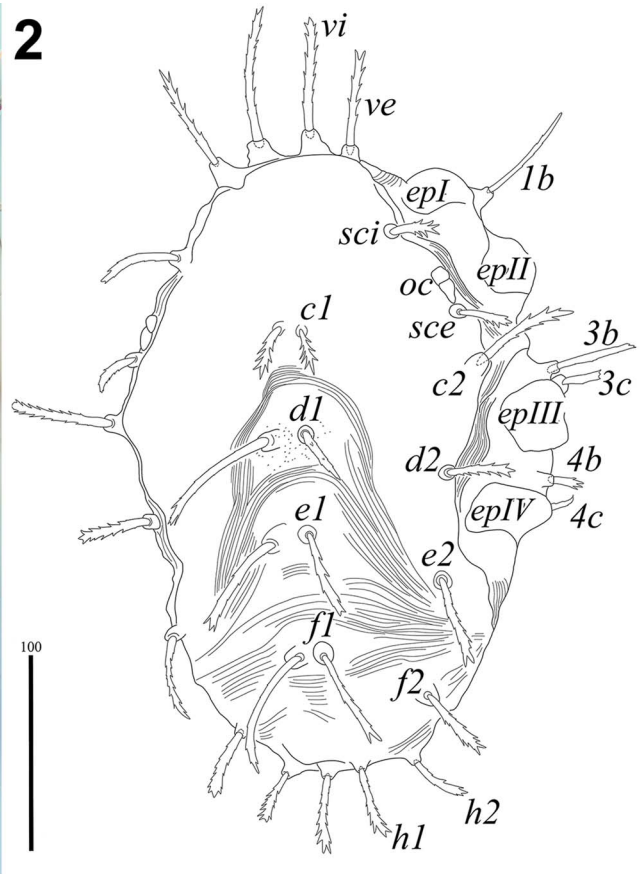


Figure 2. *Neophyllobius electrus* n. sp. (SMNG 07/36290-78a): (1) layered picture of the body in dorsal view; (2) line drawing interpretation of (1); (3) layered picture of the body in ventral view; (4) line drawing interpretation of (3). *1b, 1c, 2c, 3b, 3c, 4b, 4c* = epimeral setae; *ag* = aggenital seta; *agr* = anogenital area; *c1, c2* = idiosomal setae of row C; *d1, d2* = idiosomal setae of row D; *dF* = dorsal seta of palpfemur; *dG* = dorsal seta of palpgenu; *e1, e2* = idiosomal setae of row E; *epI–IV* = epimera of legs I–IV; *f1, f2* = idiosomal setae of row F; *g* = genital seta; *h1, h2* = idiosomal setae of row H; *ih* = cupule; *m* = subcapitular medial setae; *l'F* = lateral seta of palpfemur; *oc* = eyes; *or1, or2* = oral setae; *ps* = pseudanal setae; *sci, sce* = scapular setae of prodorsum, *st* = cheliceral stylets; *tt* = palptibia + palptarsus; *vi, ve* = vertical setae of prodorsum. Scale bars = 100 μ m.

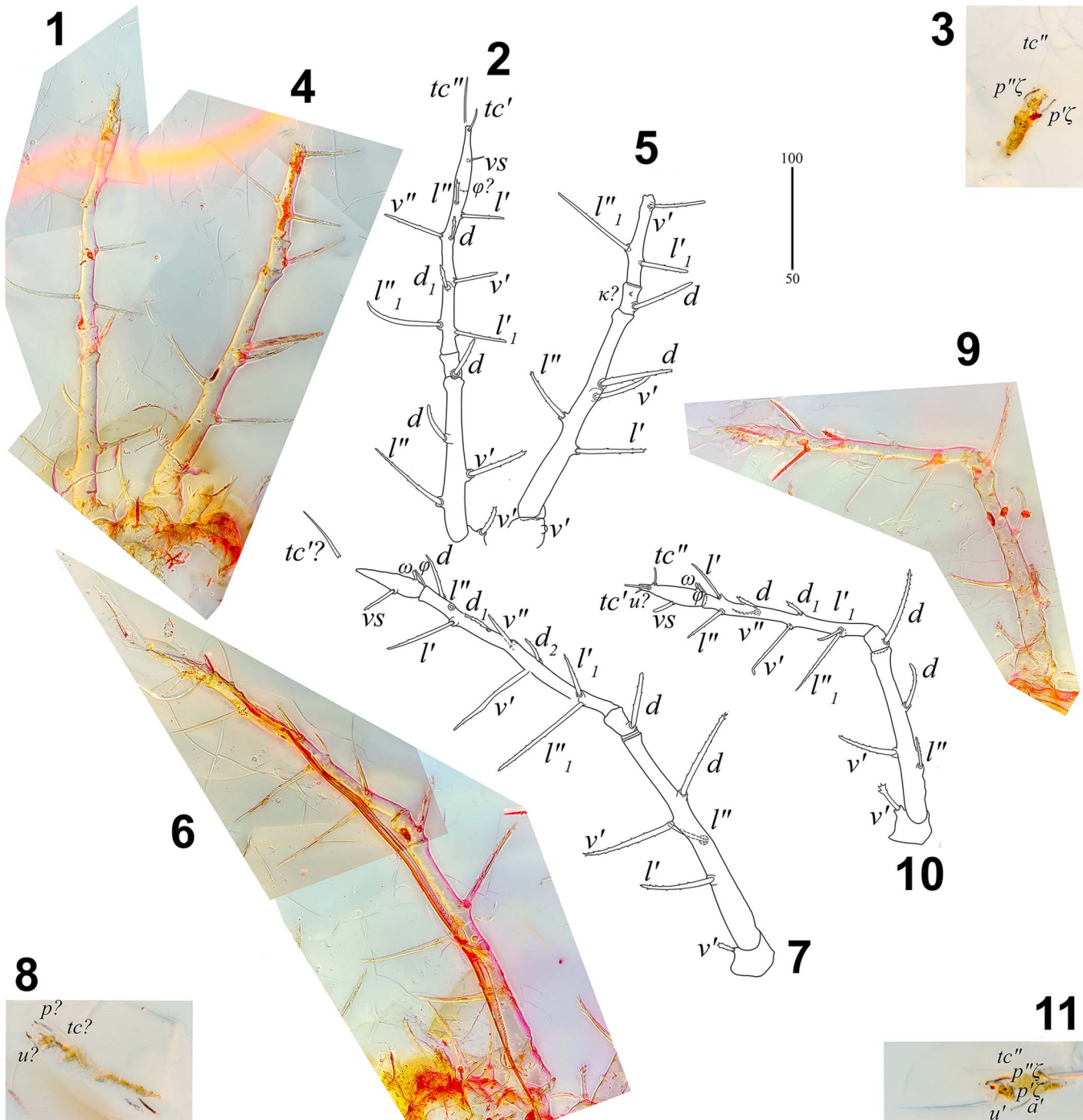


Figure 3. *Neophyllobius electrus* n. sp. (SMNG 07/36290-78b): (1) layered picture of left leg II (SMNG 07/36290-78a); (2) line drawing interpretation of (1); (3) tarsus of left leg II (SMNG 07/36290-78b); (4) layered picture of left leg I (SMNG 07/36290-78a); (5) line drawing interpretation of (4); (6) layered picture of right leg I (SMNG 07/36290-78a); (7) line drawing interpretation of (6); (8) tarsus of right leg I (SMNG 07/36290-78b); (9) layered picture of right leg II (SMNG 07/36290-78a); (10) line drawing interpretation of (9); (11) tarsus of right leg II (SMNG 07/36290-78b). *a* = anterolateral seta; *d, d1, d2* = dorsal seta; *l, l1* = lateral seta; *pζ* = eupathidial proral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs* = midventral seta of tarsus; *κ* = minute genual seta; *φ* = tibial solenidion; *ω* = tarsal solenidion; *'* = anterior; *''* = posterior. (1, 2, 4–7, 9, 10) Scale bar = 100 μ m; (3, 8, 11) scale bar = 50 μ m.

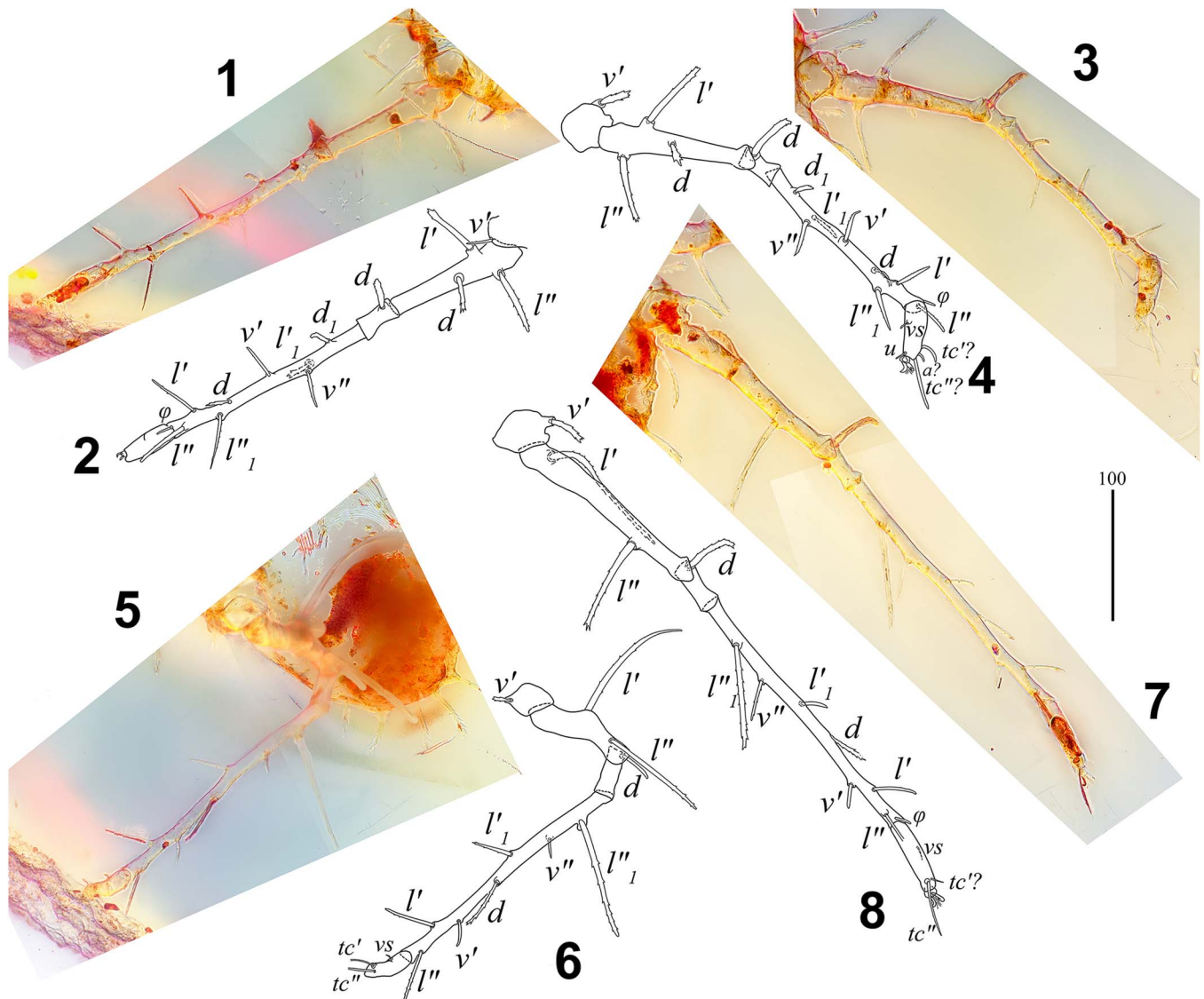


Figure 4. *Neophyllobius electrus* n. sp. (SMNG 07/36290-78a): (1) layered picture of left leg III; (2) line drawing interpretation of (1); (3) layered picture of right leg III; (4) line drawing interpretation of (3); (5) layered picture of left leg IV; (6) line drawing interpretation of (5); (7) layered picture of right leg IV; (8) line drawing interpretation of (7). *a* = anterolateral seta; *d*, *d*₁ = dorsal seta; *l*, *l*₁ = lateral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs* = midventral seta of tarsus; φ = tibial solenidion; ' = anterior; '' = posterior. Scale bar = 100 μ m.

smooth genital setae *g* (seta visible on the right side, only the base of seta visible on the left side). Three bases of pseudanal setae *ps1*–*3* present on the right, but only two bases discernible on the left. Oval breaks in the striation situated in the proximity of anogenital region visible (probably areas of simple cupules *ih*).

Legs (Figs. 3, 4) stilt-like, first and fourth pairs longer than second and third pairs; all setae barbed and situated on tubercles except those on tarsi (smooth and simple except slightly barbed midventral setae *vs*). Legs I, the total length of the right one (Fig. 3.6): 548 μ m; left one (Fig. 3.4) deficient (lacking tarsus and half of tibia). Trochanters 51 μ m long, each with single ventral seta *v*' 8–12 μ m. Femora elongated 222–223 μ m, each with four setae, from distal to proximal, *d* 70–90 μ m; *v*' 66–88 μ m; *l*' 41–54 μ m; *l*' 67–71 μ m. Genua 30–37 μ m, each with single seta *d* 51–60 μ m situated on proximal third, probably a minute

seta κ on the left one present. Right tibia elongated 206 μ m, with nine setae, from distal to proximal, *d* 41 μ m; *l*' (only base visible), *l*' 65 μ m; *d*₁ 29 μ m; *v*' 36 μ m; *v*' 86 μ m; *d*₂ 22 μ m; *l*'₁ 49 μ m; *l*'₁ 99 μ m; and one rod-like distal solenidion φ 19 μ m; left one incomplete (91 μ m) with three setae *v*' 59 μ m; *l*'₁ 51 μ m; and *l*'₁ 89 μ m. Right tarsus 64 μ m, not completely preserved, with one ventral seta *vs* and one clavate proximal solenidion ω , partially preserved setae *tc*' and at least one *p* and one *u*. Legs II (Fig. 3.1, 3.9), total lengths 403–429 μ m. Trochanter 42–47 μ m with single seta *v*' 30–32 μ m. Femora elongated 142–177 μ m, each with three setae, from distal to proximal, *d* 36–45 μ m, *v*' 55–59 μ m, and *l*' 36–71 μ m. Genua 30–31 μ m, each with single seta *d* 48–77 μ m situated on the proximal third. Tibiae elongated 150–164 μ m, each with eight setae, from distal to proximal, *l*' 41–42 μ m; *l*' 40 μ m; *d* 18–19 μ m; *v*' 55–56 μ m; *v*' 25–44 μ m; *d*₁ 22–23 μ m *l*'₁ 30–53 μ m; *l*'₁

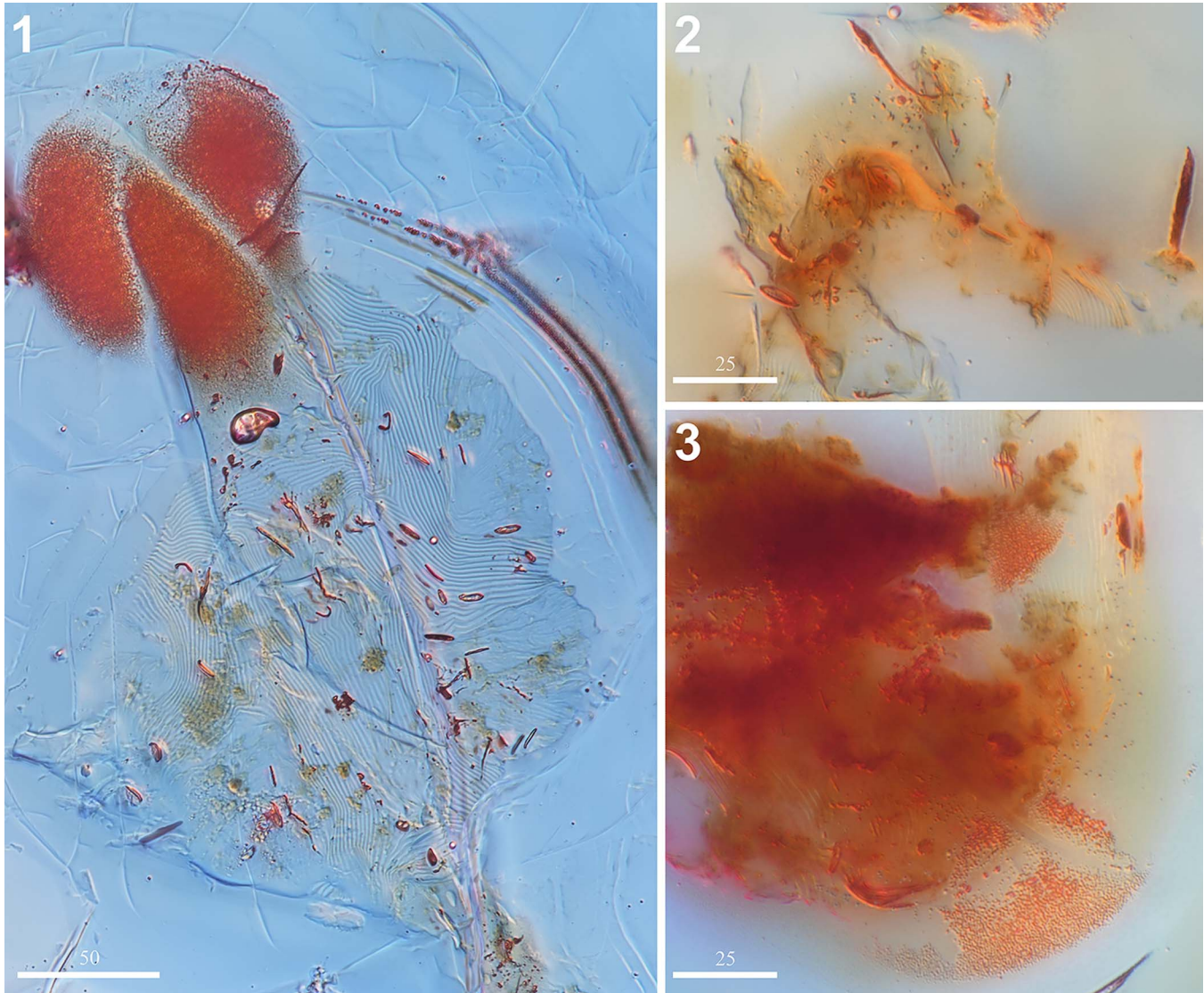


Figure 5. *Neophyllobius electrus* n. sp. (SMNG 07/36290-78): (1) imprint of ventral cuticle (SMNG 07/36290-78b); (2) gnathosoma in ventral view (SMNG 07/36290-78a); (3) opisthosoma in ventral view (SMNG 07/36290-78a). (1) Scale bar = 50 μm ; (2, 3) scale bars = 25 μm .

50–68 μm ; and one rod-like distal solenidion φ 14–18 μm . Tarsi 62–64 μm , each with one ventral seta *vs* and tectal setae (*tc*); eupathidial proral setae (*p* ζ) visible on the left tarsus; one unguinal seta *u'*, anterolateral *a'*, and two eupathidial proral setae (*p* ζ) preserved on the right tarsus; one clavate proximal solenidion ω visible on the right tarsus only. Legs III (Fig. 4.1–4.4), total lengths 345–397 μm . Trochanters 35–40 μm , each with single seta *v'* 23–24 μm . Femora elongated 111–116 μm , each with three setae, from distal to proximal, *d* 17–32 μm ; *l'* 50–55 μm ; *l''* 51–52 μm . Genua 32–34 μm , each with single seta *d* 25–42 μm situated on the proximal third. Tibiae elongated 154–169 μm , each with eight setae, from distal to proximal, *l''* 31–36 μm ; *l'* 32–42 μm ; *l''*₁ 32–38 μm ; *d* 20–21 μm ; *v'* 25–29 μm ; *v''* 27 μm ; *l'*₁ 18–21 μm ; *d*₁ 14–16 μm ; and one rod-like distal solenidion φ 9–12 μm . Tarsi 44–57 μm , no setae preserved on the left one; on the right one single slightly barbed ventral seta *vs* and probably (*tc*), *a*, and *u* present; ambulacra (claws + tenant-hair empodium) preserved on each tarsus. Legs

IV (Fig. 4.5–4.8), total lengths 364–485 μm . Trochanters 34–42 μm with single ventral seta *v'* 18–27 μm . Femora elongated 90–160 μm , each with two lateral setae, from distal to proximal, *l''* 75–89 μm and *l'* 44–95 μm . Genua 40–43 μm , each with single seta *d* 47 μm situated on the proximal third. Tibiae elongated 190–217 μm , each with seven setae, from distal to proximal, *l''* 44–46 μm ; *l'* 36 μm ; *v'* 19–21 μm ; *d* 29–37 μm ; *l'*₁ 22–32 μm ; *v''* 17–31 μm ; *l''*₁ 81–91 μm ; and one rod-like distal solenidion φ 10 μm . Tarsi 44–58 μm , each with single ventral seta *vs* and pair of tectal setae (*tc*); ambulacra preserved on the right tarsus only. Phanerotaxy formulae (trochanter to tarsus, tarsal setae estimated, κ setae not counted): (I) 1–4–1–9(φ)–9 (ω); (II) 1–3–1–8(φ)–9(ω); (III) 1–3–1–8(φ)–7; (IV) 1–2–1–7 (φ)–7.

Etymology.—The specific epithet *electrus* is an adjective derived from the Latin noun *electrum* in the nominative, which is translated into amber.

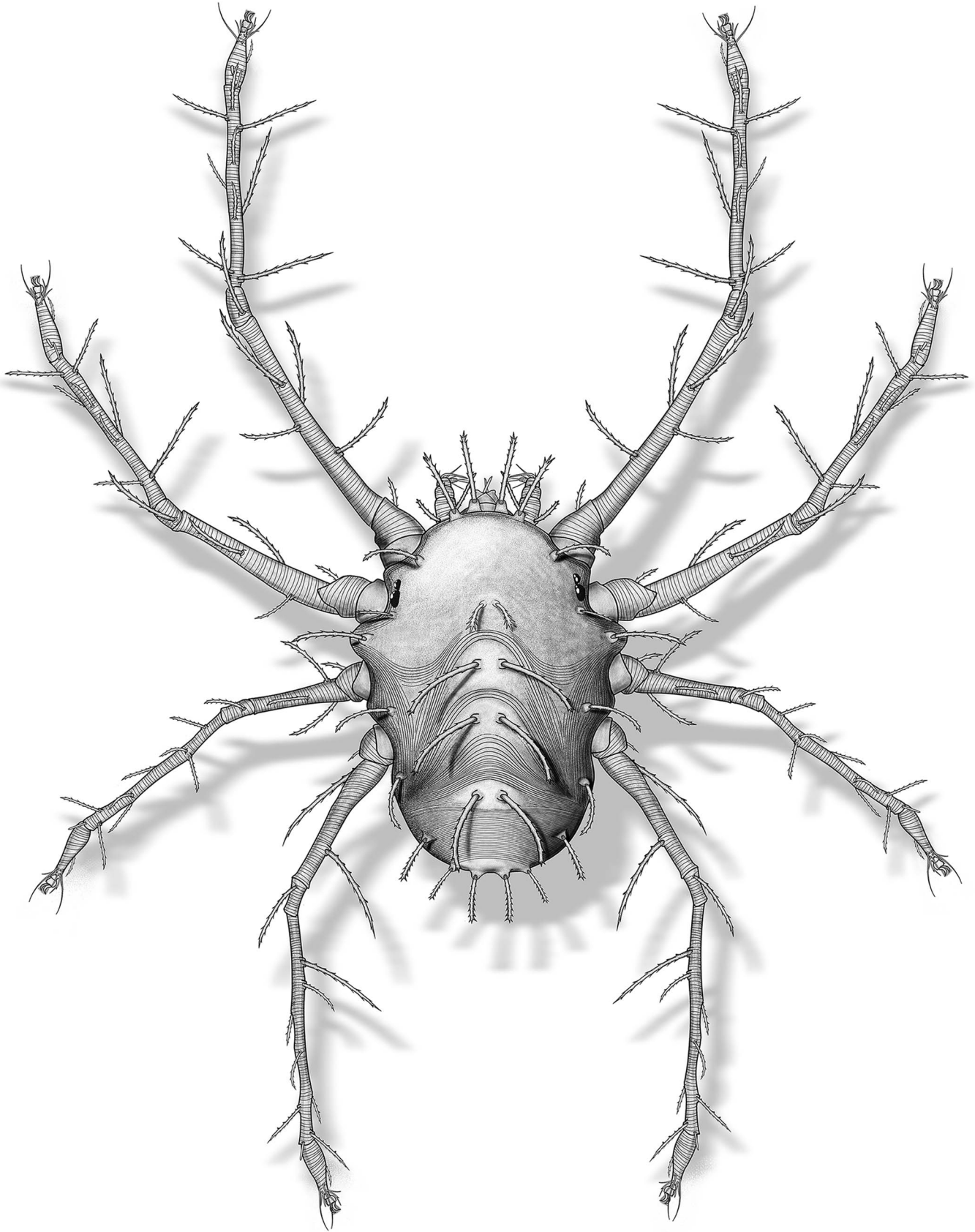


Figure 6. *Neophyllobius electrus* n. sp., reconstruction of adult female.

Table 1. Main differences between fossil *Neophyllobius* species from the Baltic amber. Units = μm .

Character	<i>N. electrus</i>	<i>N. glaesus</i>	<i>N. succineus</i>
Body length \times width	310 \times 183	255 \times 199	250 \times 218
Prodorsum covers gnathosoma	partially	completely	partially
Setae <i>pdx</i>	absent	present	present
<i>ve</i> – <i>sci</i> distance	50–52	29–36	12
Length of setae <i>cl</i>	24	37–42	47
Length of setae <i>el</i>	68	42–44	75
Length of setae <i>hl</i>	39–40	28–30	64
Midventral tarsal setae <i>vs</i>	one	two	two
Tibial setae <i>d</i> versus <i>l</i> and <i>v</i>	shorter	similar length	similar length
Setae on femora I–IV	4–3–3–2	4–3–3–2	4–3–2–2
Setae on tibiae I–IV	9–8–8–7	9–8–8–7	8–7–7–6

Remarks.—*N. electrus* n. sp. is morphologically similar to the extant species *N. meyeræ* Bolland, 1991 by the presence of only one midventral seta on each tarsus I–III. However, it differs from this species by having an additional third seta on femora III, probably *l'* (*N. meyeræ* has only two setae); lack of setae *pdx* (present in *N. meyeræ*); a slightly different idiosomal pattern, especially in terms of *vi*–*ve* distance; and significant differences in length between individual pairs within medial and lateral rows of idiosomal setae (there are only slight differences in *N. meyeræ*). There are also some similarities between the new species and the Recent cameroibiid *N. panici* Bolland, 1991. These two species have only one midventral seta *vs* on each tarsus IV, four setae on femur I, three setae on femur II, and significant differences in length ratio between the median setae. *N. electrus* n. sp. differs from this species by the presence of only one midventral seta on each tarsus I–III (two setae present in *N. panici*), lack of setae *pdx* (present in *N. panici*), having additional third setae on femora III, probably *l'* (*N. panici* has only two setae), shorter setae *d* on genua (in *N. panici* seta *d* is at least three times longer than the genu), and idiosomal setae barbed (in *N. panici* these setae are nodular). By the presence of three setae on femora III, two setae on femora IV, and the longest setae *dl* among the idiosomal setae, *N. electrus* n. sp. is also similar to the other extant species *N. trisetosus* De Leon, 1958. The new species differs by the presence of only one midventral seta on each tarsus I–IV (*N. trisetosus* has two midventral setae on each tarsus I–IV) and by the absence of setae *pdx* (which are present in *N. trisetosus*).

N. electrus n. sp. is morphologically similar to the fossil species *N. glaesus* n. sp. described herein. Both species have relatively short dorsal setae *d* of genua I–IV and the same chaetotaxy formulae of femora 4–3–3–2 and tibiae 9–8–8–7. *N. electrus* differs from *N. glaesus* by the presence of fourteen pairs of idiosomal setae (setae *pdx* present in *N. glaesus*), *ve*–*sci* distance 50–52 μm (29–36 μm in *N. succineus*), gnathosoma partially covered by the prodorsum (in *N. glaesus* prodorsum completely covers it), the presence of only one midventral seta *vs* on each tarsus (*N. glaesus* has two setae *vs* on each tarsus), and shorter dorsal setae *d* on tibiae than lateral *l* and ventral *v* setae (*N. glaesus* has these setae similar in length). A comparison of all three fossil *Neophyllobius* species from Baltic amber is summarized in Table 1.

The original sample of amber had a natural fissure filled with air that passed through the inclusion. Hence, to preserve

and polish the specimen, the sample was separated into two preparations (see Materials). Nevertheless, the mite imprint in the resin is comparable in quality to modern specimens mounted on microscope slides, even thin striae on the legs and the idiosoma, and clavate tarsal solenidia are clearly visible. Residues of the cuticle, internal organs, and probably food remnants form orange-brown artifacts that hinder the visibility of certain structures such as the anogenital area. Left leg I is incomplete (whole tarsus and a half of tibia missing); those parts were probably lost before embedding in the resin. Interestingly, the apotela of the legs are poorly preserved, so claws as relatively strongly sclerotized rigid structures should be better remained.

Neophyllobius glaesus new species
Figures 1.1, 7–13; Table 1

Holotype.—Adult female (Fig. 1.1) in two polished pieces of amber. One piece contains an almost complete specimen, and it is placed in a tube with a thymol aqueous solution (GPIH 4995a). Another contains the incomplete left tarsus II (Fig. 12.3) and is embedded in epoxy resin between two round glass coverslips (GPIH 4995b). Type material is deposited in GPIH under collection number GPIH 4995. See Zmudzinski (2020b) for original series of pictures of the specimen.

Diagnosis.—Fifteen pairs of idiosomal barbed setae present (a pair of *pdx* present). Setae *vi* and *ve* on anterior margin of prodorsum directed forward; prodorsum rectangular and covers gnathosoma from above. All idiosoma setae similar in length (except *f2* and *h1*, *h2*, which are slightly shorter). Setae *d* on genua I–IV barbed and relatively short (I, 37–48 μm ; II, 32–35 μm ; III, 26–32 μm ; IV, 48–50 μm). Each of tarsi I–IV with two midventral setae *vs*_{1–2}. Leg phanerotaxy formulae (trochanter to tarsus, tarsal setae estimated, κ setae not counted): (I) 1–4–1–9(φ)–10(ω); (II) 1–3–1–8(φ)–10(ω); (III) 1–3–1–8(φ)–8; (IV) 1–2–1–7(φ)–8.

Occurrence.—Single inclusion within the sample of Baltic amber, middle Eocene 48–38 Ma (Weitschat and Wichard, 2002).

Description of inclusion.—Gnathosoma (Fig. 12.2) situated ventrally on the idiosoma, between epimera I, wholly covered from above by anterior prodorsum, 46 μm long (measured from its base to the tip of the infracapitulum) and 48 μm wide basally. Stylophore stumpy, peritremes poorly visible, and cheliceral stylets indiscernible due to position of gnathosoma and the fossilized body remains. Subcapitulum slightly striated, with simple medial subcapitular setae: *m* (13–15 μm long; distance *m*–*m* 22 μm) situated on its middle third, and a pair of short oral setae *or* on the tip of the infracapitulum, another pair of oral setae indiscernible. Palps directed downward, their total length 30–34 μm . Individual articles hardly visible, best-visible palpfemora and sclerotized structures (most probably tibial setae and claw + tarsus). Palpfemora, each with dorsal setae *d* 24 μm and lateral setae *l'* 9–13 μm visible on the right article. Palpgenua with dorsal setae *d* 19 μm .

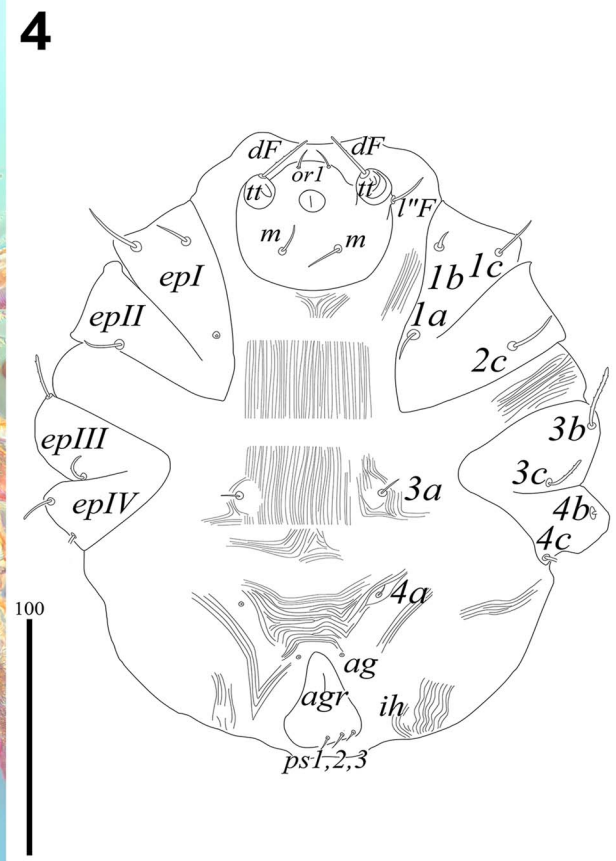
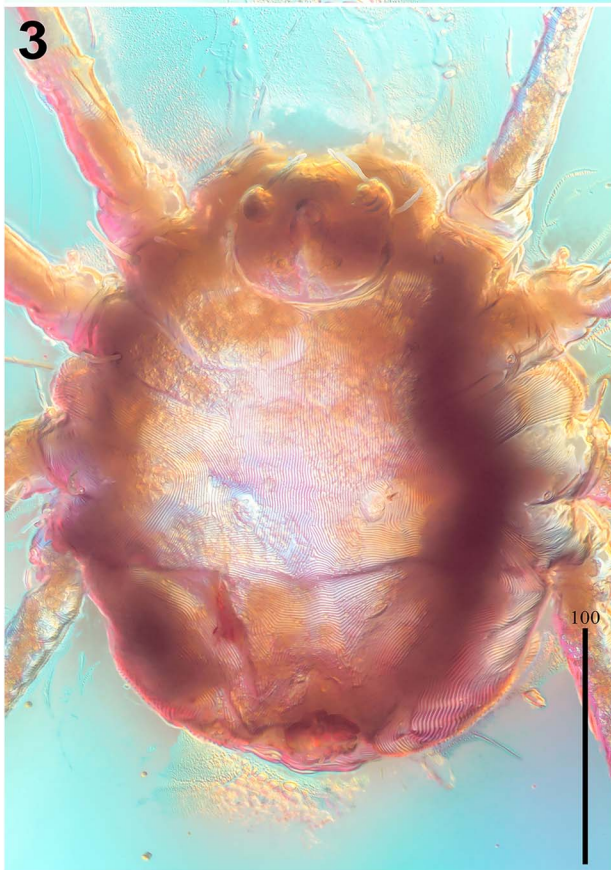
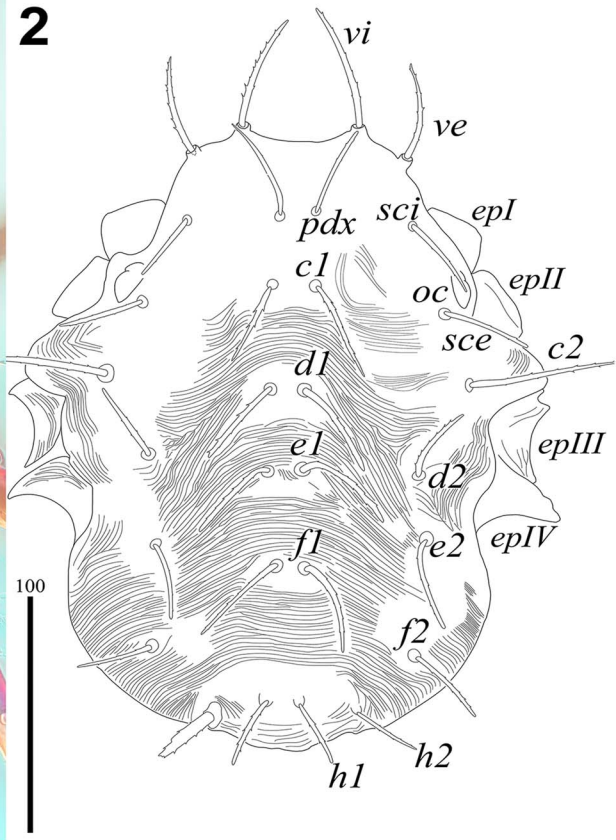


Figure 7. *Neophyllobius glaesus* n. sp. (GPIH 4995a): (1) layered picture of the body in dorsal view; (2) line drawing interpretation of (1); (3) layered picture of the body in ventral view; (4) line drawing interpretation of (3). *1a–c*, *2c*, *3a–c*, *4a–c* = epimeral setae; *ag* = aggenital seta; *agr* = anogenital area; *c1*, *c2* = idiosomal setae of row C; *d1*, *d2* = idiosomal setae of row D; *dF* = dorsal seta of palpfemur; *e1*, *e2* = idiosomal setae of row E; *epI–IV* = epimera of legs I–IV; *f1*, *f2* = idiosomal setae of row F; *h1*, *h2* = idiosomal setae of row H; *ih* = cupule; *m* = subcapitular medial setae; *l''F* = lateral seta of palpfemur; *oc* = eyes; *or1* = oral seta; *pdx* = fifteenth pair of idiosomal setae on prodorsum; *ps1–3* = pseudanal setae; *sci*, *sce* = scapular setae of prodorsum; *tt* = palptibia + palptarsus; *vi*, *ve* = vertical setae of prodorsum. Scale bars = 100 μ m.

Idiosoma (Fig. 7) oval, 255 μ m long and 199 μ m wide (measured at the level of the bases of setae *c2*), opisthosoma wider than prodorsum. Cuticle striated, except anterior prodorsum, around the setae *c1*, *d1*, *e1*, and *f1* and epimeral (coxal) fields. Dorsal idiosoma with fifteen pairs of barbed setae set on small cuticular single (not coupled) tubercles. Prodorsum rectangular; anterior margin concave. Setae *vi* (49–53 μ m long; distance *vi–vi* 44 μ m) and *ve* (41–53 μ m; *ve–ve* 83 μ m) directed forward. Setae *sci* (31–35 μ m; *sci–sci* 90 μ m) and *sce* (34–37 μ m; *sce–sce* 117 μ m) on the lateral margins of prodorsum. Between them, on each side, two eyes present, anterior one (4 μ m in diameter) a little smaller than the posterior one (7.5 μ m). Five pairs of setae of similar length in the central part present: *pdx* (34–38 μ m long; distance *pdx–pdx* 14 μ m), *c1* (37–42 μ m long; distance *c1–c1* 21 μ m), *d1* (41 μ m; *d1–d1* 16 μ m), *e1* (42–44 μ m; *e1–e1* 17 μ m), and *f1* (41 μ m; *f1–f1* 13 μ m). Lateral setae *c2* (52–53 μ m; *c2–c2* 143 μ m), *d2* (33 μ m; *d2–d2* 105 μ m), *e2* (42–54 μ m; *e2–e2* 103 μ m), and *f2* (24–33 μ m; *f2–f2* 113 μ m) situated closer to the center (not on the margins). Setae *h1* (28–30 μ m, *h1–h1* 16 μ m) situated on more-sclerotized unstriated cuticle, and *h2* (23–25 μ m; *h2–h2* 59 μ m) terminate the idiosoma; left seta *h2* hypertrophied (Fig. 12.4; see Discussion). Extremities of epimera visible from the dorsal side; the dorsolateral cuticle passes between second and third epimera. Supplementary distances: *vi–ve* 23–24 μ m; *ve–sci* 29–36 μ m; *sci–sce* 39–40 μ m; *sce–c2* 35–36 μ m; *vi–pdx* 34–37 μ m; *pdx–c1* 31–36 μ m; *c1–c2* 73–80 μ m; *c1–d1* 42–43 μ m; *d1–e1* 34–36 μ m; *e1–f1* 42–43 μ m; *f1–h1* 56–58 μ m; *d1–d2* 53–57 μ m; *e1–e2* 48–54 μ m; *f1–f2* 63–65 μ m; *h1–h2* 23 μ m; *f2–h2* 35–40 μ m; *e2–f2* 50–51 μ m; *d2–e2* 29 μ m; *c2–d2* 38–43 μ m. Coxal fields grouped into two areas: I partially fused with II, and coxal field III partially fused with IV. Epimeral setae slightly barbed and set on small cuticular protuberances: *1a* 13 μ m long (only the base of seta visible on the right side); *1b* 11–14 μ m; *1c* 19–21 μ m; *2c* 18–25 μ m; *3a* 5–10 μ m; *3b* 17–19 μ m; *3c* 18–19 μ m; *4a* 8 μ m; *4b* 14–16 μ m; *4c* 17 μ m; setae *3a* and *4a* situated in the intercoxal region, distance *3a–3a* 49 μ m; *4a–4a* 55 μ m. The anogenital area (Fig. 12.1) visible, but hard to discern its details. A pair of short, simple, smooth aggenital setae *ag* situated just above its anterior margin. Genital valves with one pair of short, simple, smooth genital setae *g* (seta visible on the right side, only base of seta visible on the left side). Three bases of pseudanal setae *ps1–3* present on the right valve but only two bases discernible on the left valve. Oval breaks in the striation situated in the proximity of anogenital region visible (probably areas of simple cupules *ih*).

Legs (Figs. 8–11) stilt-like, first and fourth pairs longer than second and third pairs, all setae barbed and situated on small tubercles except those on tarsi (simple and smooth except slightly barbed midventral setae *vs*). Legs I (Fig. 8), the total

length of the right one 412 μ m; left one deficient (lacking tarsus and a half of tibia). Trochanters 33–36 μ m long, each with single ventral seta *v'* 6–10 μ m. Femora elongated 157–162 μ m, each with four setae, from distal to proximal, *d* 48–49 μ m; *l'* 25–27 μ m; *l''* 25–38 μ m; *bv''* 9–12 μ m. Genua 34–38 μ m, each with single seta *d* 37–48 μ m situated on the proximal third. Right tibia elongated 147 μ m, with nine setae, from distal to proximal, *d* 42 μ m; *l'* 39 μ m; *l''* 44 μ m; *v''* 43 μ m; *d₁* 46 μ m; *v'* 36–44 μ m; *d₂* 34–41 μ m; *l''₁* 33–36 μ m; *l'₁* 40–42 μ m; and one rod-like distal solenidion φ 21 μ m; left one incomplete. Right tarsus 37 μ m with the complete set of setae visible: tectal (*tc*), eupathidial proral (*p ζ*), anterolateral (*a*), unguinal (*u*), midventral *vs_{1–2}*, and one proximal clavate solenidion ω ; apotele (ambulacral stalk, claws, tenant-hair empodium) preserved. Legs II (Fig. 9), the total length of the right one 300 μ m, left one incomplete, tarsus and part of tibia as a separate preparation (GPIH 4995b). Trochanter 29 μ m with single seta *v'* 9–12 μ m. Femora elongated 114–116 μ m, each with three setae, from distal to proximal, *d* 38–40 μ m; *l'* 21–27 μ m; and *bv''* 15 μ m. Genua 25–27 μ m, each with single seta *d* 32–35 μ m situated on the proximal third. Tibiae elongated 86 μ m, each with eight setae, from distal to proximal, *d* 39 μ m; *l'* 21 μ m; *l''* 28 μ m; *v'* 41 μ m; *v''* 20 μ m; *d₁* 31 μ m; *l''₁* 35–49 μ m; *l'₁* 23–26 μ m; and one rod-like distal solenidion φ 12 μ m. Right tarsus 45 μ m, with two midventral setae *vs₁* and *vs₂*, tectal (*tc*), unguinal (*u*), at least one anterolateral (*a*) and one proral (*p*) and one proximal clavate solenidion ω + complete apotele; on the left tarsus tectal and midventral setae preserved along with apotele. Legs III (Fig. 10), total lengths 383–399 μ m. Trochanters 32–34 μ m, each with single seta *v'* 14–18 μ m. Femora elongated 114 μ m, each with three setae, from distal to proximal, *d* 32 μ m; *l'* 23–24 μ m; *ev''* 21 μ m. Genua 28–32 μ m, each with single seta *d* 26–32 μ m situated on the proximal third. Tibiae elongated 163–170 μ m, each with eight setae, from distal to proximal, *l'* 45 μ m; *d* 39–40 μ m; *l''* 46–48 μ m; *v₁* 39–41 μ m; *v₂* 36–43 μ m; *l''₁* 28–42 μ m; *d₁* 24–27 μ m; *l'₁* 32 μ m; and one rod-like distal solenidion φ 13 μ m. Tarsi 52–53 μ m, each with complete set of setae: *vs_{1–2}*, (*tc*), (*a*), (*u*), and apotele. Legs IV (Fig. 11), total lengths 460 μ m. Each trochanter 31–37 μ m with single ventral seta *v'* 13–16 μ m. Femora elongated 136–146 μ m, each with two lateral setae, from distal to proximal, *l''* 24–29 μ m and *l'* 35–36 μ m. Genua 30–34 μ m, each with single seta *d* 48–50 μ m situated on the proximal third. Tibiae elongated 191 μ m, each with seven setae, from distal to proximal *l'* 45 μ m; *d* 34 μ m; *l''* 30 μ m; *v₁* 32 μ m; *v₂* 40 μ m; *l''₁* 43 μ m; *l'₁* 32 μ m; and one rod-like distal solenidion φ 11 μ m. Tarsi 64 μ m, each with preserved apotele and probably complete set of setae. Phanerotaxy formulae (trochanter to tarsus, tarsal setae estimated, κ setae not counted): (I) 1–4–1–9(φ)–10(ω); (II) 1–3–1–8(φ)–10(ω); (III) 1–3–1–8(φ)–8; (IV) 1–2–1–7(φ)–8.

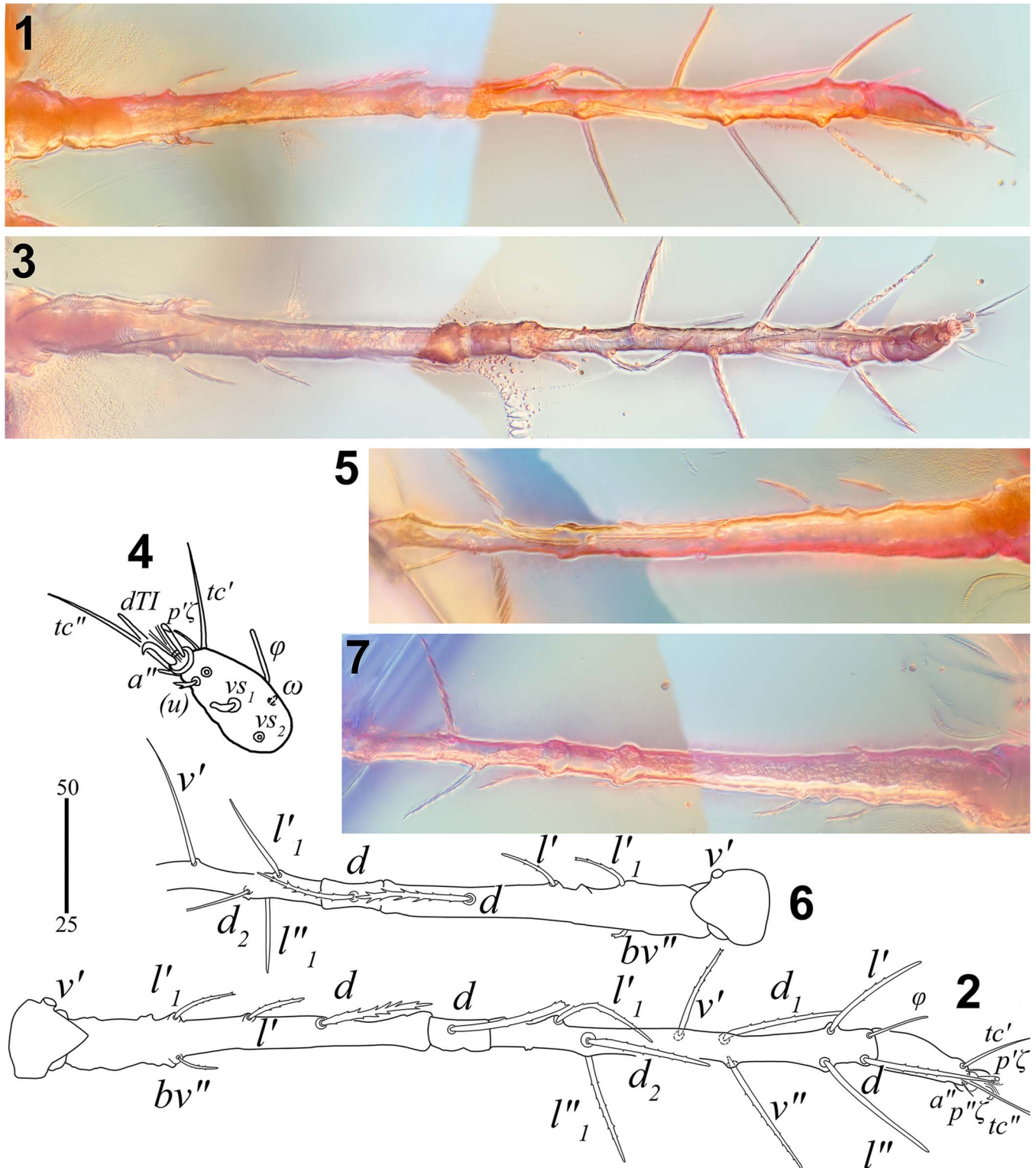


Figure 8. *Neophyllobius glaesus* n. sp., leg I (GPIH 4995a): (1) layered picture of right one in dorsal view; (2) line drawing interpretation of (1); (3) layered picture of right one in ventral view; (4) line drawing interpretation of right tarsus in ventral view; (5) layered picture of left one in dorsal view; (6) line drawing interpretation of (5); (7) layered picture of left one in ventral view. *a* = anterolateral seta; *bv* = basiventral seta of femur; *d*, *d*₁, *d*₂ = dorsal seta; *dTI* = dorsal seta of right tibia I; *l*, *l*₁ = lateral seta; *p*ζ = eupathidial proral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs*₁, *vs*₂ = midventral setae of tarsus; φ = tibial solenidion; ω = tarsal solenidion; ' = anterior; '' = posterior. (1–3, 5–7) Scale bar = 50 μm; (4) scale bar = 25 μm.

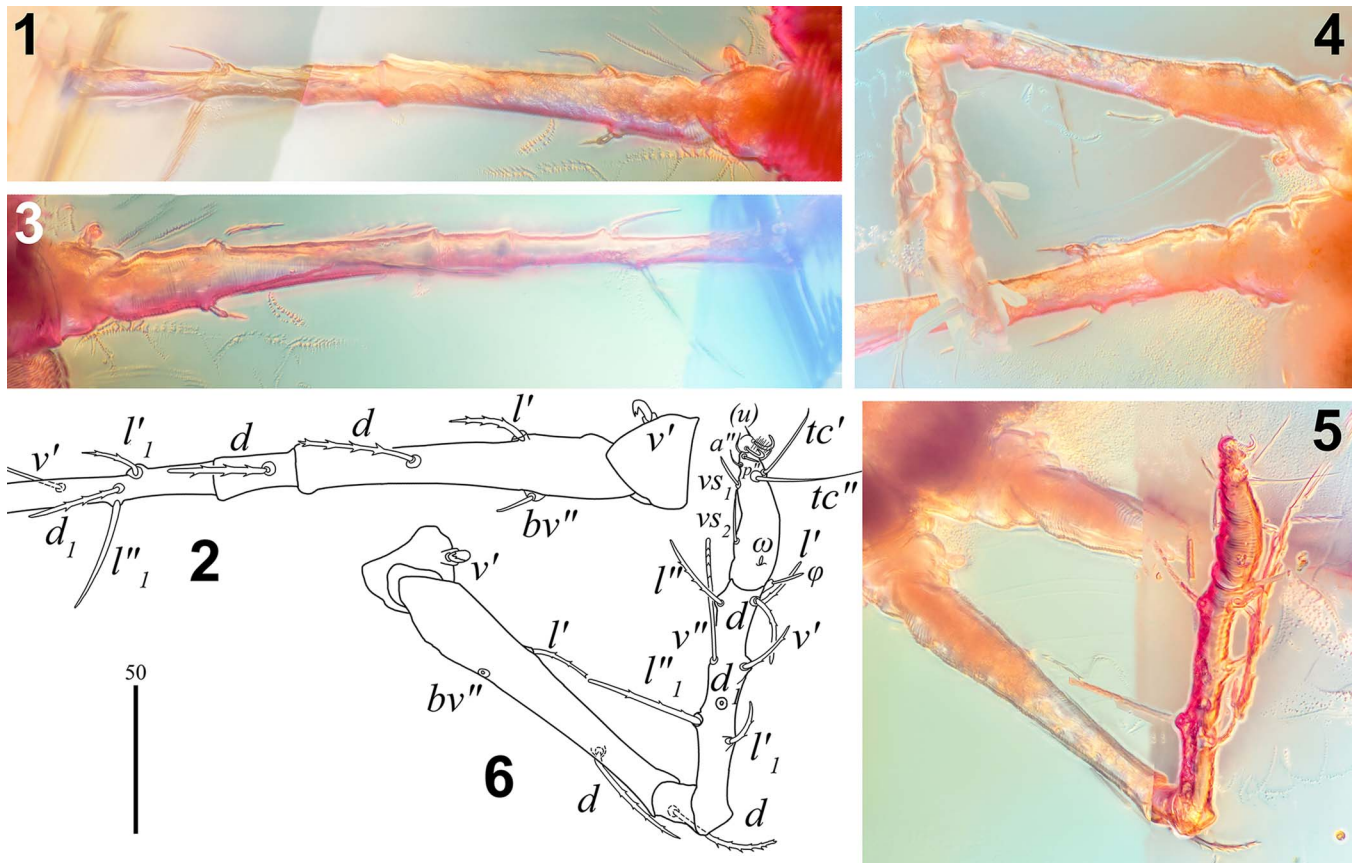


Figure 9. *Neophyllobius glaesus* n. sp., leg II (GPIH 4995a): (1) layered picture of right one in dorsal view; (2) line drawing interpretation of (1); (3) layered picture of right one in ventral view; (4) layered picture of left one in dorsal view; (5) layered picture of left one in ventral view; (6) line drawing interpretation of (5). *a* = anterolateral seta; *bv* = basiventral seta of femur; *d*, *d*₁ = dorsal seta; *l*, *l*₁ = lateral seta; *p* = proral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs*₁, *vs*₂ = midventral setae of tarsus; ϕ = tibial solenidion; ω = tarsal solenidion; ' = anterior; '' = posterior. Scale bar = 50 μ m.

Etymology.—The specific epithet *glæsus* is an adjective derived from the Latin noun *glæsum* in the nominative, which is translated into amber.

Remarks.—*N. glaesus* n. sp. is morphologically very similar to the Recent species *N. hypoleanae* Bolland, 1991. Both species have relatively short dorsal setae *d* of genera I–III; setae *c1* are shorter and *d1* longer than interval to setae next behind them; setae *bv''* (most proximal) of femora I are distinctly shorter than setae *d* (most distal); epimeral setae *1a–c* are different in length; number of setae on femora I–IV are 4–3–3–2, respectively; each tarsus of legs I–IV has two midventral setae *vs*; dorsal setae *d* of palpfemur are only slightly longer than lateral setae *l''*. However, *N. glaesus* has short dorsal setae *d* on genua IV (*N. hypoleanae* has these setae at least two times longer than the length of the genu); distances between setae *ve* and *sci* are distinctly greater (in *N. hypoleanae* bases of *ve* are situated just in front of *sci*); setae *e1* 45 μ m long and *fl* 41 μ m are distinctly shorter (these setae in *N. hypoleanae* are 60 μ m long); and setae *fl* do not reach level of bases of setae *h1* (in *N. hypoleanae* setae *fl* reach behind bases of setae *h1*).

N. glaesus n. sp. is morphologically similar to the fossil species *N. succineus* Bolland and Magowski, 1990. Both species have a relatively short dorsal setae *d* of genera I–IV; fifteen

pairs of idiosomal setae (setae *pdx* present) without significant differences in their lengths; two midventral setae *vs* on each tarsus; and the dorsal setae *d* of tibiae similar in length to the lateral *l* and ventral *v* setae. The new species differs from *N. succineus* by the presence of three setae on femora III (*N. succineus* has only two of them); chaetotaxy formulae of tibiae I–IV is 9–8–8–7 (8–7–7–6 in *N. succineus*); distinctly shorter idiosomal setae *e1* 42–44 μ m and *h1* (28–30 μ m) (75 and 64 μ m, respectively, in *N. succineus*); distance *ve–sci* 29–36 μ m (12 μ m in *N. succineus*); and gnathosoma wholly covered by the prodorsum (in *N. succineus* prodorsum covers it partially). A comparison of all three fossil *Neophyllobius* species from Baltic amber is summarized in Table 1.

Unlike the inclusion of *N. electrus*, almost the entire individual was preserved inside the preparation. The cuticle imprint is translucent, especially on the legs and in the middle of the idiosoma. Residues of the cuticle, internal organs, and probably food remains form brown artifacts within the inclusion. Their highest concentration occurs on the edges of the idiosoma forming a dense border. This makes it difficult to interpret some structures, especially on the ventral opisthosoma. The piece containing the tarsus and part of the tibia of left leg II broke off and was embedded in epoxy resin to preserve such minute amber fragment. Left tarsus I had already been cut or polished in the sample.

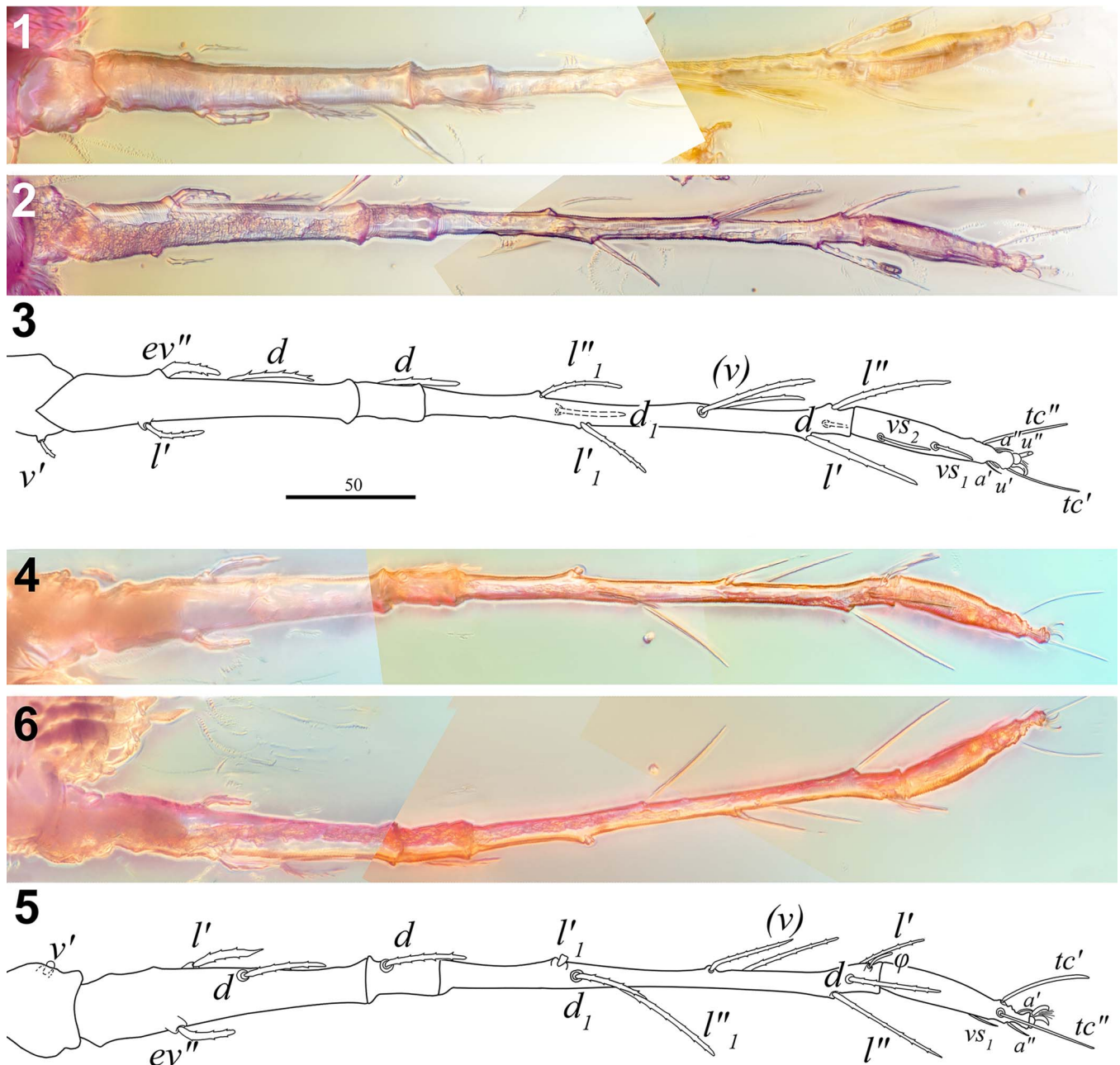


Figure 10. *Neophyllobius glaesus* n. sp., leg III (GPIH 4995a): (1) layered picture of left one in dorsal view; (2) layered picture of left one in ventral view; (3) line drawing interpretation of (2); (4) layered picture of right one in dorsal view; (5) line drawing interpretation of (4); (6) layered picture of right one in ventral view. *a* = anterolateral seta; *d*, *d*₁ = dorsal seta; *ev* = basiventral seta of femur; *l*, *l*₁ = lateral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs*₁, *vs*₂ = midventral setae of tarsus; φ = tibial solenidion; ' = anterior; ' = posterior. Scale bar = 50 μ m.

Discussion

Common remarks for studied inclusions.—The most recent and valid diagnosis of *Neophyllobius* has been proposed by Fan and Walter (2006). There is little doubt that the fossil specimens belong to this genus. Although the preservation does not reveal an exact number of peritremal loops, there is at least one in each inclusion because some peritremal structures are visible microscopically. Palptrochanters are nude, palpfemora have two setae on each, and each palpgenu has one seta. Idiosoma bears 14 or 15 pairs of setae. Genital valves have

one pair of setae *g*. Anal valves have probably three pairs of pseudanal setae *ps1*–3. Solenidion ω is present on each basal half of tarsi I and II. Phanerotaxies of legs are also typical, as in Recent representatives of *Neophyllobius*.

There is noticeable sexual dimorphism in the family Camerobiidae (already present in nymphs, see Bolland, 2001). As in other raphignathoid families, males have a sclerotized aedeagus, and the genital opening is situated terminally or dorsoterminally. In addition, there are two solenidia φ on each tibia I–II, and tarsal solenidia ω are enlarged and/or elongated. The lack of these features excludes the possibility that the specimens

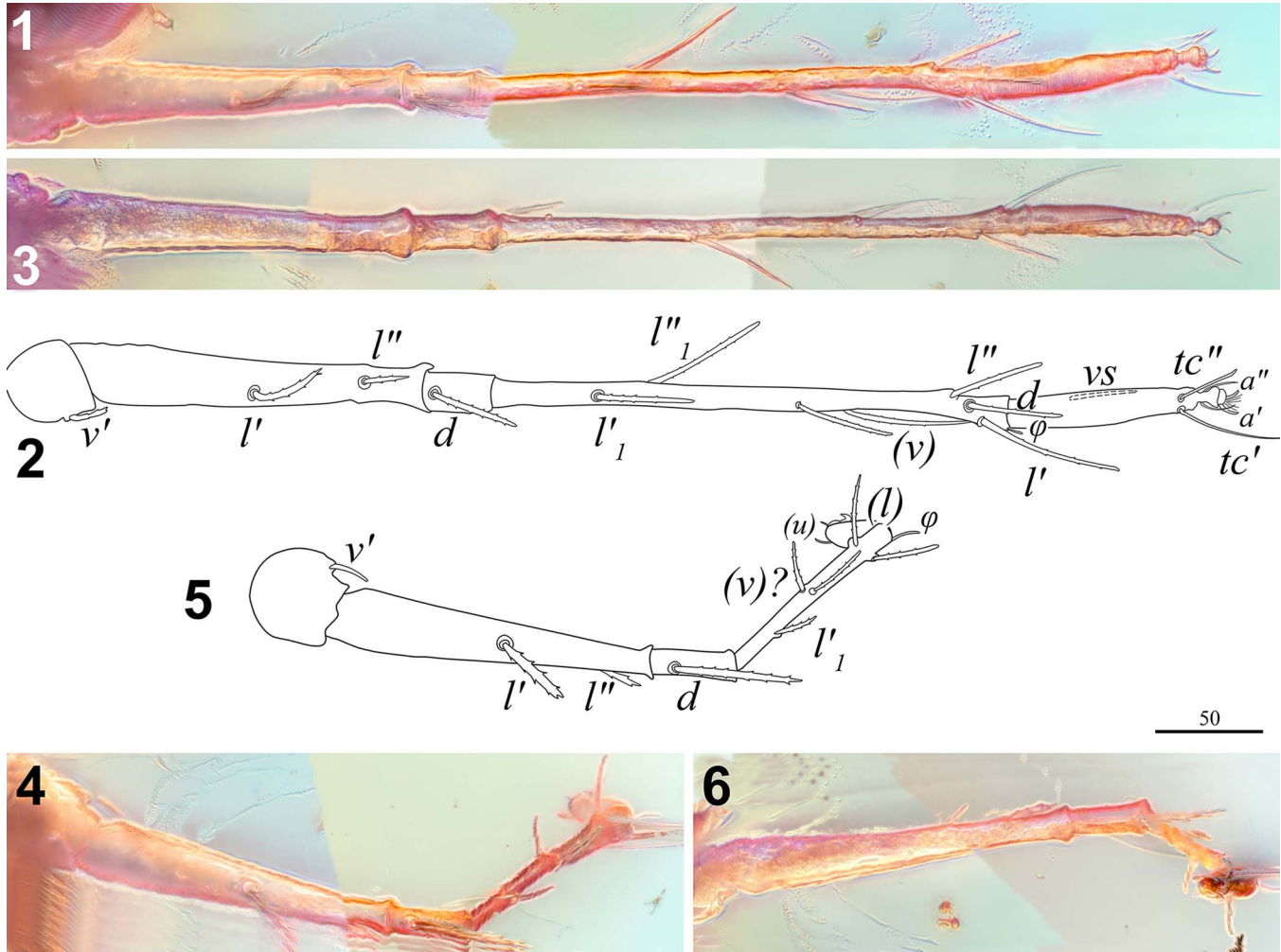


Figure 11. *Neophyllobius glaesus* n. sp., leg IV (GPIH 4995a): (1) layered picture of left one in dorsal view; (2) line drawing interpretation of (1); (3) layered picture of left one in ventral view; (4) layered picture of right one in dorsal view; (5) line drawing interpretation of (4); (6) layered picture of right one in ventral view. *a* = anterolateral seta; *d* = dorsal seta; *l*, *l*₁ = lateral seta; *tc* = tectal seta; *u* = unguinal seta; *v* = ventral seta; *vs* = midventral seta of tarsus; ϕ = tibial solenidion; ' = anterior; '' = posterior. Scale bar = 50 μ m.

are males. There are also other sex differences such as the length and position of some leg setae, but they are objectively comparable only if there are two sexes available to study. Camerobiid protonymphs are easily distinguished by the absence of setae on the epimera of legs IV and the nude trochanters IV (seta *v*' not developed yet). These setae are present on the studied specimens. Bolland (1983) stated for the first time that there are two nymphal stases within the family. However, deutonymphs are more difficult to distinguish from adults without reference material of all stases. Deutonymphs have generally longer setae *d* on the genua. Specimens of each new fossil species have relatively short genual setae, were found solely (larvae and nymphs are more commonly found in small aggregations), and probably have well-developed genital valves and complete chaetotaxy. Hence, the specimens are considered in this work as adult females, which seems to be the most probable determination of stase and sex. It is important for the reader to be aware of the difficulty of interpreting the fossil material, especially if it is present only in the form of sole individuals of rare mite groups.

Asymmetric hypertrophy of seta h2 in N. glaesus.—Mostly neglected, François Grandjean's works on deviations and their possible evolutionary significance (summarized and extended in Grandjean, 1971, 1972, 1973 but unfinished) echo even with individual discoveries, as is the case with the inclusion of *N. glaesus* n. sp. According to Grandjean, deviations can be divided into vertitions, which are important in evolutionary terms and reflect the changes that may occur in future generations permanently, and anomalies, which are more rare, random changes that are not of evolutionary significance (Grandjean, 1971). Deviations are most often asymmetrical and include the absence of some idionymous organ (any holotrichous seta is an example of such), its doubling, change of size, or different location. Other scholars have also studied morphological abnormalities, mostly in terms of teratological singularities but also in the context of regulatory genes (e.g., Southcott, 1997; Weigmann, 2010; Bingül et al., 2017). Abnormalities occurring among populations of *Tycherobius stramenticola* Bolland, 1986 and *T. polonicus* Bolland, 1986, mostly in the form of asymmetrical absence of setae, were

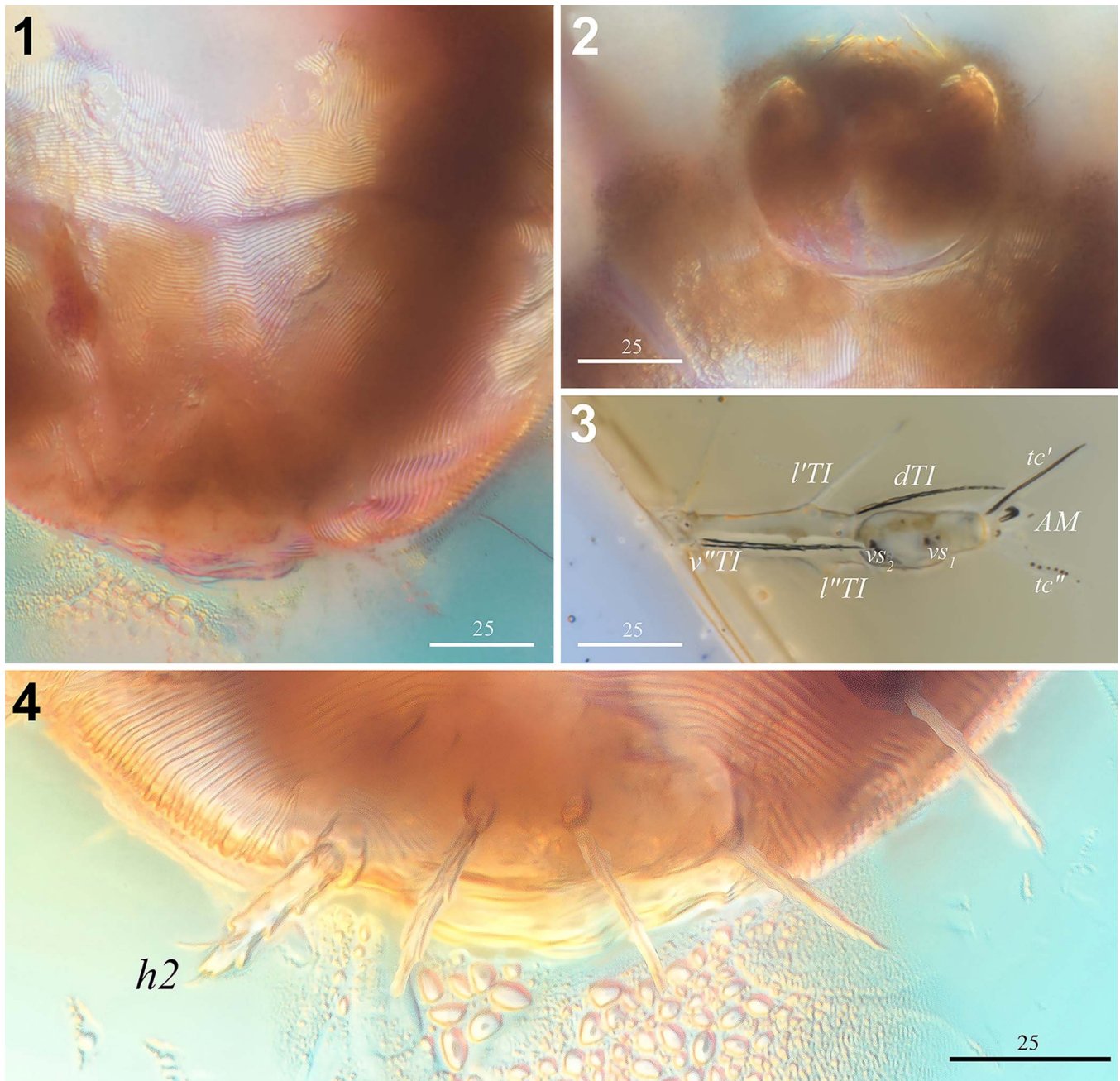


Figure 12. *Neophyllobius glaesus* n. sp. (GPIH 4995): (1) opisthosoma in ventral view (GPIH 4995a); (2) gnathosoma in ventral view (GPIH 4995a); (3) left tarsus of leg II (GPIH 4995b); (4) opisthosoma in dorsal view (GPIH 4995a). AM = ambulacrum (claws + tenant-hair empodium); dTI = dorsal seta of tibia; h2 = hypertrophied seta; lTI = lateral seta of tibia; tc = tectal seta; vs₁, vs₂ = midventral tarsal setae; vTI = ventral seta of tibia; ' = anterior; '' = posterior. Scale bars = 25 µm.

indicated (Koç and Akyol, 2007). The inclusion of *N. glaesus* n. sp. has a hypertrophied (i.e., enlarged, thickened) left seta h2 (Fig. 12.4). The right one is similar to other idiosomal setae. There are no species of *Neophyllobius* with setae h2 distinctly thicker than other idiosomal setae, and this kind of asymmetry has not been reported for Camerobiidae; hence, the observed deviation is more likely to be an anomaly rather than a vertition. It would be interesting to study the microanatomical structure of such an abnormality, whether enlargement and thickening are associated with more intense cuticle deposition, cell proliferation, or all of these factors and

whether the abnormality is affected by any individual mutation or is an error in ontogenetic development. Note also that hypertrophic setae occur in both acariform (e.g., Fernandez et al., 2014) and parasitiform mites (e.g., Mašán and Fenda, 2014) and mostly have some functions in sexual behavior. Hypertrophic setae may have originated at first from rare, random deviations (enlarging, thickening), which having a genetic background, were subject to sexual selection.

The shape of the prodorsum and position of setae h1, h2.—Specimens mounted on microscope slides, especially those

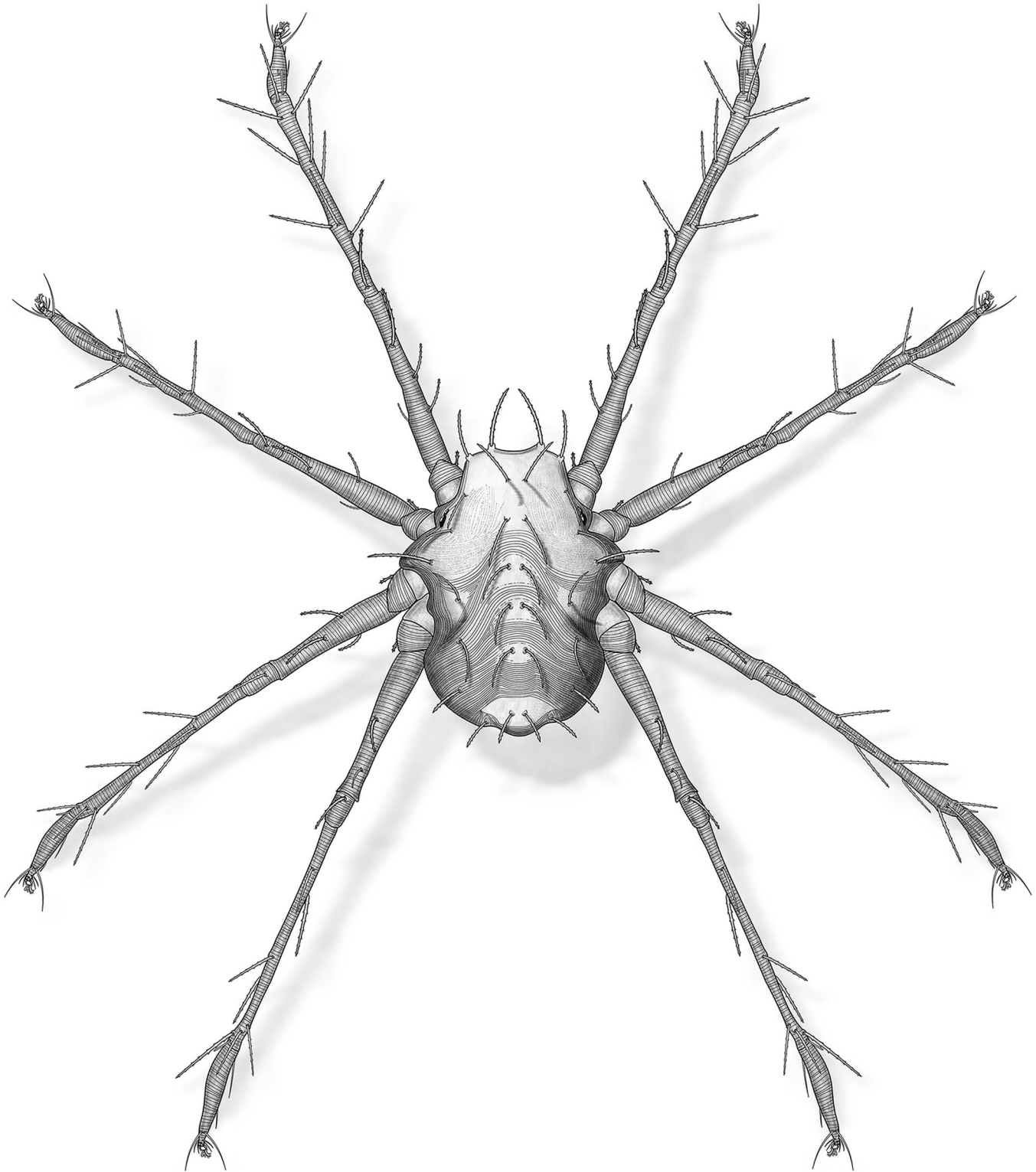


Figure 13. *Neophyllobius glaesus* n. sp., reconstruction of adult female stase.

without highly sclerotized cuticular structures, lose valuable information about the exact shape of their bodies. The flexible cuticle, which is additionally often softened before final preparation and flattened under two microscope slides (for the essential preparation techniques, see Evans, 1992; Walter and

Krantz, 2009), gives only an approximate shape of the body. In nature, it is subject to other forces and factors shaping the habitus, for example, through muscle attachments and its compositional structure (Alberti and Coons, 1999). A solid preparation made by the forces of nature, as inclusions in

amber can be called, preserves the almost intact appearance of a once-living animal. Most of the studies on Camerobiidae were carried out on the basis of just such flattened individuals mounted on microscopic slides (some recent examples: Bolland, 2001; Akyol, 2013; Zeity and Gowda, 2013; Khanjani et al., 2014). This process generally causes the gnathosoma to be unnaturally situated slightly on the ventral part of the body but usually at the same level as the idiosoma. Scanning electron microscopic techniques were used for the first time by Bolland (1986) and then by Fan and Walter (2006) to image protonymphal *Decaphyllobius gersoni* Bolland, 1986 and adult *Tycherobius stipula* Walter and Fan, 2006 among Camerobiidae. Images from their papers clearly show that the prodorsum forms a well-distinguishable part of the anterior idiosoma in the shape of a trapezoid, partially protecting the gnathosoma from above. Khaustov and Abramov (2017) also used a scanning electron microscope, but the entire individual was not imaged. The studied inclusion of *N. glaesus* n. sp. has a similarly shaped prodorsum at the edges of which are placed vertical setae directed forward, and it almost entirely covers the gnathosoma. The specimen of *N. electrus* n. sp. has a round prodorsal idiosoma, but it distinctly forms a fold over the gnathosoma. Although no comprehensive studies have been conducted on the behavior of camerobiids, it can be hypothesized that the prodorsum may serve a protective function for the gnathosoma, and its shape may be taxonomically important. This feature dates back to at least the middle Eocene, from which Baltic amber probably originates (Weitschat and Wichard, 2002).

Bolland and Magowski (1990) indicated that the terminal situation of setae *h1* in *N. succineus* is rather exceptional because, in extant species, these setae are situated rather on the dorsal side of the idiosoma. In *N. electrus* the same case can be found—setae *h1* are placed marginally terminating the idiosoma. However, in *N. glaesus*, setae *h1* are located clearly on the dorsal surface of the posterior idiosoma at some distance from the end of the body. So it seems that when interpreting this feature, the microscopic preparations of Recent specimens do not distort the true image of the setae situation. It is not excluded that the terminal location of the *h1* setae may constitute a plesiomorphic character state in the genus *Neophyllobius*, or at least this state could have been more common in the Eocene species.

Brittleness of legs in Camerobiidae.—Bolland and Magowski (1990) stated that legs of camerobiids are difficult to manipulate and are prone to breaking off; hence, the complete specimen of *N. succineus* is a quite curious finding. The studied inclusions have an almost complete set of legs. In *N. glaesus* the tarsus of left leg I had been polished before the sample reached the author. In *N. electrus*, a tarsus and a half of the tibia of left leg I are lacking, and this loss most likely happened before the mite was trapped in leaking resin. Through these observations, the following questions arise. Since the legs of camerobiids are long and prone to breaking, is there a mechanism to regenerate lost parts by adding tissues after molting? Is there a mechanism for regeneration in adults, and if not, how does limb loss affect survival and thus the fitness of individuals? It seems that the ability of limb

regeneration among Prostigmata is the weakest and with the highest mortality rate compared with other higher groups of mites (Rockett and Woodring, 1972) and takes place during molting. New, more-comprehensive studies of the regeneration capacity carried out on different representatives of prostigmatan mites may bring novel discoveries.

Lengths of genual setae d.—A curious feature among the representatives of the genus *Neophyllobius* that has never been discussed is a pattern of lengths of dorsal genual setae *d*. These setae may be short, with length equal to or slightly longer (two or three times) than that of the genu, or they may be very long, with lengths exceeding the combined length of the genu and the following tibia. Intermediate forms are probably present. However, we require more detailed studies and measurements of this character issuing precise criteria (e.g., setae reaching to half of the tibiae are common among species). *N. bequartiodendri* Bolland, 1991, *N. texanus* McGregor, 1950, and *N. trisetosus* De Leon, 1958 are examples of species with short setae *d* on each genu I–IV. *N. euonymi* Bolland and Ripka, 2000, *N. curtipilis*, De Leon, 1958, and *N. saxatilis* Halbert, 1923 have setae *d* short on genua I–III but distinctly long on genua IV. *N. farrieri* De Leon, 1958, *N. fissus* De Leon, 1967, and *N. niloticus* Bolland, 1991 all have setae *d* on genua I–IV very long. *N. armenica* Bolland, 1991 and *N. sycomorus* Zaher and Gomaa, 1979 have the setae *d* long on genua I, III, IV but short on genua II. In some other genera of Camerobiidae—*Bisetulobius*, *Camerobia*, *Decaphyllobius*, and *Tillandsobius*—these setae are always short, that is, the same length as the genu or slightly longer (Bolland, 1986). However, in *Tycherobius*, there may also be a different pattern of setae length, and *Acamerobia* has some setae *d* distinctly longer (Fan and Walter 2006, 2011). Both *N. electrus* n. sp. and *N. glaesus* n. sp. have short dorsal setae of each genu I–IV. It is noticeable that the same pattern is present in *N. succineus*; hence, this feature is common for all known fossil Camerobiidae. It may be a plesiomorphic state of that characteristic, but a sample error is also likely, so the next findings may or may not falsify this hypothesis. If these setae have begun to lengthen in the Cenozoic era, determining the primary cause and function of the final product could be an interesting task. Dorsal setae *d* are simple setae, not morphologically distinct from other leg setae, so a more probable function of them is sensory or/and protective rather than chemosensory. Minute setae κ of genua I–II, which are probably present in all species but indiscernible in fossils, may be chemostimuli-responsive.

Neophyllobius, the most numerous and the oldest genus.—Mites of the genus *Neophyllobius* have been found on all continents except Antarctica (Bolland, 1991). Their worldwide distribution can be due to their exceptional dispersal abilities or their long evolutionary history (camerobiids are slow-moving mites, and no dispersal forms or behaviors have been observed). The three known inclusions of Camerobiidae are evidence that the characteristics of the genus *Neophyllobius* were well developed in the Eocene, and the degree of morphological difference between the fossil species

is comparable to that of species living today. Organic inclusions in Baltic amber come from ecosystems of Eocene Fennoscandia (northern Europe of that time). The presence of extant Camerobiidae in northern-central Europe—*N. bialagorensis* Bolland, 1991 (northern Poland), *N. aesculi* Bolland, 1983, *N. vandebugdi* Bolland, 1991 (the Netherlands), *N. plumifer* Bolland, 1991 (central Poland), *N. saxatilis* Halbert, 1923 (Ireland)—may indicate that *Neophyllobius* returned to central and northern Europe after the last Pleistocene glacial period, which ended ca. 12,000 years ago (Weitschat and Wichard, 2002; Lomolino et al., 2010).

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References

- Akyol, M., 2013, Two new species of the genus *Neophyllobius* Berlese (Acari: Camerobiidae) from Turkey: *International Journal of Acarology*, v. 39, p. 542–546.
- Alberti, G., and Coons, L.B., 1999, Acari: mites, in Harrison, F.W., and Foelix, R.F., eds., *Chelicerate Arthropoda: Microscopic Anatomy of Invertebrates*, v. 8C: New York, Wiley-Liss, p. 515–1213.
- Berlese, A., 1886, *Acari dannosi alle piante cultivate*: Padova, Sacchetto, p. 1–31.
- Bingül, M., Doğan, S., and Doğan, S., 2017, Morphological abnormalities in some stigmatid species of *Eustigmaeus*, *Stigmaeus* and *Storchia* (Acari: Raphignathoidea: Stigmaeidae): *Systematic and Applied Acarology*, v. 22, p. 2119–2126.
- Bolland, H.R., 1983, A description of *Neophyllobius aesculi* n. sp. and its developmental stages (Acari: Camerobiidae): *Entomologische Berichten*, v. 43, p. 42–47.
- Bolland, H.R., 1986, Review of the systematics of the family Camerobiidae (Acari, Raphignathoidea). I. The genera *Camerobia*, *Decaphyllobius*, *Tilandsobius*, and *Tycherobius*: *Tijdschrift Voor Entomologie*, v. 129, p. 191–215.
- Bolland, H.R., 1991, Review of the systematics of the family Camerobiidae. II. The genus *Neophyllobius* Berlese, 1886 (Acari: Raphignathoidea): *Genus*, v. 2, p. 59–226.
- Bolland, H.R., 2001, Observations and description of *Neophyllobius piniphilus* n. sp. (Acari: Camerobiidae) from pine trees in the Netherlands: *International Journal of Acarology*, v. 27, p. 129–134.
- Bolland, H.R., and Magowski, W.L., 1990, *Neophyllobius succineus* n. sp. from Baltic amber (Acari: Raphignathoidea: Camerobiidae): *Entomologische Berichten*, v. 50, p. 17–21.
- Bolland, H.R., and Ripka, G., 2000, A new species of the genus *Neophyllobius* (Acari: Camerobiidae) from Hungary: *International Journal of Acarology*, v. 26, p. 357–361.
- Cuvier, G., 1812, Sur un nouveau rapprochement à établir entre les classes qui composent le Règne animal: *Annales du Muséum National d’Histoire Naturelle*, v. 19, p. 73–84.
- De Leon, D., 1958, The genus *Neophyllobius* in Mexico (*Acarina: Neophyllobidae*): *Florida Entomologist*, v. 41, p. 173–181.
- De Leon, D., 1967, Some Mites of the Caribbean Area. Part I. *Acarina* on Plants in Trinidad; West Indies (*Camerobiidae*, *Tenuipalpidae*, *Cheyletidae*): Lawrence, Kansas, Allen Press, 66 p.
- du Toit, B.J., Theron, P.D., and Ueckermann, E.A., 1998, A new genus and four new species of the family Camerobiidae (Acari: Raphignathoidea) from South Africa: *International Journal of Acarology*, v. 24, p. 3–19.
- Dunlop, J.A., Penney, D., and Jekel, D., 2019, A summary list of fossil spiders and their relatives: *World Spider Catalog* v. 20.0 Natural History Museum Bern <http://wsc.nmbe.ch> [Nov 2019].
- Evans, G.O., 1992, *Principles of Acarology*: Wallingford, CAB International, 563 p.
- Fan, Q.-H., and Walter, D.E., 2006, A review of the genus *Tycherobius* (Acari: Camerobiidae), with descriptions of four new species from Australia: *Zootaxa*, v. 1121, p. 1–52.
- Fan, Q.-H., and Walter, D.E., 2011, *Acamerobia inflatus* gen. n. & sp. n. from Australia (Acari: Prostigmata: Raphignathoidea: Camerobiidae) with notes on the idiosomal chaetotaxy: *Zootaxa*, v. 3045, p. 45–56.
- Fernandez, N., Coineau, Y., Theron, P., and Louwrens, T., 2014, *Nannodromus reveillei* (Acari, Anystida, Saxidromidae) a new genus and species from South Africa: *Zookeys*, v. 378, p. 17–39.
- Gerson, U., Smiley, R.L., and Ochoa, R., 2003, *Mites (Acari) for pest control*: London, Wiley-Blackwell, 539 p.
- Grandjean, F., 1971, Caractères anormaux et verticillaires rencontrés dans des clones de *Platynothrus peltifer* (Koch). Première partie: *Acarologia*, v. 13, p. 209–237.
- Grandjean, F., 1972, Caractères anormaux et verticillaires rencontrés dans des clones de *Platynothrus peltifer* (Koch). Chapitres I à VI de la deuxième partie: *Acarologia*, v. 14, p. 454–478.
- Grandjean, F., 1973, Caractères anormaux et verticillaires rencontrés dans des clones de *Platynothrus peltifer* (Koch). Chapitres VII à XIII de la deuxième partie: *Acarologia*, v. 15, p. 759–780.
- Halbert, J.N., 1923, Notes on Acari, with description of new species: *Zoological Journal of Linnean Society*, v. 35, p. 363–395.
- Kethley, J.B., 1982, *Acariformes in Parker, S.P., ed., Synopsis and Classification of Living Organisms*: New York, McGraw-Hill, p. 142–145.
- Kethley, J.B., 1990, *Acarina: Prostigmata (Actinedida)*, in Dindal, D.L., ed., *Soil Biology Guide*: New York, Wiley, p. 667–756.
- Khanjani, M., Hoseini, M.A., Yazdanpanah, S., and Masoudian, F., 2014, *Neophyllobius lorestanicus* sp. nov. and *N. ostovani* sp. nov. (Acari: Camerobiidae) from Iran: *Zootaxa*, v. 3764, p. 441–454.
- Khaustov, A.A., and Abramov V.V., 2017, A new species and a new record of raphignathoid mites (Acari: Raphignathoidea: Camerobiidae, Stigmaeidae) occurring in the galleries of bark beetles (Coleoptera: Curculionidae: Scolytinae) from Russia: *Systematic and Applied Acarology*, v. 22, p. 1385–1398.
- Koç, K., and Akyol, M., 2007, Morphometric & intraspecific variations between specimens of *Tycherobius stramenticola* and *Tycherobius polonicus* (Acari: Camerobiidae) from Turkey: *Acarologia*, v. 47, p. 139–142.
- Koch, C.L., and Berendt, G.C., 1854, Die im Bernstein befindlichen Crustaceen, Myriopoden, Arachniden und Apteren der Vorwelt, in Berendt, G.C., ed., Die in Bernstein befindlichen organischen Reste der Vorwelt, gesammelt, in Verbindung mit Mehreren bearbeitet und herausgegeben, v. 1: Berlin, Commission der Nicolaischen Buchhandlung, p. 103–111; 124.
- Kramer, P., 1877, Grundzüge zur Systematik der Milben: *Archiv für Naturgeschichte*, v. 43, p. 215–247.
- Kuznetsov, N.N., Khaustov, A.A., and Perkovsky, E.E., 2010, First record of mites of the family Stigmaeidae (Acari, Raphignathoidea) from Rovno amber with description of a new species of the genus *Mediolata*: *Vestnik zoologii*, v. 44, p. 545–547.
- Lomolino, M.V., Riddle, B.R., Brown, J.H., 2010, *Biogeography* (fourth edition): Sunderland, Massachusetts, Sinauer Associates, 878 p.
- Mašán, P., and Fenda, P., 2014, A new edaphic mite of the genus *Pachyseius* (Acari, Mesostigmata, Pachylaelapidae) from Făgăraș Mountains (Romania), with a key to world species: *Systematic and Applied Acarology*, v. 19, p. 137–143.
- McGregor, E.A., 1950, Mites of the genus *Neophyllobius*: *Bulletin of the Southern California Academy of Sciences*, v. 49, p. 55–70.
- Oudemans, A.C., 1909, Über die bis jetzt genauer bekannten Thrombidiumlarven und über eine neue Klassifikation der Prostigmata: *Tijdschrift voor Entomologie*, v. 52, p. 19–61.
- Paredes-León, R., Corona-López, A.M., Flores-Palacios, A., and Toledo-Hernández, V.H., 2016, Camerobiid mites (Acariformes: Raphignathina: Camerobiidae) inhabiting epiphytic bromeliads and soil litter of tropical dry forest with analysis of setal homology in the genus *Neophyllobius*: *European Journal of Taxonomy*, v. 202, p. 1–25.
- Reuter, E., 1909, Zur Morphologie und Ontogenie der Acariden mit besonderer Berücksichtigung von *Pediculopsis graminum*: *Acta Societatis Scientiarum Fennicae*, v. 36, p. 1–288.
- Rockett, C.L., and Woodring, J.P., 1972, Comparative studies of acarine limb regeneration, apolysis, and ecdysis: *Journal of Insect Physiology*, v. 18, p. 2319–2336.
- Seyfullah, L.J., Beimforde, C., Corso, J.D., Perrichot, V., Rikkinen, J., and Schmidt, A.R., 2018, Production and preservation of resins—past and present: *Biological Reviews*, v. 93, p. 1684–1714.
- Sidorchuk, E., 2013, New technique for preparation of small-sized amber samples with application to mites, in Azar, D., Engel, M.S., Jarzembowski, E., Krogmann, L., Nel, A., and Santiago-Blay, J.A., eds., *Insect Evolution in an Amberiferous and Stone Alphabet*. Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber: Leiden, Brill, p. 189–201.

- Sidorchuk, E.A., 2018, Mites as fossils: forever small?: *International Journal of Acarology*, v. 44, p. 349–359.
- Sidorchuk, E.A., and Vorontsov, D.D., 2016, Microscopic preparation of amber. <http://www.amber.openscience.ru/index.php?page=overview&lang=en> [Nov 2019].
- Sidorchuk, E.A., and Vorontsov, D.D., 2018, Preparation of small-sized 3D amber samples: state of the technique: *Palaeoentomology*, v. 1, p. 80–90.
- Southcott, R.V., 1957, Description of a new Australian raphignathoid mite, with remarks on the classification of the Trombidiformes (Acarina): *Proceedings of the Linnean Society of New South Wales*, v. 81, p. 306–312.
- Southcott, R.V., 1997, Dismelia and other developmental abnormalities in prostigmatid mites (Acari): *International Journal of Acarology*, v. 23, p. 93–102.
- Travé, J., and Vachon, M., 1975, François Grandjean 1882–1975 (Notice biographique et bibliographique): *Acarologia*, v. 17, p. 1–19.
- van der Hammen, L., 1980, Glossary of Acarological Terminology, Volume 1. General Terminology: The Hague, Dr. W. Junk, B.V., 244 p.
- Walter, D.E., and Krantz, G.W., 2009, Collecting, rearing, and preparing specimens, in Krantz, G.W., and Walter, D.E., eds, *A Manual of Acarology* [third edition]: Lubbock, Texas, Texas Tech University Press, p. 83–96.
- Walter, D.E., Lindquist, E.E., Smith, I.M., Cook, D.R., and Krantz, G.W., 2009, Order Trombidiformes, in Krantz, G.W., and Walter, D.E., eds., *A Manual of Acarology* [third edition]: Lubbock, Texas, Texas Tech University Press, p. 233–420.
- Weigmann, G., 2010, Anomalies of notogastral structures in poronotic oribatid mites (Oribatida: Poronota) interpreted as cryptic ancestral characters modulated by regulatory genes, in Sabelis, M.W., and Bruin, J., eds, *Trends in Acarology: Proceedings of the 12th International Congress: Dordrecht*, Springer, p. 17–22.
- Weitschat, W., and Wichard, W., 2002, *Atlas of Plants and Animals in Baltic Amber*: München, Verlag Dr. Friedrich Pfeil, 256 p.
- Zaher, M.A., and Gomaa, E.A., 1979, Genus *Neophyllobius* in Egypt with description of three new species (*Prostigmata-Neophyllobidae*): *International Journal of Acarology*, v. 5, p. 123–130.
- Zakhvatkin, A.A., 1952, Division of the Acarina into orders and their position in the system of the Chelicerata: *Parazitologicheskii Sbornik*, v. 14, p. 5–46. [in Russian]
- Zeity, M., and Gowda, C.C., 2013, A new species of *Neophyllobius* Berlese (Acari: Camerobiidae) from India: *International Journal of Acarology*, v. 39, p. 547–550.
- Zmudzinski, M., 2020a, *Neophyllobius electrus* | Baltic amber. figshare. Collection. <https://doi.org/10.6084/m9.figshare.c.4757810>.
- Zmudzinski, M., 2020b, *Neophyllobius glaesus* | Baltic amber. figshare. Collection. <https://doi.org/10.6084/m9.figshare.c.4758479>.

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