Redescription of *Tarsonemus minimax* and Definition of Its Species-Group in the Genus *Tarsonemus* (Acari: Tarsonemidae) with Descriptions of Two New Species

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ABSTRACT The *Tarsonemus minimax* species-group is established for bark beetle commensals of the genus *Tarsonemus* Canestrini and Fanzago, 1876. *T. minimax* Vitzthum 1926 is redescribed, and two new species, *T. terebrans* and *T. typographi* n. spp., are described and illustrated. A diagnostic key to the species is supplied. The systematic status of the species-group is discussed. Biogeography and associations with insect hosts and fungi are reviewed.

KEY WORDS Acari, systematics, Scolytidae, phoresy, host ranges, fungi

TARSONEMID MITE ASSOCIATES OF bark beetles have been of interest for many years. Graf von Vitzthum (1921) described the first taxon (*Pseudotarsonemoides eccoptogasteris*) from subcortical habitats as well as the first *Tarsonemus* associate of bark beetles, namely *T. minimax* (Vitzthum 1926). The tarsonemid associates of Scolytidae are among the best studied to date, mostly as a result of the works of Lindquist (1969), Moser (1985), Moser and Roton (1971) and Smiley and Moser (1974) with lesser contributions of other authors. Multiple associations with bark beetles occurred in the course of mite evolution, and the presence of these associations is continuous throughout the evolution of the major tarsonemid groupings. Primitive genera (*Pseudotarsonemoides, Ununguitarsonemus*) may be remnants of early tarsonemid radiations, which gave rise to many other fungivorous and phytophagous forms. At present, at least two derived genera are still exclusively bark beetle associates (*Heterotarsonemus, Iponemus*). *Tarsonemus,* the most diverse tarsonemid genus, includes many species associated with bark beetles or their close surroundings. Within *Tarsonemus,* at least two species groups (*T. pyrrhidi* Schaarschmidt 1959 and *T. minimax*) are known to be bark beetle associates, although not exclusively.

Representatives of the *pyrrhidi* group are infrequently reported, except in the course of bark beetles studies. Extensive treatment of this group is given elsewhere (W.L.M., unpublished data). Those of the *minimax* group (the current study) are mainly bark beetle commensals or phoronts, but can also occasionally inhabit broader habitats like foliage and litter.

The relationships among tree, beetle, mite, and fungi have been of interest to forest protection workers. In particular, the biology of tarsonemid associates of the southern ~~bark~~ pine beetle (SPB), *Dendroctonus frontalis* Zimmermann has been recently studied by Lombardero et al. (2000). They investigated bionomics and interactions of *T. krantzi* Smiley and Moser 1974 (a member of the *minimax* species-group) with its beetle host and its fungal associate/food substrate.

The key issue in studying such an association is the determination of its components and the framework of mite systematics and diagnostics. Below, we synthesize new data accumulated since the extensive treatments of Lindquist (1969) and Smiley and Moser (1974).

Materials and Methods

Most of the material was collected directly from beetles or damaged wood. Some samples from Poland were extracted from bark and forest litter by Tullgren-Berlese funnels. Beetles were often collected in pheromone traps. Mites were mounted in Berlese's medium. Morphological examination was done, and drawings were prepared with a phase-contrast microscope (Olympus BX 50) with drawing attachment.

Nomenclature for body and legs setal notation is mostly derived from Lindquist (1986). The following abbreviations are used: PrS, prodorsal shield; PrP, ventral propodosomal plate; MeP, ventral metapodosomal plate; tg, tegula; ap. 1-1, ap. 2-2, distances between

While this paper was in the late stage of preparation, a new species has been discovered, having tergital setae *d* and *f* stiff and bluntly pointed. It will be described in a subsequent work dealing mostly with redescriptions of other member-species of the *Tarsonemus* group *minimax*.

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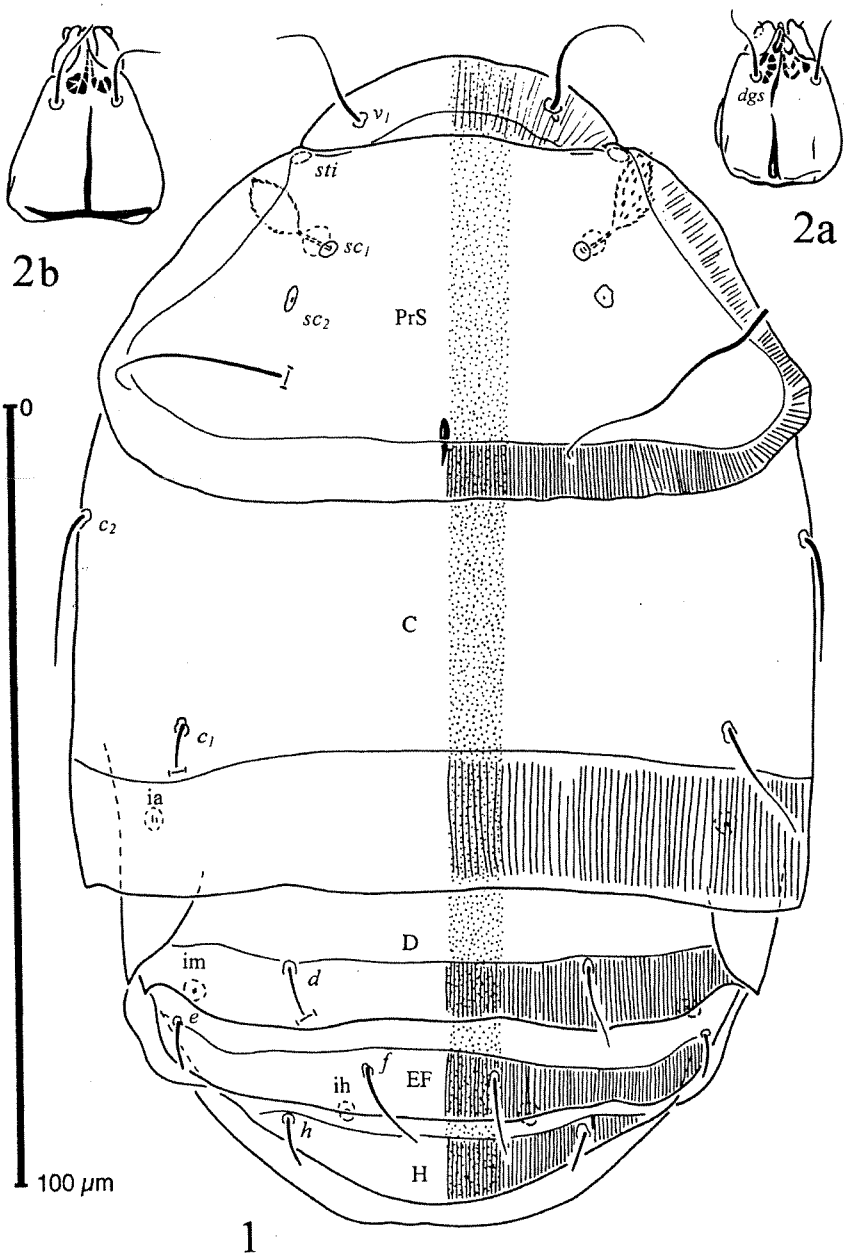


Figs. 1–2. *Tarsonemus minimax*, female dorsum: (1) lectotype idiosoma. (2) gnathosoma: (a) lectotype, (b) paralectotype. Sign [–], broken/displaced setae.

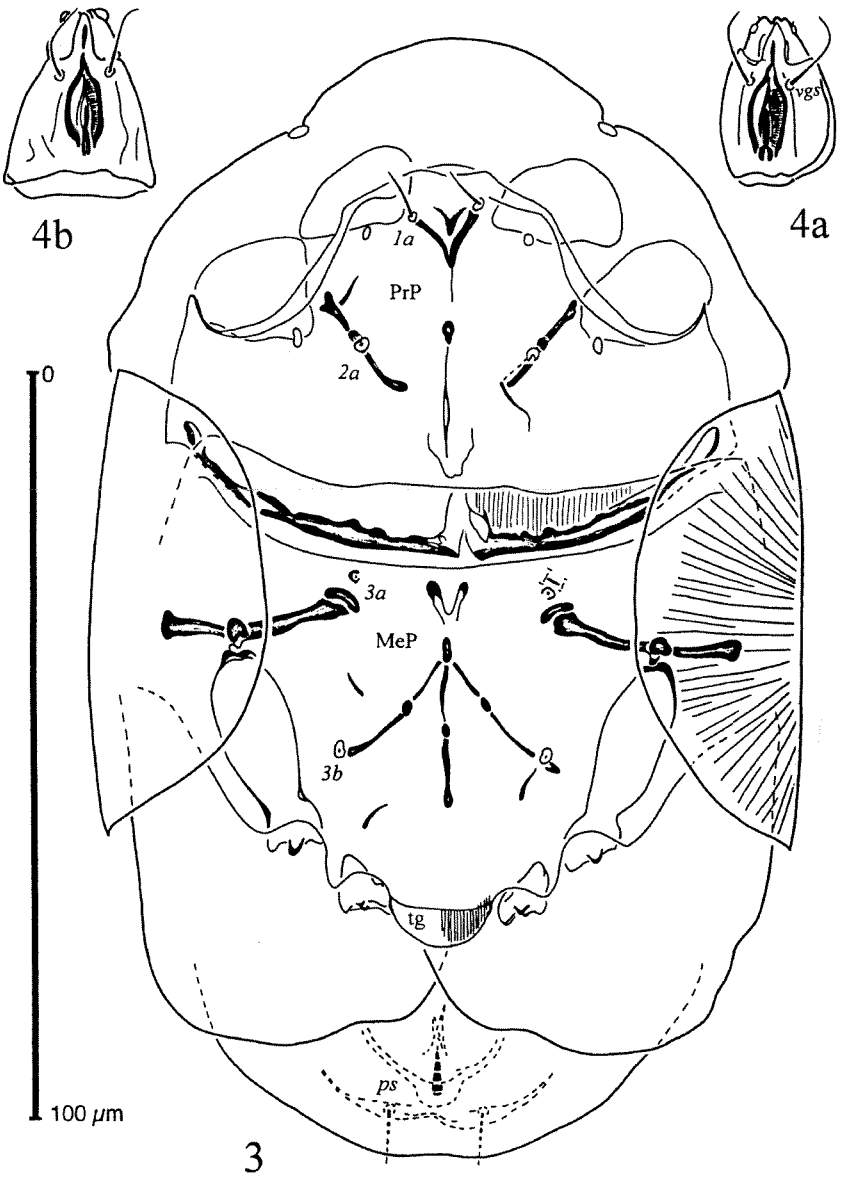
anterolateral ends of apodemes 1-1 and 2-2 respectively; Ta, tarsus; Tbt, tibiotarsus; Tb, tibia; Ge, genu; Fege, femorogenu; Fe, femur; Tr, trochanter. Excluded from the setal count are tiny, and often hardly discernible setae *u'*-*u"* flanking pretarsi; - marks separation of leg segments, + marks their fusion. All measurements are given in μm. Lengths of legs are compared excluding pretarsi and trochanters (legs measured from the apex of tarsal or tibiotarsal segment to the proximal end of femur or femurogenu).

Names of scientific institutions where types were deposited are: Bavarian State Collection (BSC), Munich, Germany; Canadian National Collection (CNC), Ottawa, Ontario, Canada; Department of Animal Taxonomy and Ecology (DATE), A. Mickiewicz University, Poznan, Poland; United States National Museum (Natural History) (NMNH), mite collection (USDA-ARS), Beltsville, MD, United States; Zoological Museum (ZMH), Hamburg University, Hamburg, Germany.

Diagnoses and Descriptions

Tarsonemus minimax Group

Diagnosis: Female: Idiosoma ellipsoidal, ≈1.5× as long as wide, pharynx with strongly sclerotized outer part, tergital setae *d* and *f* (Figs. 1 and 9) most often



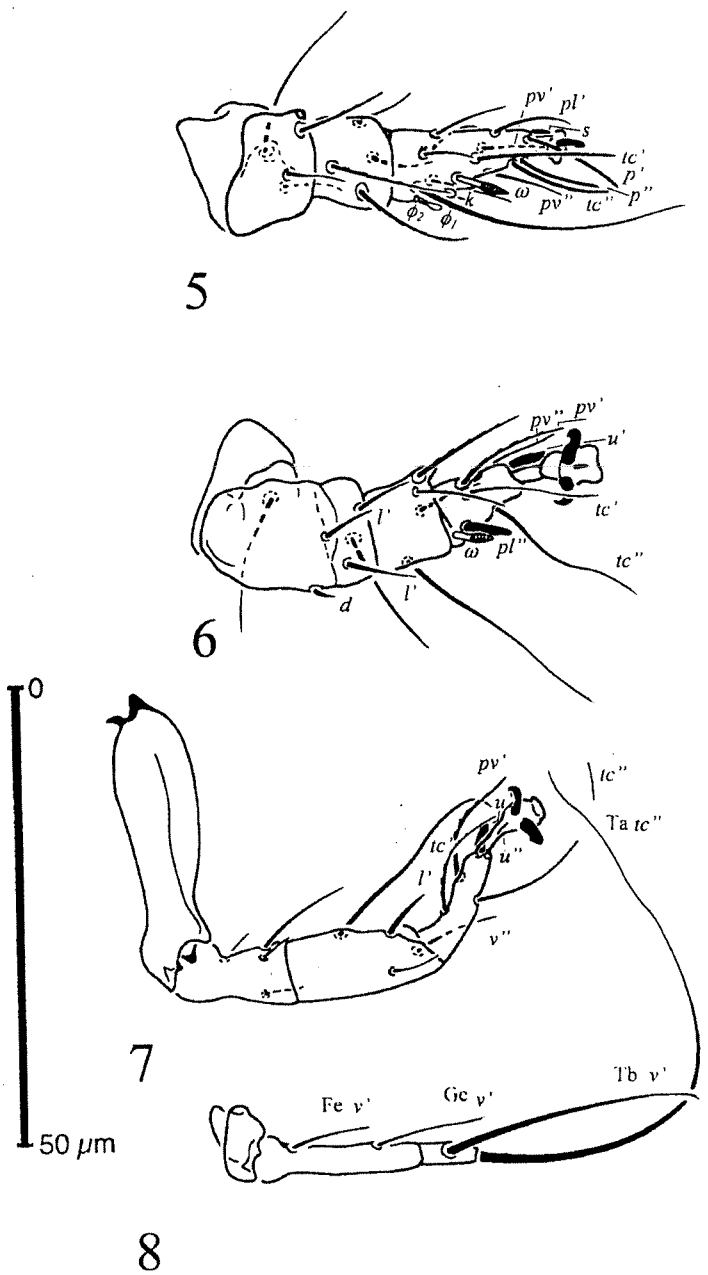
Figs. 3–4. *Tarsonemus minimax*, female venter: (3) lectotype idiosoma. (4) gnathosoma: (a) lectotype, (b) paralectotype.

attenuate, apodematal structures (particularly sejugal one) well-pronounced; tegula ("tg" in Figs. 3 and 11) broadly rounded, usually wider than the mid-diameter of trochanter IV. Legs short and stubby, tibiotarsus without ventral recurvation, claws and setae Ta I *s* and Ta II and III *u'* as well as spine Ta II *pl''* (Figs. 5, 6, and 7) strong or very strong, with rounded or curved tip. Tarsal setae *tc''* on legs II and III attenuate, most often longer than other tarsal setae.

Male: gnathosoma similar to that of females, setae c_1, *d* and *f* (see Fig. 17) stiffer than other dorsal setae, setal complement of legs complete (being the richest in the genus), claws, setae Ta I *s* and Ta II and III *u'* as well as spine Ta II *pl''* (see Figs. 19, 20, and 21) usually strong or very strong, tarsal III *pv''* and tibial III *l'* setae (one or both) most often spine-like, leg IV equal to or shorter than leg III.

Description: Female: Gnathosoma triangular-ovoid; usually as wide basally as long medially. Palpi approximate, rather short, with small palptarsal processes and two minute setae each. Pharynx with indistinct striation (sometimes oblique striae can be well visible), at most ≈0.3× of gnathosomal basal width (or narrower), with well-sclerotized lateral walls. Accessory glandular bodies usually weakly defined, inconspicuous. Postpalpal setae short and tiny. Cheliceral stylets moderate to small, levers small. Setae *dgs* about as long as (or slightly shorter than) *vgs*.

Idiosomal dorsum: prodorsal shield trapezoidal (PrS in Figs. 1 and 9), rostral shield broadly semicircular covering basal one-thirds length of gnathosoma (uncompressed state). Scapular setae (sc_2 in Figs. 1 and 9) located on or posteriad of transverse midline of the shield; their length approximate to the distance be-



Figs. 5–8. *Tarsonemus minimax*, female lectotype legs: (5) leg I; (6) leg II; (7) leg III; (8) leg IV.

tween their alveoles. Sensilli sc_1 fusiform, with two larger spines apically, finely spinose, ≈3× as long as maximum width. Stigmae (*sti* in Figs. 1 and 9) widely separated, tracheae with atria usually apparent, distinct, but never with postatrial sacs. Setae *d* and *f* most often attenuate, and longer than opisthosomal setae *e* and *h* - invariably stiff. Segment D with emarginations related to bases of setae *e* of a following segment. The distance between setae *f* shorter than between *e* and *f* on each side, that between cupuli *ih* always longer than that between bases of setae *f*.

Idiosomal venter: propodosomal apodemes pronounced; anteromedial apodeme occasionally with discontinuities; diffuses posteriorly; sejugal apodeme continuous, arcuate. Coxal setae (*1a* through *3b* in Figs. 3 and 11) variable in length but never as long as half of the distance between each other. Coxal setae *1a* and *2a* located just on or slightly below apodemes 1 and 2 respectively; *2a* located in one half or (rarely) proximal one third of length of apodemes 2. Ventral propodosomal plate with well-defined ridge between lateral ends of apodemes 1 and 2, usually with pronounced angularity. Apodemes 3 extended laterally to anterior extremities of trochanters III. Posteromedial apodeme with well defined Y-shaped fore-section. Setae *3b* placed near posterior ends of apodemes 4. Tegula relatively small, subcircular or slightly truncated, ≈2× as wide as long. Intercoxal IV interval

ranged between 1× and 2× of coxal mid-diameter. Setae *ps* small, sharply ended, delicate, shorter than the distance between their bases.

Legs: Chaetotaxy of leg I: 4-4-6(2ϕ)+8(1ω); leg II: 3-3-4-6(1ω); leg III: 1+3-4-4 or 5. Legs most often short and stubby, tibiotarsus I without ventral recurvation in its tibial portion, usually not >2× as long as wide basally, always with three attenuate setae in tarsal part. Femur II often with lateral flap, as well as tibia II with lateral spur-like process. Solenidia ω on tarsi I and II often with acute ends. Spine *pl″* on tarsus II large or very large, distad of solenidion ω. Tarsal setae *tc″* of legs II and III attenuate, usually longer than other tarsal setae of those legs (except *T. terebrans* n. sp.). Setae Ta I *s* and Ta II and III *u′* and Ta II *pl″* usually strong; when very strong, then with tips curved. Free segments of leg IV apparently shorter than combined femurogenu and tibia of leg III. Femoral *v′* seta on Fege IV always weaker than genual *v′*, subterminal seta Tb *v′* approximately as long as free segments of leg IV, terminal seta Ta *tc″* at least twice, usually 3x to 4x as long as whole leg IV. Claws from moderate to strong, curved.

Male: Idiosoma >1.5× as long as wide (copulatory complex included). Gnathosoma: shape, palpi, cheliceral stylets and levers similar to that in females. Postpalpal (*pp*) setae present, very tiny.

Idiosomal dorsum: prodorsal shield (PrS in Fig. 17) sub-triangular, truncated anteriorly. Setae v_1, v_2 and sc_1 on prodorsal shield arranged in row (on each side), but sc_2 lateral to this alignment, almost, or exactly at the same level as sc_1. Setae v_2 the weakest and shortest of all on PrS, the length of sc_2 can vary from same of v_1 to v_2. Scapular sc_1 always the longest on PrS, located posteriorly to transverse midline of the shield. The shield CD almost quadrangular, with setae c_2 ≈2× (or more) as long as c_1, the latter stiff and most often blunt, in contrast to *d* and *f* which are stiff but acute and never fully attenuate. Setae *f* on the shield EF shorter than c_1 and *d*, arranged in the same distance each to another as, or shorter than that between bases of *d*. Setae *h* very delicate, short. Genital capsule (HPs in Fig. 17) slightly wider than long, built typically for the genus.

Idiosomal venter: propodosomal apodemes strong, anteromedial apodeme sometimes with discontinuities between apodemes 1 and 2, and/or at a junction with sejugal apodeme. Coxal setae *1a* and *2a* usually stiffer than those on metapodosoma or those of a female, though not obviously blunt. Metapodosomal apodemes strong, pronounced with typical shape of a double M; coxal fields III and IV often with coarse and strong granulation anteriorly. Ventral setae of variable length but setae *1a* the shortest and *3b* usually the longest of all. Setae *3a* usually separated more widely than *3b* (except equidistant for *T. terebrans*).

Legs: Chaetotaxy of leg I: 4-4-6(2ϕ)-10(1ω); leg II: 3-3-4-6(1ω); leg III: 1-3-4-4. Legs relatively short compared with most of the other species groups; tarsus I (excluding pretarsus) most often less than twice as long as wide basally (except *T. terebrans* where the ratio approaches 2:1). Tarsus I with three attenuate setae and two small eupathidia (*ft′* and *ft″*). Solenidia ω on tarsi I and II with acute or rounded ends, spine *pl″* on tarsus II large or very large. Tarsal setae *tc″* of legs II and III attenuate, usually the longest of all setae on these segments, those on tarsi III even longer than on tarsi II. In some species tarsal III *pv″* and/or tibial III *l′* may assume the form of a spine, which may be especially prominent and strong in the case of Tb III *l′*. Setae *s* (on Ta I) and *u′* (on Ta II and III) usually strong, in one case (*T. suski* Smiley and Moser 1974) both setae flanking pretasus III (*u″* and *p′*) strong and spine-like. Claws usually strong (again except *T. terebrans*, whose claws are moderate). Entire leg IV equal to or shorter than leg III; from 2× to 2.5× as long as wide basally (claw included). Setae on genual part of femurogenu subequal in length, or seta *l″* slightly longer than *v′*; both attenuate, at least 2× as long as femoral *v′* (with possible exception for *T. suski*). Tarsus IV immovably connected with tibia, though suture still discernible. Tibial seta *v′* most often about as long as femurogenu IV, blunt, coarsely barbed, with the exception of *T. triarcus* whose *v′* is longer than the free segments leg IV, sharp, attenuate.

Larva: (known only for *T. endophloeus* Lindquist 1969 and *T. terebrans* n. sp.). Gnathosoma and its structures similar to those of adults; however pharynx realtively more narrow and less sclerotized; glandular bodies indistinct; postpalpal (*pp*) setae indiscernible. Dorsal setae v_1-c_2 slender, c_1-h_2 stiff; h_1 again attenuate. Setae h_2 are approximately as long as c_2. Chaetotaxy of leg I: 4-4-6(1ϕ)-6(1ω); leg II: 3-3-4-5(1ω); leg III: 1-3-4-4. Tibia III with seta *l′* spine-like (see Fig. 27).

Member species:

T. minimax von Vitzthum 1926 (female);
T. crassus (Schaarschmidt 1959) (female, male);
T. triarcus Lindquist 1969 (female, male);
T. subcorticalis Lindquist 1969 (female, male);
T. endophloeus Lindquist 1969 (female, male, larva);
T. krantzi Smiley and Moser 1974 (n. sp. "Smiley in prep." in Lindquist 1969, partim., female, male, larva);
T. suskii Smiley and Moser 1974 (n. sp. "Smiley in prep." in Lindquist 1969, partim., male);
T. terebrans n. sp. (female, male, larva);
T. typographi n. sp. (female).

Tarsonemus minimax von Vitzthum 1926 (Figs. 1–8)

Tarsonemus minimax von Vitzthum 1926; p. 464

Diagnosis: Female: prodorsal shield without anterolateral lobes; setae sc_2 ≈1.7× as long as v_1 and approaching the distance between its bases; setae c_2 shorter than the distance to the bases of setae c_1; setae *f* apparently shorter (1.4×) than distance between their bases. Ventral metapodosomal setae *3a* apparently (almost 2×) shorter than *2a*; setae *3a* and *3b* subequal to pseudanal *ps*. Tibiotarsus I ≈2.2× longer than wide at the base; seta Ta II *pl″* ≈2× thicker than solenidion ω at its base. Tergite C and ventral metapodosomal plate (MeP in Fig. 3) with uniform dimpled ornamentation.

Male and larva: unknown.

Description: Female: Gnathosoma: pharynx as wide as 0.3× (or less) of maximum width of gnathosoma, fusiform in outline.

Idiosomal dorsum (length = 1.8× width): relative lengths of setae (v_1: sc_2: c_2: c_1: *d*: *e*: *f*: *h*): 1: 1.7: 1: 0.7: 0.5: 0.3: 0.6: 0.3. Rostral shieldlet 3.5× wider than long. Setae v_1 in a distance of 1.3× their length. Prodorsal shield 1.6× wider than long. Tracheae and pits v_2 indiscernible. Setae sc_2 located posterior to midline of prodorsal shield, reaching with nearly 0.3× their length beyond posterior edge of prodorsal shield, in a distance between their bases equal to 1.2× their length. Setae c_2 not reaching with their tips to the bases of c_1. Setae c_1 not reaching posterior edge of a tergite C. Setae *d* slender, sharp, reaching with 0.25× of their length beyond posterior edge of tergite D, in the distance between their bases 3.7× its length. Setae *f* slender, sharp, in the distance between their bases 1.4× its length. Setae *h* in a distance longer than 6× their length.

Idiosomal venter: apodemes 1 moderately sclerotized, anteromedial apodeme weakly defined. Sejugal apodeme with numerous anterior thickenings. Setae *1a* located on apodemes 1, in a distance of 1.3× their length. Setae *2a* located on apodemes 2; the distance between their bases equaling 3× their length. Ventral propodosomal plate weakly concave anteriorly. Apodemes 4 reaching slightly posteriad of *3b* bases. Setae *3a* inserted by a distance of ≈4× of their length from bases of setae *3b* and separated by a distance between their bases of almost 5×, subequal to that between *3b*. Setae *3b* longer than *3a*, ≈3× shorter than the distance between their bases. Ventral metapodosomal plate weakly concave anteriorly, with weak protrusions between trochanters III and IV. Trochanters IV divided by the interval of almost 2× their diameters. Setae *ps* in a distance between their bases ≈1.7× their length. Sclerites of both dorsum and venter covered with uniform, finely dimpled ornamentation.

Legs: Proportions of free segments of legs: (I: II: III: IV): 1: 1.1: 1.2: 0.7.

Leg I: Claw similar to those of tarsi II and III. Spine-like seta *s* short, moderately stout, blunt-ended, similar to seta *u′* of legs II and III. Tibiotarsus ≈2× as long as wide at base. Two eupathidia inserted apically on tibiotarsus I (*p′*-longer, *p″*-shorter); *tc′* longest of all eupathidia, located distad of transverse midline of segment; *tc″* located subapically. Solenidion ω with fusiform, striated head, shorter than its stalk, apparently larger than Ta ω II. Tibial solenidion ϕ_2 smaller, ϕ_1 apparently larger, both without clear striation; famulus *k* longer than ϕ_1; located slightly proximally. Seta *l′* on genu attenuated, pointed. Femur I without apparent ventral lobe. Setae *l″* and *v″* on femur attenuate; *l′* slightly stiffer; *d* short, stiff.

Leg II: Claws medium-sized, hooked; empodium medium- sized. Tarsal spine-like seta *pl″* larger than solenidion Ta II ω located slightly more distally. Seta *tc″* longer than other setae of segment. Tibia with lateral spine-like protrusion; seta Ge *l′* attenuate, not markedly stronger than others on the segment. Femur with small ventral lobe, seta *d* very short, spine-like.

Leg III: Claws slightly smaller than those on leg II. Seta *tc″* apparently longer than the other setae of segment, *pv″* missing.

Leg IV: Free segments of leg clearly shorter than femurogenu and tibia III. Femurogenu ≈3× as long as tibiotarsus. Femoral seta *v′* shorter than genual one; the latter located in a distance of 1.2× distal width of Fege from the end of segment. Seta Tb *v′* longer than combined length of femurogenu and tibiotarsus. Seta Ta *tc″* 2.7–2.8× as long as whole leg IV.

Measurements (lectotype, followed by two paralectotypes in parentheses; unreadable measurements replaced by "**" sign)

Body and tagmata: length of body: 156 (208, 232); length of idiosoma: 156 (206, 218); width of idiosoma: 99 (108, 120); length of gnathosoma: 22 (27, 27); width of gnathosoma: 17 (23, 21); length of pharynx: 12 (13, 12) width of pharynx: 5 (6, 5).

Dorsum: length of PrS: 59 (62, 60); width of PrS: 94 (99, 94). Lengths of setae: *dgs*: 10 (12, 11); *vgs*: 11 (11, 10); v_1: 20 (21,**); sc_1: 16 (17, **); sc_2: 34 (35, **); c_2: 20 (20, 21); c_1: 16 (14, 15); *d*: 11 (10, **); *e*: 6 (7, 7); *f*: 11 (12, **); *h*: 6 (6, 6.5). Distances between setae: v_1-v_1: 26 (28, 26); sti-sti: 42 (43,41); sc_1-sc_1: 34 (40, 38); sc_2-sc_2: 42 (43, 41); c_2-c_2: 96 (101, 98); c_1-c_1: 73 (78, 71); c_1-c_2: 30 (31, 28); *d-d*: 40 (38, 37); *e-e*: 70 (72, 68); *f-f*: 17 (16, 15); *e-f*: 26 (22, 28); *h-h*: 39 (40, 38).

Venter: lengths of setae: *1a*: 7 (8, 7); *2a*: 8 (10, **); *3a*: 5 (6, 4); *3b*: ** (9,**); *ps*: 7 (7, 7). Distances between setae: *1a-1a*: 9 (10, 9); *2a-2a*: 24 (34, 24); *3a-3a*: 27 (29, 26); *3b-3b*: 29 (32, **); *ps-ps*: 13 (13, 12). Length of tegula: 7 (7, 7); width of tegula: 14 (16, 15); length of PrP: 55 (55, 52); width of PrP: 80 (103, 90); Ap. 1-1: 11 (13, 13); Ap. 2-2: 35 (40, 40).

Leg segments and setae on legs (lengths): Tbt I: 17 (16, 16); ωI: 6 (6.5, 7); ϕ_2: 3 (3, 3); ϕ_1: 5 (5, 4); *k*: 5 (6, 6); ω II: 4 (5, 5); *pl″* II: 6 (6, 6); Fege IV: 19 (19, 18); Tbt IV: 6 (7, 6); Fe *v′*: 9 (7, 10); Ge *v′*: 13 (11, 12); Tb *v′*: 29 (28, 26); Ta *tc″*: 66 (69, 40**).

Type material: LECTOTYPE: one female, AUSTRIA: Lower Austria (Nieder Österreich); Waidhofen, on Thaya, 29-V-21, on *Pityokteines* (orig. labeled "*Ips*") *curvidens* (Scolytidae), between coxae I, H. Wichmann, BSC.

PARALECTOTYPES (originally syntypes): two females, data as above.

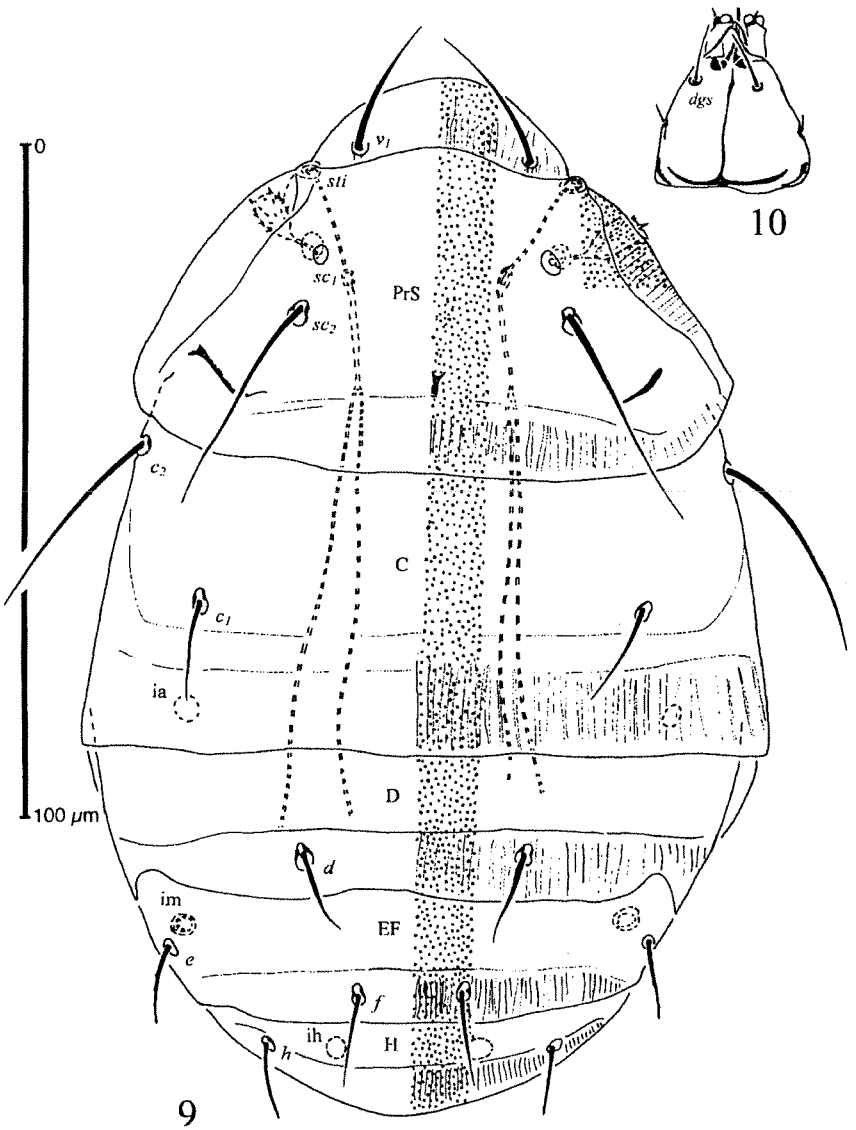
Other material: SWITZERLAND: two females, Solothurn, Bettlach, VI-VII-85, stand of *Abies alba*, phoretic on *P. curvidens*, ex pheromone trap, B. Forster, DATE.

Distribution: central Europe.

Remarks: We designate herewith the above described specimen (No V 1701/1) the lectotype of the species.

Tarsonemus terebrans n. sp. (Figs. 9–27)

Diagnosis: Females: prodorsal shield without anterolateral lobes; seta sc_2 ≈1.5× as long as v_1 and approaching the distance between its bases; setae c_2 longer than the distance to the bases of setae c_1; setae



Figs. 9–10. *Tarsonemus terebrans*, holotype female dorsum: (9) idiosoma; (10) gnathosoma.

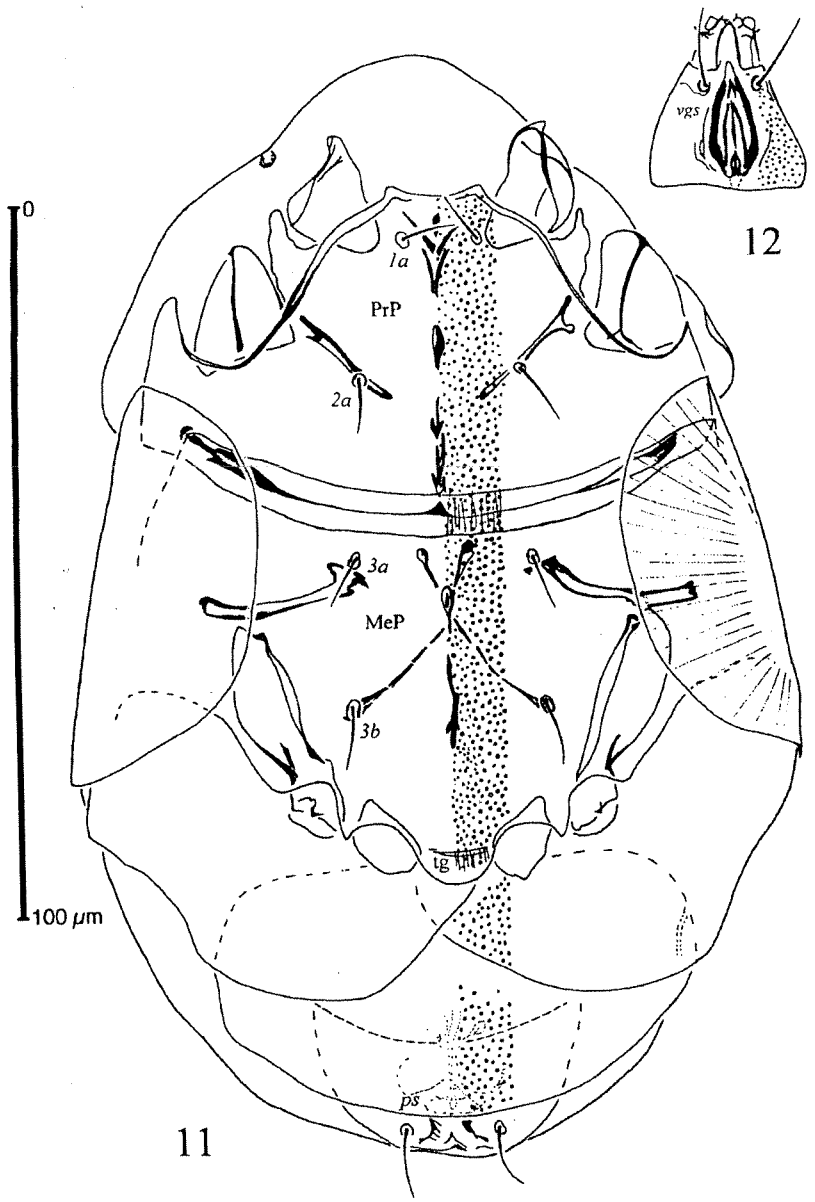
f slightly shorter than distance between their bases. Ventral metapodosomal setae *3a* subequal to *2a;* setae *3b* subequal to pseudanal *ps*. Tibiotarsus I ≈3× longer than wide at the base; seta Ta II *pl″* ≈2× thicker than solenidion *ω* at its base. Tergite C and ventral metapodosomal plate with uniform dimpled ornamentation.

Males: dorsal setae c_2 reaching the bases of c_1 but the latter placed posteriad of cupules *ia;* both latter pairs subequal, longer than *f*, reaching beyond the posterior edge of the CD shield. Coxal setae *3a* and *3b* apparently longer than *1a* and *2a; 3a* almost reaching the bases of *3b*. Tarsus I ≈2× as long as wide basally, claws weak. Tarsal setae *tc″* II and III approximately as long as other (normal) setae on those segments. Tarsal III *pv″* and tibial III *l′* attenuate.

Larvae (compared with larvae of *T. endophloeus*- the only other known): setae c_2 reaching beyond bases of c_1, and setae *d, e* and *f* reaching with at least their half-lengths beyond posterior edges of their shields.

Description: Female: Gnathosoma: pharynx as wide as 0.3× of the basal width of gnathosoma.

Idiosomal dorsum (length = 1.5× width): relative lengths of setae (v_1: sc_2: c_2: c_1: *d*: *e*: *f*: *h*): 1: 1.5: 1.2: 0.6: 0.5: 0.5: 0.5: 0.4. Rostral shieldlet almost 3× wider than long. Distance between setae v_1 approximate to their length. Prodorsal shield ≈1.5× as wide as long. Tracheae with visible atria. Pits v_2 located slightly laterad of the alignment of bases of sc_1 and sc_2. Setae sc_2 located posterior to midline of prodorsal shield, reaching with ≈0.3× their length beyond posterior edge of prodorsal shield, the distance between their bases being ≈1.1× their length. Setae c_2 with their tips reaching well beyond the bases of c_1. Setae c_1 with tips reaching two-thirds the distance from their bases to the posterior edge of tergite C. Setae *d* slender, sharp, reaching about one-half their length beyond the posterior edge of tergite D; the distance between their bases being ≈2.8× their lengths. Setae *f* slender, sharp,

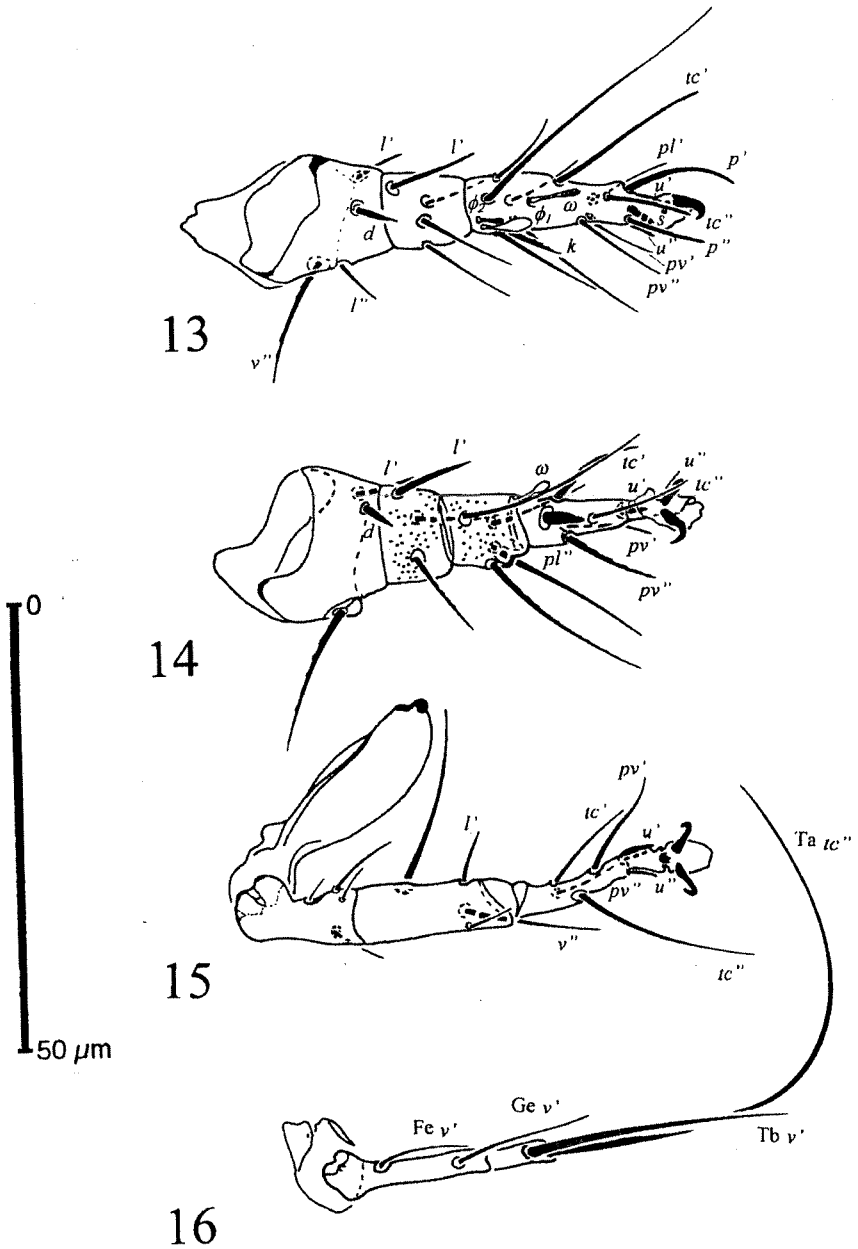


Figs. 11–12. *Tarsonemus terebrans*, holotype female venter: (11) idiosoma; (12) gnathosoma.

the distance between their bases being slightly longer than their length. The distance between bases of setae *h* approaching 4× their lengths.

Idiosomal venter: apodemes 1 weakly sclerotized, anteromedial apodeme weakly defined, discontinuous. Sejugal apodeme weak, without apparent thickenings. Setae *1a* located posteriad of apodemes 1, separated by a distance of 1.6× their length. Setae *2a* located on apodemes 2; the distance between their bases being lesser than 3× their lengths. Ventral propodosomal plate weakly concave anteriorly. Apodemes 4 not reaching posteriad of setae *3b* bases. Setae *3a* ≈2.6× their length from the bases of setae *3b*, and separated by a distance between their bases slightly shorter than that between *3b*. Setae *3b* slightly longer than *3a*, ≈3× shorter than the distance between their bases. Ventral metapodosomal plate broadly concave anteriorly, with indistinct tooth-like processes between trochanters III and IV. Trochanters IV divided by interval slightly longer than their diameters. The distance between bases of setae *ps* ≈1.6× their length. Sclerites of dorsum and venter covered with a uniform, rather sparse and coarse dimpled sculpture.

Legs: Proportions of free segments of legs: (I: II: III: IV): 1: 1: 1: 0.6. Leg I: Claw similar to those of tarsi II and III. Spine-like seta *s* moderate in size, blunt, slightly smaller than seta *u′* of legs II and III. Setae *u′* and *u″* discernible. Tibiotarsus <3× as long as wide at base. Two eupathidia inserted apically on tibiotarsus I



Figs. 13–16. *Tarsonemus terebrans*, holotype female legs: (13) leg I; (14) leg II; (15) leg III; (16) leg IV.

(p'-longer, p''-shorter); tc' longest of all eupathidia, inserted on transverse midline of segment; tc'' located subapically. Solenidion ω with fusiform, striated head, well shorter than its stalk, apparently larger than Ta ω II. Tibial solenidion ϕ_2 smaller, ϕ_1 apparently larger, only ϕ_2 with apparent striation; famulus k longer than ϕ_1; located slightly proximally. Seta l' on genu attenuated, blunt; slightly stronger than others. Femur I without apparent ventral lobe. Seta l'' on femur slender, l' slightly stiffer; v'' attenuate, d more spiculate, stout.

Leg II: Claws medium-sized, hooked; empodium medium- sized (in some specimens very delicate striation can be seen). Tarsal spine-like seta pl'' larger than solenidion Ta IIω, located more distally. Seta tc'' not markedly longer than other setae of segment; l' and l'' slightly barbed. Tibia with weakly defined lateral spine-like protrusion; seta Ge l' sparsely barbed, stronger and stiffer than remaining ones on the segment. Femur with small ventral process, seta d short, spine-like.

Leg III: Claws as large as those on leg II. Seta tc'' at least 0.3× as long as other setae of segment.

Leg IV: Free segments of leg clearly shorter than femurogenu and tibia III. Femurogenu ≈3× as long as tibiotarsus. Femoral seta v' shorter than genual one; the latter located in a distance of 1.5× distal width of Fege from the end of segment. Seta Tb v' apparently longer than length of femurogenu and tibiotarsus. Seta Ta tc'' 2.3× as long as whole leg IV.

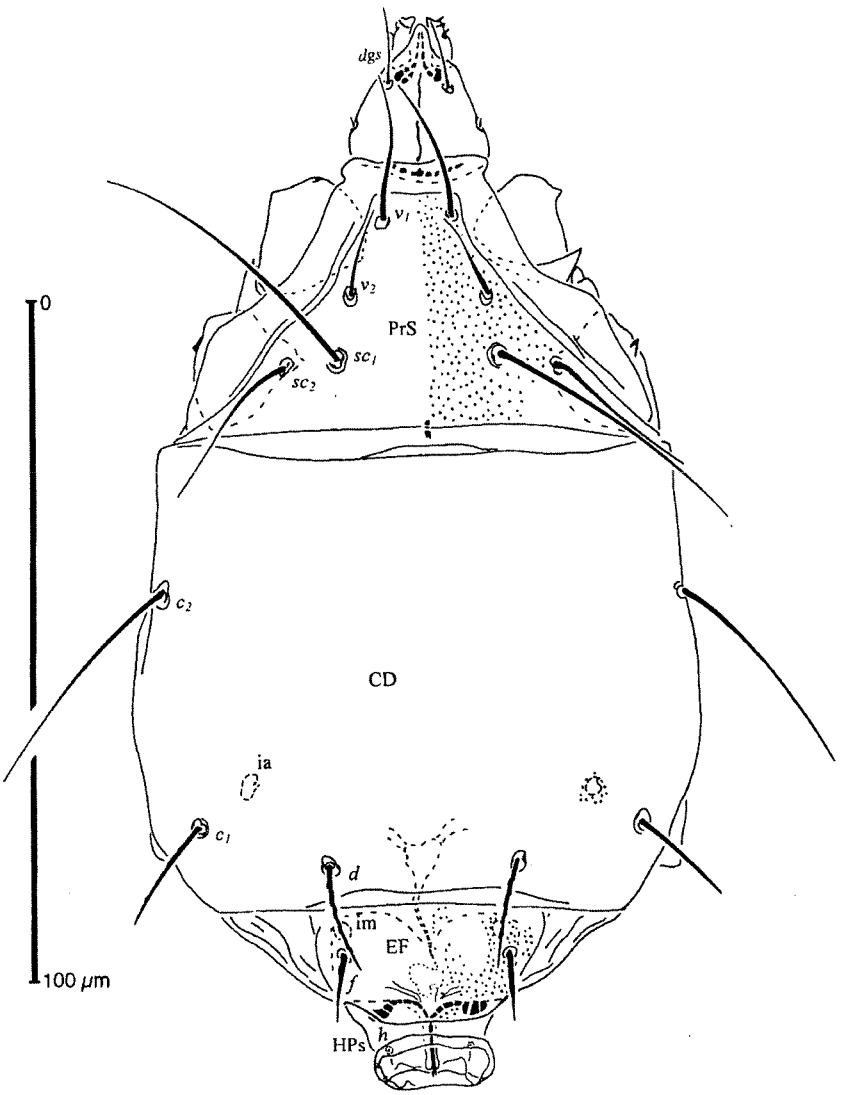


Fig. 17. *Tarsonemus terebrans*, paratype male dorsum: idiosoma and gnathosoma.

Measurements (holotype, followed by five paratypes from type locality in parentheses). Body and tagmata: length of body: 166 (163–208); length of idiosoma 155 (146–180); width of idiosoma: 102 (97–118); length of gnathosoma: 25 (24–30); width of gnathosoma: 22 (22–25); length of pharynx: 17 (15–17); width of pharynx: 6 (5–6).

Dorsum: length of PrS: 61 (57–67); width of PrS: 91 (88–104). Lengths of setae: *dgs:* 9 (9–13); *vgs:* 11 (10–12); v_1: 24 (17–25); sc_1: 16 (14–19); sc_2: 35 (34–39); c_2: 28 (21–29); c_1: 15 (15–17); *d:* 13 (12–14); *e:* 11 (11–13); *f:* 12 (11–14); *h:* 10 (9–11). Distances between setae: v_1-v_1: 26 (22–29); sti-sti: 41 (40–45); sc_1-sc_1: 36 (36–50); sc_2-sc_2: 41 (36–42); c_2-c_2: 89 (79–93); c_1-c_1: 68 (56–71); c_2-c_1: 26 (24–29); *d-d:* 33 (32–39); *e-e:* 71 (53–75); *f-f:* 16 (13–17); *e-f:* 26 (26–30); *h-h:* 42 (36–43).

Venter: lengths of setae: *1a:* 6 (5–8); *2a:* 9 (8–10); *3a:* 8 (8–10); *3b:* 9 (9–11); *ps:* 9 (7–9).

Distances between setae: *1a-1a:* 10 (9–12); *2a-2a:* 24 (21–25); *3a-3a:* 26 (23–29); *3b-3b:* 28 (26–30); *ps-ps:* 13 (12–14). Length of tegula: 5 (5–7); width of tegula: 11 (10–12); length of PrP: 50 (49–55); width of PrP: 83 (70–96); Ap. 1-1: 12 (12–15); Ap. 2-2: 39 (37–41).

Legs segments and setae on legs (lengths): Tbt I: 19 (18–21); ωI: 7 (7–9); ϕ_2: 3 (3–4); ϕ_1: 6 (5–6); *k:* 7 (7–9); ωII: 4 (4–5); *pl″* II: 5 (5–7); Fege IV: 20 (18–22); Tbt IV: 8 (7–9); Fe *v′:* 8 (7–9); Ge *v′:* 13 (12–16); Tb *v′:* 31 (28–32); Ta *tc″:* 64 (56–68).

Male: Gnathosoma: Pharynx about as wide as 0.3× of basal width of gnathosoma, as long as almost entire ventral length of capsule; with tiny glandular bodies (sclerotization defined as in female).

Idiosomal dorsum (length = 1.6× width): relative length of setae (v_1: v_2: sc_1: sc_2: c_2: c_1: *d*: *f*): 1: 0.6: 1.9: 0.9: 1.5: 0.8: 0.7: 0.5. Prodorsal shield (PrS). Setae v_1, v_2, sc_2 and sc_1 hair-like, tapering, pointed; v_1 separated by a distance of 0.5× their lengths. Setae sc_2 located near the level of sc_1. Setae sc_1 located posteriad of a mid-length of prodorsal shield, reaching with over one half their lengths beyond the posterior edge of prodorsal shield, placed in a distance of 0.6× their lengths each

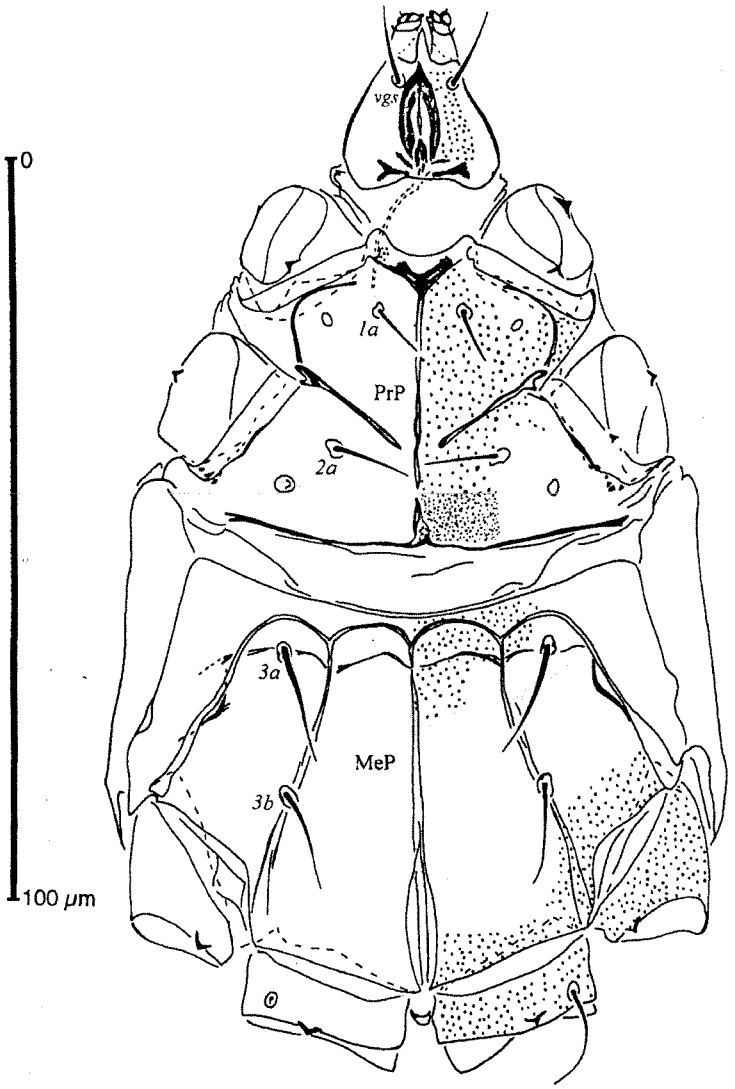


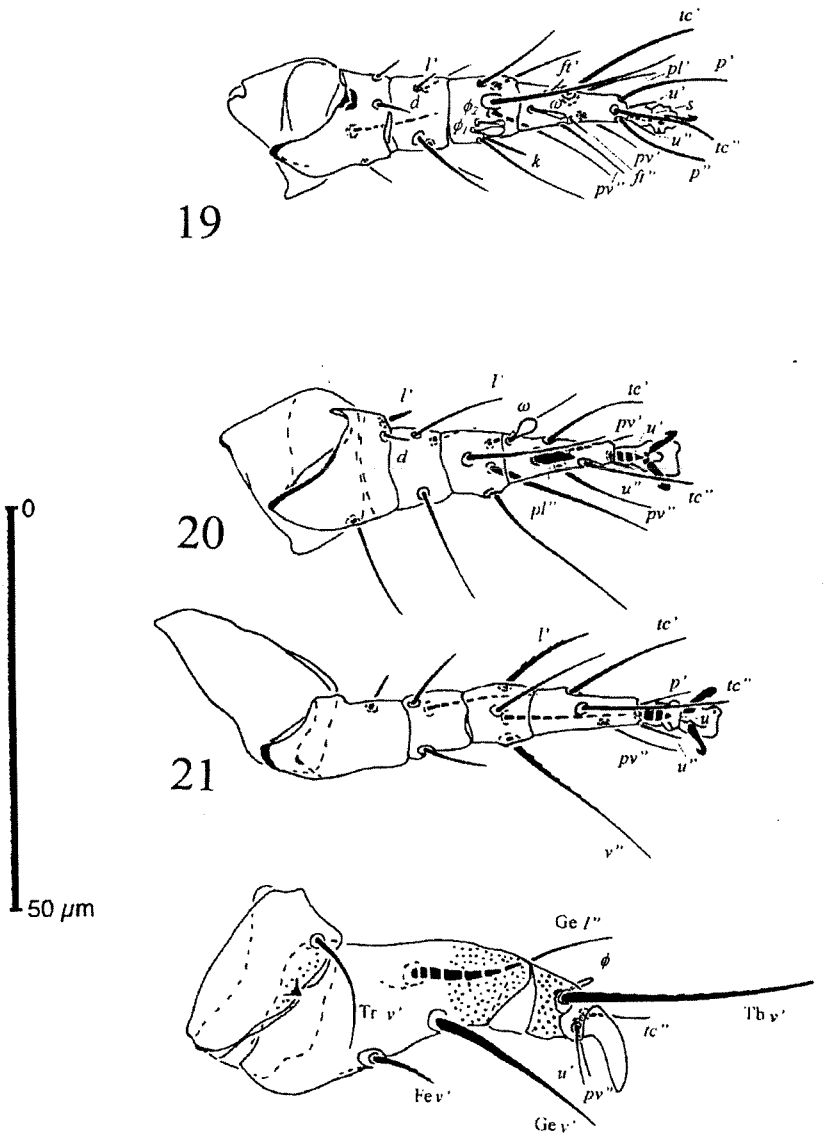
Fig. 18. *Tarsonemus terebrans*, paratype male venter: idiosoma and gnathosoma.

to another. Setae c_2 reaching with their tips to bases of c_1. Setae c_1 located by a distance almost equal to their lengths to bases of *d*. Setae *d* reaching well beyond the posterior edge of shield CD; separated by a distance of almost 1.7× their lengths. Setae *f* stronger than c_1 and *d*, located by a distance >2× their lengths; all three pairs finely barbed. Cupuli *im* located anteriorly to setae *f*. Genital capsule with hyaline rim small and narrow. Accessory stylets weak, located in posterior half of genital capsule.

Idiosomal venter: anteromedian apodeme connecting anteriorly with apodemes 1, interrupted slightly posteriad of *2a* bases. Sejugal apodeme continuous and thick, slightly bent in midsegment. Coxal setae *la* slender, located by a distance of 1.6× their lengths each to another; setae *2a* longer, displaced by a distance of more than their 2× lengths. Setae *3a* slender, subequal in length to *3b*, located by a distance to their bases subequal to their length, and separated by a distance of 2.6× their length, i.e., equal or slightly longer than that between *3b*. Setae *3b* separated by a distance of ≈2.3× of their lengths. Ventral metapodosomal plate with apodemes 4 and 3 joining anteriorly with each other and with strong posteromedial apodeme. Dorsum covered with uniform, rather sparse and coarse dimpled sculpture; ornamentation of ventral propodosomal plate, coxal fields III and IV sparsely dimpled, lateral fields of ventral metapodosomal plate smooth.

Legs: Proportions of free segments of legs (I: II: III: IV): 1: 1: 1.1: 1.1.

Leg I: Claw apparently weaker than those of tarsi II and III. Seta *s* weakly spine-like, less pronounced than setae *u'* of Ta II and III. Setae *u'* and *u''* pronounced. Tarsus ≈2× as long as wide at the base. Two subequal eupathidia (*p'* and *p''*) inserted apically on tarsus; one (*tc''*) inserted slightly more proximally, and one (*tc'*-the longest) on transverse midline of the tarsus. Solenidion ω inserted almost at the base of segment, with small, striated head, shorter than its pedicel and smaller than Ta II ω. Both tiny fastigial eupathidia



Figs. 19–22. *Tarsonemus terebrans*, paratype male legs: (19) leg I; (20) leg II; (21) leg III; (22) leg IV.

present, *ft''* at the level of eupathidion *tc'*. Tibial solenidion smaller ϕ_2 and ϕ_1 slightly larger with head as long as its stalk; eupathidion *k*, rod-like, twice as long as ϕ_2, located almost at the same level with solenidia. Seta *l'* on genu smaller than other setae of segment, femoral *d* strong though not spine-like.

Leg II: Claws strong, hooked; empodium moderate. Spine *pl''* slightly curved apically, slightly larger than the solenidion ω. Seta *tc''* subequal to other setae of segment, reaching slightly beyond the tip of empodium. Solenidion ω stronger than that on Ta I. Tibia similar to that of female, seta Ge *l'* smooth, slender. Femoral setae *d* slender, *l'* stiffer; both short.

Leg III: Claws and empodium as in leg II. Setae flanking pretarsus, *p'* and *u'* pronounced. Seta *tc''* reaching slightly beyond the end of empodial pad, tarsal *tc'* and *pv''* attenuate. Tibial seta *v''* the longest on the leg, barbed.

Leg IV: Free segments of leg IV approximately as long as those of leg III. Tarsal claw weakly curved, 2× as long as wide at the base; not much longer than tibia and tarsus IV. Tarsus not fused with tibia, with three small setae (all subequal in length). Tibial solenidion ϕ approximately as large as tarsal solenidia of legs I and II, rod-like, smooth. Seta Tb *v'* strong, stiff, barbed and obtuse, about as long as Fege IV. Femurogenu IV <2× as long as wide at the base, without any marked posterior ridge or protrusion; setae Ge *v'* and *l''* strong, Fe *v'* the shortest, all attenuate, though strong. Seta *v'* on trochanter intermediate between Ge *v'* and Fe *v'*.

Measurements (four male paratypes). Body and tagmata: Length of body: 151–160; length of idiosoma: 130–139; width of idiosoma: 80–90; length of gnathosoma: 24–25; width of gnathosoma: 17–22; length of pharynx: 14–15; width of pharynx: 5–6; *dgs:* 11–12; *vgs:* 10–12. Length of PrS: 36–41; width of PrS: 65–74.

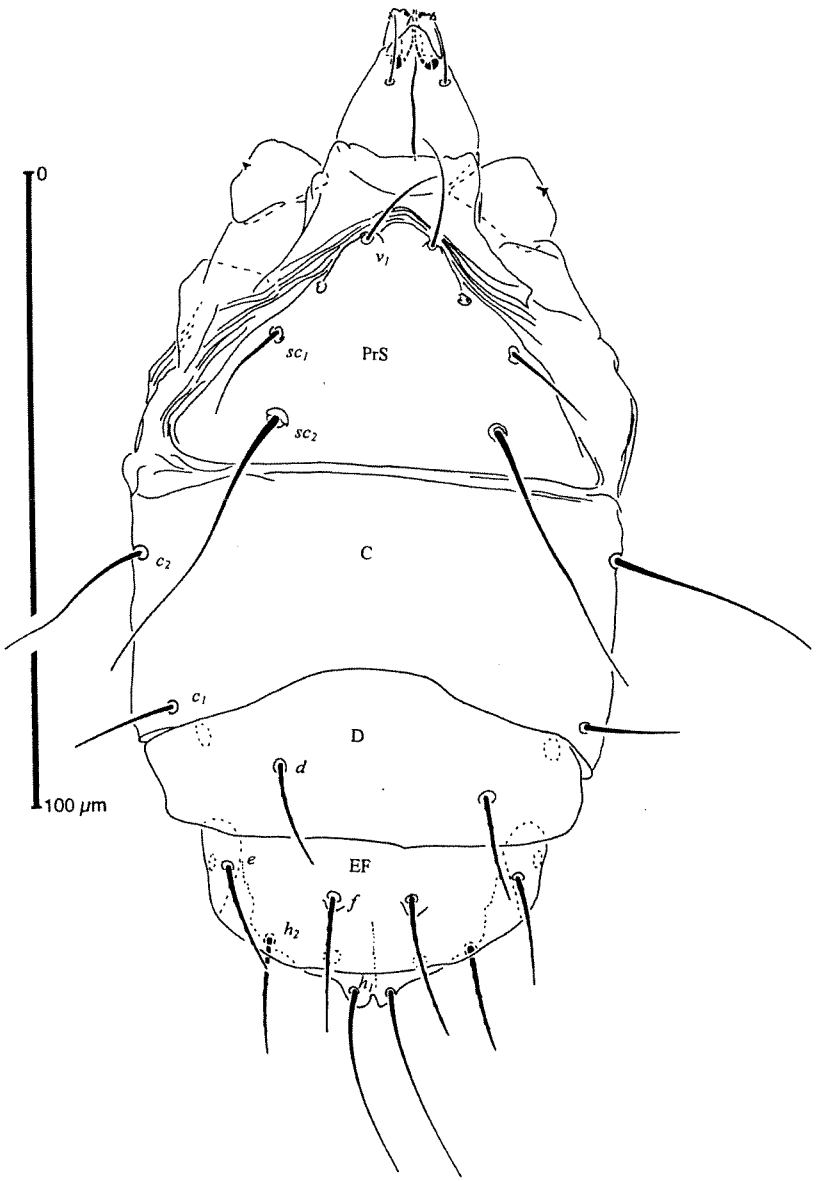


Fig. 23. *Tarsonemus terebrans*, paratype larva dorsum: idiosoma and gnathosoma.

Length of genital capsule: 24–26; width of genital capsule: 25–28.

Dorsum: Lengths of setae: v_1: 22–25; v_2: 14–15; sc_2: 42–45; sc_1: 20–24; c_2: 31–35; c_1: 16–18; *d*: 16–18; *f*: 10–13; *h*: 2–4. Distances between setae: v_1-v_1: 11–12,; v_2-v_2: 21–23; sc_2-sc_2: 42–45; sc_1-sc_1: 20–24; c_2-c_2: 74–83; c_1-c_1: 59–69; c_1-c_2: 33–40; *d-d*: 26–32; c_1-*d*: 17–20; *f-f*: 24–28; *h-h*: 11–12.

Venter: Lengths of setae: *1a*: 7; *2a*: 10–12; *3a*: 11–17; *3b*: 13–17. Distances between setae: *1a-1a*: 10–12; *2a-2a*: 21–26; *3a-3a*: 35–40; *3b-3b*: 32–39. Length of PrP: 38–41; width of PrP: 66–72; Ap 1-1: 10–12; ap 2-2: 30–34.

Leg segments and leg setae (lengths): Ta I: 14–15; ωI: 5; ϕ_2: 4; ϕ_1: 5; *k*: 6–7; ωII: 4–6; *pl″* II: 4–5; Fege IV; 33–41; Tb-Ta IV; 8–9; Ge IV *v′*: 21–27; Tb IV *v″*: 27–30; Tb IV *ϕ*: 5; claw length: 10–11; width: 4–5.

Larva: Gnathosoma: slightly larger and more triangular than in adults. Pharynx as wide as ≈0.25× basal width and clearly shorter than the ventral length of gnathosoma. Setae *dgs* and *vgs* reaching to the apices of palpi. Cheliceral stylets and levers as strong as in female. Palpi pronounced; palptibial claw indiscernible.

Idiosomal dorsum (length = 1.7× width); relative length of setae (v_1: sc_1: sc_2: c_2: c_1: *d*: *e*: *f*: h_2: h_1): 1: 0.8: 2.4: 1.7: 0.8: 0.8: 0.8: 1: 0.8: 1.4. Prodorsal shield (PrS) ≈1.6× as wide as long. Setae v_1 smooth, located in a distance of 0.5× their length each to another. Setae sc_2 located on prodorsal shield near the posterior edge, reaching with 0.8× their length beyond the posterior edge of prodorsal shield, separated by a distance of ≈0.7× their lengths. Setae c_2 slender, reaching with their tips slightly beyond bases of c_1. Setae c_1-h_2 ta-

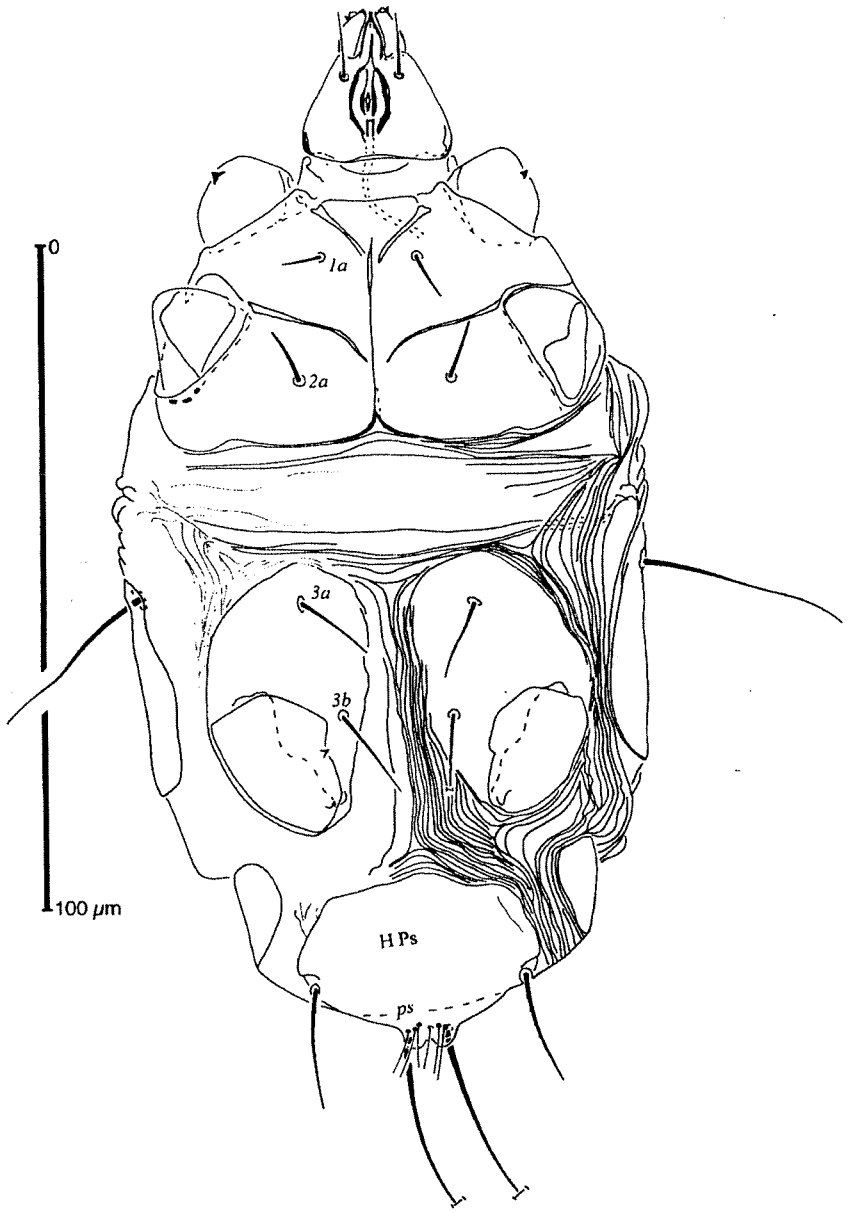


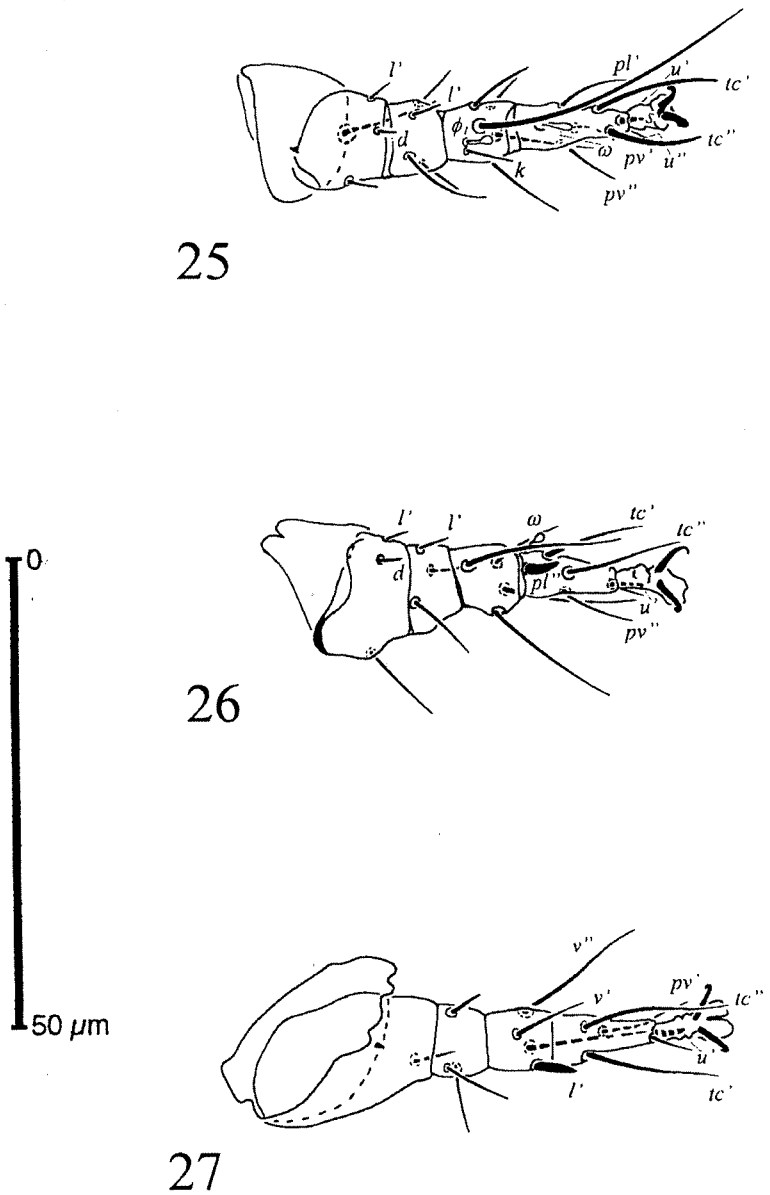
Fig. 24. *Tarsonemus terebrans*, paratype larva venter: idiosoma and gnathosoma.

pering but stiff (d-h_2 apparently barbed), c_1 separated by a distance of ≈4× their lengths. Cupuli *ia* located laterally and anteriorly to bases of setae *d*. Setae *d* reaching well beyond the posterior edge of tergite D; arranged by a reciprocal distance of almost 2× their lengths; setae *e* located by a distance subequal to their lengths to *f*, the latter in a reciprocal distance of ≈0.6× their lengths. Cupuli *im* contiguous to bases of *e*. Setae h_2 displaced by a distance ca. equal to their 2× lengths; h_1 almost 5× as long as a distance between their bases. Cupuli *ih* located slightly posteromediad of line of h_2.

Idiosomal venter: apodemes 1 and 2 and anteromedial apodeme expressed; the latter one continuous to posterior edges of coxal fields 2. Setae *1a* the shortest, stiff, located posteriorly of apodemes 1, by a distance of almost 2× their lengths. Setae *2a* short, stiff, located posteriad of apodemes 2, by a reciprocal distance of almost 2.5× their length. Ventral propodosomal plate with straight edge anteriorly between anterolateral extremities of apodemes 1 and bi-convex posteriorly. Setae *3a* and *3b* (slender, pointed) longer than *2a*; *3a* subequal to *3b*, by a distance from bases of *3b* slightly more than their length. Three pairs of short and slender setae *ps* symmetrically arranged between bases of h_1. Dorsal and ventral shielding smooth; ventral plates divided by large areas of densely striated pleura.

Legs: Proportions of free segments of legs (I: II: III): 1: 0.9: 1.2.

Leg I: Claws strong, but shorter, than those of legs II and III. Seta *s* spine-like, similar to *u'* on tarsi II and



Figs. 25–27. *Tarsonemus terebrans*, paratype larva legs: (25) legI; (26) leg II; (27) leg III (left).

III. Tarsus over 2× as long as wide at the base. Eupathidion *tc'* longer than *tc''*, both located subapically. Solenidion ω approximately as large as Ta II ω. Solenidion ϕ_1 with smooth head, apparently shorter than famulus *k*. Seta *l'* on genu stiff, pointed. Setae *l'* and *d* on femur delicate, pointed.

Leg II: Claws and empodium medium-sized. Spine *pl''* strong, blunt, distally, located slightly distad of the level of solenidion ω. Seta *tc''* not apparently longer than others on segment, reaching to the distal edge of empodium. Seta Ge *l'* small, pointed. Setae *d* and *l'* on femur tiny, stiff, short.

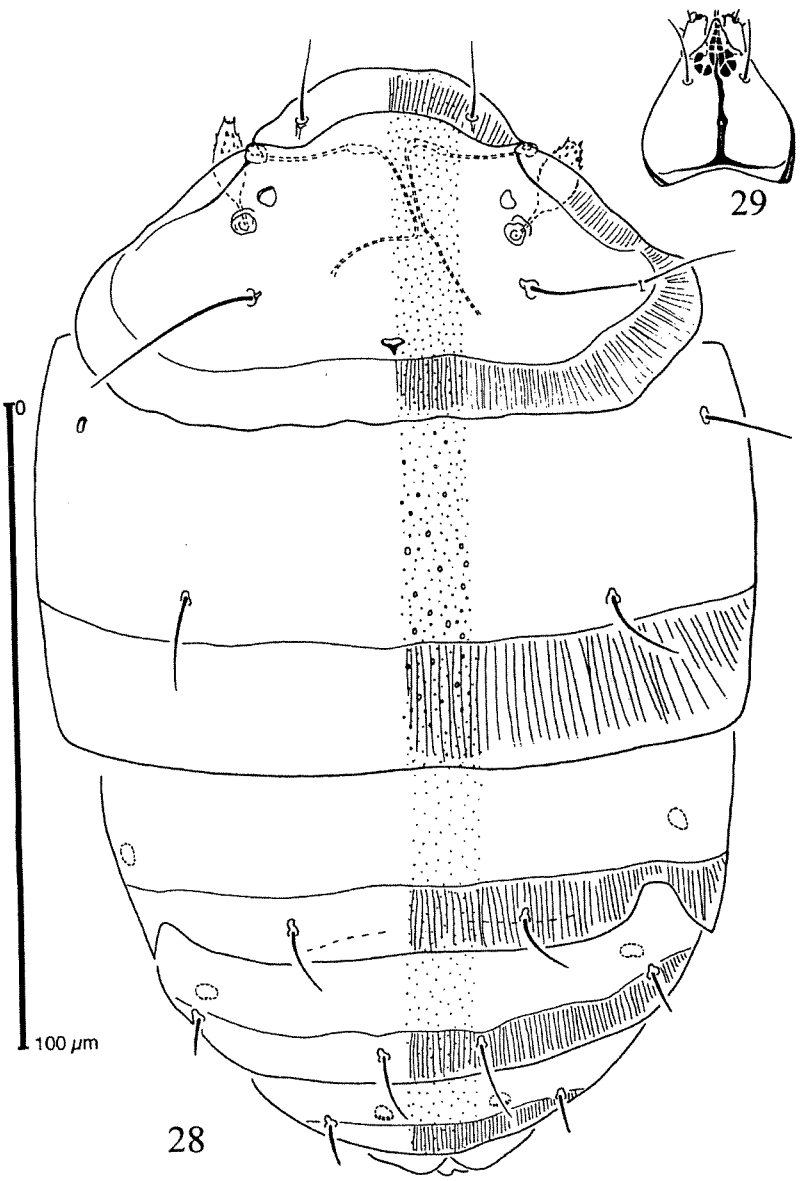
Leg III: Claws as those on leg II. Seta *tc''* similar to others on segment. Tibial setae *d*, *v'* and *v''* attenuated, slender.

Measurements (two larval paratypes): Body and tagmata: Length of body: 160, 165; length of idiosoma: 136, 143; width of idiosoma: 81, 83; length of gnathosoma: 26; width of gnathosoma: 23, 25; length of pharynx: 13, 14; width of pharynx: 6; *dgs:* 12; *vgs:* 11.

Dorsum: length of PrS: 45, 46; width of PrS: 71. Lengths of setae: v_1: 21, 24; sc_1: 17; sc_2: 49, 57; c_2: 36, 41; c_1: 17; *d:* 18, 19; *e:* 17, 18; *f:* 17, 18; h_2: 17; h_1: 32. Distances between setae: v_1-v_1: 11; sc_1-sc_1: 39, 42; sc_2-sc_2: 36, 38; c_2-c_2: 76, 78; c_1-c_1: 66, 71; c_1-c_2: 27, 28; *d-d:* 33; *e-e:* 46, 47; *f-f:* 12, 13; h_2-h_2: 32; h_1-h_1: 6, 8.

Venter: Lengths of setae: *1a:* 7, 9; *2a:* 9, 10; *3a:* 12, 13; *3b:* 12, 15; *ps:* 6–8. Distances between setae: *1a-1a:* 15; *2a-2a:* 22, 23; *3a-3b:* 18, 19; *ps-ps:* 5, 6. Length of PrP: 36, 38; width of PrP: 64, 66. Ap. 1-1: 16; ap 2-2: 35, 36. Length of HPs: 25, 26; width of HPs: 38.

Leg segments and leg setae (lengths): Ta I: 11, 12; ωI: 5; ϕ_1: 4; *k:* 5, 6; ωII: 3, 4; *pl''* II: 3, 4.



Figs. 28–29. *Tarsonemus typographi*, female dorsum: (28) idiosoma; (29) gnathosoma.

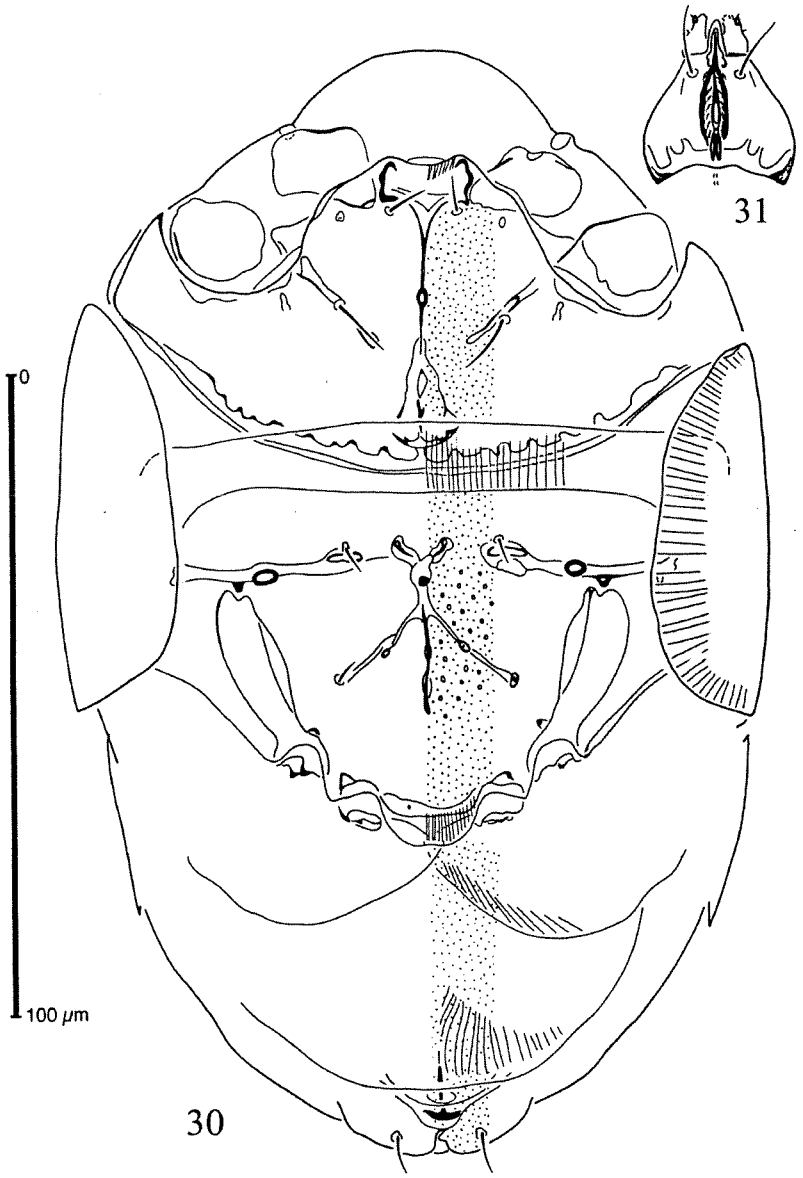
Type material: HOLOTYPE: one female, UNITED STATES: Louisiana, Elizabeth; XI-70, ex inner bark of pine *Pinus taeda; Dendroctonus terebrans* adults emerged, J. Moser, NMNH.

PARATYPES: four females, four males and two larvae, same data as in the holotype (one female, one male and one larva in NMNH; one female, one male and one larva in DATE; one female, one male in CNC, one female, one male in ZMH); UNITED STATES: one female, Louisiana, Winnfield, 10-VIII-63, phoretic ex. thorax venter of *D. terebrans* ex loblolly stump, inner bark, J. Moser, CNC; UNITED STATES, Florida, Baker County, three females, 17-VII-85, phoretic on *D. terebrans* ex. pheromone trap, C. Fatzinger, DATE; one female, 7-VI-85, phoretic on *D. terebrans* ex. pheromone trap, C. Fatzinger, NMNH.

Distribution: southeastern United States.

Tarsonemus typographi sp. n. (Figs. 28–35)

Diagnosis: Females: prodorsal shield without anterolateral lobes; seta sc_2 ≈2.3× as long as v_1 and approaching the distance between its bases; setae c_2 shorter than the distance to the bases of setae c_1; setae *f* slightly shorter than distance between their bases. Ventral metapodosomal setae *3a* apparently shorter than *2a;* setae *3a* and *3b* apparently shorter (almost twice) than pseudanal *ps.* Tibiotarsus I 2.3× longer than wide at the base; seta Ta II *pl″* 2× thicker than solenidion ω at its base. Tergite C and ventral metapodosomal plate with ornamentation differentiated into smaller and larger dimples.



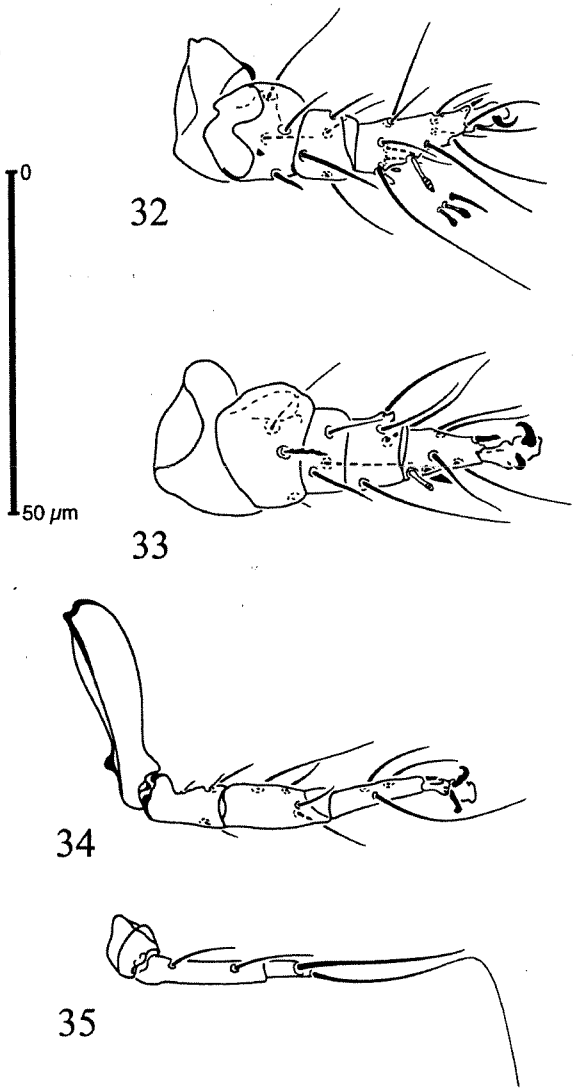
Figs. 30–31. *Tarsonemus typographi*, female venter: (30) idiosoma; (31) gnathosoma.

Males and larvae: unknown.

Description: Female: Gnathosoma: pharynx as wide as ≈0.2× of maximum width of gnathosoma, narrow-oval in outline.

Idiosomal dorsum (length = 1.8× width); relative lengths of setae (v_1: sc_2: c_2: c_1: *d*: *e*: *f*: *h*): 1: 2.3: 1.1: 1: 0.8: 0.5: 0.9: 0.4. Rostral shieldlet 3.4× wider than long. Setae v_1 in a distance of 2.1× their length. Prodorsal shield, ≈1.7× wider than long. Tracheae with visible atria. Pits v_2 separated slightly more narrowly than bases of sc_1 and sc_2. Setae sc_2 located beyond one half length of the prodorsal shield, reaching with nearly 0.3× their length beyond posterior edge of prodorsal shield, by a distance between their bases of ≈1.5× their length. Setae c_2 almost reaching with their tips by one-half-distance to bases of c_1. Setae c_1 reaching with their tips only one-half the distance from their bases to the posterior edge of a tergite C. Setae *d* slender, sharp, reaching ≈0.5× their length beyond the posterior edge of tergite D, by a distance between their bases of 3.7× its length. Setae *f* slender, sharp, by a distance between their bases slightly shorter than their lengths. Setae *h* by a distance <7× their lengths.

Idiosomal venter: apodemes 1 moderately to weakly sclerotized, anteromedial apodeme very weakly defined (but an isolated nodule anteriad of *2a* level). Sejugal apodeme with numerous anterior thickenings. Setae *1a* located posteriad of apodemes 1, in a distance of 2.3× their length. Setae *2a* located on apodemes 2, by a distance between their bases equaling to 3× their lengths. Ventral propodosomal plate weakly concave anteriorly. Apodemes 4 not reaching posteriad of setae *3b* bases. Setae *3a* short, inserted in a distance of ≈6× their length from bases of setae *3b* and separated by a



Figs. 32–35. *Tarsonemus typographi*, female legs: (32) leg I; (33) leg II; (34) leg III; (35) leg IV.

distance between their bases almost 7× their lengths; and slightly shorter than that between *3b*. Setae *3b* subequal to *3a*, separated by a distance of 7.7× their lengths. Ventral metapodosomal plate weakly concave anteriorly, angular between trochanters III and IV. Trochanters IV separated by an interval of ≈2× their diameters. Setae *ps* separated by a distance between their bases slightly exceeding their 2× lengths. Dorsal tergite C and ventral metapodosomal plate covered with diversified ornamentations composed of larger and smaller dimples; remaining sclerites of dorsum and venter densely dimpled.

Legs: Proportions of free segments of legs: (I: II: III: IV): 1: 1: 1.1: 0.7.

Leg I: Claw slightly smaller than those of tarsi II and III. Spine-like seta *s* short, relatively weak, blunt-ended, slightly smaller than seta *u'* of legs II and III. Tibiotarsus almost 2.5× as long as wide at base. Two eupathidia (*p'-p''* subequal in length) inserted apically on tibiotarsus I; *tc'* longest of all eupathidia, located distad of transverse midline of tibiotarsus; *tc''* located subapically. Solenidion *ω* with fusiform, striated head, clearly shorter than its stalk, apparently larger than Ta *ω* II. Tibial solenidion ϕ_2 only slightly smaller than ϕ_1, both with indistinct striation; famulus *k* longer than ϕ_1; located proximally. Seta *l'* on genu weakly tapering, stiffer at the base. Femur I with small ventral process. Setae *l''* and *v''* on femur attenuate; *l'* slightly stiffer, *d* rigid, blunt.

Leg II: Claws medium-sized, hooked; empodium small. Tarsal spine-like seta *pl''* subequal to solenidion Ta II *ω*, but located more distally. Seta *tc''* only slightly longer than other setae of segment. Tibia with lateral spine-like protrusion; seta Ge *l'* attenuate, slightly stronger than others on the segment. Femur with pronounced rounded ventral lobe, seta *d* very short, weak.

Leg III: Claws slightly smaller than those on leg II. Seta *tc''* ≈2× as long as other setae of segment, *pv''* missing.

Leg IV: Free segments of leg about as long as femurogenu and tibia III. Femurogenu ≈2.7× as long as tibiotarsus. Femoral seta *v'* shorter than genual one; the latter located in a distance of 1.3× distal width of Fege from the end of segment. Seta Tb *v'* about as long as length of femurogenu and tibiotarsus. Seta Ta *tc''* ≈2× as long as whole leg IV.

Measurements (holotype, followed by four paratypes in parentheses; unreadable measurements replaced by "**" sign): Body and tagmata: length of body: 197 (175–210); length of idiosoma: 177 (160–210); width of idiosoma: 104 (94–118); length of gnathosoma: 29 (26–29); width of gnathosoma: 24 (23–25); length of pharynx: 12 (11–12); width of pharynx: 5 (4–5).

Dorsum: length of PrS: 54 (54–64); width of PrS: 101 (95–105). Lengths of setae: *dgs*: 9 (9–12); *vgs*: 10 (10–11); v_1: 13 (12–14); sc_1: 17 (16–18); sc_2: 23** (28–31); c_2: 12 (12–18); c_1: 14 (13–14); *d*: 12 (9–12); *e*: 7 (5–7); *f*: 12 (11–13); *h*: 6 (5–6). Distances between setae: v_1-v_1: 28 (26–29); sti-sti: 43 (43–47); sc_1-sc_1: 43 (43–63); sc_2-sc_2: 45 (43–47); c_2-c_2: 98 (96–104); c_1-c_1: 67 (65–73); c_1-c_2: 32 (30–34); *d-d*: 37 (35–41); *e-e*: 72 (68–78); *f-f*: 16 (16–17); *e-f*: 29 (27–32); *h-h*: 37 (36–40).

Venter: Lengths of setae: *1a*: 5 (4–5); *2a*: 8 (7–11); *3a*: 4 (3–4.5); *3b*: 4 (3–4.5); *ps*: 6 (5–8). Distances between setae: *1a-1a*: 10 (10–10); *2a-2a*: 27 (26–27); *3a-3a*: 25 (25–27); *3b-3b*: 28 (26–30); *ps-ps*: 6 (5–8). Length of tegula: 9 (7–9); width of tegula: 15 (15–16); length of PrP: 50 (46–53); width of PrP: 95 (91–95); Ap. 1-1: 11 (11–13); Ap. 2-2: 43 (43–45).

Leg segments and setae on legs (lengths): Tbt I: 19 (18–20); *ω*I: 6 (6–8); ϕ_2: 3.5 (3.5–4); ϕ_1: 5 (4.5–5); *k*: 6 (5–6); *ω* II: 4.5 (4–5); *pl''* II: 5 (4–5.5); Fege IV: 20 (19–22); TbT IV: 8 (7–8); Fe *v'*: 10 (9–13); Ge *v'*: 11 (11–16); Tb *v'*: 25 (25–27); Ta *tc''*: 45** (50–64).

Type material: HOLOTYPE: one female, GERMANY: 25 km East of Freiburg, 16-VI-80, phoretic on *Ips typographus* ex pheromone trap, H. Bogenschütz, NMNH.

PARATYPES: two females with same data as in the holotype, DATE; GERMANY: nine females, 15–30 km S, E, SE of Freiburg, V-80 – IV-81, H. Bogenschütz, seven females NMNH, one female CNC, one female ZMH; 1 female, St. Margen, 10-VI-80, phoretic under elytrae of *I. typographus*, ex pheromone trap, H. Bogenschütz, DATE; 1 female, Kappel, 18-VI-80, phoretic under elytrae of *I. typographus*, ex pheromone trap, H. Bogenschütz, DATE; 1 female, Kirchgarten, 16-VI-80, phoretic on *I. typographus*, ex pheromone trap, H. Bogenschütz, DATE; SWEDEN: seven females, 18 km East of Uppsala, 19–24-V-83, phoretic on *I. typographus* ex pheromone trap, J. Regnander, one female NMNH, one female CNC, five females DATE.

Distribution: central and northern Europe; probably covering the geographic range of *I. typographus*

Remarks: this species was earlier reported as *T. subcorticalis* by Moser and Bogenschütz (1984) and Moser et al. (1989).

New distribution record for other species of the *T. minimax* group

T. subcorticalis Lindquist 1969

REPUBLIC OF SOUTH AFRICA: one female, Cape Province, Grabouw, 19-X-84, ex. alcohol sediments. *Orthotomicus erosus* ex. emergence traps, M. Wingfield, DATE; AUSTRALIA: three females, South Australia, 60 km North- East of Adelaide, Crawford Mt, 17-VII-85, phoretic ex. reared *Ips grandicolis* ex. *Pinus radiata*, alcohol sediments, A. Austin, DATE; POLAND: eight females, Wielkopolska, Morasko near Poznań, 26-V-90, ex leaf litter under fern *Dryopteris filix-mas*, in moist alder (*Alnus glutinosa*) forest, W. Magowski, DATE; two females with the same data except for date: 27-VII-90, DATE.

T. endophloeus Lindquist 1969

REPUBLIC OF SOUTH AFRICA: one female, Cape Province, Grabouw, 19-X-84, ex. alcohol sediments, *Hylurgus ligniperda*, ex. emergence traps, M. Wingfield, DATE.

Discussion

Remarks on Morphology

Common features resulting from phoresy on bark beetles vary by species. The consistent body shape, small size, and relatively short legs in the majority of species are phoretic characters found in unrelated phoretic species of *Tarsonemus* (Magowski 1986). An interesting characteristic, infrequent in tarsonemids, is the unusual form of subpretarsal setae of legs I-III (*s-u'*); the bent tips improve the fastening of the mite to the host body (e.g., in *T. krantzi*). Apical bending sometimes occur in spine *pl''*. The enormous size of this spine (in females) is characteristic for the group and may also be associated with the ability to travel on the host.

Systematics

The *minimax* group forms a coherent set of species, but it is not clear from which of the lineages of *Tarsonemus* arose. A possible kin might be the *T. gladifer* group (as suggested by cladistic study by Magowski unpublished data).

Superficially similar, but less related forms are *T. ravus* Kaliszewski 1993 and *T. orbiculatus* Livshits, Mitrofanov and Sharonov 1979. Both species have their opisthosomal setae *d* and *f* attenuated, however, other features (e.g., placement of setae *1a* far posteriad of apodemes 1) place them outside the group. Moreover, attenuated opisthosomal setae are generally accepted as the plesiomorphic condition; thus, they do not define natural groupings. The female of *T. ravus* has its pharynx more narrow and the C tergite more attenuate than any species of *minimax* group and is tentatively allocated in the *Tarsonemus floricolus* group (Magowski unpublished data). However, *T. orbiculatus* has the rostral shield weakly protruding from the prodorsal shield, sejugal apodeme almost indistinct in its medial part, broader and shorter tegula, and tarsal II spine *pl''* located far distad of solenidion ω. This species may also represent a different lineage within the genus *Tarsonemus* s. lato.

Host Range and Geographic Distribution

Mite material consisted of samples from the collection of Moser mainly from North and Central America but also from South Africa, Australia, and Europe. These specimens represent a source of new biogeographical record for some species.

Except for *T. krantzi*, the host affiliation and biogeography of the *minimax* group is insufficiently known (Table 1). Scientific interest has largely been limited to forest ecosystems of economic importance. The mite fauna of forests in the world remain very poorly known even where extensive collections of insects exist. Therefore, knowledge of host/spatial distribution of mites remains fragmentary. A further difficulty is that some species (as apparently is true for *T. subcorticalis*) do not obligatorily coexist with beetles. In Poland, the latter species is found on the forest floor and on low vegetation (W.L.M., unpublished data). Perhaps other species are also less bound to their host than indicated by the collection record. This study suggests that the origin of the *minimax* group may lie in warm regions of America. Five out of nine species are known only from North and Central America; of these, only three come from the Southern United States, Mexico and Central America. However, records of two undetermined species from China (Moser 1985, Moser et al. 1995) suggest that more extensive studies are necessary before an hypothesis on the geographic origin and dynamics of the group is proposed.

Table 1. Distribution and associations of species from *T. minimax* group

Species	Host	Phoresy	Galleries	Fungus	Sporotheca	Distribution	Sources
minimax	*P. curvidens*	+	–	–	–	E	Vitzthum 1926
crassus	*S. multistriatus*	–	+	–	–	E	Suski 1970
triarcus	*I. grandicollis, D. frontalis, D. adjunctus, O. mexicanus*	+	+	–	–	MA, M, WUS, CD	Lindquist 1969, Moser et al. 1974
subcorticalis	*D. simplex, D. frontalis, D. valens, , O. caelatus, O. ornatus, P. curvidens* (?), *P. sporsus, I. spp.* (?)	+	+	*P. (A)* sp., *O. bicolor, O. europhioides, H.* sp. (?)	+	MA, M, US, CD, AU, C(?)	Lindquist 1969, Moser et al. 1974, Lindquist 1969, orig.
endophloeus	*D. frontalis, D. brevicomis, D. pseudotsugae* (?)[1]	+	–	*O. minus, O. nigrocarpa, O. piceae, C. ranaculosus* (?)[2]	+	WUS, CD, M, MA, SA	Lindquist 1969, Moser 1985, Lindquist 1969, Moser et al. 1974, Moser 1985, orig.
krantzi	*D. frontalis*	+	–	*O. minus, P. (T)* sp.	+	SUS, EUS, MA, M	Smiley and Moser 1974, Moser and Bridges 1986, Moser 1985, Moser et al. 1974, Bridges and Moser 1983
suskii	*D. frontalis*	–	+	–	–	EUS	Smiley and Moser 1974
terebrans	*D. terebrans*	+	–	–	–	SUS	orig.
typographi	*I. typographus*	+	–	–	–	E	Moser et al. 1989, Moser and Bogenschutz 1984
sp. nr. *subcorticalis*	*I. acuminatus*	+	–	*C. nr. ranaculosus*	+	CH	Moser et al. 1995
sp. nr. *endophloeus*	*I. nitidis*	+	–	*O. nr. minus*	+	CH	Moser 1985

Distribution: E-Europe, MA-Mesoamerica, M-Mexico, US-USA (all territory), EUS-Eastern USA, WUS-Western USA, SUS-Southern USA, CD-Canada and Alaska, CH-China, SA-South Africa, AU-Australia, C-cosmopolitan.

Beetles: *D.-Dendroctonus, I.-Ips, O.-Orthotomicus, P.-Pityokteines, S.-Scolytus.*

Fungi: *C.-Ceratocystiopsis, O.-Ophiostoma, H.-Hansenula, P.-Pyxidiophora, (T)-Thaxteriola* type ascospores, *(A)-Acariniola* type ascospores.

Other: "+" phoretic and/or in galleries, "–" not found (=no data).

[1]Mite determination uncertain-perhaps a new species.

[2]*C. ranaculosus* may be restricted to the Southern US populations. Hsiau and Harrington (1997) have described *C. brevicomi* from *D. brevicomis* in California. Marmolejo and Butin 1990 have described *C. colliferi* from *D. valens* in Mexico.

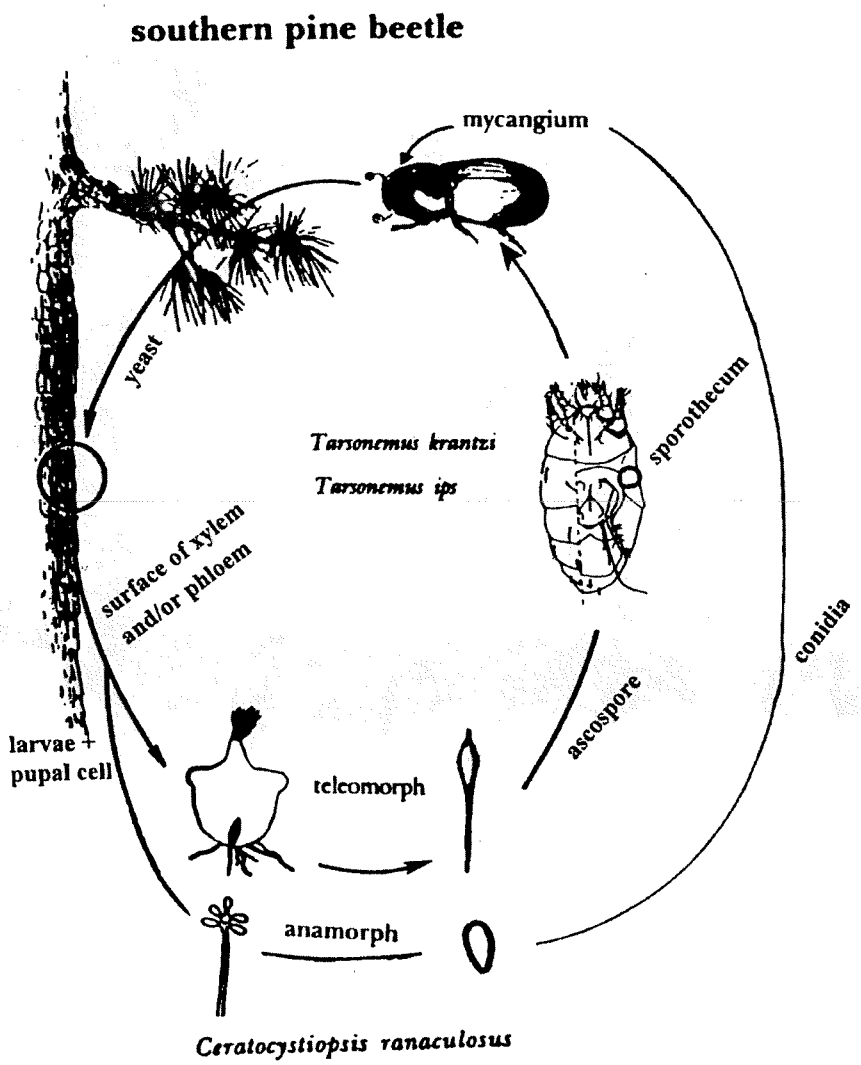


Fig. 36. Diagram of the life cycle of *Ceratocystiopsis ranaculosus*. Ascospores are released from the perithecium on the inner bark where they enter sporotheca of adult female mites. Some mites are phoretic on emerging southern bark beetles, which disperse not only the mite, but also the fungus. Inside the SPB pupal chamber, anamorph conidiophores release conidia, which enter the beetle mycangium. Here they become yeast, which multiply and are transported to a beetle gallery becoming hyphae, which produce both conidia and ascospores in the next tree that the beetle attacks.

The Sporothecum as a Taxonomic Character and Sporophory

The presence or absence of ventral flaps of tergite C as a functional sporotheca may be an important clue to the taxonomic position of a species and its biology. A number of species of *Tarsonemus* possessing sporothecae have probably coevolved with those bark beetles possessing mycangia (Moser et al. 1995). All but one of these species (*T. ips* Lindquist) belong to the *minimax* group. The best known of these associations is that of *T. ips* and *T. krantzi* with *Ceratocystiopsis ranaculosus* Perry and Bridges, the mycangial fungus of the southern bark beetle, *Dendroctonus frontalis* Zimmermann (SPB) (Bridges and Moser 1983).

Species of *Tarsonemus* whose phoretic bark beetle hosts do not have a mycangium have so far never been observed to contain spores beneath tergite C. For example, both *T. terebrans* and the population of *T. subcorticalis* phoretic on the three species of *Ips* attacking southern pines apparently mingle more or less freely with the two species of *Tarsonemus* associated with SPB. Yet there is no evidence of spores being transported under tergite C in either *T. terebrans* or this population of *T. subcorticalis*.

The yeast anamorph multiplies in the beetle mycangium but not in the tree. The yeast is transmitted to the tree when the female burrows in the inner bark and lays her eggs. But the yeast spores do not multiply. Instead, the yeast spores then grow and produce hyphae, which then divide and multiply. The sperm-shaped, sexual teleomorph also multiplies in the tree and is transported in the sporothecae of the mite. But the conidia are apparently phoretic only on the beetle (Fig. 36).

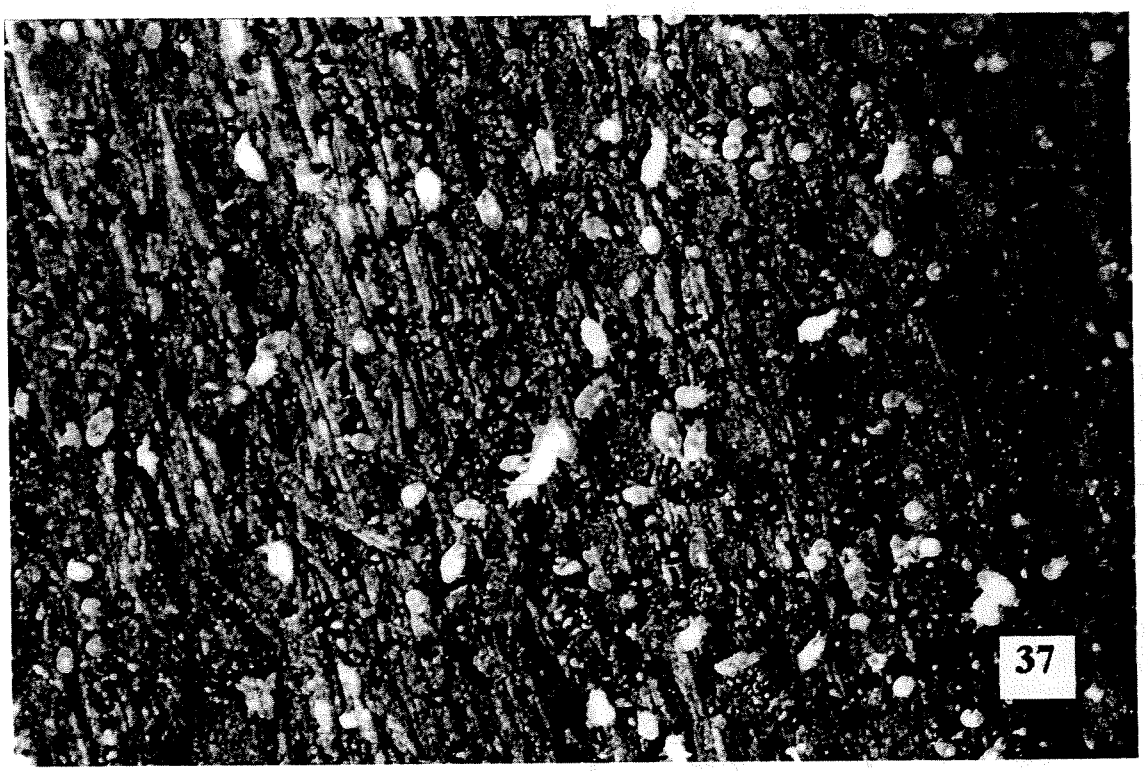


Fig. 37. Numerous eggs, larvae and adults of *T. krantzi* and/or *Tarsonemus ips* on patch of bluestain (*Ophiostoma minus*) in the inner bark of SPB-infested *Pinus taeda*.

Colonies of both *T. krantzi* and *T. ips* are often intermingled beneath the bark of SPB-infested trees on patches of *Ophiostoma minus* (Hedgcock) H. and P. Sydow (Moser and Roton 1971; Smiley and Moser 1974) (Fig. 37). Here, the mites feed on growing hyphae of *O. minus* and *C. ranaculosus* (Lombardero et al. 2000). Both anamorph and teleomorph spores of *O. minus* are carried on the external surfaces of SPB, but not in the mycangium. However, the crescent-shaped teleomorph spores are also transported within the lateral pocket-like spaces of C tergite (sporothecae) of both mites (Moser 1985). *T. ips* associated with SPB have functional sporothecae, whereas the other *T. ips* populations examined do not, suggesting that *T. ips* may be a sibling species complex rather than a presently assumed cosmopolitan entity.

The unique sperm- or tadpole-shaped ascospores of *Ceratocystiopsis* have also been observed in sporothecae of *T.* sp. n. near *endophloeus*, phoretic on *Dendroctonus brevicomis* LeConte in California, and that of *T.* sp. near *subcorticalis* phoretic on *Ips acuminatus* from China (Moser et al. 1995). Both of the latter bark beetles also possess mycangia. Hence, the phenomenon of *Tarsonemus* mites transporting ascospores of *Ceratocystiopsis sp*(p). may extend geographically over the range of the group *minimax* at least to China.

Key for the Determination of Species of the *Tarsonemus minimax* Group

[Note: Key for determination of males is provisional, because of the lack of data. Wherever male determination is involved, one is encouraged to search for and determine females of the population in question.]

Females:

1. Prodorsal shield triarcuate. Apodemes 3 contiguous . . . . . *T. triarcus*
   Prodorsal shield without anterolateral lobes. Apodemes 3 not contiguous 2
2. Setae sc_2 only slightly longer than v_1 and as long as half of the distance between their bases . . . . . *T. crassus*
   Setae sc_2 apparently (1.5- 2.5x) longer than v_1 and approaching the distance between their bases . 3
3. Tergite C and ventral metapodosomal plate with ornamentation differentiated into smaller and larger dimples. Both ventral metapodosomal setae *3a* and *3b* apparently shorter (almost twice) than pseudanal *ps* . . . . *T. typographi*
   Tergite C and ventral metapodosomal plate with uniform dimpled ornamentation. Ventral metapodosomal setae *3a* and/or *3b* subequal to pseudanal *ps* 4
4. Tibiotarsus I ≈3× longer than wide at the base, tarsus II over 2× longer than wide at the base. . . . . *T. terebrans*
   Tibiotarsus I <2.5× longer than wide at the base, tarsus II <1.6× longer than wide at the base . 5
5. Seta *pl″* on tarsus II apparently (3×) thicker than solenidion ω at its base . . . . . *T. krantzi*

Seta *pl''* on tarsus II only slightly (2× or less) thicker than solenidion ω at its base 6

6. Setae c_2 longer than the distance to the bases of setae c_1, femorogenu and tibiotarsus IV longer than femorogenu and tibia III. . . . . *T. endophloeus*

Setae c_2 shorter (though sometimes slightly) than the distance to the bases of setae c_1, femorogenu and tibiotarsus IV shorter than femorogenu and tibia III 7

7. Setae *f* apparently shorter (0.75×) than distance between their bases, ventral setae *3a* apparently (almost 2×) shorter than *2a*. . . . . *T. minimax*

Setae *f* approximate in length to distance between their bases, ventral setae *3a* subequal to or very slightly shorter than *2a*. . . . . *T. subcorticalis*

Males:

1. Seta *l'* on tibia III attenuate 2

Seta *l'* on tibia III spine-like 3

2. Seta *d* on shield CD not reaching the base of seta *f* on the shield EF, tarsi I and II not longer than 2× their lengths . . . . . *T. subcorticalis*

Seta *d* on shield CD reaching clearly beyond the base of seta *f* on the shield EF, tarsi I and II evidently longer than 2.5× their lengths . . . . . *T. terebrans*

3. Seta *pv''* on tarsus III spine-like 4

Seta *pv''* on tarsus III attenuate 6

4. Seta *p'* flanking adaxially pretarsus III stout . . . . . *T. suski*

Seta *p'* flanking adaxially pretarsus III hair-like . 5

5. Seta sc_2 three times as long as sc_1; setae *d* slightly longer than c_1 . . . . . *T. endophloeus*

Seta sc_2 less than three times as long as sc_1; setae *d* slightly shorter than c_1 . . . . . *T. krantzi*

6. Seta *3a* reaching to the half distance to base of *3b*, seta *v'* on tibia IV ≈3× as long as Ge IV *v'* . . . . . *T. triarcus*

Seta *3a* almost reaching to base of *3b*, seta *v'* on tibia IV ≈1.5× as long as Ge IV *v'*. . . . . *T. crassus*

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