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Phase morphs and phoresy: New species of *Antennoseius* (*Vitzthumia*) mites (Acari: Mesostigmata: Ascidae) associated with pyrophilous carabids (Carabidae: *Sericoda* spp.) in Alberta, Canada

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Abstract

The mite genus *Antennoseius* is composed of free-living species in soil and litter, as well as species that are phoretic on carabid beetles as adult females. Among approximately 60 described *Antennoseius* species, one North American species, *A. janus*, was found in laboratory cultures to have two female morphs: one granular, free-living morph, and one smooth, putatively phoretic morph. We here describe the adult females of *A. perseus* **n. sp.** and *A. pyrophilus* **n. sp.** collected from under the elytra of carabid beetles (*Sericoda quadripunctata* and *S. bembidioides*) associated with recently burned forests in Alberta, Canada. We also describe the female and male of a distinct, granular, non-phoretic morph of *A. perseus*, obtained from soil and by rearing the offspring of phoretic females. A key to the females of *Antennoseius* species having an ambulacrum on leg I (i.e. subgenus *Vitzthumia*) is provided.

Key words: predatory mites, phoretic morph, dimorphism, ground beetles, fire fauna

Introduction

The Mesostigmata is an ecologically diverse taxon comprising over 10,000 described species of mites. The best known mesostigmatans are predators of agricultural pests (e.g. the phytoseiid mites used as biocontrol agents), parasites of vertebrates (e.g. poultry mites), and associates of other organisms of human interest, e.g. the varroa mite of honeybees or the hummingbird-flower mites (Walter & Proctor 1999). About half of all described species of mesostigmatans, however, are predators of invertebrates in detritus-based systems such as soil, rotting wood, compost, carrion, and dung. Those living in patchy habitats often disperse to new patches by forming temporary associations with insects, a behaviour called phoresy. In the Mesostigmata, the phoretic stage is usually either the last immature instar (the deutonymph) of both sexes, or the adult female (Athias-Binche 1993; Walter & Proctor 1999).

Although phoretic deutonymphal stages that differ in morphology from free-living deutonymphal stages (i.e. heteromorphs) are known in the Mesostigmata (Athias-Binche 1993), in general, phoretic adult female mesostigmatans are morphologically identical to free-living females of a given species. The single probable exception known is *Antennoseius janus* Lindquist & Walter (Ascidae), a free-living predator of small invertebrates in montane meadows in the Rocky Mountains, which produces two distinct female morphs in laboratory cultures (Lindquist & Walter 1989). Species of *Antennoseius* are mostly found in open habitats such as

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meadows, fields, and marshes and in the nests of rodents and birds, and adult females of several species are phoretic under the elytra of carabid beetles (Costa 1969; Lindquist & Walter 1989; Fain *et al*. 1995; Halliday *et al*. 1998; Eidelberg 2000). Because one of the female morphs of *A. janus* resembles other *Antennoseius* species found on carabid beetles and the other morph resembles the form usually collected from soil and nests, Lindquist & Walter (1989) proposed that one morph was a phase morph associated with dispersal (phase) on carabid beetles (the phoretomorph); however, they were not able to find beetles with phoretic *A. janus*.

Beetles of the carabid genus *Sericoda* Kirby (previously *Agonum*) (Coleoptera: Carabidae) are considered to be pyrophilous (attracted to burned areas) because they are often abundant in recently burned forests (Holliday 1984; Burakowski 1989; Wikars 1995; Koivula *et al*. 2006). Two circumpolar species of *Sericoda* in particular, *S. quadripunctata* (DeGeer) and *S. bembidioides* Kirby, are frequently found together in burned forests throughout much of Canada. In Canada, *S. quadripunctata* occurs in all provinces except Prince Edward Island, but *S. bembidioides* is known only in provinces west of Manitoba (Bousquet 1991). Both species are collected primarily in the first three years after a fire (Holliday 1984, 1991; Wikars 1995; Koivula *et al*. 2006). The factors attracting these beetles to burned areas are unknown; however, post-fire abundances of the two species seem to be positively correlated with burn severity, and their rapid disappearance in the following years may be due to subsequent vegetative cover (Koivula *et al*. 2006) or increasing interspecific competition (Holliday 1991).

In this paper we describe two new species of *Antennoseius* in the subgenus *Vitzthumia* that are commonly phoretic on *S. quadripunctata* and *S. bembidioides* and rarely on other carabids in recently burned boreal forest in Alberta, Canada. We were able to rear offspring from one of these phoretic mites and produce an adult female of a second form—similar in shield granulation and setae shape to that in the putatively free-living morph of *A. janus* — and thus demonstrate that dimorphic adult females may be widespread in the subgenus.

Materials and methods

Beetle collections. In 2002, *Sericoda* species and other carabid beetles were collected as part of a large-scale study investigating the cumulative impacts of natural and anthropogenic disturbances on boreal ground beetles in Alberta, Canada. All sites were located in and around the Chisholm fire (~116,000 ha) (54º55'N, 114º10'W) that occurred near Chisholm, Alberta in the spring of 2001. Beetles were collected in pitfall traps filled with silicate-free ethylene glycol, from three sites of each of the following treatments: (1) unharvested sites burned in the Chisholm fire; (2) sites burned and then salvage logged in 2001; and (3) sites clear-cut harvested in 2001, and then burned by the Chisholm fire. Beetles were preserved in 70% ethanol.

Mite removal and rearing. A total of 4,160 *S. quadripunctata*, 1,078 *S. bembidioides*, and 10 individuals of each of the 10 most abundant carabid species other than *Sericoda* (*Agonum placidum* (Say), *Amara obesa* (Say), *Bembidion grapii* Gyllenhal, *Calathus ingratus* Dejean, *Calosoma calidum* (Fabricius), *Harpalus laevipes* Zetterstedt, *Patrobus foveocollis* (Eschscholtz), *Platynus decentis* (Say), *Pterostichus adstrictus* Eschscholtz and *Stereocerus haematopus* (Dejean)) were examined for mites. Using a dissecting microscope and forceps, one of us (AD) removed 3,456 *Antennoseius* mites from the sub-elytral space of the beetles and placed them in individual 1.5 ml centrifuge tubes containing 70% ethanol. One hundred haphazardly selected mites were mounted on slides in PVA and identified to species. Holotypes and a few paratypes are deposited at the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, and many paratypes at the Royal Alberta Museum, Edmonton, Canada.

To obtain live specimens for rearing, single female *Antennoseius* were removed by immobilizing individual *Sericoda* beetles with CO_2 gas, opening the elytra and gently transferring the mites with a brush into separate plastic vials (60 ml) with a plaster-charcoal bottom. Both the beetles and the mites regained consciousness within about five minutes.

We attempted rearing late in autumn when few live beetles were available, and therefore, few mites. The first two food sources used (cricket food and the nematode *Caenorhabditis elegans* (Maupas) reared on agar) did not support development, but a second nematode, *Panagrellus silusiae* (de Man) (cultured in moist oatmeal), was readily eaten and supported development. A drop of *P. silusiae* suspension was added to the charcoal-plaster floor of the mite culture every two days. Within three weeks eggs were laid in the vials and hatched within a week. Fungal infection was minimal, but when growth was observed, it was scraped from the surface with a small piece of paper towel. Cultures were maintained at approximately 22°C.

Mites were cleared in Nesbitt's solution and mounted in PVA on microscope slides (Krantz & Walter 2009). Measurements (minimum-maximum in µm) were made from slide-mounted specimens using a stage-calibrated ocular micrometer. Lengths of shields were measured along their midlines and setae from the bases of their insertions to their tips. The setal notation used follows those of Evans (1963) and Lindquist & Evans (1965) as applied to *Antennoseius* by Lindquist & Walter (1989). Notation of pore-like structures on the idiosoma mostly follows the system of Johnston & Moraza (1991), and the distinction between glandular openings and poroids (lyrifissures) was derived from Athias-Henriot (1971, 1975), Krantz & Redmond (1987), Lindquist & Moraza (1998) and Moraza & Lindquist (2008). The species key was prepared using species descriptions in the literature and the species on hand (*A. janus* and the new species described below). Authorships of *Antennoseius* (*Vitzthumia*) species are given in the key.

Antennoseius Berlese, 1916 (subgenus *Vitzthumia* Thor, 1930)

Diagnosis. The subgenus is characterized by the retention of the pulvillus and claws on legs I and sometimes by the retention of 9 setae on tibia III (*pl2* may be present). The ambulacrum and usually *pl2* are lost in *Antennoseius* (*Antennoseius*).

Remarks. The type species for the genus, *A.* (*Antennoseius*) *delicatus* Berlese, 1916, was originally placed in the Laelaptidae (= Laelapidae s. lat.) by Berlese, as was the first described species of the genus *Vitzthumia*, *V. oudemansi* Thor, 1930. However, Thor (apparently not aware of its close relative *Antennoseius*) stated that the then monotypic genus *Vitzthumia* would possibly be best placed later in a new, distinct family, Vitzthumiidae, but he clearly opted not to take that action in his 1930 paper. Since then, *Antennoseius* has been placed in the Rhodacaridae Oudemans, 1902 (Athias-Henriot 1961), in the Halolaelapidae Karg, 1965 (Karg 1969, 1993), or is given its own family, Antennoseiidae Karg, 1965 (Eidelberg 1989, 2000), but we consider it to be a member of the Ascidae Oudemans, 1905, after Lindquist & Evans (1965), Lindquist & Walter (1989), Halliday *et al*. (1998), and Krantz & Walter (2009).

Antennoseius (*Vitzthumia*) *perseus* sp. nov.

(Figs 1–19)

Material examined. ALBERTA: *Holotype*. Female, under elytra of *Sericoda quadripunctata* (DeGeer) ex pitfall traps in recently burned boreal forest near Chisholm (54°56'N, 114°7'W), 22 July 2002. *Paratypes*: 49 females, under elytra of *Sericoda quadripunctata* (DeGeer) and *S. bembidioides* ex pitfall traps; 2 females under elytra of *Calathus ingratus* Dejean**,** same collection data; 2 females and 5 males (granular morph) obtained from rearing females collected on carabids.

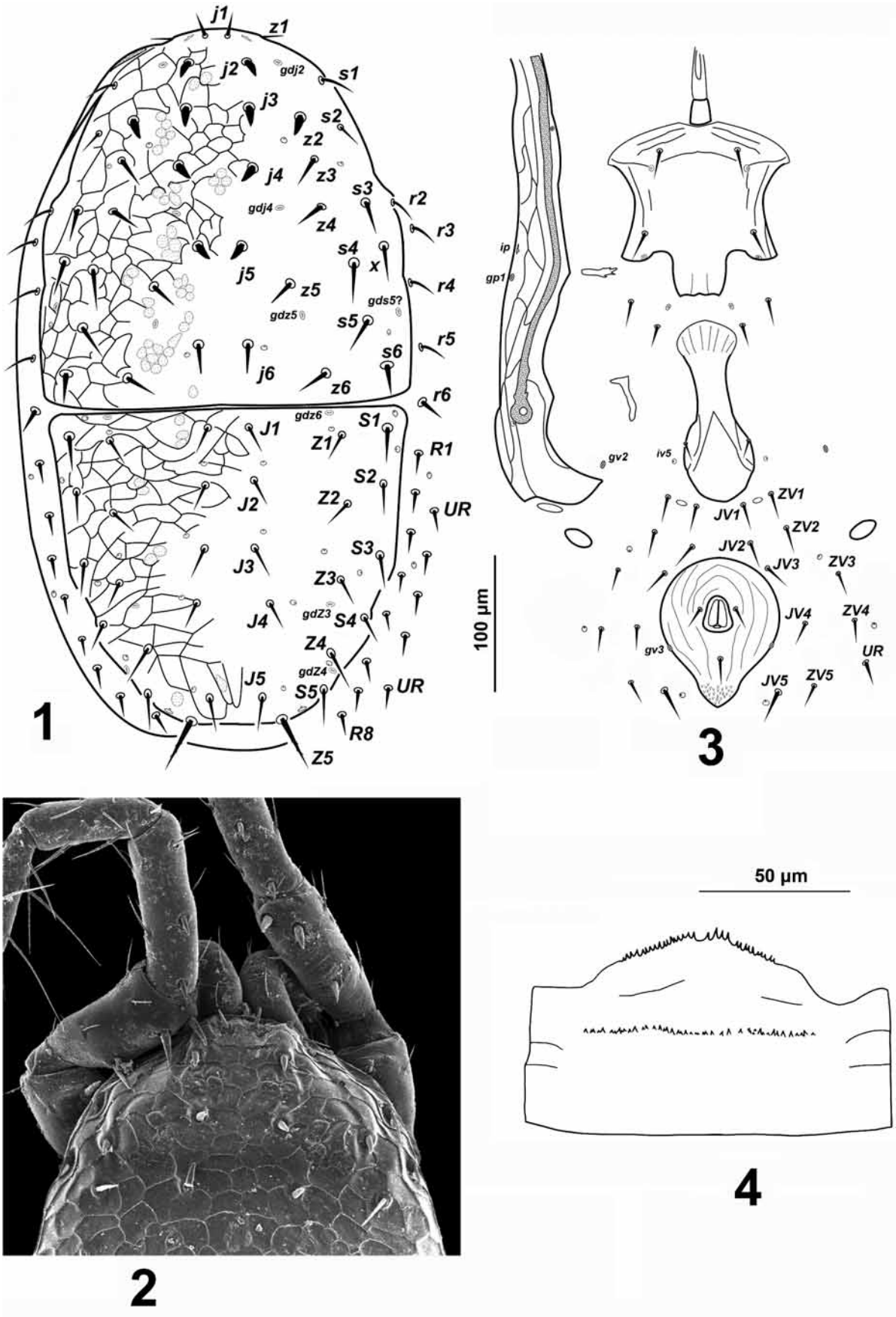
Diagnosis. *Antennoseius* species with adult females of smooth (phoretic) morph lacking granular tubercles on shields and soft cuticle: soft cuticle plicate; dorsal and peritrematal shields with reticulate pattern; ventral shields weakly lineate. Podonotal shield with 20 (rarely plus *r3* asymmetrically attached) pairs of setae, including an additional pair *x*, laterad *s4*; opisthonotal shield with 15 pairs of setae. Most idiosomal setae sim-

ple, but podonotal setae *j2-5* and *z2* short, spur-like; opisthonotal seta *Z5* about twice as long as others and lightly barbed in distal half. Sternal shield bearing *st1-2* and *stp1-2*; postero-lateral margins eroded leaving *st3* and *stp3* in soft cuticle; *st4* in soft cuticle. Anal shield with 3 circum-anal setae. Hypostomal setae *h1-3* simple; *pc* swollen basally and with fine, acuminate tip; palpal setae simple except *al* of femur and *al1-2* of genu thickened. Leg I with ambulacrum; seta *pl2* absent on tibia III. Most leg setae simple to sparsely barbed, except the following setae spur-like (thick, and usually blunt): dorsal seta on trochanter I; *ad1, pd1, pd2* on femur I; and *pd2, pd3* on genu I. Coxae I–II each with a seta with swollen base, and fine, acuminate tip.

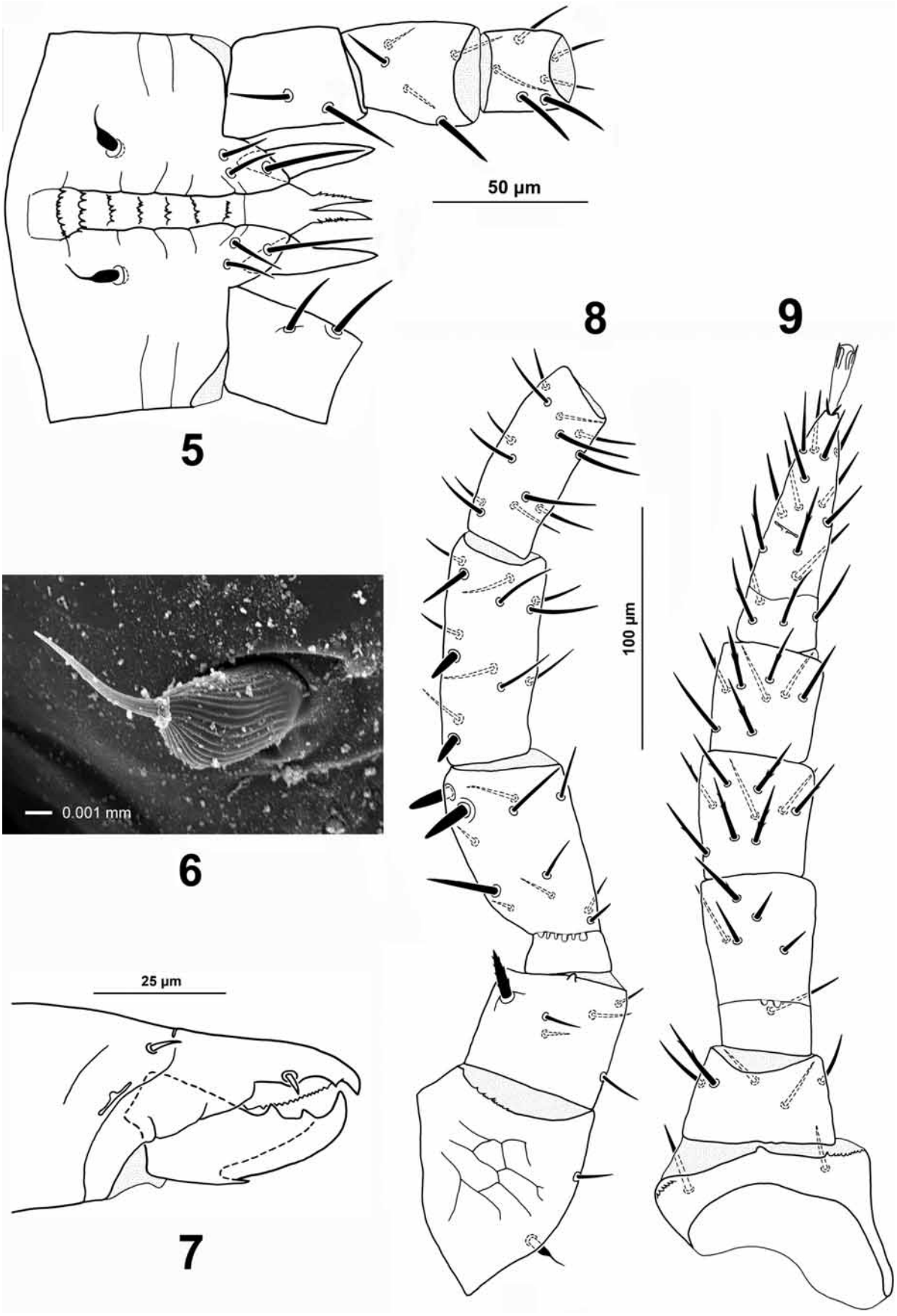
Adults of granular morph without spur-like podonotal setae or swollen setae having hair-like tips on subcapitulum or coxae. Surface of adults with dense coating of small tubercles and secondary pattern of larger tubercles forming reticulations on podonotal, opisthonotal, ventri-anal shields, and lateral region of peritrematal shield. Soft cuticle plicate and covered with small tubercles. Adult female podonotal shield with 20–22 pairs of setae, including an additional pair *x*, laterad *s4*; setae uniformly short, bushy, except *z1* thin, sparsely barbed; *j1* larger, swollen; opisthonotal shield truncate posteriorly with 14 pairs of short, bushy setae, except *Z5* thicker, about 1.5–2 × length of other opisthonotal setae. Seta *S1* off shield. Sternal shield lineate, bearing setae *st2-3, stp1-3, st1* in soft cuticle in pre-sternal region posteriad a pair of well developed pre-sternal sclerites; *st4* in soft cuticle. Ventri-anal shield with 7 setae (*JV2-3* captured). Leg I with ambulacrum; seta *pl2* absent on tibia III; all leg setae simple, most dorsal and lateral setae barbed. Adult male granular ornamentation similar to female but with podonotal and opisthonotal shields fused laterad *z-Z* series, free to irregularly fused medially and separated by narrow band(s) of soft cuticle. Sterno-genital shield lineate, bearing *st1-5*, stp *1-3*; pre-sternal platelets present. Spermatodactyl simple, with rounded tip, slightly longer than movable digit.

Description of phoretic female (smooth morph). Soft cuticle evenly plicate. Anterior dorsal shield (265–308 long × 270–310 wide) and posterior dorsal shield (230–258 × 257–288) both with smoothly angular reticulate ornamentation throughout (Figs 1–2). Anterior shield with 20 pairs (*j1-6, z1-6, s1-6, x, r2,* + *r3* rarely captured asymmetrically) of mostly short (24–30), acicular setae; *j1* (12–20) somewhat thickened; *z1* similar in length to *j1* but more slender; *j2-5* (13–15) and *z2* (13–14) short, stout (4 wide) and spur-like, usually blunt apically; *j6* and *z5* (17–22) intermediate between setiform and spiniform, sometimes blunt. Posterior shield with 15 pairs of mostly short (21–31), acicular setae (*J1-5, Z1-5, S1-5*); *Z5* (38–44) longest, sparsely barbed in distal half. Marginal setae *r3-6* and *R1-8* short (17–23), acicular, in soft lateral cuticle. Peritreme extending to near seta *z1*, peritrematal shield with elongate cells laterally, smooth in exopodal shield laterad coxae III–IV and parapodal region, joined to anterior dorsal shield near seta *s1*. Dorsal shields with 23 pairs of discernible pore-like structures (9 on anterior shield, 14 on posterior shield), of which 7 appear secretory (gland pores, *gd*, Fig. 1) and 16 non-secretory (lyrifissures). Gland pore *gds5*? apparently corresponds to *gd4 sensu* Athias-Henriot (1971, 1975). Gland pores are slit-shaped and lyrifissures are generally ovoid except those laterad setae *j1* and *Z5*.

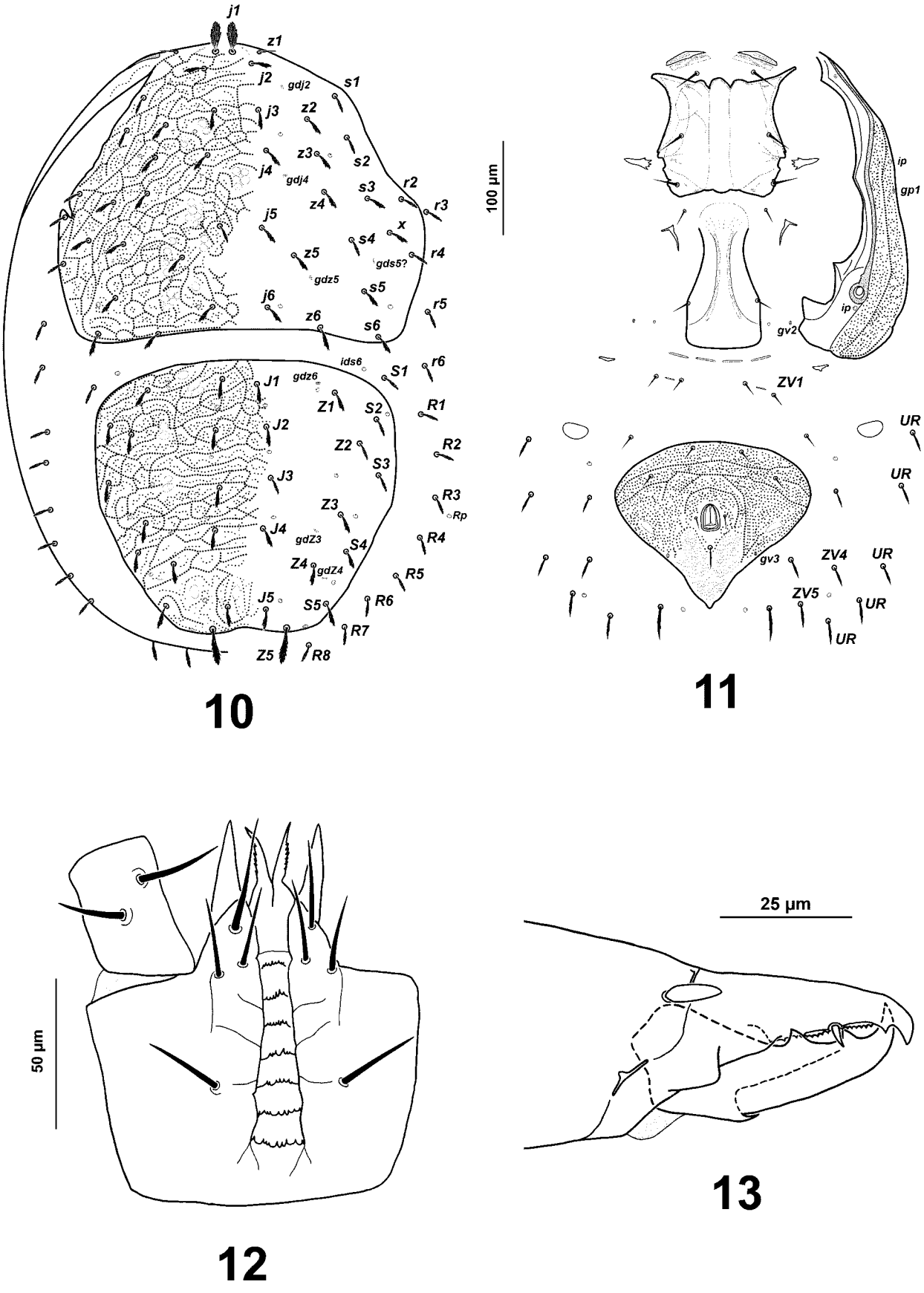
Tritosternum base (30–39) with 8–12 denticles fringing distal end around base of laciniae (54–65). Sternal shield (length 123–126 including median process, narrowest width between legs II, 89–94) (Fig. 3), lineate laterally and anteriorly, bearing simple setae *st1* (23–26), *st2* (20–23) and lyrifissures *stp1-2*; transverse ridge across shield at level of *stp1*; *stp2* on posterior margin; shield deeply but evenly notched postero-laterally, median process irregularly truncate. Small endopodal plate posteriad coxa II separated from sternal shield by soft cuticle. Setae *st3-4* (20–24) and lyrifissure *stp3* in soft cuticle. Epigynial shield (130–139 long) (Fig. 3) with membranous anterior margin, narrow stem (24–29 wide), and oval posteriorly (45–55 wide), bearing setae *st5* on margin and a few faint lines. Metapodal plates oval (11–12 × 22–23). Anal shield (105–126 long × 94–105 wide) pear-shaped, faintly lineate, usually with 3 simple circum-anal setae, post-anal seta (20–22) slightly longer than para-anal setae (17–20); shield sometimes capturing ventral seta *JV3*; cribrum in terminal tuft. Soft cuticle with simple ventral setae *JV1-5, ZV1-5*, and 4–8 pairs of simple submarginal setae (*UR*'s) (Figs 1, 3).



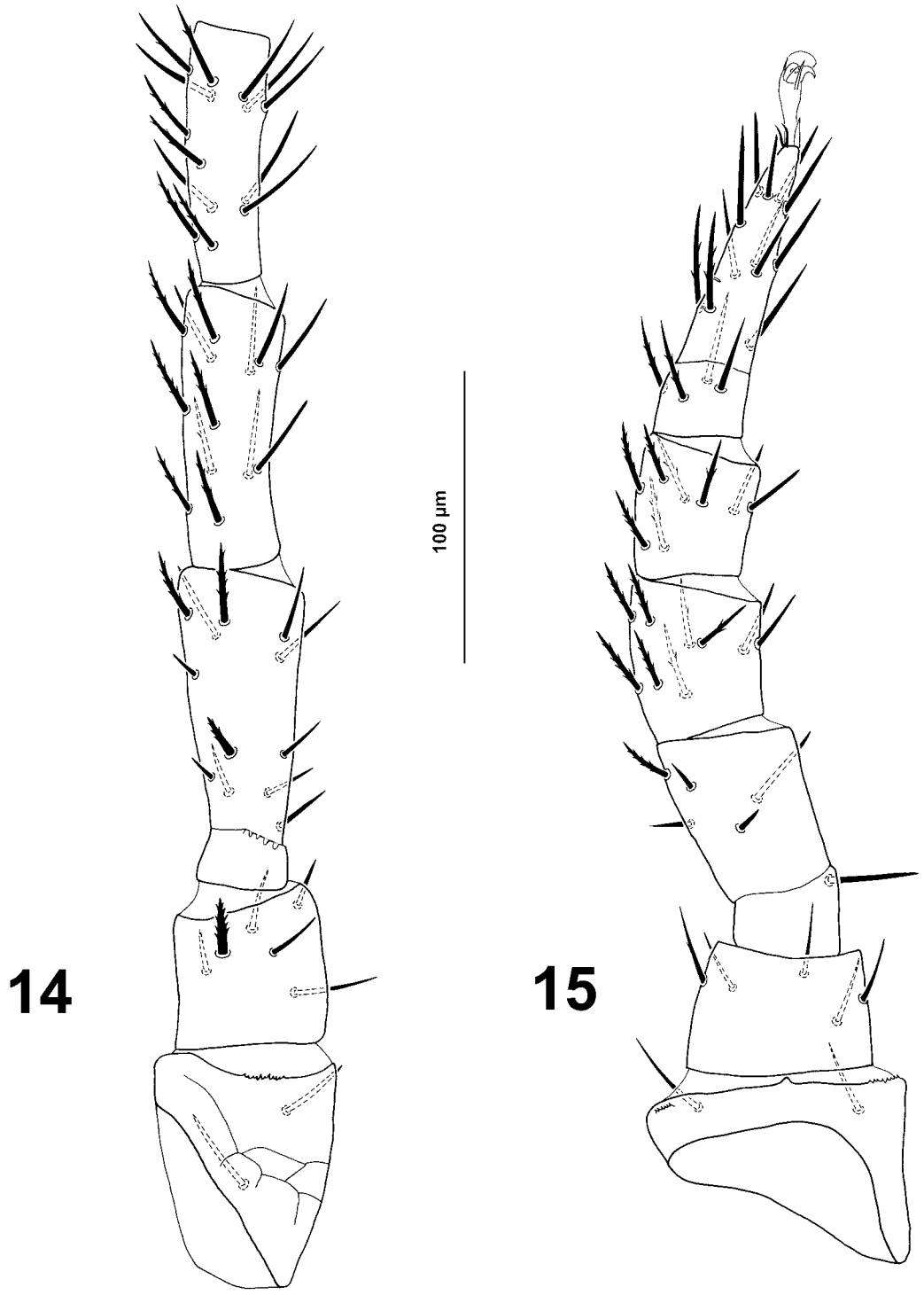
FIGURES 1–4. *Antennoseius perseus* **n. sp.**, female, phoretic form. 1, Dorsal shields; 2, Scanning electron micrograph of anterior portion of podonotal shield and most of leg I; 3, Ventral shields; 4, Tectum.



FIGURES 5–9. *Antennoseius perseus* **n. sp.**, female, phoretic form. 5, Subcapitulum; 6, Scanning electron micrograph of palpcoxal seta; 7, Right chelicera, lateral (antiaxial) view; 8, Right leg I (except tarsus), postero-lateral view; 9, Right leg III, dorsal view.



FIGURES 10–13. *Antennoseius perseus* **n. sp.**, female, free-living form. 10, Dorsal shields; 11, Ventral shields; 12, Subcapitulum; 13, Right chelicera, lateral view.



FIGURES 14–15. *Antennoseius perseus* **n. sp.**, female, free-living form. 14, Right leg I (except tarsus), postero-dorsal view; 15, Right leg III, postero-dorsal view.

Tectum (Fig. 4) with anterior medial margin denticulate, and dorsal surface with a transverse line of denticles; subcapitulum (Fig. 5) with 7 rows of 4–11 deutosternal denticles, ridges of some rows extending onto genae; corniculi horn-like (40–43), extending to distal margin of palptrochanter; hypostomal setae *h1-3* simple; palpcoxal seta *pc* swollen basally, with fine, acuminate tip (Figs 5–6). Fixed digit of chelicera (35–38, from dorsal lyrifissure) with short, rounded dorsal seta, row of 12–17 serrations, setiform pilus dentilis, and subapical offset large tooth; movable digit (41–46) bidentate and paraxial ridge leading to a ventral projection typical for the genus (Fig. 7). Palps (138–155) less than twice the length of subcapitulum (from base to tip of

corniculi: 115–117); palpal setae simple except *al* of palpfemur and *al1-2* of palpgenu thickened; setation normal for genus; palp apotele 2-tined.

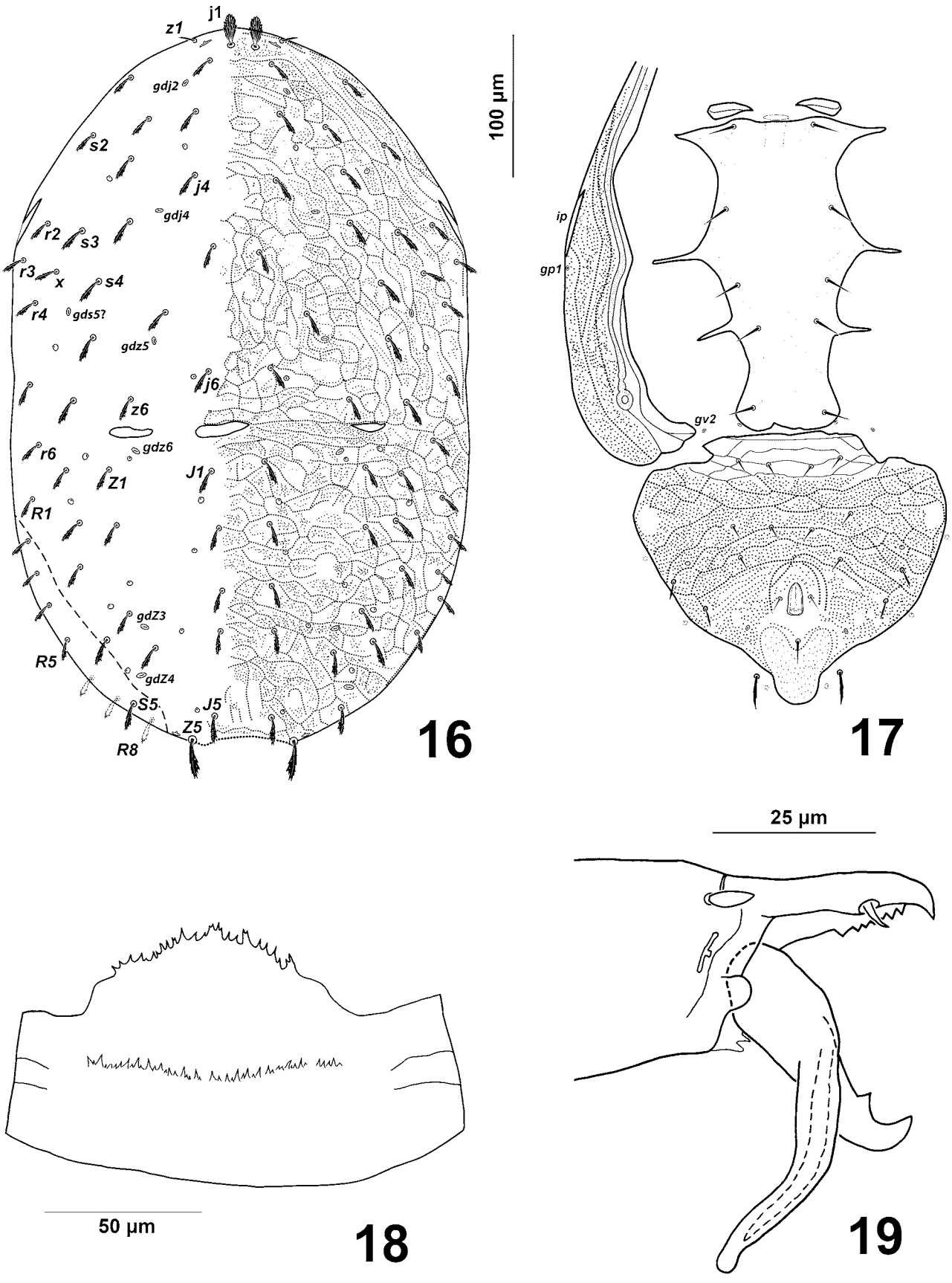
Excluding ambulacra, lengths of leg I 468–505, leg II 317–351, leg III 312–352, leg IV 440–479 (Figs 8–9). Tarsus I with ambulacrum (12–14, excluding stalk) on short stalk (8–10), claw subequal in size to claws of tarsi II–IV; ambulacra II–III (26–32), IV (34–36). Tarsus I (107–118) less than twice as long as tibia (71–78) or genu (90–96). Tarsi II–III (90–101) and IV (131–139) about as long as combined length of tibia and genu; tibiae II–III (42–49) and tibia IV (65–68) equal or subequal to genua. Setation of leg segments I–IV, respectively: coxae 2-2-2-1, posterior seta on coxae I–II swollen basally, with fine, acuminate tip (Fig. 8), as in seta *pc*; trochanters 6-5-5-5, dorsal seta on trochanter I spine-like, sparsely barbed; femora 12-11-6-6, dorsal setae *ad1*, *pd1*, *pd2* on femur I spur-like, *pd2* on femur I spine-like (Fig. 8); genua 13-11-9-9, dorsal setae *pd2*, *pd3* on genu I spur-like, *pd1* slightly thickened (Fig. 8); tibiae 13-10-8-10, seta *pl2* absent on tibia III (Fig. 9); tarsi II–IV 16-16-16, plus two short apical seta-like processes. Most dorsal setae and a few lateral setae on femora, genua, and tibiae II–IV, and a few dorsal setae on tarsi II–IV sparsely barbed (Fig. 9), others simple (acicular) or spine-like as noted above. Tarsus I with 4 long (75–83), slender setae subapically.

Description of free-living female (granular morph). Soft cuticle plicate and covered with small tubercles except in regions surrounding epigynial and sternal shields. Anterior dorsal shield (315–335 long × 395–410 wide) and posterior dorsal shield (290–310 long × 330–345 wide) both with granular colliculate ornamentation throughout (Fig. 10). Anterior shield with 20–22 pairs (*j1-6*, *z1-6*, *s1-6*, *x*, *r4*, *+/- r2* and *r3*) of mostly short (22–27 long × 5–6 wide), bushy setae, *j1* (28–34 long × 10–13 wide) inflated, *z1* (12–16 × 2 wide) shortest and slender; *r5-6* (+/- *r2-3*) in soft cuticle; posterior shield with 14 pairs of mostly short (24–28), bushy setae (*J1-5*, *Z1-5*, *S2-5*); *Z5* longest (37–39); *S1* in soft cuticle between shields. Marginal setae *R1-8* short (20–22), bushy, in soft lateral cuticle. Peritreme extending to near seta *z1*, peritrematal shield lineate tuberculate laterally, smoothly lineate in exopodal shield laterad coxae III-IV and parapodal region, joined to anterior dorsal shield between setae *s1* and *z1*. Dorsal shields with 22 pairs of discernible pore-like structures (9 on anterior shield, 13 on posterior shield), of which 7 appear secretory (gland pores, *gd*, Fig. 10) and 15 non-secretory (lyrifissures). Lyrifissure *ids6* occurs in soft cuticle mesiad seta *S1*.

Tritosternum as in phoretic morph. Sternal shield (Fig. 11) (median length 120–135, narrowest width between legs II 96–98) slightly notched at level of lyrifissure *stp2*, lineate laterally, with two faint median lines; *st1* (28–36) in soft cuticle anterior to shield; *st2-3* (29–30) and lyrifissures *stp1-3* on shield; small endopodal plate posteriad coxa II separated from sternal shield by soft cuticle. Setae *st4* (20–23) in soft cuticle. Epigynial shield (130 long) (Fig. 11) with membranous anterior margin, expanded posteriorly (77 wide) with somewhat truncated margin, bearing setae *st5* on margin and a few faint lines. Metapodal plates (22–25 long × 13–15 wide) irregularly oval. Ventri-anal shield (165–172 long × 193–200 wide) reticulate-tuberculate, bearing 7 simple setae, *JV2-3* (*+JV4* present on one side of one specimen) and circum-anal setae, post-anal seta (21–26) less than twice as long as para-anal setae (13–14); cribrum in terminal tuft. Soft cuticle with ventral setae *JV1*, *ZV1-ZV2* simple, and *JV4-5*, *ZV3-5* and 4–5 pairs of submarginal setae (*UR*'s) thick and barbed.

Gnathosoma (Figs 12–13) as in phoretic morph except the following: palpcoxal seta *pc* simple and *pd1* of palpfemur lightly barbed; palps (150–170), subcapitulum (127) and movable digit (48–50) slightly longer; dorsal seta of chelicera broad and flattened.

Legs (Figs 14–15) as in phoretic morph, except the following: legs I (561–563), II (405–411) and III (380–381) slightly longer, leg IV of similar length (470–498); setae on coxae all simple; no spine- or spur-like setae on trochanter, femora and genua, but dorsal seta on trochanter I and *pd2* on femur I short, barbed and somewhat spine-like (Fig. 14); leg setae, including of leg I, more often and more densely barbed than in phoretic morph: some dorsal setae on femora I–IV, all dorsal setae on genua and tibiae I-IV, nearly all lateral setae on genua and tibiae II–IV, and a few dorsal setae on tarsi II-IV barbed. Ambulacrum I (7–10) on short stalk (7–9), but shorter than in phoretic morph. The 4 subapical setae on tarsus I longer (103–130) than in phoretic morph.



FIGURES 16–19. *Antennoseius perseus* **n. sp.**, male. 16, Dorsal shield; 17, Ventral shields; 18, Tectum; 19, Right chelicera, lateral view.

Male. Podonotal and opisthonotal shields (Fig. 16) fused laterad *z-Z* series, sometimes also irregularly fused medially (therefore with 1–3 central narrow band(s) of soft plicate cuticle, as in Fig. 16), combined length 499–520 × 231–345 wide, similar in ornamentation to free-living female; more expanded than in female, bearing all 47 pairs of mostly short (19–24 long × 4–5 wide) bushy dorsal setae (*j1-6*, *z1-6*, *s1-6*, *x*, *r2-r6*; *J1-5*, *Z1-5*, *S1-5*, *R1-8*); *j1* (22–26 × 10–12) inflated; *s1-s2*, marginal setae (*r-R*) and additional seta *x* slightly shorter (17–22); *z1* shorter and slender (10–13 × 2); *Z5* longest (30–35). Peritrematal shield joined to dorsal shield near setae *r2* or *r3*. Sterno-genital shield (Fig. 17) smooth medially, lineate laterally, bearing 5 pairs of tapered, simple setae (20–29), anterior pairs (*st1-3*) longest (25–29). Ventri-anal shield (Fig. 17) broad, almost abutting peritrematal shield and dorsal shield; smoothly lineate anteriorly, reticulate and densely covered with small rounded tubercles over most of surface, bearing 7 pairs of ventral setae (*JV1-4*, *ZV1-3*) (16–20), mostly simple but *ZV3*, *JV4* bushy; *JV5* (22–27) bushy, in soft cuticle; no submarginal setae; soft cuticle covered with small tubercles as in free-living female.

Gnathosoma (Figs 18–19) as in female free-living morph except slightly shorter setae, palps (152–158), corniculi (38) and subcapitulum (97); chelicera (Fig. 19) with fixed digit (32–33) with 7–8 denticles; movable digit (37–41) with one tooth and spermatodactyl (from articulation with digit: 40–45) slightly longer than digit, curves ventrad about mid point, then straightens in last quarter to tapered, rounded tip.

Legs as free-living female, except the following: leg segments approximately 10% shorter than free-living female; some setae on trochanters and femora can be more or less barbed than in free-living female; ambulacrum I (12–16; stalk 8–12) longer than in free-living female, other ambulacra of similar length.

Etymology. The specific name *perseus* is a noun in apposition, derived from the Greek mythological demigod Perseus, who rode the winged horse Pegasus and decapitated the Gorgon Medusa.

Remarks. Among *Antennoseius* species with an ambulacrum on leg I, adult females of the smooth (phoretic) morph of *A. perseus* resemble those of *A. bregetovae* Chelebiev and *A. ranikhetensis* Bhattacharyya in having no granular tubercles on shields and soft cuticle, some setae in the *j* and *z* series short and spur-like, 1 or 2 spur-like setae (with hair-like processes in *A. perseus* and *A. bregetovae*) on coxae I and II, one or more dorsal spines on trochanter, femur and genu I, and an anal shield bearing only 3 circum-anal setae. It differs from *A. bregetovae* by having 5 spur-like setae on the anterior dorsal shield instead of 4 (in the description of *A. bregetovae*, it is not clear whether *j2-j5* are spur-like, or rather *j2-3*, *j5* and *z3*; Chelebiev 1984); only 1 spur-like seta on coxa I instead of 2; 3 spine- or spur-like dorsal setae on femur I instead of apparently only 1 in *A. bregetovae*; 2 spur-like dorsal setae on genu I instead of 1, setae *pc* of the subcapitulum spur-like with hair-like process, and setae *st3* on soft integument rather than captured by the sternal shield. It differs from *A. ranikhetensis* by having setae *j2-j5* and *z2* spur-like instead of *j2-3*, *z2-4* and *s4*, different spine-like setae on femur and genu I, and a sternal shield more eroded on the posterolateral corners and with a posterior median process.

The spur-like setae in the *j* and/or *z* series make the phoretic morph of *A. perseus* also similar to a few *Antennoseius* s. str. species, such as *A. pannonicus* Willmann and *A. imbricatus* Ishikawa. However, *A. perseus* differs from those in part by having an ambulacrum on leg I and a different set of spur-like setae on the anterior dorsal shield.

Adult females of the granular (presumably free-living) morph of *A. perseus* resemble those of *A. belajevi* Bregetova and *A. janus* Walter & Lindquist (granular morph) in having granular tubercles all over (as well as forming the reticulate patterning itself) the dorsal and opisthogastric shielding and on the soft integument, and setae on dorsal shields all barbed and almost uniform in appearance (*j1* is thicker and longer, as well as *Z5*, at least in *A. perseus*). They also resemble those of *A. belajevi* in having 2 pairs of ventral setae in addition to the 3 circum-anal setae on the ventri-anal shield, but differ in having truncated posterior dorsal shield and epigynial shield, 1 more seta in the area occupied by *s3-s4* and *r2-r4* on the anterior dorsal shield, *S1* off posterior dorsal shield, and no unpaired seta on dorsal shields (the drawing of *A. belajevi* shows an unpaired seta between *j2* setae). They differ from granular females of *A. janus* mostly in having 2 pairs of ventral setae in

addition to the 3 circum-anal setae on the ventri-anal shield, 8 setae on tibia III instead of 9, *S1* and *R1* setae off the posterior dorsal shield, and setae *j1* and *Z5* more inflated.

Phoretic (smooth) females were mostly found on the ventral surface of the beetles' elytra, while fewer than 5% of females were under or between the two folded wings. Typically 2–3 individuals were found on the same beetle, and were spread evenly under the elytra, though when more than 10 females were on the same beetle they were packed in rows of three across with individuals of the next row slightly overlapping. One of us (DEW) has recently seen a granular morph female collected from soil in a more northern site in Alberta, supporting our presumption that this morph is non-phoretic. This species is a voracious nematophage.

Antennoseius (*Vitzthumia*) *pyrophilus* sp. nov.

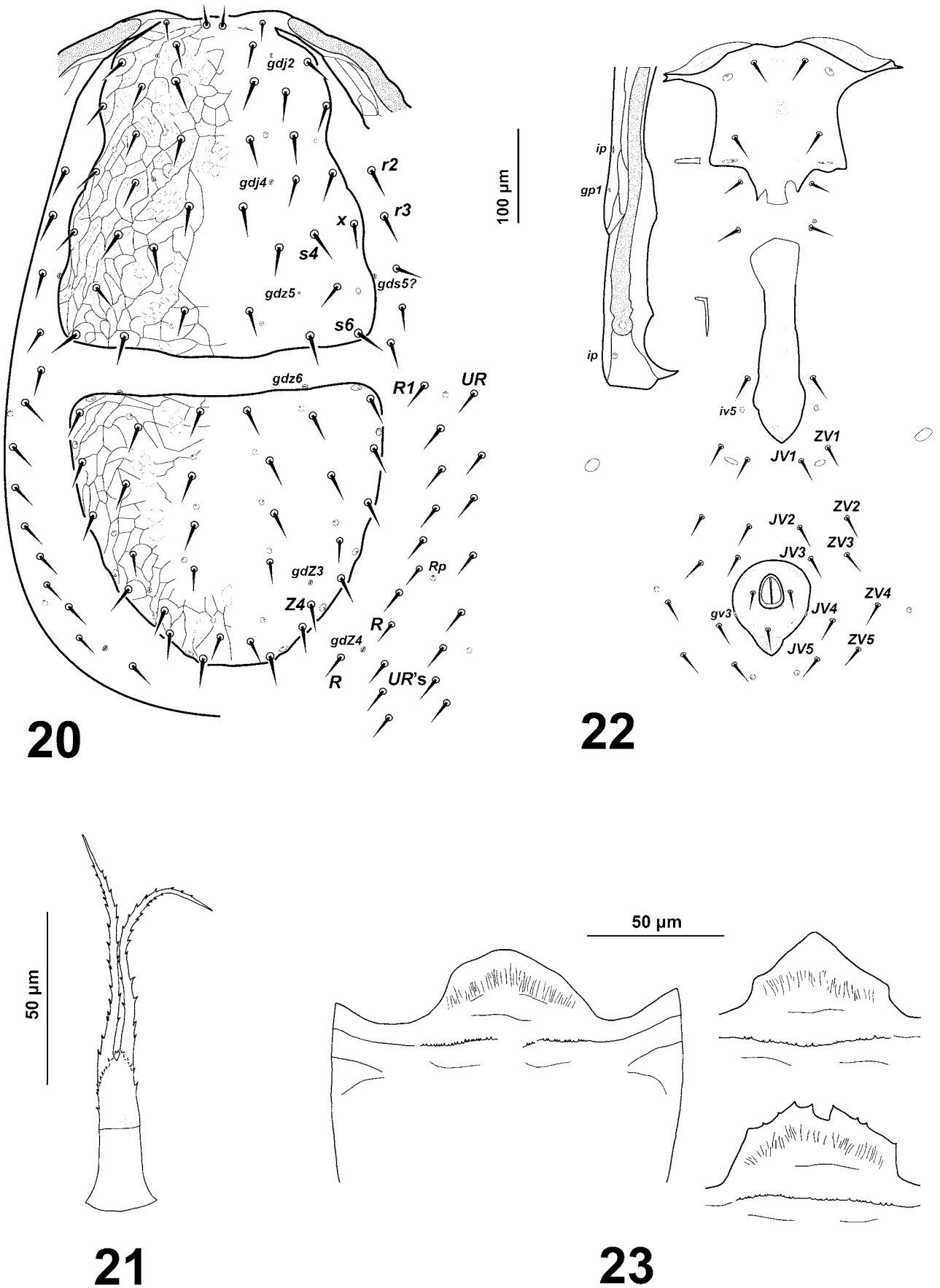
(Figs 20–28)

Material examined. ALBERTA: *Holotype*. Female, under elytra of *Sericoda bembidioides* Kirby, ex pitfall trap in burned boreal forest near, Chisolm, Alberta (54°56'N, 114°7'W), 8 August 2002. *Paratypes*: 9 female from under elytra of *Sericoda quadripunctata* (DeGeer) and *S. bembidioides* ex pitfall traps, same location as holotype, July–September 2002; 1 female each under elytra of *Calathus ingratus* Dejean and *Agonum placidum* (Say), same collection data except 22 July 2002.

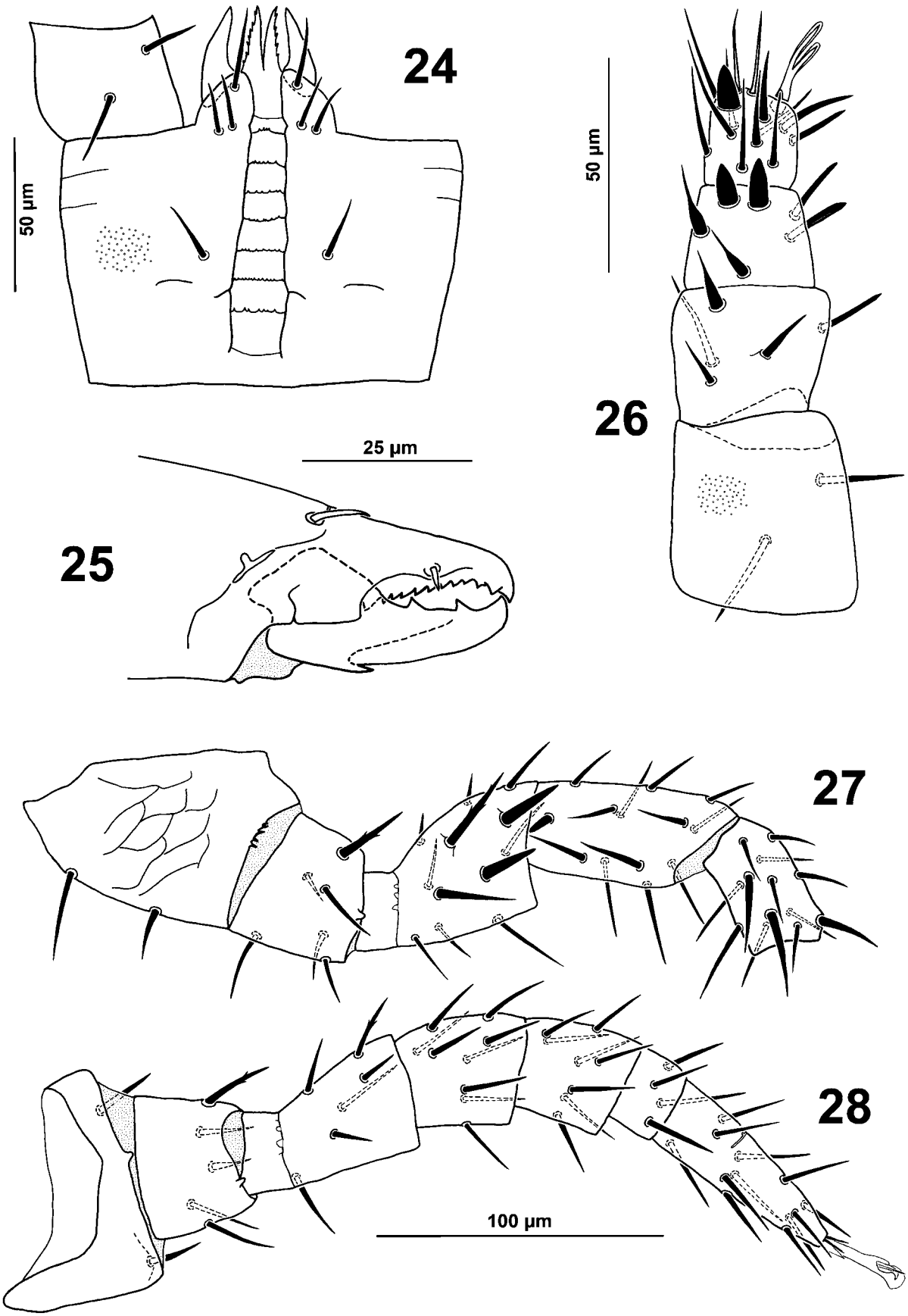
Diagnosis. *Antennoseius* species with adult females of smooth (phoretic) morph lacking granular tubercles on shields and soft cuticle; dorsal and peritrematal shields with reticulate pattern and with fine, longitudinal or oblique lineae on most of the anterior dorsal shield and the margins of the posterior dorsal shield; ventral shields weakly lineate. Podonotal shield with 19 pairs of setae, including an additional pair *x*, laterad *s4*; opisthonotal shield with 15 pairs of setae. All idiosomal setae simple, of similar length. Sternal shield bearing *st1-2* and *stp1-2*; postero-lateral margins eroded leaving *st3* and *stp3* in soft cuticle; *st4* in soft cuticle. Tectum with anterior margin mostly smooth. Hypostomal setae *h1-3* and *pc* simple; palpgenu and palptibia with two and one very stout, spur-like setae dorso-distally, respectively; *al* of palpfemur, *al1-2* of palpgenu, and *al1-2* of palptibia sword-shaped. Leg I with ambulacrum; seta *pl2* absent on tibia III. Most leg setae simple, with few dorsal setae on trochanter and femora sparsely barbed; dorsal seta on trochanter I, *pd1-2* and *pl1-2* of femur I, *pd3* of genu I, *ad1* and *pl1* on tibia I thickened, spur-like or spine-like. Tarsus I without conspicuously elongate subapical setae.

Description of phoretic female. Soft cuticle evenly plicate. Anterior dorsal shield (245–260 long × 212–232 wide) and posterior dorsal shield (193–207 long × 209–231 wide) both with reticulate ornamentation throughout (Fig. 20). Most of the anterior dorsal shield and edges of the posterior dorsal shield covered with lineae, giving a rugose appearance. Anterior dorsal shield with 19 pairs (*j1-6*, *z1-6*, *s1-6*, *x*) of mostly short (20–25), simple setae, *j1* (13–16) and *z1* (15–18) shortest. Posterior dorsal shield with 15 pairs of mostly short (18–23), acicular setae (*J1-5*, *Z1-5*, *S1-5*); *Z5* (20–27) longest. Marginal setae *r2-6* (20–24) and *R* series (15–20) short, simple, in soft lateral cuticle; between 8 to 12 *R* setae. Peritreme approaching seta *z1*, peritrematal shield narrow, lineate, joined to anterior dorsal shield near seta *z1*. Dorsal shields with 22 pairs of discernible pore-like structures (9 on anterior shield, 13 on posterior shield), of which 6 appear secretory (gland pores, *gd*, Fig. 20) and 16 non-secretory (lyrifissures); gland pore *gdZ4* appears to have migrated in soft cuticle laterad posterior shield. Gland pores are slit-shaped and lyrifissures are generally ovoid except mostly those laterad setae *j1*.

Tritosternum (Fig. 21) base (44–46 long × 11–13 wide for most length, 19–21 wide at proximal end) with 14–17 denticles fringing base of laciniae (65–69). Sternal shield (Fig. 22) attached to lineate pre-sternal lobes, with weak lineate pattern, bearing simple setae *st1-2* (19–25) and lyrifissures *stp1-2*; shield notched or eroded postero-laterally, median process irregularly produced, dissipating posteriorly; small endopodal plate posteriad coxa II separated from sternal shield by soft cuticle. Setae *st3-4* (21–24) and lyrifissure *stp3* in soft cuticle. Setae *st1-3* with a lightly swollen base and acuminate tip. Epigynial shield (Fig. 22) narrowly lanceolate,



FIGURES 20–23. *Antennoseius pyrophilus* **n. sp.**, female, phoretic form. 20, Dorsal shields; 21, Tritosternum; 22, Ventral shields; 23, Tectum and its variants.



FIGURES 24–28. *Antennoseius pyrophilus* **n. sp.**, female, phoretic form. 24, Subcapitulum; 25, Right chelicera, lateral view; 26, Left palp (tarsus not shown except palp apotele), dorsal view; 27, Right leg I (except tarsus), postero-dorsal view; 28, Right leg III, postero-dorsal view.

125–139 long × 37–41 wide, with lineate ornamentation; setae *st5* (23–24) in soft cuticle. Metapodal plates oval (diameter 13–20). Anal shield suboval (73–77 long × 57–62 wide), faintly lineate with 3 simple circumanal setae, para-anal setae (17–20) almost as long as post-anal seta (19–24). Soft cuticle with simple ventral setae *JV1-5*, *ZV1-5*, and 10–16 pairs of submarginal setae (*UR* series) (Figs 20, 22).

Gnathosomal tectum (Fig. 23) with mostly smooth margin, dorsal surface with a transverse line of denticles; subcapitulum (Fig. 24) with 7 rows of 4–13 deutosternal denticles; corniculi (30–34) horn-like; hypostomal setae *h1-3* and palpcoxal seta *pc* simple (17–25). Fixed digit (28–30, from dorsal lyrifissure) of chelicera (Fig. 25) with short, rounded dorsal seta (8), row of 10–11 serrations, setiform pilus dentilis, and subapical offset large tooth; movable digit (38–39) bidentate, paraxial ridge leading to a ventral projection typical for the genus. Palps (128–134) (Fig. 26) about as long as subcapitulum (from base to tip of corniculi: 124–130); palpal setation normal for genus, but palpgenu and palptibia with respectively two and one very stout, spur-like setae dorso-distally; anterolateral setae of femur, genu and tibia ensiform; *pd1* of palpfemur, *ad2* and *pd2* of palpgenu and many dorsal setae of palptibia swollen basally with a fine, acuminate tip; palp apotele 2-tined.

Excluding ambulacra, lengths of leg I 402–424, leg II 294–312, leg III 286–307, leg IV 361–388 (Figs 27–28). Tarsus I with ambulacrum (21–26, excluding stalk) on short stalk (11–12), claw subequal in size to claws of tarsi II–IV. Ambulacra II–III 28–32, ambulacrum IV 33–38. Tarsi II–III (85–93) and IV (113–119) about as long as combined length of tibia and genu; tarsus I (106–112) slightly shorter than combined length of tibia (44–54) and genu (70–74); tibiae II–III (38–44) and IV (56–62) equal or subequal to genua. Setation of leg segments I–IV, respectively: coxae 2-2-2-1, all setae normal or slightly swollen basally; trochanters 6-5-5-5, dorsal seta of trochanter I thickened, spine-like, and sparsely barbed (Fig. 27); dorsal seta on trochanter II–IV also sparsely barbed, and one *pl* on trochanters III–IV slightly swollen basally; femora 12-11-6-6, femur I with *pd1* and *pl1* spur-like (thicker), *pd2* and *pl2* spine-like and *pd2* with a few barbs (Fig. 27), most dorsal setae on femora II–IV sparsely barbed; genua 13-11-9-9, seta *pd3* of genu I short, blunt and spur-like; tibiae 13-10-8-10, seta *pl2* absent on tibia III (Fig. 28), seta *ad1* and *pl1* on tibia I thickened, somewhat spine-like; tarsi II–IV 16-16-16, plus two short apical seta-like processes. Subapical setae (30–41) on tarsus I not conspicuously longer than other setae on tarsus.

Etymology. The specific name *pyrophilus* was chosen for the mite's association with carabids of the genus *Sericoda*, which thrive in recently burned forests.

Remarks. Females of *A. pyrophilus* can be distinguished from any other species in the genus by the following combination of characters: the very strong spur-like dorsal setae on palpgenu and palptibia (Fig. 26), the fine, (almost) longitudinal ridges on the dorsal shields, the almost completely smooth margin of the tectum, the spur-like or spine-like setae on trochanter, femur, genu and tibia of leg I, and the absence of conspicuously elongate subapical setae on tarsus I.

As for *A. perseus*, phoretic females of *A. pyrophilus* were mostly found on the ventral surface of the beetles' elytra.

Discussion

The systematics of *Antennoseius* requires revision for several reasons: (1) the subgenus *Vitzthumia* appears to be based on plesiomorphies; (2) an obscure but older generic name, *Anystipalpus* Berlese, 1911 (long misplaced in the Laelapidae), may represent *Antennoseius* (see Lindquist & Walter 1989); and (3) the apparent presence of two adult female morphs in some (and possibly many) species. As with other species of *Vitzthumia*, the two species described here possess an ambulacrum on tarsus I, but contrary to other species in *Vitzthumia* (e.g. *A. janus*), they lack *pl2* on tibia III, as do the species of *Antennoseius* s. str. that we examined. Therefore, the presence of *pl2*, an apparent plesiomorphy, is an inconsistent character in *Vitzthumia*, and the genus rests weakly on the ambulacrum of leg I.

Sklyar (1995) hypothesized that the shorter, robust, spur-like or peg-like setae in the *j* and *z* series (as *j2-j5* and *z2* in the *A. perseus* phoretomorph) have evolved to support the pressure of the carabid's elytra, beneath which the mites lodge themselves before dispersing on the beetle. Sklyar also suggested a transformation series from species having only three pairs of stout setae in the *j* series, to species having 4–5 pairs both in the *j* and *z* series. Sklyar used data on nine species, scattered across the spectrum of the transformation series, including seven *Antennoseius* (*A.*) species (*bytinskii* Costa, *imbricatus* Ishikawa, *masoviae* Sellnick, *pannonicus* Willmann, *sabulicola* Bregetova, *shcherbakae* Balan, *ukrainicus* Sklyar), as well as *Antennoseius* (*V.*) *bregetovae* (it is unclear whether the ninth species, *A. vysotskajae* Sklyar, has an ambulacrum on leg I or not). At least four of these species (*A. bytinskii*, *masoviae*, *ukrainicus*, *vysotskajae*) are known associates of carabids. Two more species of *Antennoseius* s. str. collected from carabids (*A. livshitsi* Eidelberg, 1989, *A. maltzevi* Eidelberg, 1994) have spur-like setae on the podonotal shield, as well as on coxae I–II. Other phoretic *Antennoseius* s. str. (*A. nataliae* Eidelberg, 1990, *A. matsjuki* Eidelberg, 2001) don't have such setae on the podonotal shield, but do have some on coxae I–II. Among *Antennoseius* (*Vitzthumia*) species, five species, namely *A. deyi*, *A. orientalis*, *A. garurensis*, *A. perseus* (phoretic morph), and *A. ranikhetensis*, all except *A. perseus* collected in soil or under moss, also have such setae in the *j*, *z*, and/or *s* series, and usually also on coxae I–II. If these species are indeed closely related (and less so to the species with no such spur-like setae, even in the phoretomorph, e.g. *A. janus*), then the division of *Antennoseius* into the two current subgenera based on the presence or absence of ambulacra I is artificial. However, if these spur-like setae on the podonotum, and on the coxae or other leg segments (e.g. femur and genu I of *A. perseus*; ventral surfaces of coxa I to genu I in *A. ukrainicus*), do help secure the mite to subelytral surfaces, then convergence in form among the setae contacting these surfaces would not be surprising. For instance, spur-like setae that may have a similar function occur on coxae (especially I–II), on other segments of legs I–II, on the subcapitulum, and/or on dorsal or ventral shields of phoretic or parasitic stages of other Mesostigmata, such as *Proctolaelaps nauphoetae* (Womersley) (Melicharidae), presumably parasitic on cockroaches, *Saintdidieria* spp. (Halolaelapidae), phoretic on beetles, and *Dyscinetonyssus*, *Dinogamasus*, and *Scolopendracarus* spp. (Laelapidae), parasitic or symbiontic on scarabs, bees and millipedes, respectively (Evans 1955; Ryke 1961; Moss & Funk 1965; Lundqvist 1998). Another attribute shared by some species of both *Antennoseius* s. str. and *Antennoseius* (*V.*) that may be of phylogenetic value is longitudinal or oblique lineae in the cells of the dorsal shield. They occur in *A.* (*V.*) *pyrophilus* (this paper), *A.* (*A.*) *calathi* Fain *et al.* (1995), *A.* (*A.*) *rugosus* Mašán (1997) as well as in two undescribed species of *Antennoseius* s. str. collected from carabid beetles in Canada.

As for *A. janus*, phoretic and free-living morphs of *A. perseus* are strikingly different and, without prior knowledge of such dimorphism, they would normally be classified as two distinct species. They differ mostly in the shield ornamentation, the shape of setae, and the extent and shape of idiosomal shields, which capture a different number of setae. In addition to having their soft integument and dorsal, peritrematal and ventri-anal/anal shields granular, the free-living female morphs of *A. perseus* and *A. janus* have densely barbed dorsal setae, a subtrapezoidal opisthonotal shield that is slightly concave posteriorly, and a sternal shield usually notched at the level of lyrifissures *stp2*. Except for species with modified spur-like setae in *j*, *z* or *s* series, which may prove to be phoretic as implied by Sklyar's hypothesis, most other putatively free-living morphs of *Antennoseius* (*V.*) species (*A. belajevi*, *granulatus*, *indicus*, *koroljevae*, *oudemansi*) also have granular shields (although only the anal shield is granular in *A. spinosus*), densely barbed dorsal setae (not in *A. spinosus*), and tend to have a subtrapezoidal opisthonotal shield (not *A. belajevi*; unknown in *A. spinosus*). Some of them also have a sternal shield notched at the level of lyrifissures *stp2* (*A. belajevi*, *A. granulatus*), setae *st1* off sternal shield (*A. belajevi*, *indicus*, *perseus*) or on a weakly sclerotized portion of shield (*A. janus*), and a ventri-anal shield that captures 1–2 pairs of ventral setae (*A. belajevi*, *indicus*, *perseus*). In contrast, the phoretomorph of *A. perseus* and the putative phoretomorph of *A. janus* have smooth shields and integument, smooth or sparsely barbed dorsal setae, a posteriorly rounded opisthonotal shield, and a sternal shield so deeply eroded or notched postero-laterally that it does not capture setae *st3*. All other *Vitzthumia* species collected on carabids

(*A. multisetus*, *ovaliscutalis*, *pyrophilus*) also have non-granular shields with smooth setae (sparsely barbed in *A. ovaliscutalis*), opisthonotal shield posteriorly rounded (tapered in *A. multisetus*), and setae *st3* on soft cuticle. All other *Antennoseius* (*V.*) species with dorsal spur-like setae (*A. bregetovae*, *deyi*, *garurensis*, *orientalis*, *ranikhetensis*), as well as *A. hyperboreus*, which was collected from a mice, have similar characters except that *st3* is usually on the sternal shield (on soft cuticle in *A. ranikhetensis*). Based on all of the described and undescribed species of *Antennoseius* s. str. that we examined, we can say that these suites of characters are generally partitioned into free-living or phoretic forms.

Species in which two morphs have been discovered (*A. janus* and *A. perseus*) are characterized by an ambulacrum on tarsus I, and that is true in both morphs. Whether there is such phase polymorphism within species lacking an ambulacrum on leg I (*Antennoseius* s. str.) is unknown. However, we believe it is likely because some species of the subgenus *Vitzthumia*, including one with two confirmed morphs (*A. perseus*), share a morphological attribute that may be of phylogenetic importance—the stout, spur-like setae on the podonotal shield—with several species of *Antennoseius* s. str. Note that it is of course possible that two separately described species actually represent the two morphs of the same species. This should be suspected when any two apparently distinct species, especially when one is phoretic and one free-living, are collected from the same locality. The question of whether two morphs exist in other species might be elucidated by rearing species under varying crowding conditions. The phoretic morph of *A. janus* was discovered in high density cultures (=11 individuals per 3 cm diameter vial) (Lindquist & Walter 1989) and the free-living morph of *A. perseus* was found simply by rearing its phoretic morph (this paper).

Although males are known for only a few *Antennoseius* species, the partial fusion of the podonotal and opisthonotal shields observed in males of *A. perseus* seems to be rare in the genus. We are not aware of any other similar cases of sexual dimorphism in the degree of fusion of the dorsal shields in the Ascidae. In the parasitid subfamily Parasitinae, males have similar fusion patterns to *A. perseus*, with anterior and posterior dorsal shields narrowly fused laterad *s-S* series (as well as to ventri-anal or holoventral shield), whereas females usually have completely divided shields (Hyatt 1980). However, this fusion in parasitine males seems partly due to the expansion of both anterior and posterior shields into lateral and ventral regions. Somewhat conversely, in the parasitid subfamily Pergamasinae, the males of some species have separate (though generally abutting) podonotal and opisthonotal shields (the latter fused to the ventri-anal shield, as for all parasitid males) whereas the females have a (free) holodorsal shield (Bhattacharyya 1963). The same situation occurs in some species of Ologamasidae (e.g. *Geogamasus skoshi* Lee, *Gamasellus discutatus* Lee) (Lee 1966, 1970).

Based on about 60 *Antennoseius* species described to date, 17, including the two species described here, can be considered in the subgenus *Vitzthumia* by the presence of an ambulacrum on leg I. However, it is unclear whether *Antennoseius garurensis* and *Antennoseius indicus* have a full ambulacrum with claws; *Antennoseius garurensis* has "leg I with pulvillus" (Bhattacharyya 1994) and the *A. indicus* holotype has a leg I broken off, and "the other is with a pedicel only" (Bhattacharyya 1972).

In the following key, species names followed by an asterisk (*) are represented by individuals that were collected on carabid beetles. The symbol ‡ indicates that individuals were taken from rodent nests (*A. bregetovae*, *A. koroljevae*) or from a rodent itself (*A. hyperboreus*, on mice caught in pitfall traps). A cross (†) indicates that the morph was obtained only in rearing culture. The absence of a symbol indicates that individuals were collected free-living from soil, litter or moss.

Key to adult females of *Antennoseius* species with ambulacrum on leg I

1. Anterior dorsal shield with 1 or more pairs of setae among *j2-j5* or *z2-z4* strongly thickened, short, smooth and spur-like (some may also have a hair-like tip); one or more setae on coxae I–II similarly shaped 2

- Most setae of anterior dorsal shield similar in length and shape, none spur-like; coxal setae not spur-like 7

2. Anterior dorsal shield with 1 or 2 pairs of spur-like setae (*j3* and/or *j4*) 3
- Anterior dorsal shield with 4 or more pairs of spur-like setae 5
3. Anterior dorsal shield with 2 pairs of spur-like setae (*j3* and *j4*); posterior dorsal shield with 5 pairs of barbed setae; India ..... *deyi* Bhattacharyya
- Anterior dorsal shield with 1 pair of spur-like setae (*j3*); remaining setae simple, not barbed 4
4. Anterior dorsal shield with 19 pairs of setae (*r2* off shield); peritreme extending to level of *z1*; idiosoma 700–750 µm; India ..... *orientalis* Bhattacharyya, Sanyal & Bhattacharyya
- Anterior dorsal shield with 20 pairs of setae; peritreme shorter, extending only to level of coxa I; idiosoma about 600 µm; India ..... *garurensis* Bhattacharyya
5. Anterior dorsal shield with 4 pairs of spur-like setae; coxa I with 2 spur-like setae with hair-like tip; femur I with only 1 spine-like seta; seta *st3* on sternal shield; Kazakhstan ..... *bregetovae* Chelebiev ‡
- Anterior dorsal shield with 5 or 6 pairs of spur-like setae; coxa I with only 1 spur-like setae (with or without hair-like tip); femur I with 3 or 4 spur or spine-like setae; seta *st3* on soft cuticle 6
6. Anterior dorsal shield with 5 pairs of spur-like setae (*j2-j5, z2*); seta *pc* of subcapitulum spur-like with hair-like tip; genu I with 2 spur-like setae; posterolateral corners of sternal shield deeply eroded, producing a broad median process posteriorly; Canada (Alberta) ..... *perseus* **n. sp.** (smooth morph)*
- Anterior dorsal shield with 6 pairs of spur-like setae (*j2-j3, z2-z4, s4*); seta *pc* of subcapitulum simple; genu I with 3 spur-like setae; sternal shield not as deeply eroded, without median process; India .... *ranikhetensis* Bhattacharyya
7. Dorsal shield setation strongly neotrichous, anterior dorsal shield with about 31 pairs of short, smooth setae and several unpaired setae; posterior dorsal shield with 20 pairs of setae; Moldavia, Ukraine (Crimea), Russia (Novosibirsk Province, Krasnodar Territory) ..... *multisetus* Eidelberg *
- Dorsal shields at most weakly neotrichous, anterior dorsal shield typically with 19–26 pairs of setae, posterior dorsal shield with 12–17 pairs of setae 8
8. Dorsal and opisthogastric shielding and surrounding soft integument covered with small granular tubercles; most dorsal setae distinctly barbed; generally nonphoretic forms 9
- Dorsal and opisthogastric shielding generally smoothly reticulate and surrounding soft integument smoothly striate, lacking granular tubercles; most dorsal setae, excepting *j1*, smooth or nearly so (may be slightly pilose apically); commonly phoretic forms 15
9. Ventri-anal shield with 3 circum-anal setae and 1 or 2 pairs of ventral setae; *st1* off sternal shield, on soft cuticle in between sternal shield and pre-sternal plates 10
- Ventri-anal shield with 3 circum-anal setae only (rarely, an unpaired ventral seta asymmetrically on shield margin); *st1* on sternal shield 12
10. Ventri-anal shield with 3 circum-anal setae and 1 pair of ventral setae; fixed digit of chelicerae unidentate; India ..... *indicus* Bhattacharyya
- Ventri-anal shield with 3 circum-anal setae and 2 pairs of ventral setae; fixed digit of chelicerae typically serrated (unknown for *A. belajevi*) 11
11. Posterolateral margins of posterior dorsal shield gently rounded, giving nearly semicircular outline; epigynial shield rounded posteriorly; anterior dorsal shield with 1 unpaired median seta; Russia (Magadan province) ..... *belajevi* Bregetova
- Posterolateral margins of posterior dorsal shield somewhat truncated, giving a somewhat (inverse) trapezoidal outline; epigynial shield truncated posteriorly; dorsal shields with no unpaired median seta; Canada (Alberta) ..... *perseus* **n. sp.** (granular morph)
12. Dorsal shields densely granulate-tuberculate, lacking reticulate patterning; Central Europe .... *granulatus* (Willmann)

- Dorsal shields with reticulate patterning of tubercles superimposed on granulate-tuberculate surface ... 13

13. Idiosoma 800–900 µm; posterior dorsal shield with 12–14 pairs of setae, including only 3 or 4 pairs of *S* setae; northern Europe ..... *oudemansi* (Thor)
- Idiosoma 500–600 µm; posterior dorsal shield with 14–17 pairs of setae, including 5 or 6 pairs of *S* setae 14

14. Anterior dorsal shield with about 17 pairs of setae, apparently lacking 1 or 2 setae in area normally occupied by *z2-z4* on either side, and with only *r4* of marginal series on edge of shield; pre-sternal platelets apparently absent, and lateral margins of sternal shield apparently entire between sternal setae 2 and 3; Kazakhstan ..... *koroljevae* Chelebiev ‡
- Anterior dorsal shield with 20–25 pairs of setae, with *z* series complete, with 1 or 2 extra setae usually present on either side in area occupied by *s3-s6*, and with *r2* and often *r4* on edge of shield; pre-sternal platelets present but weakly defined, and lateral margins of sternal shield usually notched at level of lyrifissures 2; USA (Colorado) ..... *janus* Lindquist & Walter (granular morph)

15. Vertical seta *j1* sparsely to densely barbed and larger or thicker than other setae on anterior dorsal shield 16
- Vertical seta *j1* similar to others, not noticeably enlarged or barbed 17

16. Vertical seta *j1* about 1.5× longer than other setae on dorsal shields; *Z5* thickened and barbed; other setae slightly pilose apically; Moldavia, Ukraine (Crimea), Russia (Rostov province), Kazakhstan ....*ovaliscutalis* Eidelberg *
- Vertical seta *j1* not longer than other setae on dorsal shields; other setae including *Z5* narrowly bicarinate; USA (Colorado) ..... *janus* Lindquist & Walter (smooth morph)†

17. Palptibia and palpgenu with respectively 1 and 2 strongly thickened, short, smooth, spur-like setae dorsodistally; cells in most of anterior shield packed with longitudinal or oblique lineae; anterior margin of tectum mostly smooth, with no or very few denticles; seta *st3* on soft cuticle; sternal shield with a broad postero-median process; idiosoma 425–500 µm; Canada (Alberta).....*pyrophilus* **n. sp.** *
- Palptibia and palpgenu with normal setae dorso-distally; dorsal shields without longitudinal lineae; anterior margin of tectum with numerous denticles; seta *st3* on sternal shield, although sometimes on the edge; sternal shield without broad postero-median process; idiosoma 600–675 µm.....18

18. Sternal shield with anterior margin without a notch; four subapical setae on tarsus I only slightly longer than other setae; anal shield finely tuberculate; Central Europe ..... *spinosus* (Willmann)
- Sternal shield strongly notched anteriorly; four subapical setae 2/3 length of tarsus I; anal shield probably smooth (not mentioned in description); Russia (Taymyr region) ..... *hyperboreus* Nikolskij ‡

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