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Steneotarsonemus ananas (Acari: Tarsonemidae): a complementary description from Australian pineapples and a new pest on *Neoregelia* spp. (Bromeliaceae) in Costa Rica

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Original research

ABSTRACT

The pineapple tarsonemid mite *Steneotarsonemus ananas* (Tryon), 1898 is associated with pineapple around the world, including Costa Rica. Here, we report its association with *Neoregelia* sp. (Bromeliaceae) for the first time. These mites damaged the plantlets considerably, affecting the esthetic quality of the product and thus causing economic losses to the local growers. This discovery prompted us to redescribe the adult females and males from the type host and locality (pineapple in Queensland, Australia) and compare it with the original description, subsequent descriptions, and material collected from the USA, Costa Rica, and Colombia on pineapple, *Neoregelia*, and an unidentified bromeliad. Further specimens from pineapple in Guatemala were identified as the same species and represent the first record for this country. We concur with previous observations that the original description by Tryon is not the same species in subsequent descriptions. We tentatively consider all specimens examined the same as those described as *S. ananas* in succeeding descriptions, i.e., *Steneotarsonemus ananas* Tryon *sensu* Beer.

Keywords *Steneotarsonemus ananas*; Tarsonemidae; mites; *Neoregelia*; *Aechmea*; Bromeliaceae; Australia; Colombia; Costa Rica; Guatemala; USA (California; Hawaii)

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Introduction

Several phytophagous mite species are associated with pineapple (*Ananas comosus* [L.] Merr., 1917) including two significant pest species, the red-pineapple mite *Dolichotetranychus floridanus* (Banks, 1900) (Tenuipalpidae) and the pineapple blister mite *Phyllocoptruta sakimurae* Keifer, 1966 (Eriophyidae). Additionally, six species of Tarsonemidae are reported: three species of *Tarsonemus* (*T. bilobatus* Suski, 1965, *T. buchelerei* Smiley, 1967, and *T. merus* Lin & Zhang, 2002) and three species of *Steneotarsonemus* (*S. ananas* (Tryon, 1898), *S. perezi* Cromroy, 1958, and *S. comosus* Ochoa, 1991 (Ochoa *et al.*, 1991a, 1991b, 1994; Lin and Zhang 2002). Of these species, the best known species of *Steneotarsonemus* is the pineapple tarsonemid mite, or leathery pocket mite, *S. ananas*.

Steneotarsonemus ananas was described by Tryon (1898) associated with pineapple fruit in Australia. Since then, it has been collected from Brazil, Costa Rica, Cote d'Ivoire,

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Ecuador, India, Netherlands, Peru, Philippines, Poland, South Africa, and USA (Hawaii) (e.g., Illingworth 1931; Beer 1954; Jeppson *et al.*, 1975; Mourichon *et al.*, 1987; Mourichon and Sarah 1993; Rohrbach and Johnson 2003; Corpuz-Raros 2005; Petty *et al.*, 2006; De Moraes and Flechtmann 2007, 2008; Pijnakker and Ramakers 2009; Aguilar and Murillo 2012; Joy *et al.*, 2016; Kolicka *et al.*, 2016; Bazan 2018). The species is often linked with leathery pocket disease in pineapple (e.g., Petty 1989; Mourichon 1997). Furthermore, Pijnakker and Ramakers (2009) recorded this species from ornamental bromeliads, and Kolicka *et al.* (2016) found it associated with the bromeliaceous genera *Tillandsia* sp. and *Aechmea* sp. Thus, these mites are associated with several genera in the family Bromeliaceae.

Costa Rica exports a great number of ornamental plants of commercial interest to different markets around the world, including bromeliads in the genera *Bromelia* and *Neoregelia*. Although mites often associate with Bromeliaceae (e.g., Nesbitt 1985; Guerra *et al.*, 2012), including *S. ananas* from pineapples in Costa Rica (Ochoa *et al.*, 1991), no mite species were reported as pests of *Bromelia* and *Neoregelia* in Costa Rica. Here, we provide the first record of *S. ananas* found associated with the ornamental bromeliad *Neoregelia* spp. Its discovery raised questions about the identity of the species on both pineapple and the new host plant, leading us to redescribe *S. ananas* from pineapple so that it could be reliably compared to other material. We also describe the symptoms induced by this tarsonemid mite on *Neoregelia*.

Material and methods

Like many bromeliad genera, *Neoregelia* is native to the South American rainforests, specifically from southeastern Brazil (Royal Botanic Garden, Kew Science, n.d.), as are pineapples (Coppens d'Eeckenbrugge and Leal 2003), but the first *Neoregelia* cuttings were brought to Costa Rica from Europe more than 20 years ago and now mother plants are all produced in Pococí, Limón, Costa Rica. Some of the cuttings are developed to the seedling stage on another farm located in the province of Alajuela (810 masl). When they are ready for production, they are transported to the province of Limón to continue their growth. Mother plants are also produced on the farm in Limón, consequently materials from both places are mixed and grown together. Farm workers are responsible for the selection of mature plants and packing them in boxes for shipment to the different markets around the world.

A commercial plantation in Costa Rica, comprising many different bromeliad plant species, was visited on February 2018 because numerous plants were attacked by a small mite, causing visible symptoms. The damage was negatively affecting the quality of the product for export, particularly bromeliads in the genus *Neoregelia*. Plants for export should lack any injury and foliage must be free of spots, deformations, or any other visible damage.

The plantation, which utilized a black shade cloth (Saran) system, is located in the canton of Pococí, province of Limón, at 467 m above sea level. This zone is known for having high temperatures (24 to 30 °C throughout the year) and humidity (90-100% during the year), as well as considerable annual precipitation mostly through the rainy season. Eighteen samples, consisting of whole plants, were collected in plastic bags and placed into a cooler. The samples were transported to the Laboratory of Acarology at the University of Costa Rica and processed according to the laboratory protocols.

The samples were observed under a stereoscope-microscope, individual leaves were detached manually; then, the symptoms and mite behavior were recorded. The mites were collected in a Syracuse dish with 70% ethanol and mounted on slides in Hoyer's medium (Krantz and Walter 2009). The slides were processed in an oven at 50°C for three days or until the mites were completely clarified.

Once the mites were ready, the slides were sealed with glossy polyurethane varnish and examined with the help of Olympus BX 51 and Zeiss Axio Imager D1 microscopes, both with phase contrast and DIC (Differential interference contrast), as well as an Axio Imager D1 with DIC.

For the material from Costa Rica, five slides were deposited in the mite collection of the Laboratory of Acarology (CIPROC), University of Costa Rica and two slides with male and female specimens, as well as two larvae, at the Smithsonian (NMNH), National Insect and Mite Collection, Washington DC. Additionally, three larvae, two females and one male from Costa Rica were later prepared and deposited in the Queensland Museum (QM). The Australian material of *S. ananas* was found as an unidentified tarsonemid mite species in the Queensland Agriculture collection housed at the Queensland Museum (QM). This material, from pineapple in southeast Queensland (the type locality), was examined with phase contrast (Leica DMLB) and DIC (Leica DM2500). Other material examined is housed in the NMNH. A photograph of the first record in the USA of *S. ananas* on *Aechmea* (Figure 1) is provided. Morphological terminology follows Lindquist (1986).

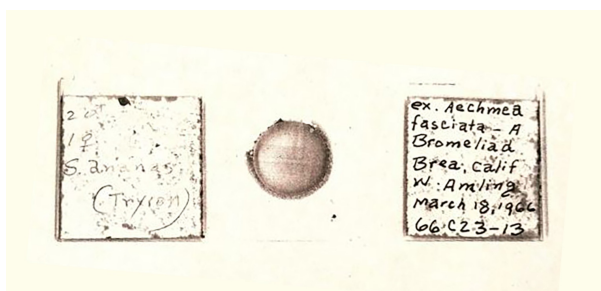


Figure 1 First record of *Steneotarsonemus ananas* (Tryon) 1898 (Tarsonemidae) on *Aechmea fasciata* (Lindl.) Baker 1879 (Bromeliaceae).

Results

Steneotarsonemus Beer

Steneotarsonemus Beer, 1954: 1229. Type-species *Steneotarsonemus hyaleos* Beer, 1954, by original designation.

Parasteneotarsonemus Beer & Nucifora, 1965: 40, Lindquist, 1986: 274.

Neosteneotarsonemus Tseng & Lo, 1980: 127; Lindquist, 1986: 274.

Steneotarsonemus are characterized for having: females with stigmata close to setae *vl*, body elongate-slender, sejugal and poststernal apodemes reduced; males often with round lobes on femorogenu IV; both genders with small pharynx and subcircular to subquadrate gnathosoma (Beer 1954; Lindquist 1986). A full description is provided by Lindquist (1986).

Steneotarsonemus (*Steneotarsonemus*) *ananas* (Tryon, 1898)

Tarsonemus ananas Tryon, 1898: 458.

Steneotarsonemus ananas (Tryon), Beer, 1954: 1276.

Diagnosis

All life stages: femur II with three setae; tarsi II-III elongate, longer than wide, setae *tc'* on tarsus I distinctly proximal to *tc''*. **Female** (Figure 2). Posterior margin of prodorsal plate medially concave and crenate; seta *vl* positioned at anterolateral corner of prodorsal plate, anterior of stigmata; bothridial seta *scI* capitate, its head obovate; seta *c2* positioned far anterior of seta *c1*; pore *ia* positioned far anterior of seta *d*; setae *c1*, *d*, *e*, *f* slender to slightly thickened, stiff; seta *h* thickened; *c2* about twice as long as *c1* and filiform; setae *e* and *h* with minute barbs. Paired remnants of sejugal apodeme each highly curved, boomerang-like;

apodemes 3 reaching level of seta *3a*; apodemes 4 well developed, almost reaching mid-line; seta *2a* positioned on or slightly behind apodeme 2; seta *3a* short, not reaching trochanter III; leg IV moderately long, extending to or just beyond idiosomal margin; femur I seta *d* lanceolate, *l'* and *l''* thickened; femur II seta *l'* thick; genu II seta *l'* thick; seta *G v' IV* not reaching base of seta *Ti v' IV*. **Male** (Figure 3). Prodorsum with four pairs of setae; seta *sc1* at least three times as long as seta *sc2*; seta *c2* not reaching base of *c1*; seta *c1* not reaching base of seta *d*; coxisternal plates smooth; apodeme 5 well-developed, forked; femur, genu, tibia II–III without sexually-dimorphic spine-like setae *l'*, *v'*; leg IV with small abaxial femorogenual flange and large, semi-circular adaxial flange; seta *v' Ti* 30–54 long, thick. **Larva**. Setae *v1* short, tips not overlapping; setae *h1* long, about twice length of *h2*.

Differential diagnosis

Seeman *et al.* (2016) brought together the two existing subgeneric classifications of *Steneotarsonemus*, recognizing six subgenera. *Steneotarsonemus ananas* is best placed in nominate subgenus *Steneotarsonemus*. However, it does not match this subgenus perfectly as the small abaxial flange on the male femorogenu IV is present in *S. ananas* and *Parasteneotarsonemus*. However, this feature is easily missed, and may be present elsewhere in *Steneotarsonemus*.

Many descriptions of *Steneotarsonemus* are rudimentary and sometimes lack even basic illustrations of females (e.g., Cromroy 1958) which are essential for classification. Thus, our proposed diagnostic features are tentative. Nevertheless, *Steneotarsonemus ananas* is unique in *Steneotarsonemus* by having females with a crenate posterior margin of the prodorsal plate. However, the crenate prodorsal margin does occur in some females of *Tarsonemus* such as *T. stammeri* Schaarschmidt, 1959, as well as on *Deleonia aguilar* Goldarazena & Ochoa, 2002 (Goldarazena *et al.*, 2002).

The two other species of *Steneotarsonemus* found on pineapple are *S. comosus* and *S. perez*. *Steneotarsonemus ananas* is differentiated from *S. comosus* by having females with setae *c2* about twice the length of *c1* (*c1* and *c2* subequal in *S. comosus*) and coxal setae *3a* and *3b* subequal (*3a* about twice as long as *3b* in *S. comosus*); and a male with leg IV with a large rounded flange (versus a narrower rectangular flange in *S. comosus*). *Steneotarsonemus perez* is distinguished from *S. ananas* and *S. comosus* by having males with setae *v1* much longer than *v2* (versus *v1* shorter than *v2*).

Description

Female (Figures 4–7). Measurements are given in Table 1. Idiosoma elongate. Gnathosoma rounded. Dorsal gnathosomal setae *ch* finely pilose, longer than ventral setae *su*. Palpi approximate, small, directed anteriorly. Cheliceral stylets short, strongly curved, with basal levers conspicuous. Pharynx short, with muscular, thinly sclerotized walls.

Dorsum. Prodorsal plate truncated anteriorly, not projected beyond basal part of gnathosoma, posterior edge concave, crenated with 7 to 8 fine lobes (Figure 6A). Stigmata on anterior margin of prodorsal plate, situated closely posterolaterad of setae *v1*; main tracheal trunks with small, fine sclerotized atria, each atrium divided into two elongate halves. Setae *v1* filiform, finely pilose; setae *sc2* long, filiform, about twice the length of *v1*. Bases of *sc2* posterolaterad setae *sc1*. Bothridial setae *sc1*, capitate, finely pilose. Setae *c1*, filiform, shorter than setae *c2*, also filiform. Bases of *c2* located anterolaterad *c1*. Cupules *ia* anterolaterad setae *d*. Setae *d*, *e* and *f* simple, finely barbed, similar in length, setae *e* slightly thicker than setae *d* and *f*. Tergite EF with base of setae *e* located anterolaterad setae *f*. Cupules *im* anteromedial of setae *e*. Setae *h* stout, barbed, slightly longer than *v1*.

Venter. Apodemes I short, united with prosternal apodeme; apodemes II conspicuous and curved, not united with prosternal apodeme. Prosternal apodeme not extending posteriad of apodemes II, with a bifurcated ending. Sejugal apodeme reduced to two lateral highly-curved, boomerang-like fragments. Apodemes III slender, conspicuous, curving posteromedially near setae *3a*. Apodemes IV slender (Figure 6B), extending anteriorly about $\frac{3}{4}$ distance to *3a*.

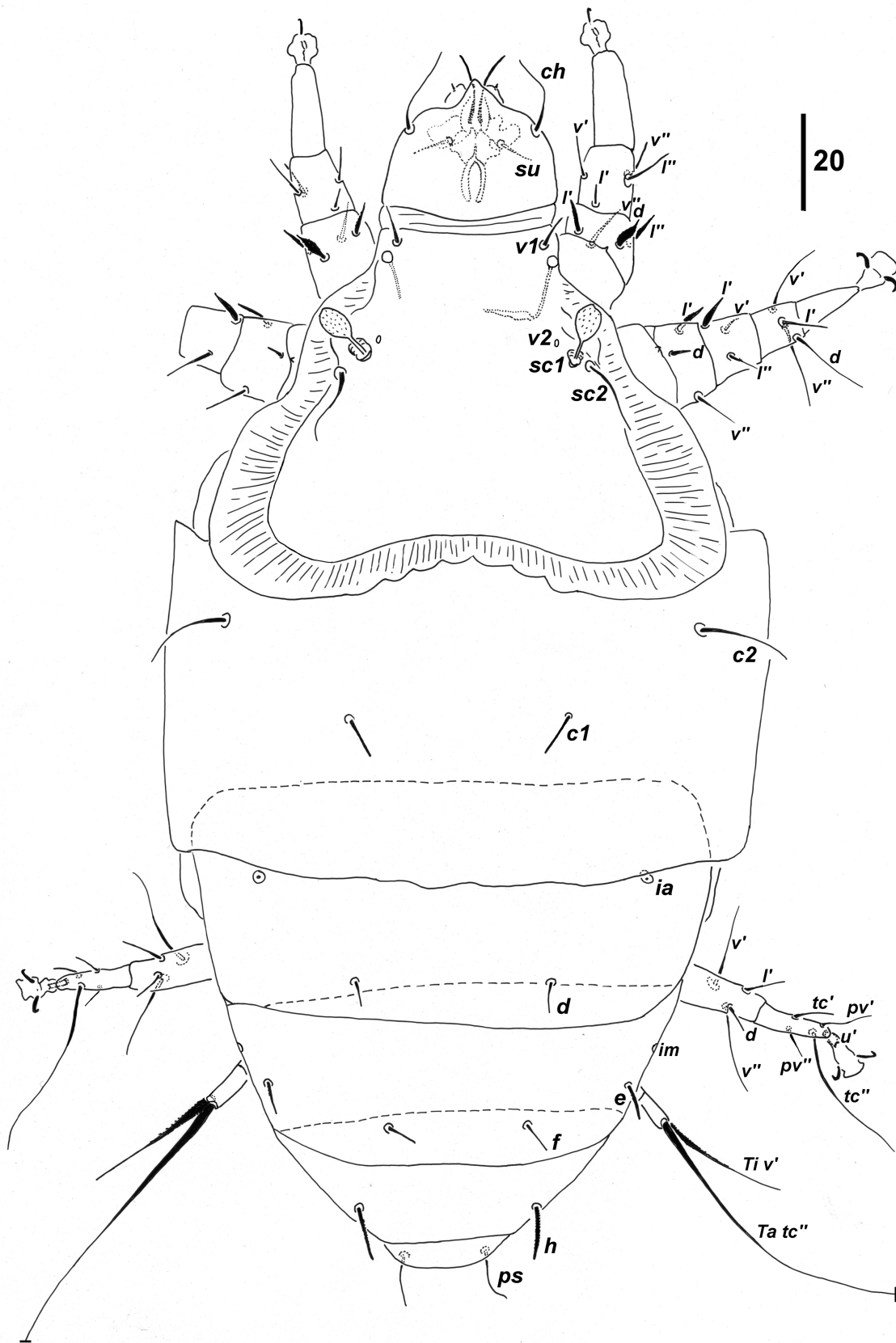


Figure 2 *Steneotarsonemus ananas* (Tryon). Female, dorsal view.

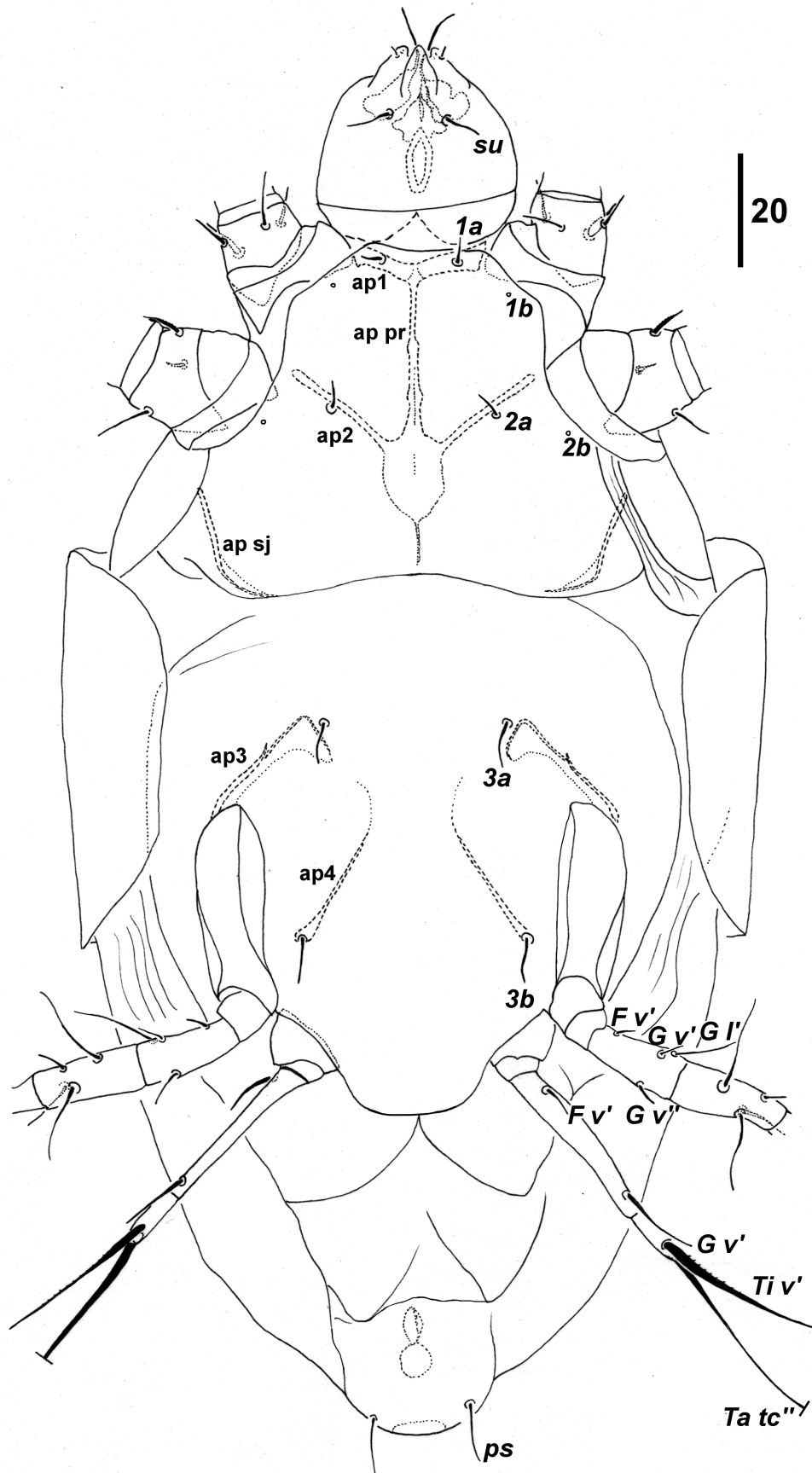


Figure 4 *Steneotarsonemus ananas* (Tryon). Female, ventral view. Idiosoma and legs III and IV.

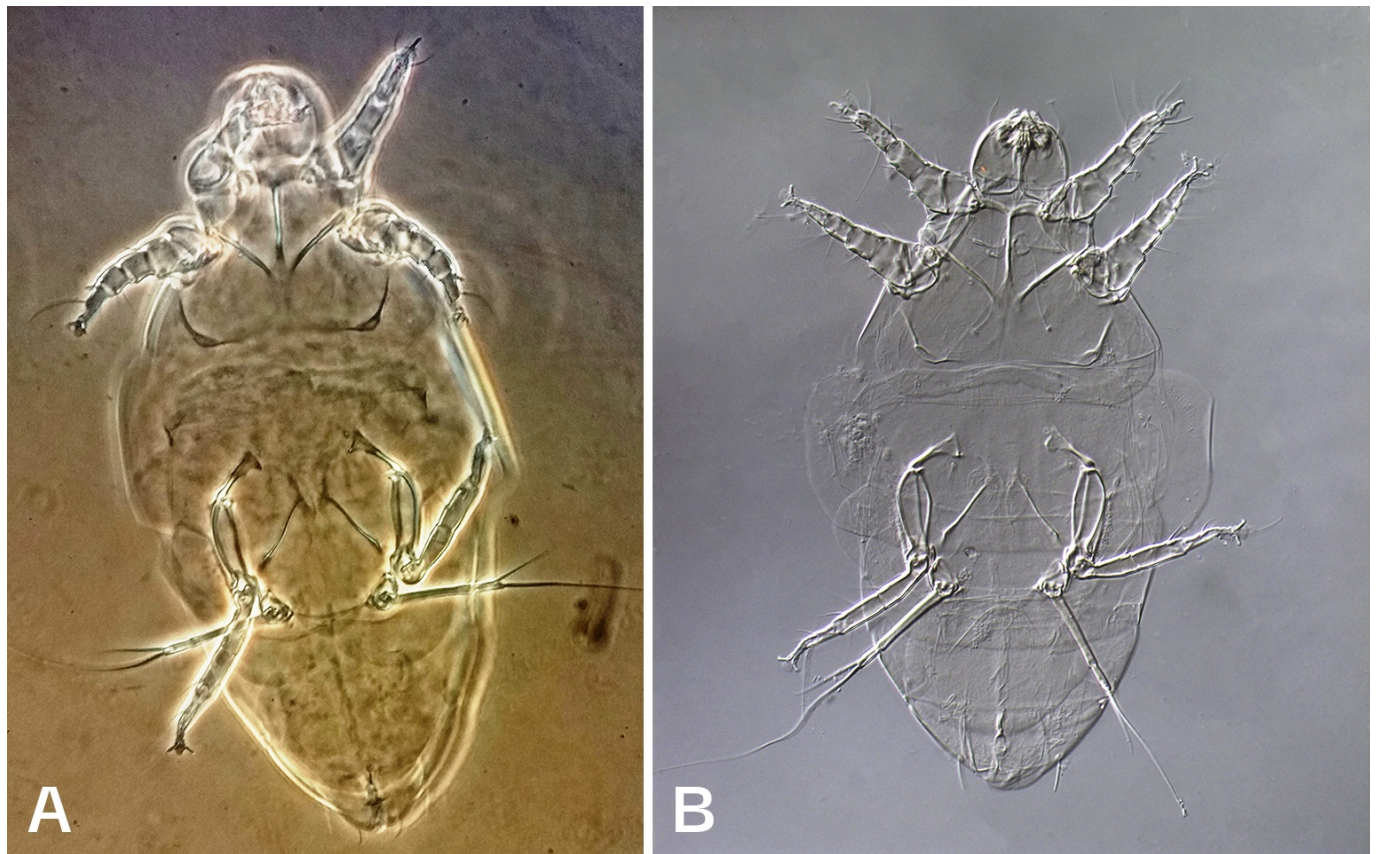


Figure 5 *Steneotarsonemus ananas* (Tryon). Female, ventral view. A – phase contrast; B – differential interference contrast.

Poststernal apodeme absent. Setae *1a*, *2a*, *3a*, *3b* slender, similar in length, *3a*, *3b* longest. Tegula 3-4 times longer than wide, truncated apically. Pseudanal setae slender, slightly longer than *vI*.

Legs (Figure 7). Leg III longer than legs I, II and IV. Leg IV cylindrical; terminal seta *tc''* filiform, about three times longer than subterminal seta *v'Ti*; subterminal setae stout, finely pilose; femorogenu with genual seta *v'G* slightly shorter than seta *v'F*.

Setal counts for legs I–III (femur to tarsus): leg I (Fe-Ta) 4-4-6(+2φ)+8(+ω), 3-3-4-6(+ω), 1+3-4-5. Setae smooth, slender, unless otherwise mentioned. Leg I: femur I, *d* lanceolate, barbed, 7–8, *l'* thickened, weakly barbed, 6–7, *l''* narrowly lanceolate, weakly barbed, 7–8, *v''* 10–12; genu I, *l'* shortest, 5, *l''* longest, 10–12; tibiotarsus I, *d* longest, 23–28, *φI* 5, *φ* 3–4, *k* 5, *p'* 10–11, *p''* 12–14, *tc'* 15–16, *tc''* 16–18, *s* with weakly bifid tip, 3, *ω* 6–7. Leg II: femur II, *d* thickened, 4–5, *l'* narrowly lanceolate, barbed, 6–8, *v''* 5–8; genu II, *l'* narrowly lanceolate, 6–7, *l''* weakly barbed, *v'* 4–5; tibia II *l'* shortest, 8–9, *d*, *v'*, *v''* 18–23; tarsus II, seta *pl'* thick, thorn-like, 4, *tc''* longest, 20–26, *u'* with weakly bifid tip, 3, *ω* 4–5. Leg III: femorogenu III *Fv'*, *Gv'*, *Gv''* short, 3–5, *Fl'* longer, 11–14; tibia III, *d* shortest, 4–6, *v'*, *v''* longest, 15–21; tarsus III, *tc''* longest, 26–32, *u'* with weakly bifid tip, 3–4. Leg IV with seta *Ti v'* barbed, thick (measurements in Table 1).

Male (Figures 8–10) (n = 5 from *Neoregelia*; n = 2 from Queensland pineapple). Measurements are given in Table 2. Idiosoma broadest near level of *c2*, body length variable in Costa Rican population (ca. 20% length variation versus 2.5% width variation). Gnathosoma oval rounded. Dorsal gnathosomal setae finely barbed basally, ventral gnathosomal setae smooth. Cheliceral stylets moderately short, straight. Pharynx small, same as female, with muscular, thinly sclerotized walls.

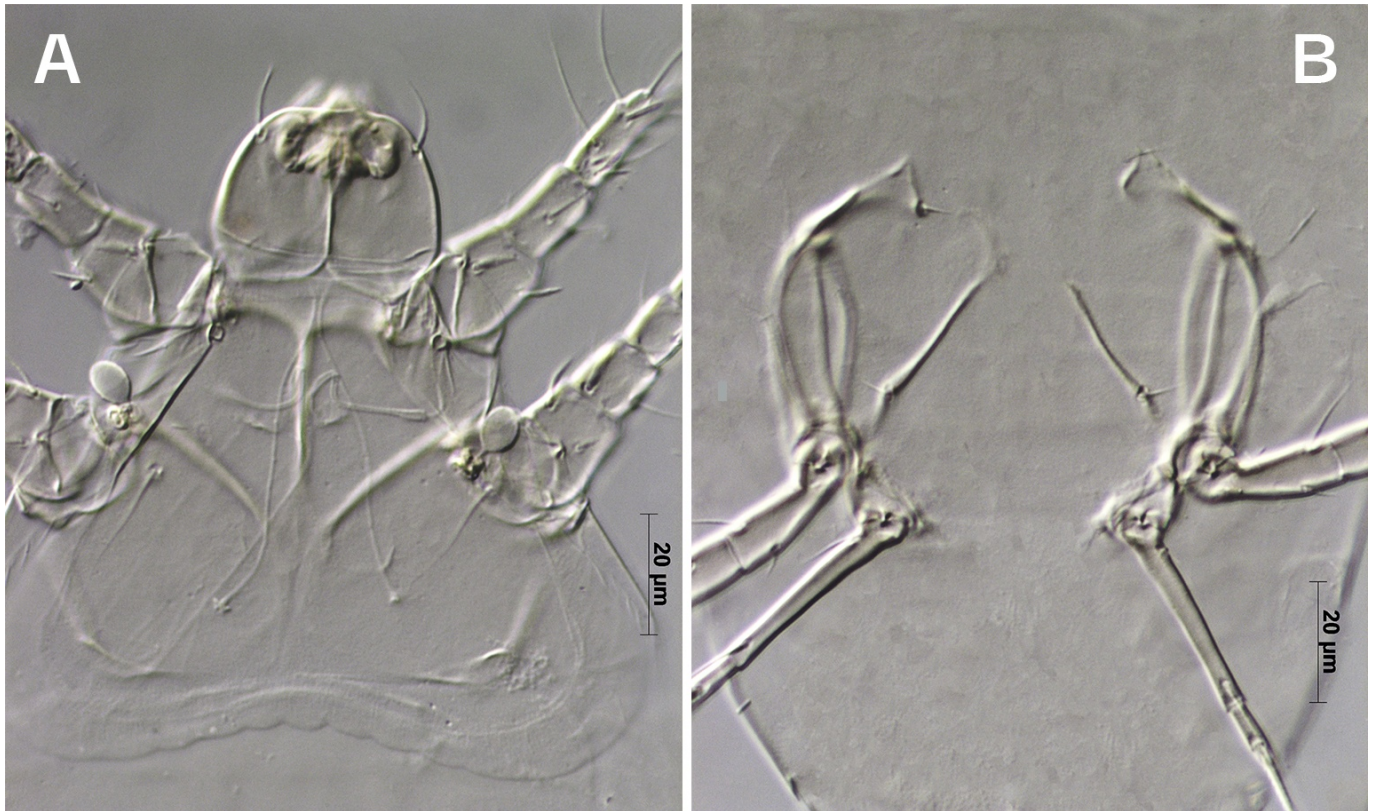


Figure 6 *Steneotarsonemus ananas* (Tryon). Female. A – Propodosoma, dorsal view (crenulation); B – Leg IV, and apodemes III and IV.

Dorsal plates unornamented (Figure 10A). Prodorsal plate weakly sclerotized, subtriangular. Vertical setae *v1*, slender, slightly barbed, shorter than *v2*. Scapular setae *sc1* simple, slightly pilose, longer and thicker than *sc2*. Base of *sc2* aligned with *v2-sc1*.

Plate CD with setae *c2*, filiform, two times longer than *c1*. Setae *c1* and *d* stout, barbed. Plate EF with setae *f*, stout, pilose. Setal lengths vary between populations: Australian specimens with much shorter setae compared with Costa Rican and Colombian populations, USA intermediate (Table 2). Genital capsule as long as wide, with accessory copulatory structures *ps1* spinelike, pointed apically.

Venter. Apodemes I short, united with prosternal apodemes; apodemes II conspicuous and distally curved, weakly united with prosternal apodemes. Prosternal apodemes not reaching posterior podosomal margin. Sejugal apodemes absent. Apodemes III, IV, poststernal apodeme united; apodemes V separate, joining poststernal apodeme.

Legs. Legs I-II, IV subequal in length; leg III longer than leg IV. Leg IV with large adaxial rounded flange and narrow distal abaxial flange (Figure 10B).

Leg setation for legs I-III same as female except for addition of small *ft''* on tarsus I. Setal form similar except for: femur I, all setae smooth, slender or only slightly thickened, *d* 5–7, *l'* 4–5, *l''* 6–7, *v''* 7–8; genu I setae 8–14, *l'* not obviously shorter than other setae; femur II setae smooth, slender or only slightly thickened; genu II setae smooth, slender; femur III setae *v'*, *l'* similar length, 13–17; tibia III seta *d* long, 16–22. Measurements from Australian specimens; males from Costa Rica with longer setae (Table 2).

Larva (from *Neoregelia* spp. material) (Figures 11–13). Idiosoma length 170–270, width 95–115. Gnathosoma rounded, length 32–33, width 32–33; setae *ch* 13–14, *su* 7–8.

Prodorsal plate with setae *v1* 4–8, *sc1* 6–8, *sc2* 22–26; opisthosoma with setae *c1* 5–9, *c2* 8–10, setae *c2* usually longer than *c1*; *d* 6–9; *e* 11–13, *f* 10–12; caudal setae *hl* 22–25, about

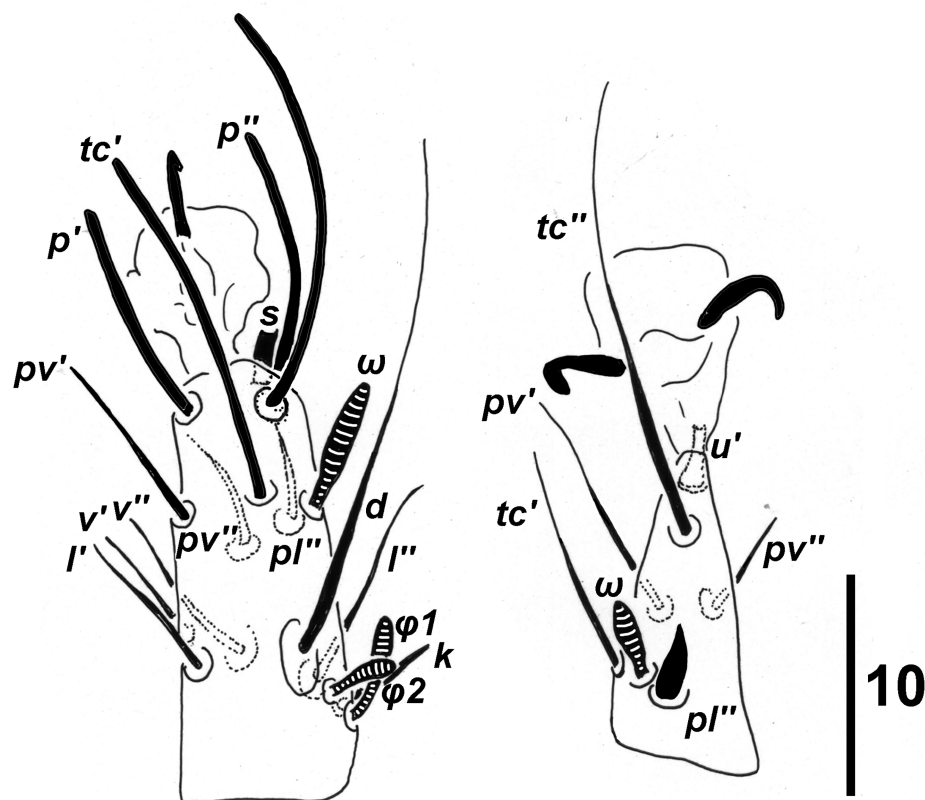


Figure 7 *Steneotarsonemus ananas* (Tryon). Female. A – tibiotarsus I; B – tarsus II.

twice as long as *h2* 11-13, setae *ps1* and *ps2* 4–5. All idiosomal setae slightly thickened and minutely pilose, setae *sc2*, *c1*, *d*, *e*, *f* thicker than other setae, their tips blunt; setae *ps1-2* fine, smooth.

Ventral apodemes *ap1*, *ap2* and *appr* distinct, *ap2* not reaching *appr*; sejugal apodeme not apparent; *ap3* indistinct. Setae *1a*, *2a* small, slender, length 3; setae *3a*, *3b* longer, length 4–6.

Legs. Leg setation for legs I-III similar to female except lacking $\phi 2$ on tibia I, proral setae on tarsus I and *pv'* on tarsi II-III. Form of setae similar to female except for: femur I seta *d* only slightly thickened, peg-like, 2–3, other setae slender, smooth; genu II seta *l'* not shorter than other setae; femur II, genu II setae slender, smooth; tibia III with short, thick thorn-like seta *l'*, 3.

Material examined. 56 females, 35 males, 2 pharate males, 6 larvae as follows. **Australia:** 6 females, 2 males, 1 pharate male, Cooroy, Queensland, 4 Apr. 1968, C. Dodson, ex pineapple (mount by J.J. Davis, in Hoyers), deposited in QM. **Colombia:** 12 females, 9 males, 1 pharate male, Fusagasuga, Cundinamarca, 13 Dec. 1997, D. Navia, ex Bromeliaceae (cup), deposited in NMNH, Smithsonian, USA. **Costa Rica:** 17 females, 11 males, 5 larvae, Pococí Limón, 28 Feb. 2018, H. Aguilar, ex *Neoregelia* spp. (8 females, 3 males, 2 larvae, deposited in NMNH; 9 females, 8 males, deposited in the Laboratory of Acarology, Univ. of Costa Rica; 2 females, 1 male, 3 larvae deposited in QM); 10 females, 3 males, 1 larva, Venecia, San Carlos, Alajuela, 25 Feb. 2009, A. Obando, pineapple, deposited in the Acarology Lab., Univ. of Costa Rica; 1 female, 1 male, interception, Philadelphia, PA, from Costa Rica 28 Nov. 1994, F. Salantri, ex *Ananas comosus*, deposited in NMNH; 2 females, 1 male, interception Philadelphia CBP,

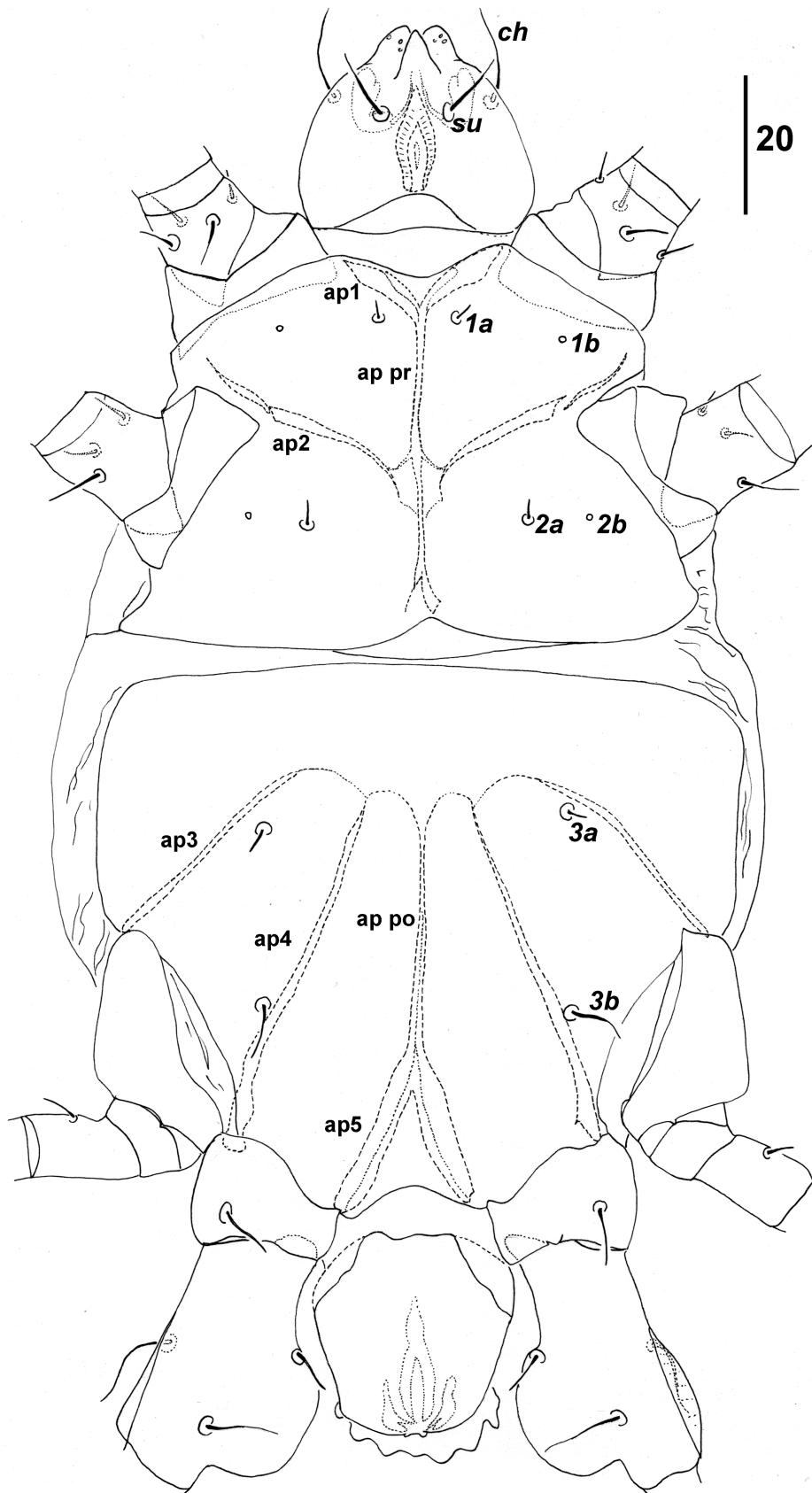


Figure 8 *Steneotarsonemus ananas* (Tryon). Male. Ventral view. Idiosoma.

PA, from Costa Rica 14 Mar. 2016, G. Evans, ex *Ananas comosus*, deposited in NMNH. **Guatemala:** 2 females, 2 males (poor condition), interception Wilmington CBP, DE, from Guatemala, 2 Aug. 2016, E. McDonald, ex *Ananas comosus*, deposited in NMNH. **United States:** 4 females, 5 males, Brea, CA, 18 Mar. 1966, R. Smiley, ex *Aechmea fasciata*, deposited in NMNH.

Discussion

Tryon (1898) described *S. ananas* from mites collected on pineapples showing severe symptoms of fruitlet core rot, which is caused by *Fusarium* fungi and linked to the feeding of *S. ananas* by Tryon (1898) and later by several studies (e.g., Petty *et al.*, 2006).

Unfortunately, Tryon (1898) did not mention the specimens on which the species is based:

Table 1 Morphometric data (presented as ranges, in μm) for females of *Steneotarsonemus ananas* collected from Australia (ex pineapple), Costa Rica (ex *Neoregelia*), Colombia (ex unidentified bromeliad), and USA (ex *Aechmea fasciata*).

Morphological character	Australia	Costa Rica	Colombia	USA
Idiosoma length	210–235	230–270	240–278	230–232
Idiosoma width	107–130	99–121	110–132	100–102
Gnathosoma length	33–37	33–35	36–40	27–29
Gnathosoma width	34–39	35–39	34–39	31–32
Gnath. dorsal seta	16–17	16–18	15–18	15–16
Gnath. ventral seta	8–10	8–10	8–10	7–9
Tracheal atrium length	5–6	6–7	6	Not measured
Tracheal atrium width	2–3	2–3	2–3	Not measured
Seta v1 length	7–9	9–11	9–11	8–10
Setae sc1 length	12–14	12–14	12–14	12–14
Setae sc2 length	16–19	15–18	16–23	17–19
Seta c1 length	8–10	10–12	10–11	9–10
Seta c2 length	16–19	16–21	17–22	16–18
Setae d, e, f lengths	8–9	8–9	7–10	7–9
Seta h length	11–13	13–15	12–15	13–14
Setae 1a, 2a, 3a lengths	4–5	3.5–5	4–6	4–5
Seta 3b length	7–10	6–8	7–9	6–8
Tegula length	28–30	29–33	28–30	26–27
Tegula width	6–9	7–8	7–9	6–7
Seta ps length	9–11	14–17	11–14	9–10
Leg I length	63–65	62–73	65–74	64–66
Leg II length	64–69	62–72	68–71	65–71
Leg III length	104–105	104–109	107–110	108–109
Leg IV length	47–50	45–50	48–56	47–49
Leg IV seta tc''Ta length	100–110	110–130	90–110	93–95
Leg IV seta v'Ti length	28–38	38–42	31–38	34–35
Leg IV seta v'G length	8–11	12–14	8–10	9–10
Leg IV seta v'F length	13–14	15–16	12–15	12

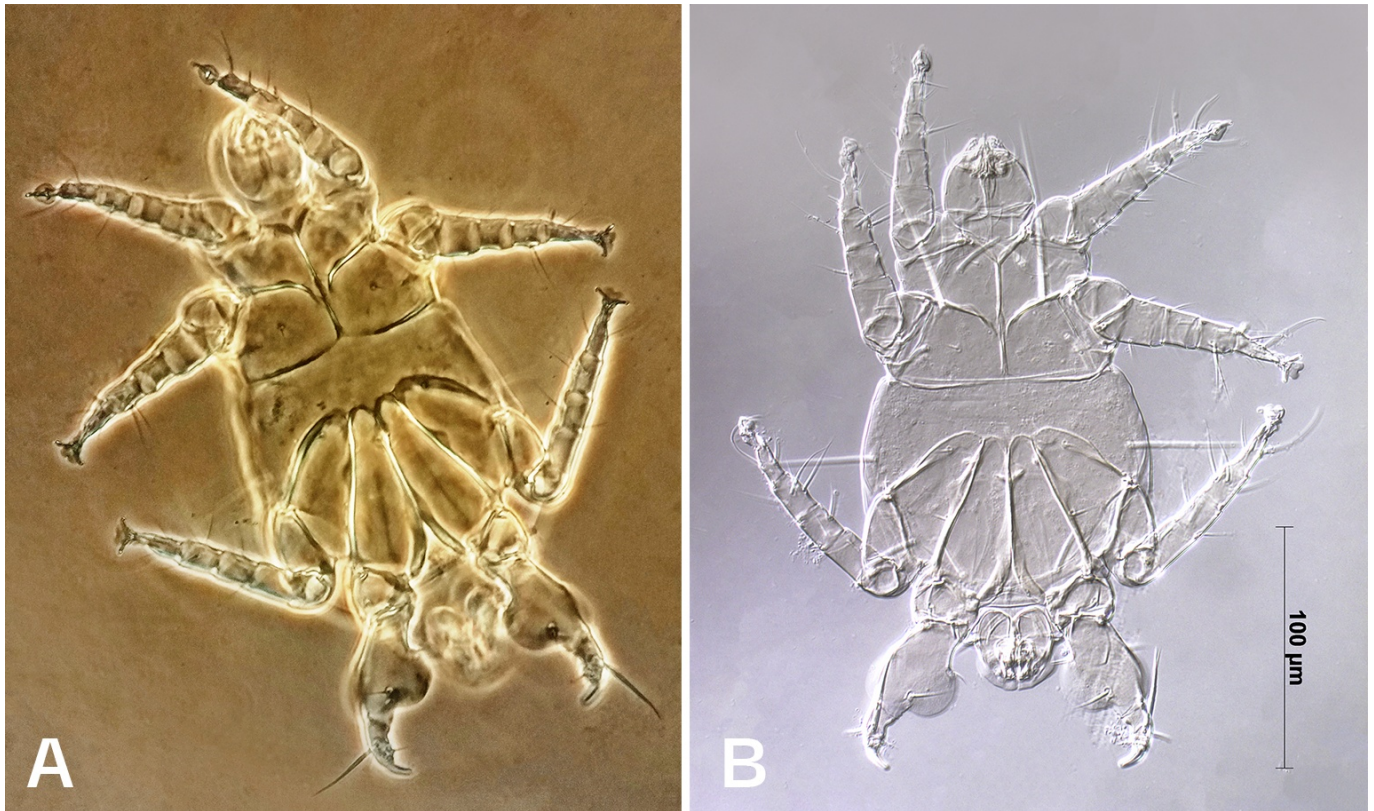


Figure 9 *Steneotarsonemus ananas* (Tryon). Male. Ventral view. A – phase contrast; B – differential interference contrast.

they are merely an undisclosed number of mites from pineapples in southern Queensland. Ewing (1939) did not examine type specimens, instead relying on Tryon's manuscript and female and larval material from Hawaii. Beer (1954) considered the whereabouts of Tryon's material "unknown", again relying upon Ewing's material from Hawaii. In the past decade or so, several unsuccessful efforts were made to locate these type specimens at the Queensland Department of Agriculture collection, the Queensland Museum, and the Australian National Insect Collection.

Tryon's drawings and descriptions are, not surprisingly for their time, rudimentary, however, we doubt that the species described by Tryon (1898) is the same species later called *S. ananas* by subsequent authors. Tryon (1898) provided ventral views of each sex. The male shows a few significant differences from later descriptions (Beer 1954; Jeppson *et al.*, 1975). First, the flange on leg IV is absent in Tryon (1898), but with a low-powered microscope, it is unlikely but possible that the flange was misinterpreted as a spine-like process. Second, in his original description the male is widest just anterior to seta *c1*, whereas in subsequent descriptions of the male, it is widest just anterior to seta *c2*. Third, Tryon (1898) also shows an undivided apodeme 5, but male *S. ananas* have a posteriorly forked apodeme 5. The female presents further significant differences that are incongruous not only with *S. ananas* in subsequent descriptions (Ewing 1939; Beer 1954; Jeppson *et al.*, 1975) but also with *Steneotarsonemus*. Instead of an elongate body as in *Steneotarsonemus*, it is ovate; rather than short setae *h*, they are long; contrary to separate apodemes 3, they are joined; instead of lacking a post-sternal apodeme, it is present; rather than separate apodemes 4, they join the post-sternal apodeme. Therefore, the mite described by Tryon is not *S. ananas* as currently defined. It is not *Steneotarsonemus*. A similar conclusion is reached in Kolicka *et al.* (2016), who doubted that *S. ananas* (Tryon, 1898) was the same species described by later authors as *S. ananas*.

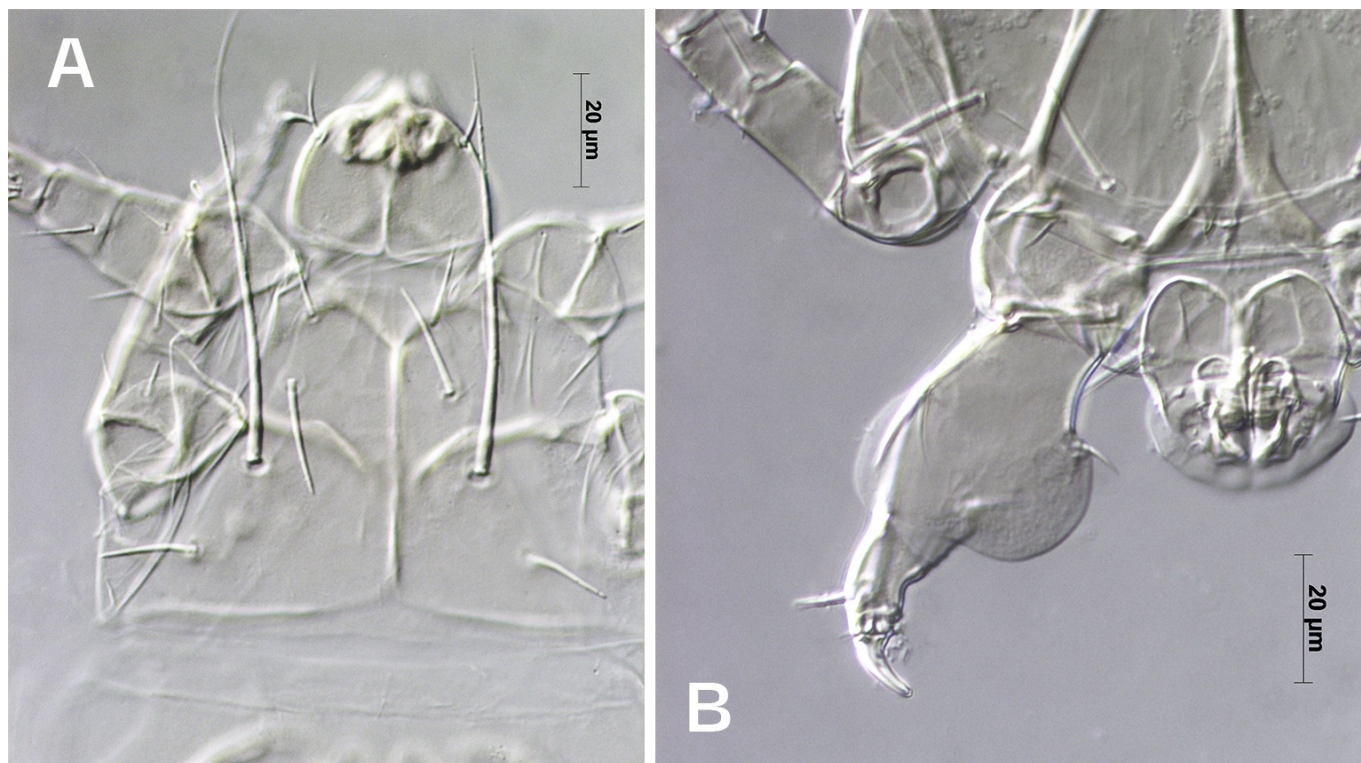


Figure 10 *Steneotarsonemus ananas* (Tryon). Male. A – Dorsal view of propodosoma; B – Ventral view of leg IV (detailed).

What is *S. ananas* (Tryon, 1898)? We are unaware of any species of tarsonemid that matches his original description. The only tarsonemid mites described from Bromeliaceae are the six species known from pineapple and records of *S. ananas* from other bromeliad hosts (Lin and Zhang 2002; Kolicica *et al.*, 2016). Thus, as *Tarsonemus* is the only other tarsonemid genus known from Bromeliaceae, perhaps Tryon (1898) described a species of *Tarsonemus* rather than *Steneotarsonemus*. This genus at least has females with an ovate body and more complete apodemes. Unfortunately, the three species of *Tarsonemus* recorded on pineapples (*T. bilobatus*, *T. bucheleri*, and *T. merus* (Suski 1965; Smiley 1967; Flechtmann 1971; Lin & Zhang 2002)) bear no great similarity with *S. ananas* sensu Tryon (1898). Until material matching Tryon's description is found, the true identity of *S. ananas* will remain a mystery.

Ewing (1939) provided the first description of *S. ananas* after Tryon (1898). While he copied the description of the male from Tryon, his description of the female was new. However, the specimens examined, two females and a larva ("nymph"), were poorly and incompletely described making the description unsuitable for identification purposes or comparison with Tryon (1898). Thus, the first complete description is that of Beer (1954), who also provided the first description of the male, and we thus consider the species *Steneotarsonemus ananas* (Tryon, 1898) sensu Beer (1954). Unfortunately, the specimens of Ewing (1939) have not been located, and Beer's (1954) material in the University of Kansas is not available.

The specimens from Australia, described here, are from the type locality and host for *S. ananas*, but are clearly not the same species described by Tryon (1898) and instead match *S. ananas* sensu Beer. Comparisons between females from Queensland pineapple, Costa Rican *Neoregelia* and pineapple, Colombian bromeliad and Californian (USA) ornamental bromeliad demonstrated not only concordance with diagnostic features but also measurements (Table 1). However, males were less similar (Table 2). While they all agree in general diagnostic features, some setal lengths differ considerably in size with males from Queensland pineapple having

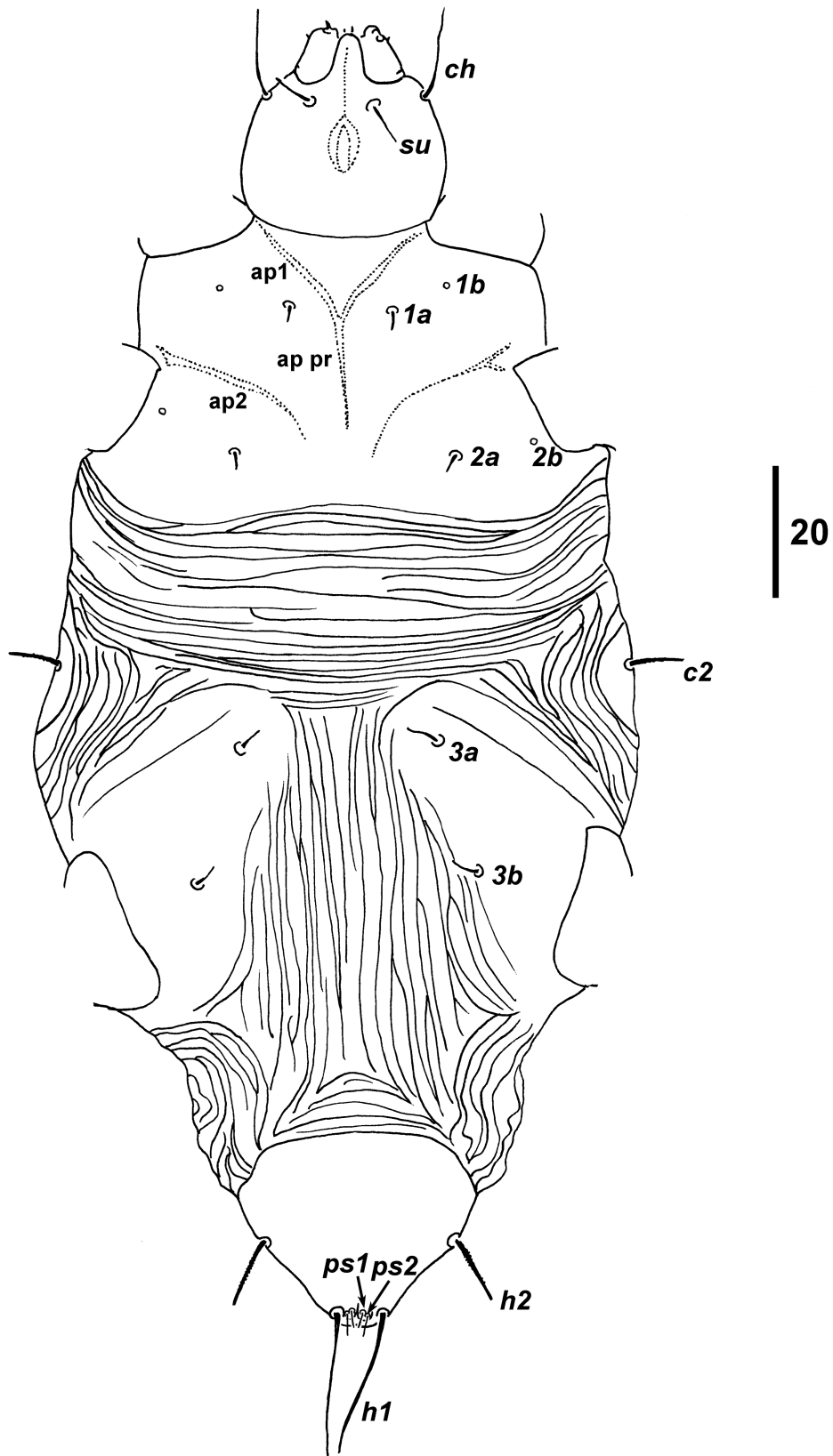


Figure 12 *Steneotarsonemus ananas* (Tryon). Larva. Ventral view.

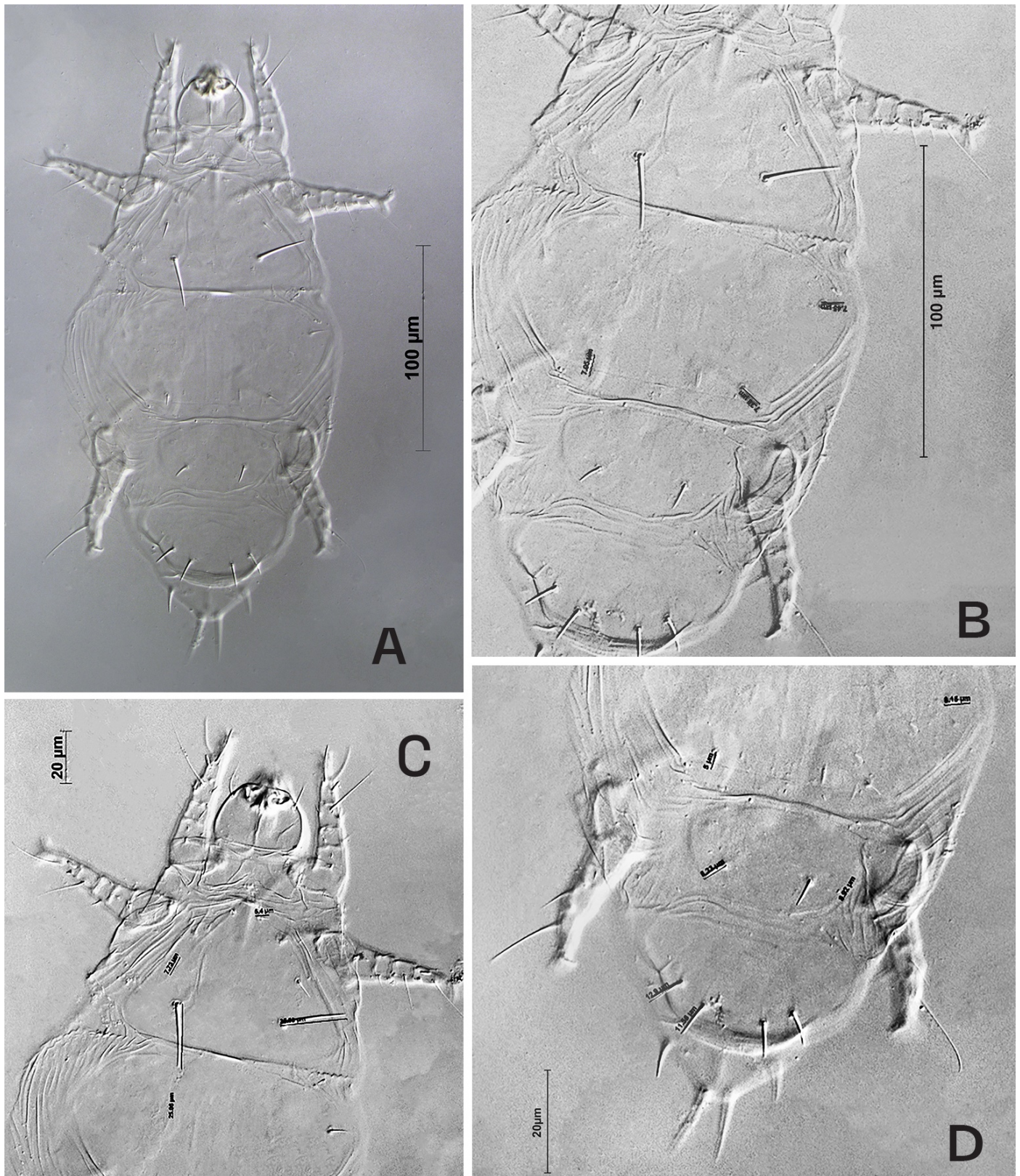


Figure 13 *Steneotarsonemus ananas* (Tryon). Larva. A – Dorsal view; B – Idiosoma; C – Prosoma; D – Hysterosoma.

much shorter setae than those found on Costa Rican *Neoregelia* and Colombian bromeliads. As intraspecific variation in males is known in Tarsonemidae (e.g., *Tarsonemus waitei* Banks, Lindquist (1978)) and other collections from USA pineapples were intermediate in size, we tentatively consider these differences as intraspecific. Thus, they are all *S. ananas* sensu Beer (1954), pending further studies into the identity of *Steneotarsonemus* species on pineapple throughout the world.

Description of symptoms on *Neoregelia* spp. (Bromeliaceae)

Mites were observed grouped in the interior of the plant, especially hidden on the underside of the leaves, near the axils of the younger foliage. The leaves also form rosettes, which compose microreservoirs in the axils, beneath the main phytotelmata of the plant. This provides a good habitat for many organisms, including tarsonemid species, which require warm temperatures, high humidity and low light intensity to develop (Jeppson *et al.*, 1975). The feeding damage shows a light brown color, mostly in the middle of the young leaf surface (Figures 14A and 14B), while the apex remains green and the base of the leaf white in color, which serves as a depository camouflaging a high concentration of wandering mites and eggs.

When the leaves develop and become more coriaceous, red spots of different diameters appear along the leaves upper side. These spots are the remnants of the earlier feeding damage by *S. ananas*. The dimensions of the brownish discolorations could be associated with the population density at the time of feeding (Figure 14C).

It is at this point in the plant's development, when the mites are no longer present, that these symptoms are most likely to be noticed by farm personnel in charge of monitoring the plants. Plants exhibiting such damage are not commercially acceptable for export.

Table 2 Morphometric data (presented as ranges, in μm) for males of *Steneotarsonemus ananas* collected from Australia (ex pineapple), Costa Rica (ex *Neoregelia*), Colombia (ex unidentified bromeliad), and USA (ex *Aechmea fasciata*).

Morphological character	Australia	Costa Rica	Colombia	USA
Idiosoma length	180–190	169–243	196–205	192–194
Idiosoma width	102–113	103–113	94–109	89–92
Gnathosoma length	30–33	28–36	34–37	30–32
Gnathosoma width	34–35	29–36	34–39	32–34
Seta v1 length	9–11	12–16	10–20	9–10
Seta v2 length	13–15	23–27	17–29	22–24
Setae sc1 length	49–61	70–99	63–93	69–72
Setae sc2 length	14–16	18–25	16–27	16–17
Seta c1 length	12–14	27–35	30–33	18–20
Seta c2 length	32	60–76	60–69	47–53
Seta d length	13–15	20–25	26–28	18–19
Seta f length	13	14–17	16–20	12–13
Genital capsule length	30–37	31	26–28	27–28
Leg IV large flange length	28–33	31–36	30–36	27–29
Leg IV seta v'Ti length	30–34	37–47	39–54	32–39
Leg IV solenidion ϕ length	8–9	8–9	9–10	9–10
Leg IV seta v'G length	11	9–11	14–18	13–16
Leg IV seta l'G length	13–14	16–17	14–17	13–15
Leg IV seta v'F length	6–7	10–12	10–12	7–10

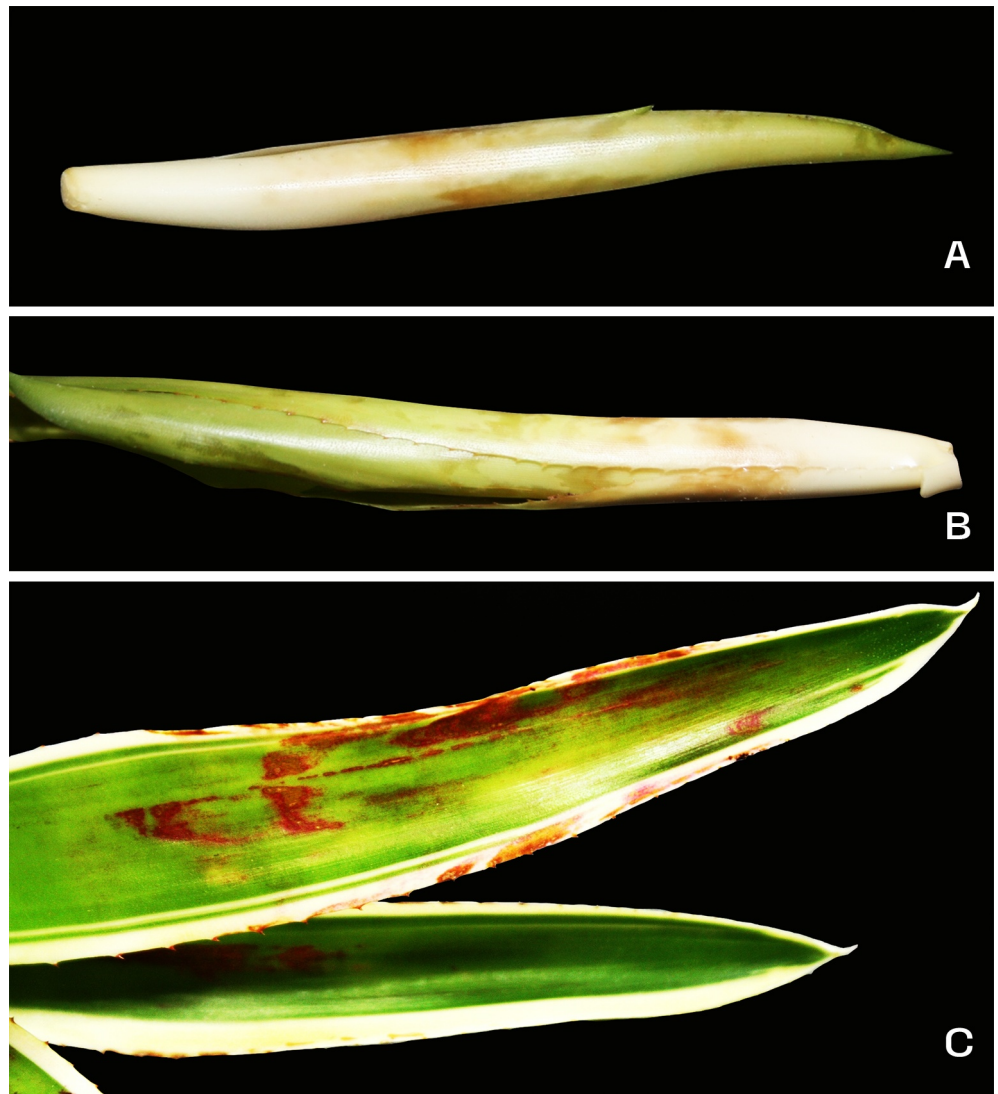


Figure 14 A – Damage caused by *Steneotarsonemus ananas* on *Neoregelia* spp., Limón, Costa Rica; B – Symptoms provoked by *S. ananas* on *Neoregelia* spp. Limón, Costa Rica; C- Old damage caused by *S. ananas* on *Neoregelia* spp. Limón, Costa Rica.

The damage caused by *S. ananas* on pineapple occurs on growing plants during the development of the inflorescence, fruit and crown (Jeppson *et al.*, 1975; Py *et al.*, 1987; Rohrbach and Johnson 2003), which is similar to the symptoms caused by this organism on *Neoregelia*. As noted, the pineapple tarsonemid mite has also been associated with *Fusarium* and also in the pathogenesis of *Penicillium funiculosum* Thom, (1910) (Rohrbach *et al.*, 1981). Another important factor is the presence of an entomopathogenic fungus, *Hirsutella* spp. (Umaña *et al.*, 1990; Zoebisch *et al.*, 1992; Quesada-Sojo and Rivera-Mendez 2016), associated with soil and bromeliads in Costa Rica; species of this fungus genus could be used for the control of phytophagous mites like *S. ananas* that live in concealed places on their host plants. Further studies on the biology of the mite are required for effective monitoring, focused on the plant phenology, as well as control measures, both chemical and biological.

In conclusion, we consider *Steneotarsonemus ananas* sensu Beer (1954) to be the species found on pineapple and several other bromeliaceous plants world-wide, where it causes damage through both its feeding and association with pathogenic fungi. Its taxonomy remains difficult,

in part due to the lack of types, and that at least two species are involved: the species originally described by Tryon (1898) and that described by Beer (1954), Jeppson *et al.* (1975), and also probably by Ewing (1939). However, the presence of other species of *Steneotarsonemus* on pineapple, and the intraspecific variation in males noted here, suggest the problem requires a much larger revision involving fresh samples from numerous hosts and countries, combining both morphology and molecular methods.

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