

Endoparasitic mite infections of anuran amphibians from Bolivian montane rain forests, with descriptions of two new *Hannemania* species (Acari: Parasitengona: Trombiculidae: Leeuwenhoekiiinae)

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Received 23 March 2005; accepted 20 July 2005

Abstract

Endoparasitic chiggers were collected from juvenile *Bufo quechua* (Bufonidae) and adult *Eleutherodactylus platydactylus* (Leptodactylidae) sampled in perhumid montane forests in Bolivia. Complete taxonomic descriptions are given for *Hannemania yungicola* n. sp., which parasitizes both amphibian hosts in higher montane rain forests, and for *H. chaparensis* n. sp., which seems to be restricted to lower montane rain forests. In histological sections, the mites are completely embedded in capsules produced by the host. The parasites' mouthparts obviously are adapted to rupturing host cells, the contents of which are ingested. The life style of *Hannemania* species, its evolution, and the parasites' potential influence on their hosts are discussed.

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Keywords: Amphibia; Anura; Trombiculidae; New species; Endoparasites; Parasite–host associations

Introduction

During herpetological fieldwork in montane rain forests on the eastern Andean slopes of Bolivia, frog specimens with pustules under their skin were frequently recorded. The occurrence of these 'cysts' was first mentioned for that region by Lynch and McDiarmid (1987) from a specimen of *Eleutherodactylus mercedesae* (Leptodactylidae). Subsequently, Köhler et al. (1995) reported similar pustules on specimens of *Bufo quechua* (Bufonidae) and *E. platydactylus*, and De la Riva and

Lynch (1997) for *E. fraudator*. However, the pustules were tentatively referred to strigiid trematodes by Lynch and McDiarmid (1987) and De la Riva and Lynch (1997). Later, De la Riva (1998) stated that they are caused by larvae of trombidiid mites.

The first report of a *Hannemania* sp. (Acari: Parasitengona: Trombiculidae: Leeuwenhoekiiinae), the causative agent for these pustules, was made by Oudemans (1910). The mite was embedded in the skin of a Brazilian leaf frog (Sambon 1928, cited after Sladky et al. 2000). Early reports of this phenomenon from North America derive from Ewing (1926). At present, 11 *Hannemania* species are known from South America, another 10 species occur in North America. The New

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Caledonian *Hannemania rouxi* Oudemans, 1916 needs confirmation. Prior to the present study, no *Hannemania* species was reported from Bolivia.

During examination of Bolivian amphibians collected in December 1994 and December 1997, these were found to be parasitized by mites of the genus *Hannemania*. Morphological analysis revealed that the acarine parasites belonged to two distinct but hitherto unknown species, which are described below. The respective parasite–host associations are analysed as well.

Material and methods

Specimens of *Hannemania* were collected from juvenile *B. quechua* (Bufonidae; $n = 2$ hosts; ZFMK 60263, 60266) and adult *E. platydictylus* (Leptodactylidae; $n = 3$ hosts; ZFMK 60212, 66980, 67129). Collected frog specimens were anaesthetized in chlorobutanol solution, fixed in 95% and preserved in 70% ethanol. Bolivian host specimens were collected at two localities in the upper montane rain forests of the Provincia Carrasco, Departamento Cochabamba (Sehuencas, 17°29'S, 65°17'W, 2200 m a.s.l., sampled December 1994; Incachaca, 17°15'S, 65°49'W, 2350 m a.s.l., sampled December 1997), as well as in lower montane rain forest in Provincia Chapare, Departamento Cochabamba (30 km on old road from Paracitito to Cochabamba, 17°07'S, 65°34'W, 1300 m a.s.l.). The general area is characterized by very steep slopes (inclination 40–85°) with perhumid montane rain forests and cloud forests. Many small and large streams are present. The precipitation in this area ranges among the highest recorded in Bolivia. Kessler (1999) suggested the yearly amount to be around 8000 mm in some parts of the Carrasco National Park. Heavy downpours with 400 mm rainfall per day were reported by Ibisch (1996).

For histological examinations, three *Hannemania* n. sp. parasitic on *B. quechua*, including the surrounding host capsule, were embedded in Technovit 7100[®] following standard procedure; histological sections (2–3 µm) were stained with toluidine methylene blue.

Drawings and measurements of mites were made after specimens had been cleared in hot 1 mol KOH, removed from the host, cleared in lactic acid, and mounted in polyvinyl-lactophenol. Photographs, drawings, and measurements were made using an Olympus BH2 microscope equipped with differential interference phase contrast, a camera lucida, and a reflex camera (Olympus OM-4).

Measurements based on a maximum of 15 larvae are given in µm. For morphological terminology and abbreviations, see Mąkol and Wohltmann (2000).

Museum abbreviations: ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMH = Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany.

Results

The new species

Hannemania yungicola n. sp.

Etymology: The specific name is derived from the forest-covered eastern Andean slopes in Bolivia, well-known as the 'Yungas'.

Type material: Holotype (inventory no. ZMH A7/05) and one paratype (inventory no. ZMH A08/05) deposited at ZMH; additional paratypes deposited at ZFMK, and in first author's collection.

Type locality: Upper montane rain forest in Bolivia, Departamento Cochabamba, Provincia Carrasco, Sehuencas, 2200 m a.s.l., 17°29'S, 65°17'W.

Description: Larva (Fig. 1; Tables 1 and 2). All specimens engorged; idiosoma (before mounting) length 945–1550 µm, total width 570–950 µm.

Gnathosoma (Fig. 1c): Digitus mobilis is arrow-like, widened proximally, outer side provided with a row of about 12 teeth, inner margin with bottle-opener-shaped incision. Dorsolaterally at anterior part of gnathosoma, one pair of pointed deutorostrals (os) (26–27); ventrally near base of gnathosoma, a pair of tritorostrals (bs) (34–36), each with 4–5 prominent setules. No protostrals, no supracoxal setae detected.

Palpal synthetic formula: 0-N-N-NNN-ωNNNNN. Palp tibia with two smooth setae dorsally, laterally with one setae with 3–5 prominent setules. Odontus with an additional pair of smaller claws laterally.

Idiosoma, dorsum: Scutum (Fig. 1b) pentagonal with anteriorly projecting naso; with three pairs of serrate setae plus one pair of trichobothria with smooth sensillae. Lateral of scutum two pairs of eyes, each pair on a common ovoid sclerite (17–20 × 30–36). Anterior eye (14–17) slightly larger in diameter than posterior lens (10–12). Posterior to scutum about 60 barbed setae (length 45–50) arranged in rows.

Idiosoma, venter: With smooth cuticle, one pair of Claparède's organs laterally between coxae I and II. Coxa I with setulose setae 1a and 1b, coxa II with smooth seta 2b, and coxa III with setulose seta 3b. One pair of setulose intercoxal setae 3a medially of coxae III. About 40 setae (length 32–40) around the unsclerotized anal opening (about 15 µm long).

Legs (Fig. 1d): Segmentation formula: 6-6-6. Leg segments with internal cuticular stiffenings. Pretarsus on legs I–III each with paired claws and claw-like empodium. Lateral claws with lateral rows of minute spurs (onychotriches).

Hannemania chaparensis n. sp.

Etymology: The specific name refers to the Chapare province in the Departamento Cochabamba, Bolivia, where the species was found.

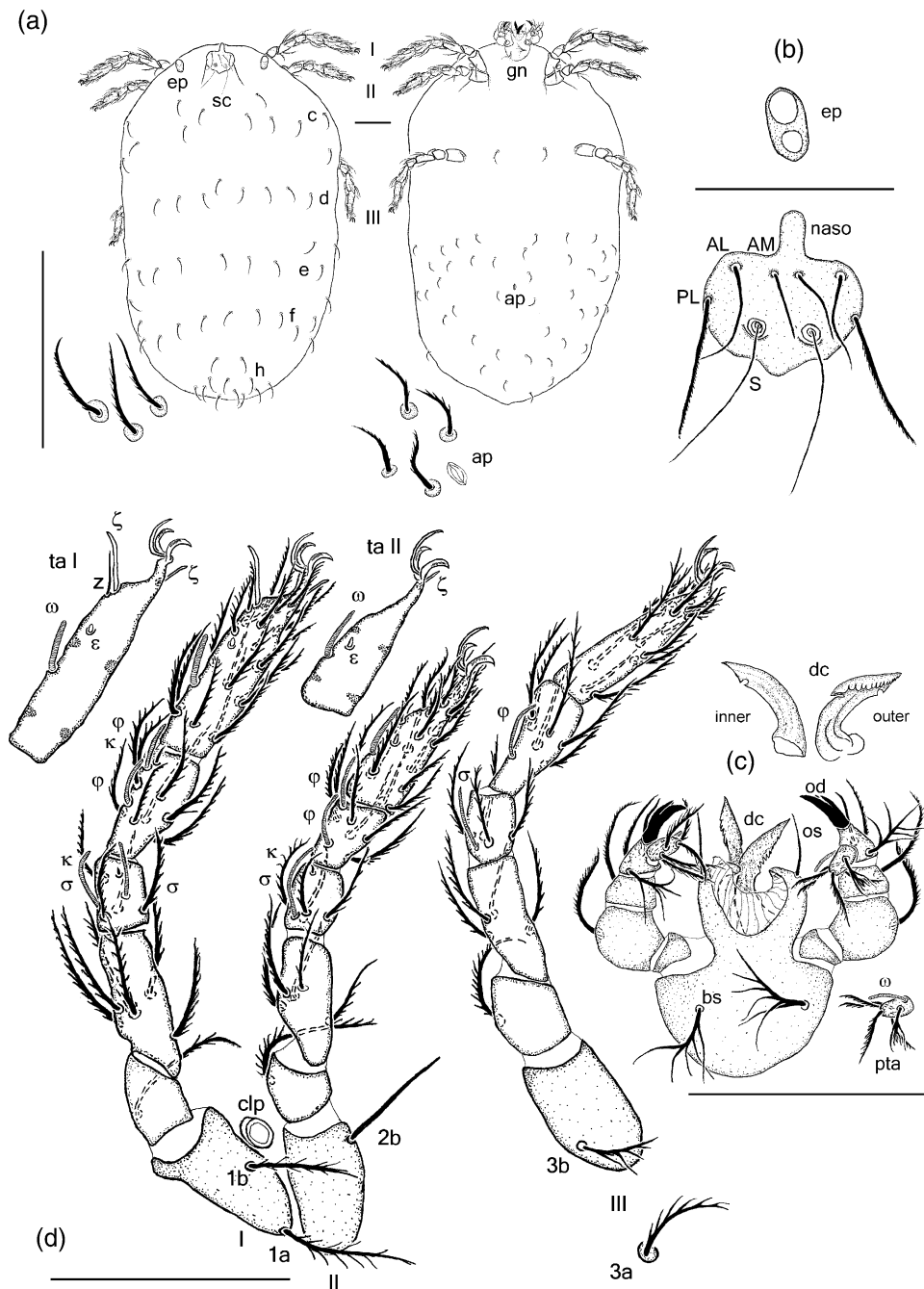


Fig. 1. *Hannemania yungicola* n. sp., larva; scale bars: 100 μ m. (a) Habitus; left: dorsal view (gnathosoma omitted) and detail of dorsal setae; right: ventral view and detail of ventral setae and anal pore; ap = anal pore, c–h = rows of dorsal idiosomal setae, ep = eye-plate, gn = gnathosoma, sc = scutum, I–III = legs I–III. (b) Eye plate (top) and scutum; AL = anterior lateral setae, AM = anterior median seta, PL = posterior lateral seta, S = sensilla of trichobothrium. (c) Gnathosoma (ventral view) and details of cheliceral digitus (top) and palp tarsus with solenidion (bottom right); bs = tritorrostral seta, dc = cheliceral digitus, od = odontus (palp tibial claw), os = deutorostral seta, pta = palp tarsus, ω = solenidion. (d) Legs; details of tarsi I and II show specialized setae only; for labels of setae, see text; clp = Claparède's organ, ta I = tarsus I, ta II = tarsus II.

Type material: Holotype (inventory no. ZMH A5/05) and one paratype (inventory no. ZMH A06/05) of *H. chaparensis* n. sp. is deposited at ZMH, further paratypes deposited at ZFMK, and in first author's collection.

Type locality: Lower montane rain forest in Bolivia, Departamento Cochabamba, Provincia Chapare, 30 km

on old road from Paractito to Cochabamba, 1300 m a.s.l., 17°07'S, 65°34'W.

Description: Larva (Fig. 2, Tables 1 and 2). All specimens engorged.

Gnathosoma (Fig. 2c): Form of digitus as in *H. yungicola*, outer side with a row of about eight teeth.

Table 1. Leg setae of *Hannemania yungicola* n. sp. ($n = 18$) and *H. chaparensis* n. sp. ($n = 6$); for seta labels, see Fig. 1; B = non-specialized seta

| | <i>H. yungicola</i> | <i>H. chaparensis</i> |
|----------------------------|---|---|
| Palp trochanter | — | — |
| Palp femur | 1 B | 1 B |
| Palp genu | 1 B | 1 B |
| Palp tibia (excl. odontus) | 3 B | 3 B |
| Palp tarsus | 5 B, 1 ω | 5 B, 1 ω |
| Coxa I | 2 B | 2 B |
| Trochanter I | 1 B | 1 B |
| Femur I | 6 B | 6 B |
| Genu I | 4 B, 2 σ , 1 κ | 4 B, 7 (6–8) σ , 1 κ |
| Tibia I | 8 B, 2 φ , 1 κ | 8 B, 2 φ , 1 κ |
| Tarsus I | 24–26 B, 1 ω , 1 ε , 2 ζ , 1 z | 22–23 B, 1 ω , 1 ε , 2 ζ , 1 z |
| Coxa II | 1 B | 1 B |
| Trochanter II | 1 B | 1 B |
| Femur II | 5 B | 5 B |
| Genu II | 4 B, 1 σ , 1 κ | 4 B, 1 σ , 1 κ |
| Tibia II | 6 B, 2 φ | 6 B, 2 φ |
| Tarsus II | 17–18 B, 1 ω , 1 ε , 1 ζ | 16–18 B, 1 ω , 1 ε , 1 ζ |
| Coxa III | 1 B | 1 B |
| Trochanter III | 1 B | 1 B |
| Femur III | 4 B | 4 B |
| Genu III | 4 B, 1 σ | 4 B, 1 σ |
| Tibia III | 6 B, 1 φ | 6 B, 1 φ |
| Tarsus III | 14–16 B | 15–16 B |

Deutorostrals (os) (18–24) with short serrae, tritorostrals (bs) (30–35) each with 3–5 prominent setules. No protostrals, no supracoxal setae detected.

Palpal synthetic formula: 0-N-N-NNN- ω NNNNN. Odontus trifold.

Idiosoma, dorsum: Form of scutum (Fig. 2b) as in *H. yungicola*. On each side two eyes (diameters: anterior 9–12, posterior 9–11) on common sclerite (23–26 \times 12–14). Posterior to scutum about 54 barbed setae (length 32–47) arranged in rows.

Idiosoma, venter: Coxa I with setulose setae 1a and 1b, coxa II with smooth seta 2b, and coxa III with setulose seta 3b. One pair of setulose intercoxal setae 3a medial of coxae III. About 52 setae (length 34–48) around the unsclerotized anal opening (about 10 μ m long).

Legs (Fig. 2d): Segmentation formula: 6-6-6. Leg segments with internal cuticular stiffenings. Pretarsus on legs I–III with paired claws and claw-like empodium. Lateral claws with lateral rows of minute spurs (onychotriches).

Comparisons to other *Hannemania* species

The presence of only two solenidia on genu I separates *H. yungicola* n. sp. from the North American *H. monticola* Welbourn and Loomis, 1970 (3–7 soleni-

dia); *H. saxicola* Welbourn and Loomis, 1970 (6–10); *H. eltoni* Sambon, 1928 (8–10); *H. hegeneri* Hyland, 1956 (8–13); *H. anurae* Welbourn and Loomis, 1970 (6–9); *H. hylae* (Ewing, 1925) (3–7); *H. bufonis* Loomis and Welbourn, 1969 (2–6); *H. pelaezi* Hoffmann, 1965 (11–12); *H. mexicana* Hoffmann, 1965 (11–12); and from the South American *H. minor* Alzuet and Mauri, 1985(1987) (8–10) and *H. achalai* Alzuet and Mauri, 1985(1987) (2–4). Unfortunately, the taxonomic state of other South American *Hannemania* spp. (*H. argentina* Lahille, 1927; *H. edwardsi* Sambon, 1928; *H. hobdayi* Sambon, 1928; *H. hylodeus* Oudemans, 1910; *H. news-teadi* Sambon, 1928; *H. pattoni* Sambon, 1928; *H. samboni* Alzuet and Mauri, 1985(1987) syn. *H. argentina* Sambon, 1928; and *H. stephensi* Sambon, 1928) is uncertain because of inappropriate descriptions and the loss of types (W.C. Welbourn, A. Cantenazzi, pers. comms.). *H. chaparensis* n. sp. differs from other recognizable species by its particular number of solenidia on genu I; from *H. minor* by having shorter legs I–III.

Parasite–host association

All *Hannemania* larvae were found in spheroid cavities below the cuticle of their hosts, predominantly

Table 2. Standard measurements (in μm) for *Hannemania yungicola* n. sp. ($n = 10\text{--}15$) and *H. chaparensis* n. sp. ($n = 5\text{--}6$); data format: average (minimum–maximum); for seta labels, see Fig. 1

| | | <i>H. yungicola</i> | <i>H. chaparensis</i> |
|------------------|----------------------------|---------------------|-----------------------|
| Gnathosoma | Cheliceral digitus | 42 (35–50) | 28 (25–32) |
| | Palp trochanter | 6 (5–7) | 10 (8–11) |
| | Palp femur | 30 (29–31) | 24 (22–26) |
| | Palp genu | 12 (11–12) | 10 (8–11) |
| | Palp tibia (excl. odontus) | 18 (15–22) | 10 (10–12) |
| | Odontus | 16 (15–22) | 16 (14–20) |
| | Palp tarsus | 14 (13–16) | 9 (8–10) |
| | Scutum | Length | 96 (84–105) |
| Width | | 92 (83–100) | 66 (63–74) |
| AM | | 36 (31–40) | 20 (17–21) |
| Distance | | 13 (11–14) | 10 (9–10) |
| AM–AM | | | |
| AL | | 52 (47–56) | 44 (41–47) |
| Distance | | 57 (52–63) | 43 (39–44) |
| AL–AL | | | |
| PL | | 75 (67–83) | 59 (55–65) |
| Distance | | 79 (73–87) | 59 (58–61) |
| PL–PL | | | |
| Sensilla (PSens) | | 86 (83–89) | 72 (66–78) |
| Distance | | 32 (28–37) | 23 (20–25) |
| PSens–PSens | | | |
| Leg I | Coxa I | 65 (56–74) | 52 (49–56) |
| | Trochanter I | 33 (28–39) | 24 (21–26) |
| | Femur I | 67 (62–72) | 46 (42–49) |
| | Genu I | 39 (34–45) | 30 (28–32) |
| | Tibia I | 55 (50–62) | 39 (36–44) |
| | Tarsus I | 105 (90–118) | 80 (73–84) |
| Leg II | Coxa II | 65 (57–80) | 50 (49–52) |
| | Trochanter II | 31 (28–35) | 23 (20–25) |
| | Femur II | 58 (55–63) | 36 (31–39) |
| | Genu II | 31 (27–36) | 22 (20–23) |
| | Tibia II | 42 (35–47) | 34 (29–36) |
| | Tarsus II | 76 (70–85) | 59 (58–60) |
| Leg III | Coxa III | 64 (56–70) | 48 (44–50) |
| | Trochanter III | 40 (36–45) | 26 (22–30) |
| | Femur III | 58 (55–62) | 39 (32–42) |
| | Genu III | 34 (29–39) | 27 (24–31) |
| | Tibia III | 54 (48–60) | 43 (36–46) |
| | Tarsus III | 86 (73–100) | 65 (62–68) |

on the legs (Table 3). *H. yungicola* n. sp. parasitized *B. quechua* and *E. platydictylus*; all hosts were collected in montane rain forests at 2200–2300 m a.s.l. *H. chaparensis* n. sp. was found in one *E. platydictylus* (Table 3) collected in montane rain forest at 1300 m a.s.l. No differences in site specificity were evident when comparing species; all specimens of *Hannemania* were apparently engorged and had fed on their hosts. Some of the heavily infested individuals of *E. platydictylus* appeared to be anaemic.

From the longitudinal and horizontal sections, it was evident that a double-layered capsule without any opening surrounded the mite larvae (Fig. 3). The outer layer consisted of cellular tissue; the inner layer was amorphous and free of cells. Only where the mite chelicerae pierced the inner layer, cell fragments were visible in the capsule. Histological sections show that liquefied cell contents are ingested by the mite, probably by means of hypo-pressure produced by dilator muscles of the pharynx. In the anterior region of the larva, the oesophagus passes through the brain and opens into the voluminous midgut, which occupies most of the space in the larva. No feeding tube (stylostome) as reported from other Trombiculidae (Voigt 1970; Hase et al. 1978; Wohltmann 2001a) could be detected.

Discussion

The *Hannemania* parasitizing Bolivian frogs evidently belong to different species: *H. yungicola* n. sp. and *H. chaparensis* n. sp. This is indicated by the differences in metric characters as well as by the different number of solenidia on genu I. Both species are new to science and represent the first reports of *Hannemania* from Bolivia and the eastern Andes.

Our histological observations are in accordance with earlier examinations of North American *Hannemania* spp. (Hyland 1950, 1961). The capsule around the mite larva is produced by the host from connective tissue; the amorphous inner layer may be the result of histolysis due to mite-born enzymes (Grover et al. 1975). The particular design of cheliceral tips with outer teeth and an inner, bottle-opener-shaped incision is typical for the genus *Hannemania*, and probably serves to mechanically rupture host cells in the periphery of the capsule. After complete encystment, the mite may remain in the capsule for up to months (Hyland 1961), obviously dependent on external signals. When host blood flow was interrupted artificially, engorged *Hannemania* larvae left the capsule within some hours with the help of their chelicerae (Hyland 1961).

During parasitism, the mite larva increases considerably, up to fourfold, in length (Hyland 1961). Such enormous growth can hardly be explained by simply unfolding pre-folded cuticle, but much more likely is the result of cuticular growth without intermittent moult. This phenomenon, called neosomy, is known from other trombiculid larvae (Audy et al. 1972) and Parasitengona in general (Wohltmann 2001a). Although the process of cuticle production is still unclear, the smooth and thickened epidermal layer as visible in histological slides indicates that neosomy takes place throughout the area of unsclerotized cuticle.

The life cycles of *H. yungicola* and *H. chaparensis* remain unknown. Probably they are similar to those of

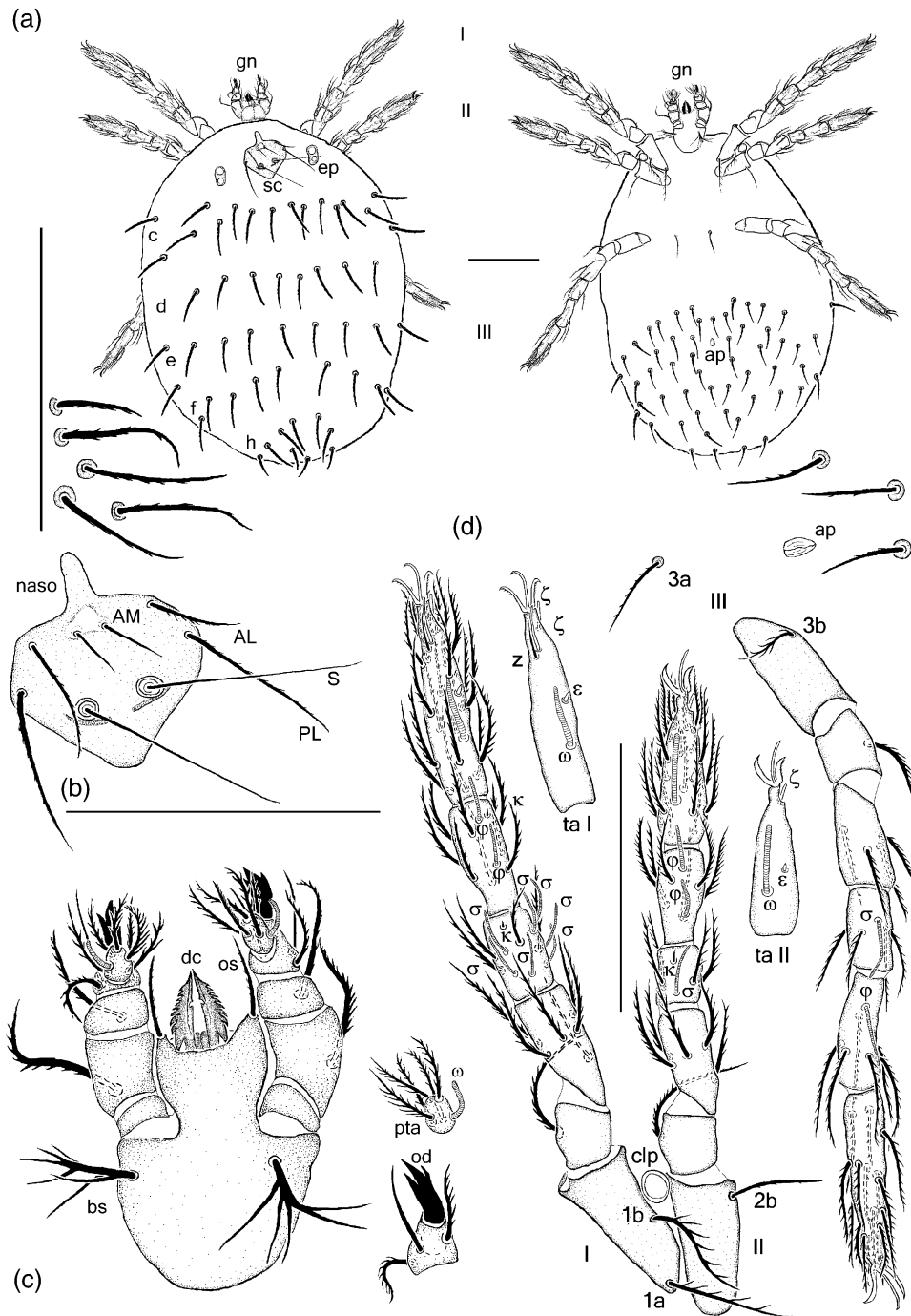


Fig. 2. *Hannemania chaparensis* n. sp., larva; scale bars: 100 μ m. (a) Habitus; left: dorsal view and detail of dorsal setae; right: ventral view and detail of ventral setae and anal pore; ap = anal pore, c–h = rows of dorsal idiosomal setae, ep = eye-plate, gn = gnathosoma, sc = scutum, I–III = legs I–III. (b) Scutum; AL = anterior lateral setae, AM = anterior median seta, PL = posterior lateral seta, S = sensilla of trichobothrium. (c) Gnathosoma (ventral view) and details of palp tarsus with solenidion (right, top) and palp tibia with odontus (right, bottom); bs = tritorostral seta, dc = cheliceral digitus, od = odontus (palp tibial claw), os = deutorostral seta, pta = palp tarsus, ω = solenidion. (d) Legs; details of tarsi I and II show specialized setae only; for labels of setae, see text; clp = Claparède's organ, ta I = tarsus I, ta II = tarsus II.

other *Hannemania* spp. and follow the typical life cycle of *Parasitengona*, including three active instars (Wohltmann 2001a), of which the larva is the only parasitic stage. Deutonymphs and adults of *H. hegeneri* (Hyland

1950, 1961) and *H. hylae* (Loomis and Welbourn 1969) have been reared successfully on a diet of collembolan eggs, but *H. bufonis* deutonymphs develop into adults without feeding (Loomis and Welbourn 1969) and thus

Table 3. Parasitic load and attachment sites; codes in brackets refer to inventory numbers of hosts deposited at ZFMK

| Host | Legs | Dorsum | Venter | Total |
|---|------|--------|--------|-------|
| <i>Hannemania yungicola</i> n. sp. | | | | |
| <i>Bufo quechua</i> (ZFMK 60263, juvenile) | 16 | 6 | — | 22 |
| <i>Bufo quechua</i> (ZFMK 60266, juvenile) | 22 | 4 | 6 | 32 |
| <i>Eleutherodactylus platydactylus</i> (ZFMK 67129) | 4 | 5 | 3 | 12 |
| <i>Eleutherodactylus platydactylus</i> (ZFMK 60212) | 5 | 1 | — | 6 |
| <i>Hannemania chaparensis</i> n. sp. | | | | |
| <i>Eleutherodactylus platydactylus</i> (ZFMK 66980) | — | 6 | 2 | 8 |

constitute an elattostatic instar. Probably, *Hannemania* larvae hatch close to winter retreats of their hosts and enter them in soil crevices (Welbourn and Loomis 1975). The larvae actively burrow into the host's skin by means of chelicerae and pedipalps; a few hours after infestation, the mites are not visible on the host surface, and the entrances of capsules are closed by host secretions (Hyland 1961). Hyland (1961) reported that in laboratory culture, *H. hegneri* may completely engorge without embedding into the host. However, such a phenomenon probably is rare because it has never been observed in infested frogs captured in the field.

The observation that *H. chaparensis* and *H. yungicola* use the same host resource, but inhabit different biotopes, is in agreement with observations on other non-trombiculid Parasitengona. Usually, closely related species either parasitize the same hosts but differ in the temporal or spatial usage of this resource; alternatively, closely related, co-occurring species differ in nutritional resource requirements of larvae (Wohltmann 2001b).

Red pustules probably caused by *Hannemania* species have been reported from the following Bolivian host species: *B. quechua*, *E. fraudator*, *E. llojsintuta*, *E. mercedesae*, and *E. platydactylus* (Lynch and McDiarmid 1987; De la Riva and Lynch 1997; Köhler and Lötters 1999). It is somewhat surprising that, despite intensive surveys, other related anuran species found in the same general area (e.g. *B. veraquensis*, *E. pluvicanorus*, *E. rhabdolaemus*) were never observed to be infested with *Hannemania*. This is also true for sympatric non-related species of the anuran families Centrolenidae and Hylidae. Differences in the degree of infestation by *Hannemania* were also reported for two sympatric plethodontid salamanders by Regester (2001). Since *Hannemania* spp. usually parasitize a range of anuran hosts and display low host specificity (Hyland 1950, 1961; Loomis and Welbourn 1969; Welbourn and Loomis 1970, 1975), the apparent preference of some anurans by *Hannemania* spp. and the apparent absence of mites on other amphibians might be the result of ecological parameters that facilitate or prevent contacts between potential hosts and *Hannemania* larvae.

Although documented for few taxa only, species in the genus *Eleutherodactylus* are assumed to deposit terrestrial egg clutches in which the eggs undergo direct development without a larval tadpole stage, with small froglets emerging directly from the clutch. Thus, the development is independent from water bodies, but generally requires high humidity. In contrast, reproduction of *B. quechua*, a member of the *B. veraquensis* species group, probably takes place in small streams, with tadpoles adapted to lotic conditions (Köhler 2000). However, both species inhabit the moist leaf litter on the ground (although *E. platydactylus* perches on low vegetation at night), and therefore may be particularly exposed to *Hannemania* mites.

Another remarkable fact is that *Hannemania* infestations seem to be restricted to those Bolivian montane forests with the highest amounts of precipitation. Infestations were never observed in montane forests with less rainfall or with a more seasonal climate, although the host species reported herein do occur there. This indicates that very high humidity is required for the survival of *Hannemania*. Necessity of nearly saturated air humidity for successful development has been demonstrated for other trombiculid Parasitengona (Wohltmann 1998) and seems to constitute a general feature of this taxon.

The effects of *Hannemania* infestations on frogs are unclear. Sladky et al. (2000) state that the mites may kill frogs or may serve as vectors for infectious diseases. In contrast, Hyland (1961) kept *Hannemania*-infested frogs alive for more than 6 months. Generally, parasitic mites should have a negative impact on the fitness of the host by reducing its competitiveness, reproduction success, and perhaps even life span. Thus, an increase of parasitism by *Hannemania* (e.g. resulting from changes in the environment) may at least contribute to population declines in amphibians of tropical montane forests. The phenomenon of a global amphibian decline has been evaluated recently by Stuart et al. (2004), but in many cases, the causes for declines remain obscure (e.g. Blaustein et al. 1994; Ron et al. 2003). However, parasite infection might be one of the factors involved.

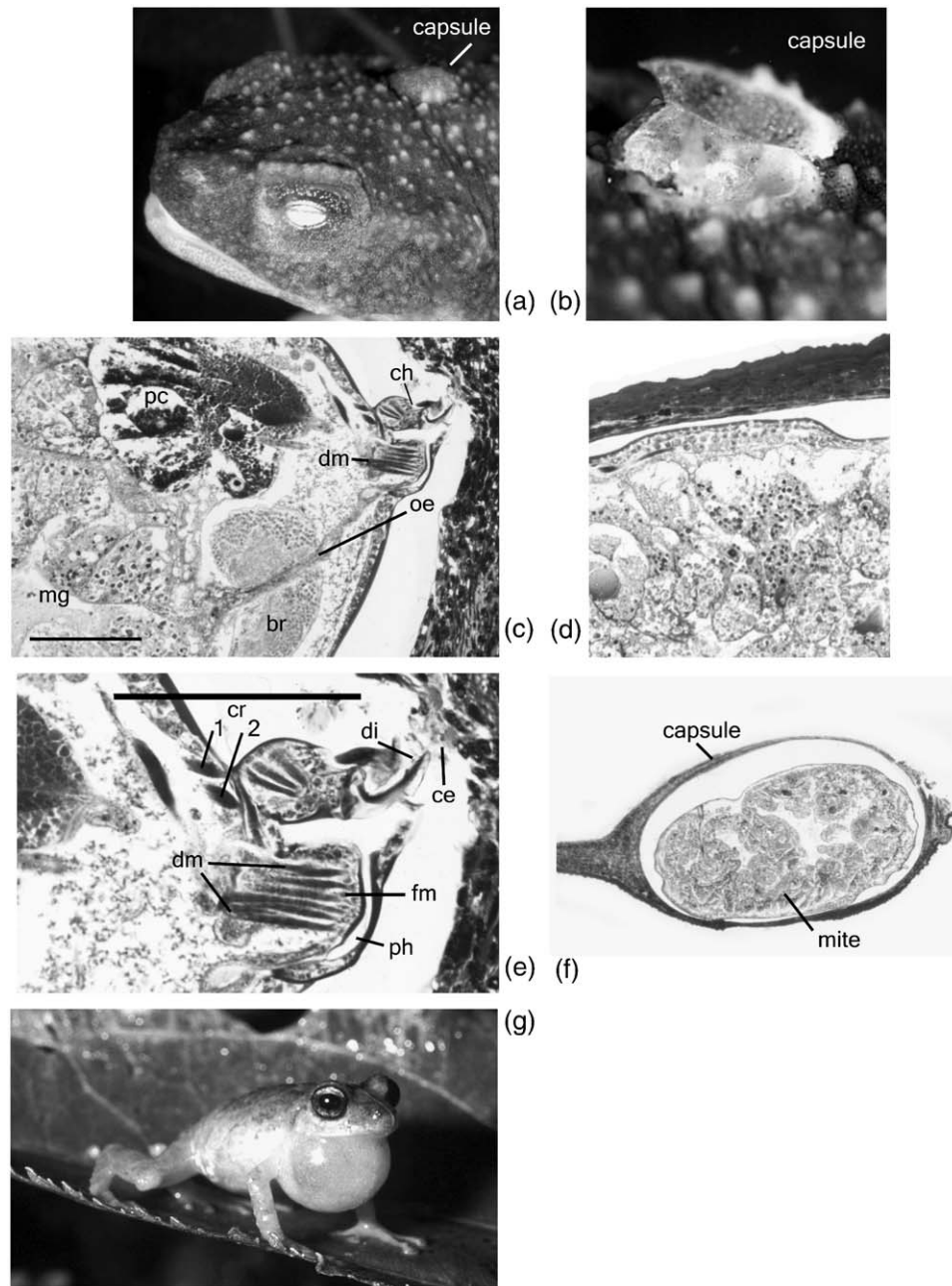


Fig. 3. Host, host capsule, and histological sections of larva of *Hannemania yungicola* n. sp. (a) Head of juvenile *Bufo quechua* with capsule containing *Hannemania*. (b) Same capsule opened, mite larva removed. (c) Longitudinal section showing anterior region of *Hannemania* in the host capsule; br = brain, ch = chelicera, dm = dilator muscle of pharynx, mg = midgut, oe = oesophagus, pc = podocephalic gland system. (d) Longitudinal section showing *Hannemania* epidermis and part of midgut separated from host-generated capsule wall (at top) by a lumen. (e) Longitudinal section of gnathosoma region; ce = disrupted cell of host tissue, cr 1, 2 = cheliceral retractor muscles 1 and 2, di = cheliceral digitus, dm = dilator muscle of pharynx, fm = flexor muscle of pharynx, ph = pharynx. (f) Situs of *Hannemania* within host capsule. (g) Habitus of *Eleutherodactylus platydactylus*.

Amphibians serve as hosts for several parasitic mite taxa of different families: apart from soft and hard ticks (Argasidae and Ixodidae of at least six genera: *Amblyomma*, *Argas*, *Hyalomma*, *Haemaphysalis*, *Ixodes*, and *Ornithodoros*; Arthur 1962), water mites and Trombiculidae constitute the most commonly reported

parasites. In water mites (Parasitengona: Hydrachnidia), so far only two species are known to parasitize amphibians: Martin and Schwoerbel (2002) found larvae of *Thermacarus andinus* parasitizing the Neotropical toad *B. spinulosus*; Goldschmidt et al. (2002) reported parasitic females of *Hygrobatas salamandarum*

attached to the newt *Pachytriton labiatus*. Within the Trombiculidae (Parasitengona: Trombidia), the genus *Endotrombicula* (Trombiculinae) is known from anurans in Africa (e.g. Spieler and Linsenmair 1999), *Vercammenia* (Trombiculinae) from Malayan and Australian frogs (Domrow et al. 1983), and *Hannemania* (Leuvenhoekiinae) from American amphibians (e.g. Duszynski and Jones 1973; Alzuet and Mauri 1987). A summary of amphibian genera reported as hosts for *Hannemania* is listed by Regester (2001). Larvae of terrestrial Parasitengona using Amphibia as hosts are characterized by subepidermal parasitism. Larvae of the water mite *Thermacarus* do not form closed capsules within the host's epidermis, but they are deeply embedded in the skin with only the posterior parts of their bodies visible (Martin and Schwoerbel 2002). Subepidermal or nearly subepidermal parasitism constitutes a phenomenon that is rare (Trombiculidae) or even unknown (all other subgroups) in Parasitengona that do not parasitize amphibians. Obviously, the moist amphibian epidermis and its toxic secretions produced by numerous epidermal glands is disadvantageous for small ectoparasites such as mite larvae. Subepidermal parasitism seems to constitute an adaptation of parasitengone larvae to this particular host character, that has evolved at least three times convergently in Leuvenhoekiinae (*Hannemania*), Trombiculinae (*Endotrombicula*, *Vercammenia*), and in water mites (*Thermacarus*). The state in *Thermacarus* is intermediate between the plesiotypic external host attachment displayed by the majority of Parasitengona and that of terrestrial species parasitizing Amphibia. This may indicate that parasitism on Amphibia evolved rather late in *Thermacarus*.

Acknowledgements

We are indebted to Wolfgang Böhme (ZFMK) for providing access to the herpetological collection under his care, to Alessandro Catenazzi for providing some unpublished information, and to Gundula Sieber-Warwass for the preparation of histological slides. Moreover, we thank Dagmar Frisch, Matthias Glaubrecht, and two unknown referees for critical comments on earlier drafts of the manuscript.

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